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YIELD, SEED WEIGHT, AND CANNING QUALITY IN KIDNEY BEAN (PHASEOLUS VULGARIS L.); AND RANDOM AMPLIFIED POLYMORPHIC DNA (RAPD) MARKERS ASSOCIATED WITH CANNING QUALITY TRAITS

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ABSTRACT

YIELD, SEED WEIGHT, AND CANNING QUALITY IN KIDNEY BEAN (*Phaseolus vulgaris* L.); AND RANDOM AMPLIFIED POLYMORPHIC DNA (RAPD) MARKERS ASSOCIATED WITH CANNING QUALITY TRAITS

By

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Two recombinant inbred populations of kidney beans (*Phaseolus vulgaris* L.) - 'Montcalm' x 'California Dark Red Kidney 82' and 'Moncalm' x California Early Light Red Kidney' - were evaluated in six year-location combinations in Michigan, Minnesota and North Dakota from 1996 to 1999. Heritability estimates were obtained for yield (0.62 to 0.63), seed weight (0.58 to 0.69), and canning quality traits - appearance (0.83 to 0.85) and degree of splitting of processed beans (0.84 to 0.85). Positive correlations were detected between yield and seed weight, and between APP and SPLT. Negative correlations were detected between yield and APP, and yield and SPLT.

Two putative quantitative trait loci (QTL) for canning quality traits were identified using eleven RAPD markers. The first region was tentatively mapped in linkage group B8 of the bean genome. The alleles in this locus, which were associated with desirable canning quality, appeared to be derived from Montcalm. The second locus, associated with 4 markers, appeared to be derived from the non-Montcalm parents. Population and environment-specificity were observed for the markers identified.

To my parents and my husband.

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INTRODUCTION

Dry bean (*Phaseolus vulgaris* L.) is an important staple in countries where animal protein is limited or expensive. In some countries in Central and South America, and Central and East Africa, large quantities of beans are consumed and provide from one-quarter to more than one-half of the dietary protein, and up to one-quarter of the energy requirements (Shellie-Dessert and Bliss, 1991). Even in the United States where beans are consumed mostly to add variety to diets, their contribution to dietary requirements is appreciable. The considerable diversity for seed characteristics and eating preferences of dry bean lead to its classification into 13 major market classes in the U.S. (U.S. Department of Agriculture, 1982). Dark and light red kidney beans, two important market classes, account for a sizable consumption. Light red kidney beans are used in chili and chili products; dark red kidney beans are used mainly in salads and constitute a significant component of restaurant salad bars, particularly in northern U.S. states.

Increased and stabilized yield over a range of environmental conditions is a major goal of breeding programs. Newer varieties with improved characteristics are always evaluated, and may be accepted or rejected commercially, with regard to their yield potentials. In developing and testing dry bean breeding lines and cultivars, plant breeders pay attention to data on yield performance, heritability of yield and components of yield, correlations between yield and other traits of interest, and genotype x environment interactions. Such information aids in planning a program to improve yield and other economically important traits, and serves as a benchmark for the evaluation of materials planted at different locations and in different years. Data on genotype x

environment interactions serve as a guide in estimating the most efficient allocation of locations, years, and replications necessary for testing and selecting genotypes with improved yield and other characteristics. Such data would also be useful indicators of the amount of genetic variability available for selection.

In addition to yield, bean breeders also include canning quality improvement as an important program objective. Although uncooked seeds may be bought in stores and then cooked on the stovetop or in the oven, a large amount of the dry bean crop produced in the U.S. is consumed as a pre-processed (canned) product. Commercial canners process beans in plain water, brine, sugar solutions, tomato sauce, molasses or mixed vegetables added during processing (Adams and Bedford, 1973; Deshpande et al., 1984). Regardless of how beans are purchased by the consumer, "dry pack" or in tin cans, beans are generally soaked or blanched, and must be cooked to render them palatable, inactivate heat labile anti-nutrients, and permit the digestion and assimilation of protein and starch (Deshpande et al., 1984). The steps used in preparing beans for eating cause structural changes in cells that influence acceptance criteria by consumers and processors. The criteria used by consumers include appearance, ease of preparation, wholesomeness, mouth feel and texture. On the other hand, processors, although constrained by consumer expectations, seek properties of beans that lend themselves to ease of commercial preparation, processing efficiency, and a high can yield per unit weight of raw product (Wassimi et al., 1990). To this end, processors desire beans that exhibit rapid and uniform seed expansion during soaking and/or blanching (Hosfield, 1998), and beans that maintain intact seed coats coupled with a high water-holding capacity during processing.

The multiplicity of characteristics used to determine whether or not processed beans are preferred and acceptable to processors and consumers is referred to as canning quality.

The evaluation of genetic materials for improved canning quality, in addition to yield and other agronomic features, is necessary because a bean cultivar with poor canning quality may be rejected by consumers regardless of how agronomically superior it is (Kelly et al., 1998). On the other hand, selections with good canning quality are discarded if they do not meet yield expectations. Incorporating the dimension of canning quality improvement into a bean breeding program places a heavy burden on the breeder to develop efficient selection practices.

Dry bean canning quality is more or less conceptual because its definition depends on a multiplicity of variables of which no single one adequately describes the properties preferred and required (Hosfield and Uebersax, 1990). Furthermore, canning quality traits are controlled by quantitative trait loci (QTLs), resulting in continuous variation among phenotypes (Hosfield et al., 1984b). The number of genes influencing canning quality, and the influence of the environment on gene expression complicate the identification of the effects of individual genes controlling canning quality traits, and thus, makes it difficult to manipulate genes for improving genotypes.

Indirect selection using linked markers - marker-assisted selection (MAS) - is a method that might increase selection efficiency within breeding programs. If a trait is difficult and expensive to evaluate, under polygenic control, or highly influenced by the environment (such as is the case for bean canning quality traits) MAS may be more efficient than traditional selection methods based on phenotype (Dudley, 1993). The use of markers to facilitate selection could shorten the breeding cycle in plants because the

breeder might be able to select a desirable trait in the early generations following hybridization. Early-generation selection increases the efficiency of breeding programs because unwanted genotypes can be discarded before they enter replicated field trials. The use of MAS can also reduce costs, especially when conventional selection methods require evaluating numerous genotypes or large samples. Various morphological and molecular markers have been used in MAS for different crops. Before such markers can be used, associations or linkages between these markers and the QTL of interest must be identified (Dudley, 1993; Miklas et al., 1996).

Walters et al. (1997) identified random amplified polymorphic DNA (RAPD) as molecular markers for canning quality in three populations of navy bean. Several RAPD markers were found to be associated with the traits: visual appeal, texture and washed drained weight of canned beans. In the published literature no studies on beans other than that of Walters et al. (1997) have been reported where MAS has been used to select for canning quality or molecular markers have been developed for this trait. Given the genetic diversity between bean market classes, kidney beans may or may not possess the same markers associated with the same traits that were identified for navy bean.

The importance of yield and processing quality in kidney bean, the paucity of published information on both, and an interest in identifying RAPD markers associated with canning quality traits prompted the present work. Information on the inheritance of these traits and on the effect of the environment and genotype x environment interactions were also sought, in order to provide insight into the amount of testing required to characterize breeding lines reliably. This research is composed of two studies, the first of which dealt with yield and seed weight of two recombinant inbred populations of kidney

beans planted in Michigan in 1996, 1997, 1998, and 1999, in Minnesota in 1996, and in North Dakota in 1999. The specific objectives of Study 1 were to a) evaluate yield and seed weight of two recombinant inbred populations of kidney beans planted in six environments; and b) estimate heritabilities and pair-wise correlations between traits. The objectives of the second study were to a) evaluate the general appearance and degree of splitting of canned beans of two recombinant inbred populations of kidney bean planted in six environments; b) estimate heritabilities and pair-wise correlations; c) identify putative RAPD markers for canning quality; and d) determine whether markers associated with canning quality are the same across market classes, specifically for kidney beans and navy beans.

CHAPTER 1: YIELD AND SEED WEIGHT OF TWO KIDNEY BEAN RECOMBINANT INBRED POPULATIONS

INTRODUCTION

Total dry bean production in the United States in 1999 was estimated at 33.3 million hundredweight (cwt). Light red kidney and dark red kidney beans respectively accounted for about 1.4 million cwt and 1.0 million cwt of this production (USDA-NASS, 2000). Three of the principal bean-producing states are Minnesota, Michigan and North Dakota. In 1999, Minnesota alone produced about 178,000 cwt and 597,000 cwt of light red and dark red kidney beans, respectively (USDA-NASS and Minnesota Department of Agriculture, 2000). Michigan's total dry bean production in 1999 was 7.34 million cwt. Of these, 306,0000 cwt and 153,000 cwt were the light red kidney and dark red kidney bean market classes, respectively (USDA-NASS and Michigan Department of Agriculture, 2000). North Dakota's total dry bean production in 1999 was 8 million cwt (USDA-NASS and North Dakota Department of Agriculture, 2000).

Sustained efforts in yield breeding in dry bean require a continuous evaluation of yield and its components. Breeders should also have some knowledge of the heritability for yield, and the magnitude of genotype x environmental interactions influencing yield in the populations in which they are selecting. The data obtained from the present study will increase the published information available for dry beans in general and kidney beans in particular. The present study on two kidney bean recombinant inbred populations was conducted in Michigan, Minnesota and North Dakota. Kidney bean production in these states contributes substantially to the bean canning industry. The

specific objectives of this study were to a) evaluate yield and seed weight of two recombinant inbred populations of kidney beans planted in Michigan from 1996 to 1999, in Minnesota in 1996, and in North Dakota in 1999; and b) estimate heritabilities and pair-wise correlations between traits.

REVIEW OF LITERATURE

Yield in dry bean can be viewed in terms of three components: number of pods per plant, average number of seeds per pod, and average seed size (Adams, 1967; Coyne, 1968; Nienhuis and Singh, 1985; Ranalli et al, 1991).

Yield and Yield Components

The contribution of number of pods per plant to total seed yield has been reported to be more important than the other two components (Coyne, 1968). Although yield components are genetically independent, negative correlations among components exist not only for beans but also for other crops (Adams, 1967). Negative correlations are caused by developmental rather than genetic factors, and result in yield component compensations and yield stability under various environmental stresses (Adams, 1967; Al-Mukhtar and Coyne, 1981). Various authors have studied the correlations between the yield components in beans planted in different environments, sometimes with varying results (Coyne, 1968; Nienhuis and Singh, 1985; Nienhuis and Singh, 1988; Zimmerman et al., 1984b).

Coyne (1968) found that most correlation coefficients among yield components were low and positive in sign, indicating the possibility of increasing one without

reducing the other two. Nienhuis and Singh (1985) observed that seed weight had negative phenotypic correlations with number of pods and seeds per pod, although no association was found between the latter two. In the Nienhuis and Singh (1985) study, both number of pods and seeds per pod were positively correlated with yield but seed weight and yield were negatively correlated. These authors suggested that selection for increased number of pods or seeds per pod should result in increased yield, but seed weight would be reduced. In a later selection experiment, Nienhuis and Singh (1988) found that the number of pods had significant negative correlations with both seeds per pod and seed weight. Selection for number of pods appeared to reduce not only seed weight but also yield and seeds per pod. Seeds per pod and seed weight were also negatively correlated. The authors (Nienhuis and Singh, 1988) suggested that selection for seeds per pod would increase yield only slightly, and reduce number of pods and seed weight. Selection for seed weight would reduce seeds per pod, and increase number of pods and yield only slightly. The conclusion drawn from this work was that selection for seed yield per se appears to be the best approach for yield improvement in dry beans (Nienhuis and Singh, 1988). In another study in beans, Ranalli et al. (1991) reported inverse relationships between the three yield components such that selection for one was detrimental to the others. Seed yield was increased by simultaneous selection for the yield components, using adequate selection intensity and a selection index composed of more than one trait (Ranalli et al., 1991).

In dry bean, the three yield components, along with yield per se, have been reported to be under the control of different modes of gene action. Pod number has been reported as completely dominant (Coyne, 1968), partially or almost completely dominant

(Sarafi, 1978) and with additive effects (Nienhuis and Singh, 1988). Sarafi (1978) reported seeds per pod as partially or nearly completely dominant. Nienhuis and Singh (1988) and Singh et al. (1991) found additive variance more significant than non-additive variance for the trait. Mean seed weight was observed to be influenced by additive effects (Coyne, 1968; Nienhuis and Singh, 1988; Singh et al., 1991) and partially or nearly completely dominant (Sarafi, 1978). Nienhuis and Singh (1988) and Singh et al. (1991) found additive genes to be significant for yield per se. Zimmerman et al. (1985) reported additive and dominance gene action, along with epistasis, as significant for yield in some crosses.

Estimates of heritabilities reported for yield and yield components in beans ranged from very low to high. In the cross Great Northern 1140 x PI 165078, low heritability estimates were obtained for total seed yield (0.09 to 0.11) and for each of the three yield components (–0.01 to –0.08) (Coyne, 1968). Sarafi (1978) found narrow sense heritability estimates to be 29% for pods per plant, 38-42% for seeds per pod and 33-37% for 100-seed weight in a cross between Iranian and American bean cultivars evaluated in the F_2 and F_3 generations. Zimmerman et al. (1984b) reported broad sense heritabilities for yield to range from 0.21 to 0.23, number of pods to range from 0.63 to 0.86, seeds per pod to range from 0.81 to 0.90 and 100-seed weight to range from 0.97 to 0.99 in beans. For beans of Middle-American origin, Nienhuis and Singh (1988) estimated narrow sense heritabilities to be 0.21 ± 0.13 for yield, 0.20 ± 0.13 for number of pods, 0.57 ± 0.13 for seeds per pod, and 0.74 ± 0.15 for seed weight. For a group of genotypes mostly of Andean origin, Singh et al. (1991) estimated narrow sense heritability values to be 0.43 ± 0.19 for yield, 0.49 ± 0.20 for number of pods, 0.63 ± 0.21

for number of seeds, and 0.76 ± 0.23 for 100-seed weight. Other authors reported the following broad-sense heritability estimates for seed yield: 0.90 (Scully et al., 1991), 0.42 ± 0.07 to 0.49 ± 0.04 (Singh and Urrea, 1995) and 0.19 ± 0.17 to 0.50 ±0.16 (Welsh et al., 1995).

Genotype x Environment Interactions

The presence of genotype x environment interactions is the reason that the performance of any genotype relative to another grown in the same environment is inconsistent. These interactions result in either a change in the ordering of the genotypes (change in rank) from one environment to another or to changes in the degree of difference between them without changing their relative order (change in variance) (Hill, 1975). Genotype x environmental interactions are especially important if the relative order of the genotypes changes (Fehr, 1987).

In tropically adapted germplasm, Beaver et al. (1985) observed that the magnitude of the genotypic variance was similar to the variances of genotype x environment interactions, indicating that these interactions are important factors to consider and that testing must be done at several locations to obtain a precise estimate of yield. Likewise, Nienhuis and Singh (1988) reported significant interactions in their work with 80 genotypes, which were mostly small-seeded and of Middle-American origin.

MATERIALS AND METHODS

Genetic Material

Two recombinant inbred populations of kidney bean provided the experimental materials on which yield and seed weight were evaluated in the present study. These populations were derived from 'Montcalm' (MCM), 'California Dark Red Kidney 82' (CDRK 82) and 'California Early Light Red Kidney' (CELRK). MCM is a dark red kidney bean with a Type I growth habit, and was released in 1974 by the Michigan Agricultural Experiment Station (Copeland and Erdmann, 1977). MCM is tolerant to halo blight disease caused by *Pseudomonas syringae* pv. *phaseolicola* (Burkholder) Young et al., matures in 90-100 days from planting, and has excellent canning quality. CDRK 82 is a Type I growth habit dark red kidney bean released in 1989 by the California Agricultural Experiment Station (CAES). CDRK 82 is resistant to bean common mosaic virus (BCMV) and has good yield potential. CELRK was released in 1989 by the CAES. CELRK has a Type I growth habit, resistance to BCMV, and good yield potential. CDRK 82 and CELRK mature in about 90 days and 80 days, respectively, near Chico and Linden, California (Peterson, California Crop Improv. Assoc., personal communication, Nov. 6, 2000).

Population 1, derived from a cross between MCM and CDRK 82, comprised of 75 dark red kidney bean recombinant inbred lines (RILs). Population 2 comprised 73 RILs and was derived from a cross between MCM and CELRK. The crosses were made in 1991 by K.F. Grafton of the North Dakota Experiment Station. The protocol used to develop the RILs of each population was as follows: The initial selection of RILs was made in the F_2 generation. F_2 plants were advanced in the greenhouse until the F_6

generation, using the single-seed descent (SSD) procedure. Seed from F_6 plants were bulked, and the seed increased in the field until the F_8 generation.

Field Plot Procedures

The 75 and 73 RILs of Populations 1 and 2, respectively, the two parents of each population, and check genotypes (Table 1) were planted to conform to a 9 x 9 balanced lattice (Cochran and Cox, 1968) for each population. The $F_{6:8}$, $F_{6:9}$, $F_{6:10}$ and $F_{6:11}$ RILs of each population were planted in 1996, 1997, 1998, and 1999 on a McBride Sandy Loam (coarse-loamy, mixed, frigid Alfic Fragiothods) at the Montcalm Research Farm near Entrican, MI. Each population was planted in a separate experiment and replicated two times, except in 1996, when the experiments were planted in three replications. The entries were planted in two-row plots, 6.1 m long and spaced 0.5 m apart. Within-row spacing was 7.6 cm. Herbicide and fertilizer applications were made following recommendations for commercial bean production for each respective year. The harvested area was 4.6 m^2. The plants were harvested by hand from 1996 to 1998 and threshed using a stationary plot thresher. In 1999, the plots were harvested mechanically and threshed using a Hege 140 Plot Harvester (Hege Equipment, Inc.).

Populations 1 and 2 were grown in Hubbard soil (sandy, mixed, frigid, Entic Hapludolls) in Perham, MI in 1996 ($F_{6:8}$) and in Gardena soil type (coarse-silty, mixed, superactive, frigid, Pachic Hapludolls) in Erie, ND in 1999 ($F_{6:11}$). Table 1 gives the details of the composition of entries for each year and location. These entries were planted in two-row plots, 6.1 m long and spaced 0.8 m apart. The harvested area was 6.0 m^2. In this location, the plants were harvested by hand and threshed using an Almaco stationary plot thresher. After harvest at both the Minnesota and North Dakota sites, the

Table 1. Parents of recombinant inbred populations 1 and 2 and varieties and breeding lines used as checks in each population, and the years and locations in which they were grown in the study.

Variety or breeding line	Year and location[a]					
	Mich 1996	Minn 1996	Mich 1997	Mich 1998	Mich 1999	NDak 1999
Population 1[b]						
MCM[de]	*	*	*	*	*	*
CDRK 82[df]	*	*	*	*	*	*
Isles	*		*	*	*	*
Red Hawk	*		*	*	*	*
K93201 (Montcalm/37-16)			*			
K94202 (Sacramento/I89021)	*		*			
K97305 (Red Hawk/Drake)				*	*	*
K97309 (Red Hawk/K93644)				*	*	*
K90122 (Lassen/Isabella/Montcalm)	*					
Population 2[c]						
MCM[de]	*	*	*	*	*	*
CELRK[dg]	*	*	*	*	*	*
CDRK 82[f]		*				
Isles	*	*				
Chinook	*		*			
Redhawk	*		*			
K93621 (CELRK/Chinook)[g]				*	*	*
K93629 (CELRK/Chinook)[g]			*	*	*	*
K93653 (Chinook/CELRK)[g]			*	*	*	*
K93654 (Chinook/CELRK)[g]	*		*			
K94515 (K89829/K88401)	*					
Chinook2000	*		*	*	*	*
K97503 (Red Hawk/CELRK)[g]				*	*	*
K97504 (Red Hawk/Foxfire)				*	*	*

[a] *- indicates that variety or breeding line was grown in that particular year and location

[b] Population 1: Montcalm x California Dark Red Kidney 82

[c] Population 2: Montcalm x California Early Light Red Kidney

[d] Parents of the population

[e] MCM - Montcalm

[f] CDRK 82 - California Dark Red Kidney 82

[g] CELRK - California Early Light Red Kidney

seeds were hand-cleaned to remove split, damaged and diseased seeds. The seeds were stored at room temperature (~22 °C) until sample preparation and analysis. The yield ($kg \cdot ha^{-1}$) and 100-seed weight (g) of each entry were recorded at constant moisture of 18%.

Statistical Analysis and Estimation of Heritability

All data were subjected to an analysis of variance (ANOVA) appropriate to a randomized complete block design, with genotypes as random effects, and years and environments (year-location combinations) as fixed effects. The SAS program *proc glm* (SAS Institute, Cary, N.C, 1998) was used to analyze data. Significance levels were set at $\alpha = 0.05$. Since the data from the study were not balanced in the sense that experiments were grown in Michigan, Minnesota and North Dakota in each of the years 1996, 1997, 1998 and 1999, analyses were conducted according to the following groups:

Analysis 1 - separate analysis for each experiment i.e., MI-1996, MI-1997, MI-1998, and MI-1999; MN-1996; and ND-1999.

Analysis 2 - combined data for Michigan over the years, 1996, 1997, 1998, and 1999.

Analysis 3 - combined analysis of all experiments such that combinations of years and locations were treated as environments; only the parents and RILs of each population were included in this analysis.

Box-plots of the data in Analysis 1 were constructed to provide a visual comparison of the ranges, means and median values in the different environments. Box-plots are interpreted as follows (Schabenberger, 1997):

a) mean - represented by (+)

b) median value - located by the line dissecting the box

c) first (Q_1) and third (Q_3) sample quartiles - determine the dimensions of the box. In an ordered data set, 25% of all observations are smaller and 75% are larger than Q_1; 25% are larger and 75% are smaller than Q_3. The difference between Q_1 and Q_3 is called the inter-quartile range (IQR).

d) whiskers - represent values within 1.5 x IQR from each end of the box

e) extreme values or outliers - Mild outliers (o) are observations beyond the whiskers but less than 3 x IQR from the respective end of the box. Extreme outliers (*) are observations more than (3 x IQR) from each end of the box.

For the estimation of heritability, two replications of the data from the RILs in Analysis 3 were used. Heritability was estimated for yield and seed mass on a progeny mean basis (Fehr, 1987) as follows:

$$H^2 = \frac{\sigma^2_g}{\sigma^2_t} = \frac{\sigma^2_g}{\sigma^2_e / rv + \sigma^2_{gv} / v + \sigma^2_g}$$

where:
- σ^2_g = genotypic variance
- σ^2_t = total variance among RILs compared in r replications and v environments ($r = 2$, $v = 6$)
- σ^2_e = experimental error
- σ^2_{gv} = variance due to genotype x environment interactions

Confidence intervals for heritability estimates were derived according to Knapp et al. (1985). Correlations among the traits for each environment were also determined using the program *proc corr* in SAS (SAS Institute, Cary, N.C, 1998). To determine correlations of seed color with the yield and seed weight, numerical values were assigned, as follows: 1 – light red seed color, 2 – non-commercial seed color (a mixture of light and dark red), and 3 – dark red seed color.

Images in this thesis are presented in color.

RESULTS

Genotypic effects were significant for both yield and seed weight in all data analyses for Population 1 (Table 2). Except for yield in Mich-1998 (Analysis 1), genotypic effects for Population 2 were significant for yield and seed weight in all experiments (Table 3). Analyses of the Michigan combined data (Analysis 2) for both populations showed significant year effects for yield and seed weight, which led to significant interactions between years and entries (Tables 2 and 3). In Analysis 3 in both populations (years and locations treated as environments), the genotype, environment and genotype x environment effects were significant for both traits (Tables 2 and 3).

For the six experiments in Populations 1 and 2 (Analysis 1), the highest yields were obtained in Mich-1999: 3197 $kg \cdot ha^{-1}$ in Population 1 (Table 4) and 3467 $kg \cdot ha^{-1}$ in Population 2 (Table 5). These data are displayed pictorially in the box plots in Figures 1a and 2a. The yield of the lowest yielding entries in Population 1 in Mich-1999 was higher than that of most of the entries in North Dakota in the same year (Figure 1a). However, due to the high amounts of variability in Minn-1996, Mich-1997 and Mich-1998, several outliers in these environments had yields comparable to some of the highest yielding entries in Mich-1999 (Figure 1a). In Population 2, mean yield was highest in Mich-1999; no extreme differences in variability were observed among the environments (Figure 2a). The yields in Mich-1996 for Population 1, and in NDak-1999 for both populations were generally low for kidney beans (Tables 4 and 5). Seed weight was highest in Mich-1999 and lowest in NDak-1996 year for both populations (Table 4, Figure 1b; Table 5, Figure 2b). Seed weight observed in Minnesota and in North Dakota was generally low for kidney beans. Ranges for seed weight, though variable, were somewhat similar across the

Table 2. Significance levels for main effects and interactions for yield and seed weight of Population 1 entries. Data analyses were according to individual experiments, years, and environments (location and years confounded).

Source of Variation	Yield ($kg.ha^{-1}$)[a]	Seed weight ($g.100\ seed^{-1}$)[a]
Data analysis number and location-year description		
1 - Individual experiments		
Michigan 1996: Genotype	**	**
Minnesota 1996: Genotype	**	**
Michigan 1997: Genotype	**	**
Michigan 1998: Genotype	**	**
Michigan 1999: Genotype	**	**
North Dakota 1999: Genotype	**	**
2 - Michigan data combined (1996, 1997, 1998, 1999)		
Genotype	**	**
Year	**	**
Genotype x Year	**	**
3 - Locations and Years Confounded, and Treated as Environments		
Genotype	**	**
Environment	**	**
Genotype * Environment	**	**

[a] ** - Significant at 0.05 level of significance

Table 3. Significance levels for main effects and interactions for yield and seed weight of Population 2 entries. Data analyses were according to individual experiments, years, and environments (location and years confounded).

Source of Variation	Yield ($kg.ha^{-1}$)[a]	Seed weight ($g.100\ seed^{-1}$)[a]
Data analysis number and location-year description		
1 - Individual experiments		
Michigan 1996: Genotype	**	**
Minnesota 1996: Genotype	**	**
Michigan 1997: Genotype	**	**
Michigan 1998: Genotype	ns	**
Michigan 1999: Genotype	**	**
North Dakota 1999: Genotype	**	**
2 - Michigan data combined (1996, 1997, 1998, 1999)		
Genotype	**	**
Year	**	**
Genotype x Year	**	**
3 - Locations and Years Confounded, and Treated as Environments		
Genotype	**	**
Environment	**	**
Genotype * Environment	**	**

[a] ** - Significant at 0.05 level of significance

Table 4. Data Analysis 1 - Yield and seed weight of Population 1 entries, including parents, RILs and checks. Analyses were conducted individually for each experiment.

Environment	Yield		Seed weight	
	Mean ($kg.ha^{-1}$)	Coefficient of variation (%)	Mean ($g.100\ seed^{-1}$)	Coefficient of variation (%)
Mich (1996)	2615	21.1	56.2	6.1
Minn (1996)	2107	23.5	53.7	7.7
Mich (1997)	2345	19.9	61.9	4.8
Mich (1998)	2602	13.7	58.2	4.6
Mich (1999)	3197	11.6	63.4	3.5
NDak (1999)	1590	18.4	44.9	7.4

Table 5. Data Analysis 1 - Yield and seed weight of Population 2 entries, including parents, RILs and checks. Analyses were conducted individually for each experiment.

Environment	Yield		Seed weight	
	Mean ($kg.ha^{-1}$)	Coefficient of variation (%)	Mean ($g.100\ seed^{-1}$)	Coefficient of variation (%)
Mich (1996)	3359	16.8	61.9	4.4
Minn (1996)	2414	17.5	58.1	6.1
Mich (1997)	2199	15.5	64.4	5.8
Mich (1998)	2711	16.6	59.5	4.7
Mich (1999)	3467	13.9	63.4	3.3
NDak (1999)	1491	21.4	47.6	6.7

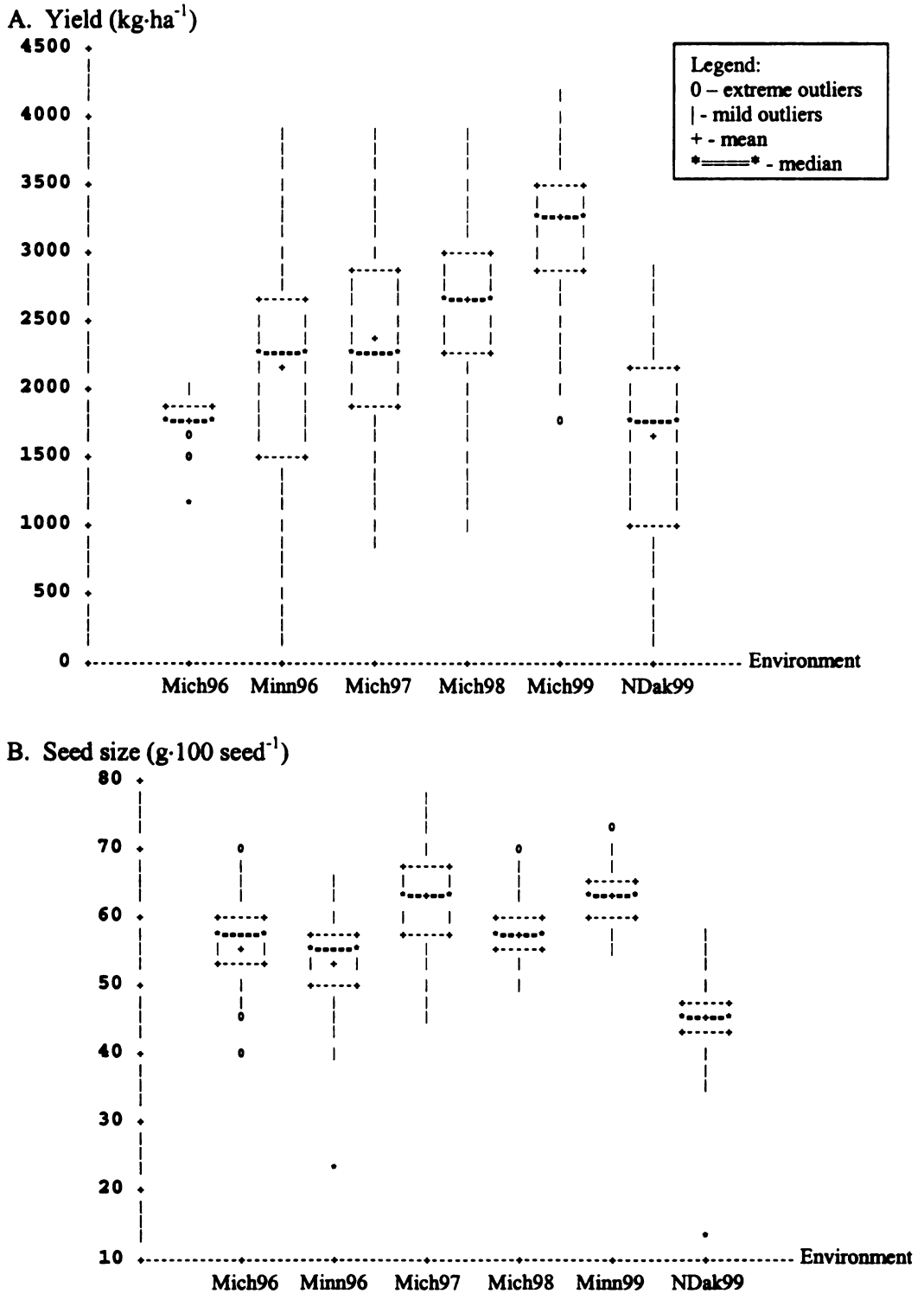


Figure 1. Data Analysis 1 - Box plots for a) yield (kg·ha^{-1}) and b) seed weight (g·100 seed^{-1}) of Population 1 RILs, parents and checks, planted in each environment.

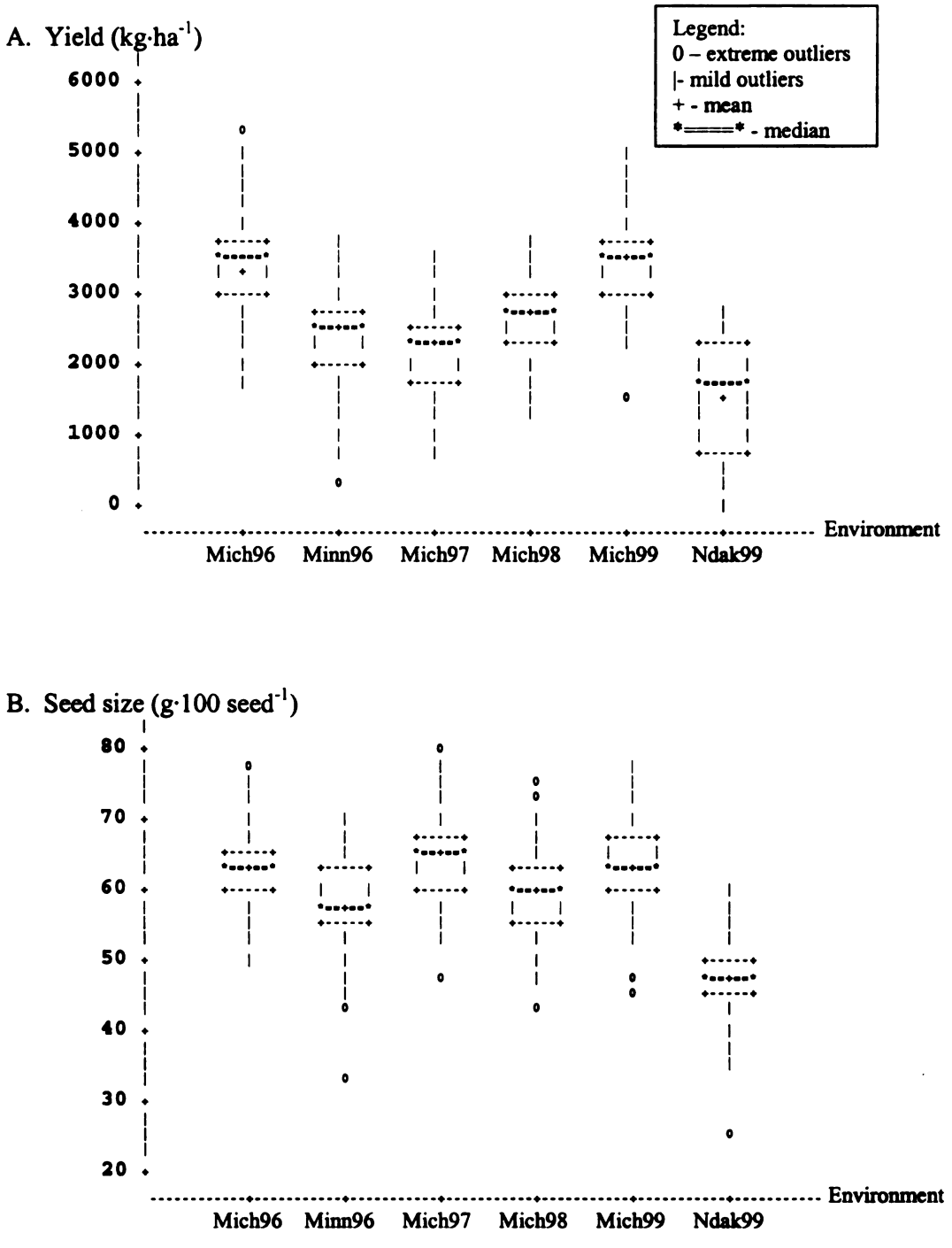


Figure 2. Data Analysis 1 - Box plots of a) yield (kg·ha^{-1}) and b) seed size (g·100 seed^{-1}) of Population 2 RILs, parents and checks, planted in each environment.

six environments for both populations. These results were reflected in the analyses based on the four years of planting in Michigan (Analysis 2) (Tables 6 and 7), and on the analyses which included only the parents and RILs (Analysis 3) (Tables 8 and 9).

High-yielding RILs in Populations 1 and 2

When the two parents of Population 1 were considered, MCM had yields higher than that of CDRK 82 in three environments and CDRK 82 had higher yields in the other three (Table 10). In Population 2, each of the two parents, MCM and CELRK, also had higher yields than the other in three environments (Table 11). In both populations, the mean yield and seed weight of all the RILs did not exceed the mean yield and seed weight of their parents (Tables 10, 11 and 12). However, in each environment, the RILs with the ten highest yields exceeded the parent with the higher yield. Differences were significant in some environments.

The 10 highest yielding RILs in Population 1 had a higher mean yield than the check entries. For example, in Mich-1999 (Table 10), the 10 highest yielding RILs had a mean yield of 3718 $kg \cdot ha^{-1}$, compared to the mean yields of MCM and CDRK 82 (3294 $kg \cdot ha^{-1}$), all the RILs (3187 $kg \cdot ha^{-1}$), and the check varieties (3339 $kg \cdot ha^{-1}$). Differences were significant only for NDak-1999. The mean seed weight of the 10 RILs with the highest yields in each environment, on the other hand, was not consistently higher than the seed weights of the parents (Table 12).

In Population 1, several RILs in the group with the ten highest yields had yields higher than or comparable to the yield of either parent in more than two environments (Table 10). One RIL of Population 1, 118-82, was common to the group with the 10

Table 6. Data Analysis 2 - Yield and seed weight of Population 1 entries, grown in Michigan from 1996 to 1999, analyzed to compare individual years.

Year	Yield[a] ($kg.ha^{-1}$)		Seed weight[a] ($g.100\ seed^{-1}$)	
1996	2622	b	56.4	d
1997	2339	c	62.0	b
1998	2590	b	58.1	c
1999	3201	a	63.4	a
Mean combined over years	2680		59.6	
Coefficient of variation (%)	17.5		5.0	

[a] - Means with the same letter are not significantly different by Fisher's LSD (0.05).

Table 7. Data Analysis 2 - Yield and seed weight of Population 2 entries, grown in Michigan from 1996 to 1999, analyzed to compare individual years.

Year	Yield[a] ($kg.ha^{-1}$)		Seed weight[a] ($g.100\ seed^{-1}$)	
1996	3337	b	62.1	c
1997	2197	d	64.6	a
1998	2722	c	59.9	d
1999	3474	a	63.5	b
Mean combined over years	2977		62.5	
Coefficient of variation (%)	16.4		4.5	

[a] - Means with the same letter are not significantly different by Fisher's LSD (0.05)

Table 8. Data Analysis 3 - Yield and seed weights of Population 1 parents and RILs grown in Michigan, Minnesota and North Dakota from 1996 to 1999, analyzed to compare year-location combinations, treated as environments.

Environment	Yield[a] ($kg.ha^{-1}$)		Seed weight[a] ($g.100\ seed^{-1}$)	
Mich 1996	2619	b	56.4	d
Minn 1996	2107	d	53.7	e
Mich 1997	2336	c	62.0	b
Mich 1998	2581	b	58.0	c
Mich 1999	3190	a	63.4	a
NDak 1999	1608	e	45.0	f
Mean combined over environments	2424		56.4	
Coefficient of variation (%)	18.8		5.7	

[a] - Means with the same letter are not significantly different by Fisher's LSD (0.05).

Table 9. Data Analysis 3 - Yield and seed weights of Population 2 parents and RILs grown in Michigan, Minnesota and North Dakota from 1996 to 1999, analyzed to compare year-location combinations, treated as environments.

Environment	Yield[a] ($kg.ha^{-1}$)		Seed weight[a] ($g.100\ seed^{-1}$)	
Mich 1996	3321	b	62.1	c
Minn 1996	2413	d	58.1	e
Mich 1997	2199	e	64.5	a
Mich 1998	2720	c	60.0	d
Mich 1999	3458	a	63.6	b
NDak 1999	1500	f	47.7	f
Mean combined over environments	2424		56.4	
Coefficient of variation (%)	18.8		5.7	

[a] - Means with the same letter are not significantly different by Fisher's LSD (0.05).

Table 10. Yields of entries in Population 1.

Entry	Environment					
	Mich 1996	Minn 1996	Mich 1997	Mich 1998	Mich 1999	NDak 1999
RIL that was common to the group with the 10 highest yields in five of the six environments[b]						
118-82	3533	3181	3119	3268	3811	-[b]
	---------- Yield (kgs.ha^{-1}) ----------					
RIL that was common to the group with the 10 highest yields in four of the six environments[b]						
118-46	3391	2986	3240	-[b]	-[b]	2383
	---------- Yield (kgs.ha^{-1}) ----------					
RILs that were common to the group with the 10 highest yields in three of the six environments[b]						
118-33	-[b]	2801	3342	3014	-[b]	-[b]
118-84	3670	-[b]	-[b]	-[b]	3604	2508
	---------- Yield (kgs.ha^{-1}) ----------					
Parents of Population 1						
CDRK 82[a]	2613	1273	2715	2670	2875	99
Montcalm	2790	2499	1381	2649	3713	2159
	---------- Yield (kgs.ha^{-1}) ----------					
Means of the experiment, checks, parents, all 75 RILs in Population 1, and 10 highest yielding RILs						
Experiment	2615	2107	2345	2602	3197	1590
Check varieties	2598	-[b]	2526	2993	3339	1244
Parents	2702	1886	2048	2660	3294	1129
All RILs	2617	2105	2344	2579	3187	1620
Ten highest yielding RILs	3224	3034	3213	3078	3718	2436
LSD (0.05)	891	1000	928	709	738	581
CV (%)	21.1	23.5	19.9	13.7	11.6	18.4
	---------- Yield (kgs.ha^{-1}) ----------					

[a] CDRK 82 - California Dark Red Kidney 82

[b] - only the yields where the RILs were among the ten highest-yielding lines are shown

Table 11. Yields of entries in Population 2.

Accession	Seed color[a]	Environment					
		Mich 1996	Minn 1996	Mich 1997	Mich 1998	Mich 1999	NDak 1999
RILs that were common to the group with the 10 highest yields in four of the six environments[b]							
119-21	Light red	-[c]	3191	-[c]	3176	4086	2274
119-32	Dark red	-[c]	3069	-[c]	3248	3991	2293
		---------- Yield (kgs.ha^{-1}) ----------					
RILs that were common to the group with the 10 highest yields in three of the six environments[b]							
119-17	Light red	-[c]	-[c]	2842	3128	4153	-[c]
119-50	Light red	3801	3006	-[c]	-[c]	-[c]	2294
119-60	Non-commercial	-[c]	3076	-[c]	3088	-[c]	2532
119-70	Light red	-[c]	3245	-[c]	3312	4342	-[c]
119-79	Light red	4621	-[c]	-[c]	-[c]	4265	2337
		---------- Yield (kgs.ha^{-1}) ----------					
Parents of Population 2							
CELRK[b]	Light red	3823	1964	2610	3242	3214	436
Montcalm	Dark red	3578	2120	1580	2610	3563	2546
		---------- Yield (kgs.ha^{-1}) ----------					
Means of the experiment, checks, parents, all 75 RILs in Population 1, and 10 highest yielding RILs, and values for LSD and CV							
Experiment mean		3359	2414	2199	2711	3467	1491
Check varieties		3836	2459	2204	2597	3582	1379
Parents		3700	1806	2095	2926	3388	1491
All RILs		3311	2423	2201	2714	3459	1500
Ten highest yielding RILs		4014	3130	2849	3177	4145	2453
LSD (0.05)		913	853	679	896	961	634
CV (%)		16.8	17.5	15.5	16.6	13.9	21.4
		---------- Yield (kgs.ha^{-1}) ----------					

[a] Non-commercial seed color: a mixture of dark and light red

[b] CELRK - California Early Light Red Kidney

[c] - only yields in the environments where the RILs were among the 10 highest-yielding lines are shown

Table 12. Seed weights of entries in Populations 1 and 2.

Accession	Environment					
	Mich 1996	Minn 1996	Mich 1997	Mich 1998	Mich 1999	NDak 1999
Population 1						
Parents of Population 1						
MCM	55.1	57.2	58.4	57.9	62.8	47.5
CDRK 82	57.8	49.1	54.2	55.6	65.7	42.1
	---------- Seed weight (g.100 seed^{-1}) ----------					
Means of the experiment, checks, parents, all 75 RILs in Population 1, and 10 highest yielding RILs						
Experiment	56.2	53.7	61.9	58.2	63.4	44.9
Check varieties	53.2	-	59.9	61.7	63.2	42.9
Parents	56.4	53.1	56.3	56.7	64.2	44.8
All RILs	56.4	53.7	62.2	58.1	63.4	45.0
Ten Highest yielding RILs	58.8	57.7	66.7	58.3	63.2	48.4
LSD (0.05)	5.5	8.4	5.9	5.4	4.4	6.6
CV[a] (%)	6.1	7.7	4.8	4.6	3.5	7.4
	---------- Seed weight (g.100 seed^{-1}) ----------					
Population 2						
Parents of Population 2						
MCM	62.8	56.0	69.0	56.3	61.9	46.9
CELRK[b]	64.0	50.2	61.6	64.5	60.9	44.2
	---------- Seed weight (g.100 seed^{-1}) ----------					
Means of the experiment, checks, parents, all 73 RILs in Population 2, and 10 highest yielding RILs, and values for LSD and CV						
Experiment mean	61.9	58.1	64.4	59.5	63.4	47.6
Check varieties	58.9	60.0	62.6	53.0	61.8	46.0
Parents	63.4	53.1	65.3	60.4	61.4	45.6
All RILs	62.1	58.1	64.5	60.0	63.6	47.7
Ten Highest yielding RILs	65.9	60.7	65.3	58.0	64.9	52.8
LSD (0.05)	4.4	7.2	7.5	5.5	4.1	6.4
CV[a] (%)	4.4	6.1	5.8	4.7	3.3	6.7
	---------- Seed weight (g.100 seed^{-1}) ----------					

[a] CV - Coefficient of variation

[b] CELRK - California Early Light Red Kidney

highest yields in five of the six environments. RIL 118-46 was common to the group with the 10 highest yields in four of the six environments. Moreover, in these environments, RILs 118-46 and 118-82 had higher yields than both the average of the parents and the yield of the better yielding parent. Three RILs, 118-94, 118-33, and 118-39, were common to the group with the 10 highest yielding RILs in three out of the six environments (Table 10).

In Population 2, the mean yield of the 10 highest yielding RILs was higher than the mean yield of the parents in all environments (Table 11). However, when the individual yields of MCM and CELRK were considered, the mean yield of the 10 highest yielding RILs was higher than the yields of both parents in only four of the six environments (Table 11). When the high yielding RILs were compared to the check varieties, the mean yield of the RILs was higher than that of the check varieties in all environments (Table 11). For example, in Mich-1999, the 10 highest yielding RILs had a mean yield of 4145 $kg \cdot ha^{-1}$, compared to the means of MCM and CELRK (3388 $kg \cdot ha^{-1}$), all the RILs (3459 $kg \cdot ha^{-1}$) and the check varieties (3582 $kg \cdot ha^{-1}$) (Table 11). Unlike the yield, the mean seed weight of these 10 high yielding RILs was not consistently higher than the mean seed weights of the parents and the check varieties (Table 12).

Several RILs in Population 2 were common to the group of the 10 highest yielding RILs in more than two environments (Table 11). Some of these RILs had high yields only in Michigan while some were high yielding in different sites in different years. In most cases, the yields of the RILs were comparable to or exceeded that of either parent. Two RILs, one a dark red and another a light red kidney bean line, were among the 10 highest yielding RILs in four environments. These two RILs, 119-21 and 119-32, were

among the highest yielding entries in Mich-1998, Mich-1999, Minn-1996 and in NDak-1999. Five RILs, four of which were light red kidney bean lines and one of which was of a non-commercial seed color, were among the 10 highest yielding RILs in three environments. One of these five, RIL 119-17, a light red kidney bean line, was in the group in three years in Michigan. The three other light red kidney bean RILs, 119-50, 119-70 and 119-79, were in the group in three different environments. The yields and seed weights of these and the rest of the RILs of the two populations, and of the check cultivars in each experiment, are shown in Appendix Tables A.1 to A.4. In each experiment, several RILs had yields higher than one or more of the commercial cultivars used as checks.

Heritability Estimates and Correlations Between Yield and Seed weight

The ANOVA tables from which the variance components were estimated from mean squares for yield and seed weight are shown in Tables A.9 to A.12. Heritability estimates for yield and seed weight were obtained using data from the 75 and 73 RILs, respectively, of Populations 1 and 2. Estimates were moderate in value (Table 13).

Table 13. Heritability estimates for yield and seed weight of the 75 and 73 RILs in Populations 1 and 2, respectively, calculated from data combined over six environments.

Population	Yield[a] (CI[b])	Seed Weight[a] (CI[b])
Population 1	0.62 (0.45 - 0.71)	0.58 (0.38 - 0.68)
Population 2	0.63 (0.45 - 0.73)	0.69 (0.55 - 0.78)

[a] - Two replications in six environments; year-location combinations treated as environments.
[b] CI – 95% confidence interval

Heritability estimates from Population 2 were higher than the values from Population 1. In Population 1, the heritability estimates for yield and seed weight were 0.55 and 0.58, respectively. In Population 2, the heritability estimates were 0.63 and 0.69 for yield and seed weight, respectively (Table 13).

Seed weight was positively correlated with yield in both populations (Table 14). In Population 1, the correlation coefficients ranged from 0.4 to 0.7 in four environments - Minn-1996, NDak-1999, Mich-1997 and Mich-1998). In Population 2, the coefficients of correlation ranged from 0.2 to 0.6 in five environments - Mich-1996, Mich-1997, Mich-1999, Minn-1996, and NDak-1999. For Population 2, seed color was also correlated with yield and seed weight (Table 14). Numerical values for seed color (1 – light red; 2 – mixture of light and dark red; 3 – dark red) were negatively correlated with

Table 14. Significant correlations between yield, seed weight and seed color in Populations 1 and 2, planted in Michigan, Minnesota and North Dakota from 1996 to 1999.

		Environment[a]						
Trait 1	Trait 2	Mich 1996	Minn 1996	Mich 1997	Mich 1998	Mich 1999	NDak 1999	Range[b]
Population 1								
yield	seed weight	*	*	*	*		*	0.42 to 0.66
Population 2								
yield	seed weight	*	*	*		*	*	0.17 to 0.60
yield	seed color	*					*	-0.21
seed weight	seed color	*	*			*	*	-0.26 to -0.45

[a] * - Significant at level of significance = 0.05.

[b] Range - Range of significant coefficients of correlation over environments.

yield in two environments (Mich-1996 and NDak-1999) with significant coefficients of correlation around –0.2. Thus, in these two environments, the light red kidney bean RILs (seed color = 1) generally had significantly higher yields than the dark red RILs (seed color = 3). In Mich-1996, the light red kidney bean lines (35 RILs) had a mean yield of 3441 $kg.ha^{-1}$, while the dark red kidney bean lines (27 RILs) had a mean yield of 3201 $kg.ha^{-1}$ (data not shown). In NDak-1999, the light red and dark red kidney bean lines had mean yields of 1691 $kg{\cdot}ha^{-1}$ and 1221 $kg{\cdot}ha^{-1}$, respectively (data not shown). The light red kidney bean lines also had a higher mean yield overall (averaged over all environments) (2686 $kg{\cdot}ha^{-1}$) than the dark red lines (2518 $kg{\cdot}ha^{-1}$).

Significant coefficients of correlation between seed color and seed weight ranged from –0.3 to –0.5 in four environments (Table 14). The negative correlations indicate that in Mich-1996, Mich-1999, Minn-1996 and NDak-1999, the light red kidney bean RILs had significantly higher seed weights than the RILs with dark red seed color. Averaged over all the environments, the light red kidney bean lines had a mean seed weight of 61.1 $g{\cdot}100\ seed^{-1}$, while the dark red kidney bean lines had a mean seed weight of 58.2 $g{\cdot}100\ seed^{-1}$ (data not shown).

DISCUSSION

Quantitative traits such as yield and seed weight are generally controlled by many genes. The loci involved in the expression of a quantitative trait are called quantitative trait loci. The effective manipulation of QTLs is required for the improvement of the traits they control. However, the individual effects of these QTLs are not readily identifiable since the environment influences QTL expression to a significant but often unknown degree. Significant environmental effects also lead to genotype x environment interactions, which obscure genetic variation. The environment affects not only the level of performance of the genotypes, but also the degree of variation expressed in a population as a whole. Thus, the reliability of cultivar performance across locations and years is an important consideration in plant breeding (Fehr, 1987). If the genotype x environmental interaction is substantial for a trait of interest, the breeder may have to test over a series of locations and for several years to assess the breeding value of genotypes under selection.

Some lines intended for commercial release perform well under a range of locations and over several seasons while other lines are more limited in performance. Information about a line's performance in a series of environments is used to determine its stability. Phenotypically stable genotypes are well buffered in the genetic sense and show a predictable response to different environmental conditions. Stability is particularly important for yield and yield components in dry bean (Kelly et al., 1998). To ascertain the stability of a given set of materials, yield testing must be replicated over a broad range of environments, including locations and years.

Genotype x environment interactions involving year effects warrant different considerations in the breeding sense than do those interactions containing location terms (Allard and Bradshaw, 1964). Genotype x year interactions generally are more unpredictable than genotype x location interactions. The breeder has little control over seasonal variations in rainfall, temperature, and cloud cover; however, environmental influences due to location effects and genotype x location interactions may be ameliorated by soil and crop management changes. Nevertheless, weather patterns and disease incidence differ across locations too.

The results of the present study indicated that testing of beans for yield and yield components (seed weight) for a period of years is necessary. In this study, the two kidney bean recombinant inbred populations were evaluated over four seasons. The variation attributed to significant year effects may be more precisely determined from a series of annual experiments such as was the case for the Michigan tests (four consecutive years) than from seasonal effects evaluated in a few randomly chosen seasons (e.g., two years). Testing should thus be conducted over several consecutive years to establish a genotype or group of genotypes' stability. Dry bean is extremely responsive to high temperature, large diurnal fluctuations in temperature, drought, etc. Testing in a limited number of seasons that are randomly chosen from a seasonal interval may preclude the breeder from accurately predicting a genotype's stability for a trait. Evaluation over several seasons will also allow a more precise estimate of the amount of variation available for selection.

Evaluation of lines in more than one location allows the assessment of their adaptation to different sites. The structure of the current study was such that location

effects cannot be determined for more than one year. In the two years in which the populations were evaluated in more than one location, the locations involved were Michigan and Minnesota in 1996, and Michigan and North Dakota in 1999. The experiments involving two locations may be compared only within the year in which they were conducted, using the results of Analyses 1 and 3 (Tables 4, 5, 8 and 9; Figures 1 and 2). In 1996, yield was significantly higher in Minnesota than in Michigan for Population 1, but for Population 2, yield was significantly higher in Michigan. In 1999, yield in Michigan was significantly higher than in North Dakota for the two populations.

Seed weight was significantly higher in Michigan than in either Minnesota or North Dakota in 1996 and in 1999. In other yield trials, the yield of dry beans in Michigan has been consistently higher than in either Minnesota or North Dakota (unpublished data from cooperative dry bean nurseries from 1994 to 1999). Comparisons across different locations must be conducted over several years to obtain an accurate assessment of location effects on yield and seed weight of bean genotypes. In this study, Michigan can be compared with Minnesota or North Dakota in only one year. Thus, other than the observations already given, no conclusions can be made about variable yield and seed weight responses in the three locations, or about the plant characteristics and developmental aspects that could account for these differences.

In the two populations tested in this study, no single RIL was superior yielding and manifested a high seed weight in all environments. Instead, ten RILs, which had the highest yields in each environment, were identified. Although the mean yield of each population (all RILs) was not higher than the mean of the respective parents, the mean yield of these 10 RILs was higher than the means of both the parents and the checks.

Transgressive segregation of genes for yield might have contributed to these RILs outyielding their respective parents. These results suggest that yield in kidney bean can be increased by crossing established cultivars among themselves or cultivars by the breeding lines. However, since the increases in yield were small, other sources of genes for yield need to be introduced.

Some RILs were high yielding in at least two years in Michigan only. The development of these RILs specifically for Michigan may be the appropriate and practical approach. Some lines in both populations were among the highest yielding RILs in more than one location, with yields higher than the parents and checks. Two RILs in Population 1 (118-82 and 118-46) and two in Population 2 (119-18 and 119-32) were common to the group with the 10 highest yields in four of the six environments in which the study was evaluated (Tables 10 and 11). Thus, the significant effects of the environment did not affect the ranking of some genotypes. At least some of RILs in these kidney bean populations are apparently sufficiently stable across environments in yield and seed weight. These results are not surprising since the three parents, MCM, CDRK 82, and CELRK, had acceptable yields in these locations in previous yield trials (unpublished data from cooperative dry bean nurseries from 1994 to 1999), suggesting that it may be possible to select particular genotypes that will perform well in all three locations.

In addition to the statistical treatment of the environment as fixed effects, the presence of significant interactions places a condition on inferences that can be made about the main effects of genotypes, years, and year-location combinations (environments). The estimates of these main effects are conditional, such that the

genotypic effects that may be concluded are only as observed in the years and environments where the tests were conducted, and not over all possible environments (Freeman, 1973). Given similar climatic conditions in future years of testing, the performance of the RILs in the three locations, Michigan, Minnesota and North Dakota, from 1996 to 1999 may be used only as a benchmark for potential yield. Environmental fluctuations not sampled in these four years may cause results dissimilar to those reported here. Likewise, the RILs may perform differently in areas other than these three locations; i.e., no conclusions or predictions can be made about their yield potential in other production areas.

Heritability estimates for yield and seed weight were mid-value for Population 1 and mid- to high-value for Population 2 (Table 13). These were similar to those reported by Singh et al. (1991) for a group of mostly Andean genotypes. However, the variances due to year, location and year x location interactions were confounded in the present study, thus possibly causing an upward bias in the heritability estimates (Fehr, 1987). Although these estimates aid in understanding the genetic control of these traits in kidney beans, the very nature of heritability makes it clear that any estimate is specific both to the material under study and to the structure of the experiment (Simmonds, 1979). The heritability estimates from this study, along with the observed stability and yield potential of some of the RILs, indicate yield in kidney bean can be increased through breeding and selection. The high yielding RILs reported here may be used as parents in developing lines with high yields and stable performance over several seasons. Lines that performed well in Michigan over several years may be further developed specifically for the state

while those lines that had high yields in more than one location showed a wider adaptation.

Yield and seed weight were positively correlated in at least four environments in the two populations. The correlation was in contrast to the findings reported by Nienhuis and Singh (1985), who found negative correlations between the two traits. The relationship between yield and seed weight is particularly important in dry bean, due to the strict seed size requirements placed on each market class. Kidney bean cultivars must have seed size acceptable to the processing industry. The standard seed size for this market class is 50-65 gm per 100 seeds (Adams and Bedford, 1975). Beans that are perceived as too small are undesirable by both producers and consumers. Breeders and farmers, on the other hand, desire high yields. Thus, the positive correlations observed here for the two kidney bean populations bode well for both bean breeders and processors. The requirements of consistently high yielding lines and sufficiently large seeds may be met without compromising one or the other.

Based on previous work by other authors (Adams, 1967; Nienhuis and Singh, 1985, 1988; Ranalli et al., 1991), the possibility that the correlated increases in yield and seed weight were accompanied by compensatory reductions in number of seeds per pod and/or number of pods per plant exists. These relationships between yield components are developmental in nature, are influenced by the environment, and may be due to competition among plant structures for a common and limited nutrient supply (Adams, 1967). Environmental fluctuations may have triggered these mechanisms in the kidney bean RILs used in this study. Further research is necessary to test this hypothesis. Low but positive correlations between yield components were reported by Coyne (1968), who

also suggested the feasibility of selecting for one trait without an accompanying reduction in the others. In the present study, since data on number of seeds per pod and number of pods per plant were not taken, yield component compensation involving these two traits, as they relate to yield and seed weight in kidney beans, warrant no further discussion.

In dry bean, several factors – lack of favorable alleles, low heritability, high genotype x environment interactions, yield component compensation, low or negative GCA within and between gene pools, and reliance on visual selection in early generations contribute to the slow progress in yield improvement (Kelly et al., 1998). The results from the present study with RILs from two kidney bean populations underscore the influence of the environment on the expression of QTL controlling yield. Moderate heritabilities for yield and seed weight indicate sufficient genetic control over the trait to permit successful breeding for increased yield.

The major limitation in yield breeding in dry bean is not low heritability, stability or genotype x environment interactions, but a lack of favorable genes for yield in the current cultivated germplasm (Kelly et al., 1999). Since kidney beans have a narrow genetic base, new sources of genetic material are necessary to introduce new genes for yield into existing germplasm pools. There is a need to identify and utilize favorable genes from other sources such as plant introductions and wild accessions of *P. vulgaris*. Kelly et al. (1999) proposed a three-tiered approach to yield breeding, which utilizes a broad genetic base as a source of genes for elite lines. Such approaches will take advantage of the diversity of bean germplasm and ensure continued success in increasing the yield of kidney beans and other classes of dry bean. Utilizing new sources of genes for yield, however, may have undesirable effects on other traits considered important for

commercial kidney bean cultivars, such as canning quality. Unadapted germplasm may have the necessary genes to increase yield in cultivated genotypes but have not been subjected to selection for traits such as wholeness of beans after processing and general acceptability for consumption. Thus, the introduction of genes from these unadapted sources may compromise canning quality. Such negative correlations, if present, retard progress in breeding for yield (Yan and Wallace, 1995). Both sets of traits must be evaluated and monitored throughout the breeding process in order to meet the desired goals for yield breeding without compromising other important traits.

CHAPTER 2: EVALUATION OF CANNING QUALITY IN KIDNEY BEAN, AND THE IDENTIFICATION OF RANDOM AMPLIFIED POLYMORPHIC DNA (RAPD) MARKERS ASSOCIATED WITH CANNING QUALITY TRAITS

INTRODUCTION

Much of the dry bean production in the U.S. that is canned commercially is consumed domestically. Due to their nutritional composition, dry bean is a valuable addition to the diet of consumers. Kidney beans, for example, are composed of approximately 22% protein, 4.0% ash, 67% carbohydrates and 7.0% fiber (Sathe et al., 1984). In addition, beans have a long shelf life and cost less than most animal, fruit and vegetable products.

Since dry beans are eaten as whole grains and not milled into flour, consumers have been conditioned by years of use to expect certain characteristics of the dry, soaked, and cooked beans. Likewise, processors have their own set of criteria that are mostly concerned with processing efficiency and profitability. Due to consumer expectations and processing standards for beans, the dry bean processing industry has made processing characteristics a major consideration in their choice of bean varieties. Plant breeders and food scientists collaborate to ensure that newly released bean varieties meet, not only yield expectations, but also the acceptability standards established by the processing industry for the various market classes of dry bean.

In view of the steps necessary to prepare beans for eating, a priori tests that evaluate components of canning quality have been developed (Hosfield and Uebersax, 1980; Hosfield et al., 1984a; Ghaderi et al., 1984; and Walters et al., 1997). These tests measure distinct physical and chemical properties of bean seeds that are logically related

to canning quality (Hosfield et al., 1984b). Several canning tests have been adopted for use in private and public breeding programs. The test measurements do not fall into discrete measurement classes and hence, are quantitative in nature. Moreover, canning quality methodology in dry bean generally requires the use of advanced generation plant material to ensure sufficient seed for evaluation.

Breeding for canning quality in dry bean provides a difficult challenge to the plant breeder because of the quantitative nature of the component traits, and the necessity of waiting until the F_5 or F_6 generation when sufficient seed is available for canning tests. Indirect selection using linked molecular markers, termed marker-assisted selection (MAS), has received attention as a method for increasing selection efficiency within breeding programs. If a trait is expensive to evaluate, under polygenic control, or considerably influenced by the environment, MAS may be more efficient than traditional (direct) selection methods based on phenotype. The use of MAS has proven to be effective in shortening the time involved in the improvement of quantitative traits in many crops (Dudley, 1993), and may prove useful in breeding for canning quality in beans, in general, and kidney beans, in particular.

Kidney beans constitute a significant percentage of dry bean production in the U.S. Light red kidney beans are used in chili products, while the dark red varieties are a significant component of restaurant salad bars. A large portion of the annual kidney bean crop in the U.S. is canned prior to commercial distribution, and thus must meet the standards required by the bean canning industry and by consumers. Canning quality thus continues to be an important focus for kidney bean breeding programs. In addition to conventional approaches, improved technology, such as the development of molecular

markers for complex traits, has afforded the use of methods not previously available to plant breeders. The future of plant breeding includes the assessment of the feasibility of using these methods and their effective application to problems with which breeders have been dealing for decades. This present study seeks to address and remedy the lack of information on RAPD markers associated with canning quality traits in beans in general and kidney beans in particular.

The study was conducted on two recombinant inbred populations of kidney bean. The populations were planted in Michigan from 1996 to 1999, in Minnesota in 1996, and in North Dakota in 1999. The objectives of the research were to a) evaluate canning quality of the two recombinant inbred lines in six environments; b) estimate heritabilities and correlations between canning quality traits; c) identify putative RAPD markers for canning quality; and d) determine whether markers associated with canning quality in navy bean are useful for kidney bean.

REVIEW OF LITERATURE

The importance of canned beans in the diets of many people has prompted studies dealing with the various components of canning quality and the development of methods for evaluating these components (Hosfield and Uebersax, 1980; Hosfield et al., 1984a; Ghaderi et al., 1984). Advances in biological research, such as the use of molecular markers, have opened the possibility that such markers may facilitate canning quality evaluation and lead to the development of varieties that meet the requirements of processors and consumers (Walters et al., 1997).

Canning Quality

Canning quality is composed of traits that affect the hydration characteristics of seeds, thermal conditions that render the seed palatable and provide for the digestion of nutrients, and consumer expectations for the cooked product. Some traits that processors and consumers pay attention to are: rate of water uptake, volume increase of seeds, expansion coefficients of soaked and blanched seeds, brine characteristics, uniformity of seed size and shape, seed color and appearance, mouthfeel, texture, digestibility, degree of clumping and splits, visual appeal (perceived overall acceptability), net weight after canning (processors' yield), flavor, and ease of preparation and cooking (Adams and Bedford, 1975; Hosfield and Uebersax, 1980, 1990; Uebersax and Bedford, 1980; Ghaderi et al., 1984; Hosfield et al., 1984a; Hosfield, 1991; Forney et al., 1990; and Walters, 1995). Although these physical and chemical attributes of cooked beans all contribute to the definition of processing quality, no single trait defines overall acceptability (Hosfield and Uebersax, 1990; Hosfield, 1991).

Components of canning quality. Rapid and uniform uptake of water during soaking is a desirable trait of beans for canning (Hosfield and Uebersax, 1990; Adams and Bedford, 1975). A moisture content of 55% after soaking is considered optimum (Uebersax, 1985). Soakability is generally measured as the difference in weight of a bean sample before and after soaking, and is expressed as the hydration coefficient (HC) (Adams and Bedford, 1975).

Texture (TXT) is another primary canning quality character. TXT affects the perceived stimulus for chewing, and hence, influences to a large degree a consumer's acceptance of a food product. TXT of processed beans has three components: firmness,

gumminess, and adhesiveness. Firmness is defined as the resistance of a bean to deformation after a mechanical force is applied. Lu and Chang (1996) and Van Buren et al. (1986) reported contrasting effects of firmness on the degree of splitting of cooked beans. According to Van Buren et al. (1986), a low incidence of splitting is associated with a lower WDWT and firmer cooked beans. Lu and Chang (1996), on the other hand, reported that high firmness values are associated with a more viscous medium after cooking and more splits, and thus contribute to a lower overall acceptability (visual appeal) of the cooked beans. Harvest date appears to affect the firmness of processed beans, with later dates resulting in firmer textures (Kays et al., 1980). Gumminess is measured by the energy required to disintegrate the sample and adhesiveness is the degree of stickiness or difficulty of removing the substance from a smooth surface, e.g., the roof of the mouth. A panel of judges who render an opinion of a perceived stimulus may subjectively evaluate TXT. TXT can also be estimated objectively by using an Allo-Kramer Shear Press (Food Technology Corp., Rockville, MD). Although the firmness of a food, as determined with a shear press, ignores other perceptions, such as viscosity of the medium, adhesion, or gumminess, it estimates TXT in a practical sense. As such, the measurement serves as an index for consumer acceptance. In the case of cooked beans, beans may be unacceptable if perceived as too firm ("tough beans") or too soft ("mushy beans") (Hosfield et al., 1984a).

The hydration properties of cooked beans are expressed as the washed drained weight (WDWT), which is the net weight of processed beans after rinsing under cold tap water and draining (Wassimi et al., 1990; Hosfield and Uebersax, 1980). This trait is important to canners who seek high can yields because, when the WDWT is high, fewer

beans are required to fill a can of a particular volume. Beans with a high WDWT usually have high swelling capacities and high physical entrainment brought about by water-macromolecule interactions. A low WDWT may occur when beans lose excessive solids during processing. With excessive solids loss, water entrainment is low, and low WDWT occurs because the solids lost are heavier than the water absorbed. In general, WDWTs for canned beans with initial fresh weights equivalent to 100g total solids (TS) range from 275-375g. Higher WDWTs have been associated with softer beans after canning (Lu and Chang, 1996).

The degree of clumping and splitting are physico-chemical attributes of cooked beans that have a marked influence on visual appeal, which is one of the primary criteria of consumers of beans. Clumping may be due to excessive starch exudation during canning (Adams and Bedford, 1975) and is undesirable (Wang et al., 1988). Fewer splits in canned beans contribute to higher acceptability (Lu and Chang, 1996; Forney et al., 1990). Splitting appears to be affected by seed size, with larger seeds showing more splits (Forney et al., 1990). Later harvest dates seem to result in fewer split seeds (Kays et al., 1980). Splitting may also be affected by threshing and post-harvest handling conditions, as well as soaking and processing conditions.

Brine characteristics after processing are also important for beans processed in tin cans or glass jars. Consistency, graininess or cloudiness, and color of the brine are considered in rating brine characteristics for acceptability. Brine of good quality is slightly viscous, clear, without obvious starch granules, and drains easily from the whole beans (Adams and Bedford, 1975). Brine that is highly viscous has been correlated with

greater clumping than less viscous brine. Correlations have shown that the more starch in the brine, the lower the overall acceptability of beans (Lu and Chang, 1996).

Other factors affecting overall visual appearance are uniformity of seed size and shape in a sample, the intensity and uniformity of seed color, wholeness of the beans, and absence of loose seed coats and other extraneous material (Adams and Bedford, 1975; Ghaderi et al., 1984; and Forney et al., 1990). Although most of the qualities discussed above are based on sensory perception, certain procedures have been established in order to objectively evaluate each component trait (Hosfield and Uebersax, 1990).

Procedures in processing. Canning methods employed during genotype evaluation should simulate those used in the commercial canning industry, with the primary purpose being aroma development and rendering the beans tender enough for human consumption. Processing also removes or inactivates beany or bitter flavors and antinutritional factors such as protease inhibitors, lectins, phenolic compounds and phytates (Deshpande et al., 1984).

According to Adams and Bedford (1975), the procedures appropriate for the evaluation of canning quality are as follows: selection of good quality raw dry beans, equilibration of moisture content, soaking, blanching, filling in cans, cooking, equalization of cooked beans and evaluation. In addition to bean genotype and moisture level, the different conditions produced by these procedures affect the quality of canned beans.

Uebersax (1972) studied the effects of storage and soaking methods on the processing quality of navy beans. The temperature and relative humidity under which beans are stored were found to affect processed bean color, flavor and firmness

(Uebersax, 1972). In the same study, the temperature and composition of the soak water was found to significantly affect water uptake, bean volume and texture. Further research (Uebersax and Bedford, 1980; Wiese and Jackson, 1993) corroborated these results.

If processing evaluations are to measure true differences between varieties, the moisture content of each seed sample should be equilibrated to a common value of about 14 to 18% (Deshpande et al., 1984). Adams and Bedford (1975) suggested moisture levels of 12-14%, if the beans are to hydrate and cook readily. Beans stored under high RH, which would consequently have high moisture contents, require a longer cooking time (Kon and Sanshuck, 1981). On the other hand, Deshpande et al. (1984) observed that, if the moisture content is too low, the beans may not imbibe water normally and become hard to cook, or the seed coats may become brittle and crack during processing.

Soaking ensures tenderness and uniform expansion of the beans during canning (Hoff and Nelson, 1965), shortens the processing time, and reduces the amount of toxic compounds found in raw beans (Deshpande et al., 1984; Uebersax et al., 1991). Van Buren et al. (1986) reported that higher concentrations of calcium in the soaking medium (150-350 ppm) and higher soak temperatures (66-71°C) significantly reduce splitting.

Uebersax and Bedford (1980) determined that the following two-step process provided optimum soaking conditions for canning beans: 30 minutes at 23°C and 30 minutes at 88°C with at least 50 ppm calcium in the soak water. Addition of 100 ppm calcium ion resulted in beans with minimum damage due to splitting and beans becoming mushy (Hosfield and Uebersax, 1980). Beans soaked at 82°C or 93°C for 30 minutes had short rehydration times and hydration coefficients similar to beans soaked in many processing plants (Ogwal and Davis, 1994). In the same study, processing conditions at

121°C for 21 minutes were found to result in higher WDWTs, softer beans, and less splitting than the control, which was processed at 116°C for 41 minutes.

Blanching eliminates air and equalizes moisture in the samples. However, overblanching beans causes the seed coats to split (Adams and Bedford, 1975). Steam blanching at a high temperature for a short time produced canned beans with good quality, although quality varied with cultivar and length of time of the blanching process (Drake and Kinman, 1984).

Addition of both calcium chloride ($CaCl_2$) and ethylenediaminetetraacetic acid (EDTA) to the processing medium improved both the firmness and color of processed beans, and resulted in less splitting in kidney beans (Van Buren, 1986). The use of $CaCl_2$ alone reduced clumping and splitting of beans (Wang et al., 1988; Wang and Chang, 1988). Shorter cooking times also reduced splitting in kidney beans (Van Buren, 1986). After beans are processed, they continue to imbibe water until they reach a moisture content of approximately 65% (Adams and Bedford, 1975). Storing processed beans for two weeks before evaluation ensured that water imbibition in the can was complete (Hosfield and Uebersax, 1980).

In addition to storage conditions and processing procedures, processing quality in dry bean depends on the genotype, environment, their interactions, and the condition of seeds at harvest (Wassimi et al., 1990; Hosfield, 1991; Lu and Chang, 1996; Nordstrom and Sistrunk, 1979; Junek et al., 1980; Hosfield et al., 1984b). In studies by Uebersax and Bedford (1980), Ghaderi et al. (1984), Hosfield et al. (1984b), Wassimi et al. (1990) and Walters et al. (1997), environmental effects on certain processing quality traits were found to be significant. The variations in the phenotype caused by the environment are

usually unpredictable. The responses of different genotypes relative to one another may vary over sites and years, and frequently lead to genotype by environment interactions, which complicate the interpretation of results (Hosfield, 1991). Significant interactions between genotype and environment must be considered in interpreting the effect of genotype or environment alone.

Genetics of Canning Quality. Genetic variation with respect to processing quality has been reported in dry beans (Hosfield and Uebersax, 1980, 1990; Hosfield et al., 1984b; Wassimi et al., 1990). As for any complex trait, the breeder must have knowledge of the genetic control and heritability of the traits comprising canning quality in order to ascertain and utilize phenotypic variability for the traits under selection.

Wassimi et al. (1990) confirmed the mode of inheritance of physico-chemical traits related to processing quality in dry bean. Genes that behaved in an additive fashion predominated over non-additive ones for soaked bean weight (SBWT), soaked bean water content (SBWC), splitting (SPLT), and the washed-drained weight coefficient (WDWTR). Clumping (CLMP), WDWT and TXT were influenced by genes that behaved in both an additive and a non-additive fashion. In the same study, most genes for WDWT and TXT were found to be completely dominant. Heritability estimates obtained by Walters et al. (1997) were moderate to high: 0.59 for visual appeal (VIS), 0.64 for TXT and 0.67 for WDWT.

Correlations exist among the various parameters of canning quality. Hosfield and Uebersax (1980) reported that soaking properties were not correlated with textural differences among the tropically adapted genotypes included in their study. However, Ghaderi (1984) reported a negative correlation between TXT and WDWT (a hydration

property) of cooked beans. Hosfield et al. (1984a) looked into the question of trait interrelationships in black seeded dry bean in a multivariate analysis of processing quality. Factor analysis (Catell 1965 a, b; Kim, 1975) indicated that soaking, cooked color, thermal and dry color traits were orthogonal although TXT and WDWT, two thermal traits, were negatively correlated (Hosfield, et al., 1984a). In three populations of navy bean, Walters et al. (1997) detected negative correlations between TXT and WDM ($r = -0.53$ to -0.83), and between VIS and WDM ($r = -0.26$ to -0.66). In the terminology used by Walters et al. (1997), VIS was visual appeal, a perception of the overall appearance of canned beans, and WDM was the washed drained mass, equivalent to WDWT. The same authors (Walters et al., 1997) reported significant and positive correlations between VIS and TXT ($r = 0.19$ to 0.66). Since the correlations are phenotypic in nature, they may be due to the combined effects of genotype and the processing environment, and do not necessarily reflect associations due to genetic factors such as linkage or pleiotropic effects (Nienhuis and Singh, 1985).

Use of Markers in Crop Improvement

A quantitative trait is more difficult to improve than a Mendelian character because the type and degree of influence of several loci acting in concert on a particular trait cannot be identified easily (Dudley, 1993), unlike for a single-gene trait where each allele results in a distinct phenotype. The number of genes involved and the interactions among them imply that several loci must be manipulated at the same time to obtain the desired phenotype (Ribaut and Hoisington, 1998).

Canning quality in dry bean is viewed as a "super trait" because no single variable can adequately describe the properties preferred in and required of a sample (Hosfield

and Uebersax, 1990). In view of the inherent complexity, a "super trait" is difficult to improve. At best, the breeder seeks to dissect them into a number of component characters that can be individually measured and selected (Hosfield and Uebersax, 1990). In improving the processing quality of dry beans, the breeder must consider that additive and/or dominance effects influence each of the component traits separately. The effect of the environment on the expression of each component trait must also be taken into account. Thus, the evaluation of a large number of samples with small differences using objective and/or subjective methods would be difficult (Ghaderi et al., 1984). Furthermore, for traits that have low heritabilities and high additive variance, selection using conventional methods should be done in later generations, such as the F_6 generation, when the lines are nearly homozygous (Elia et al., 1997). Technological advances in the last decade have given plant breeders an impetus to reevaluate the use of genetic markers to address these problems in various crops.

For simply-inherited traits, marker-assisted selection (MAS) has been used to select in early generations and to reduce the size of the population used during selection (Staub and Serquen, 1996). MAS is of particular value in breeding for characters with low heritabilities and when the marker is associated with additive genetic variance (Staub et al., 1996). In quantitative trait analysis and breeding, the use of markers and genetic maps has permitted the identification of regions of the genome that most likely contain the genes or groups of genes [quantitative trait loci (QTL)], responsible for the expression of these traits. Molecular markers may also aid in understanding genotype x environment interactions when significant marker-QTL associations are compared in different environments (Dudley, 1993). Markers also allow the comparison of the genomes of

different but related taxa with regards to the location of common QTL (Paterson, 1995). By knowing the locations of important QTL in the genome, one can facilitate their precise manipulation in breeding programs. However, even if the exact locations of QTL in the genome are not known, the associations of the genes with easily identifiable markers may aid in trait improvement by combining MAS with conventional breeding.

MAS is an indirect selection method that appeals to breeders because it enables them to select in early generations, which can reduce both the time and the cost of the selection process. Eathington et al. (1997) used marker-QTL associations to predict the yield performance of maize in later generations of testcrosses using data from earlier generations. Knapp (1998) proposed the use of MAS to increase the probability of selecting superior genotypes and predicted that, for traits with low to moderate heritabilities, MAS will require fewer resources to reach a selection goal when the selection intensity is high. Markers have also been used successfully to improve disease and insect pest resistance, and other characteristics of crop species (Haley et al., 1993; Young and Kelly, 1996; Kelly and Miklas, 1998; Kelly and Miklas, 1999). But before MAS can be used in a breeding program, associations between appropriate marker alleles and QTL must be identified.

Morphological and Protein Markers. The first markers reported were easily observed phenotypic characteristics associated with economically important traits. Associations of simply inherited traits (markers) with more complex characteristics were reported as early as 1923 when Sax documented the association of seed size with a seed coat color marker in *P. vulgaris*. Since then, numerous authors working with various crops have found other associations between simply inherited characters and quantitative traits.

The use of physical and chemical characteristics to predict dry bean canning quality has been proposed by various authors. The pasting viscosity of whole bean flour was highly correlated with the texture or firmness of canned navy beans in separate studies (Ruengsakulrach, 1994; Lu et al., 1996). The authors of the two studies suggested that pasting characteristics might be useful in screening breeding lines for canning quality in early generations. Lu et al. (1996) found correlations between pasting viscosity and WDWT, and between viscosity of the canned bean medium and overall acceptability. Lu et al. (1996) also suggested using the hydration ability of raw navy beans to predict the degree of color of cooked beans, and the turbidity of micro-cooked bean liquid to predict the clarity of the canned bean medium. However, Ruengsakulrach et al. (1994) suggested that the color of cooked beans might be a function of processing time and the caramelization of sugars during heating, implying that physico-chemical processes such as hydration will not have any effect on the final color of the cooked beans.

In kidney beans, significant correlations have been reported between the relative amount of damaged beans after processing and both bean density and seed coat weight (Heil et al., 1992). These researchers (Heil et al., 1992) suggested that these physical properties could be used to estimate bean damage during processing, and in aiding dry bean breeders in improving processing qualities. In addition, soluble pectin content was highly correlated with firmness in various dry bean cultivars (Wang et al., 1988). These authors suggested that pectin content could thus be used as a parameter for screening lines for desirable firmness of cooked beans.

Some disadvantages of using physical and chemical traits as markers are the limited number available and undesirable phenotypes of many of these markers, and, in

the case of cytological markers, the large size of the chromosomes and chromosome segments used (Dudley, 1993). Morphological markers also rely on recessive mutations and require much time to develop (McClean et al., 1994). One improvement on the use of morphological markers for selecting QTL was the employment of isozymes, which have been used in MAS in several crops such as maize (Stuber and Edwards, 1986). Although these marker systems have proved useful in genetic studies, their biochemical nature and function limit the number of enzyme systems commonly used for analysis to about 40-60 reactions (Gabriel, 1971; Gottlieb, 1982; Burow and Blake, 1998). The lack of potential isozyme markers limits their use in QTL analysis, fine mapping, and MAS. The same limitation exists for other protein marker systems. As a consequence, molecular markers that function at the DNA level have largely replaced protein marker analysis in gene-tagging experiments (Burow and Blake, 1998).

DNA Markers. DNA markers first became widely used in genetic analysis in the 1980s, with the advantage of an increased number of potential markers available (Burow and Blake, 1998). DNA markers have also proved to facilitate faster recovery of genomic segments, more efficient selection, and even the transfer of favorable alleles from wild relatives to elite cultivars (Ribaut and Hoisington, 1998).

There are several criteria to be met in selecting molecular markers for use in MAS. The value of a molecular marker depends on its inherent repeatability, map position and linkage with an economically important trait (Weeden et al., 1992; Staub and Serquen, 1996). Linkage of 10 cM or less is helpful to increase gain from selection (Paran et al., 1991; Kennard et al., 1994; Timmerman et al., 1994). Miklas et al. (1995) listed criteria necessary for a marker to be useful for indirect selection of quantitative

traits: 1) relative stability across environments; 2) variation that accounts for as much as or more than the heritability of the trait being considered; and 3) in the case of disease resistance, presence only in the resistant germplasm.

The first DNA markers used in QTL analysis were restriction fragment length polymorphisms (RFLPs). Labeled probes detect RFLPs as variable sized DNA fragments generated by restriction enzymes that cut the DNA at specific sites in the molecule. RFLPs behave as codominant markers, viewed as bands on cellulose-acetate film (Staub et al., 1996). They were first used to construct a human genetic map (Botstein et al., 1980). Since the time of their pioneering use in human genetic studies, RFLPs have been applied in the construction of genetic linkage maps in crops such as maize and tomato (Helentjaris et al., 1986), and the tagging of QTL such as those controlling the amount of soluble solids in tomato (Osborn et al., 1987). Other examples of DNA marker systems are restriction landmark genome scanning (RLGS), microsatellite systems, sequence-tagged sites (STS) and amplified fragment-length polymorphism (AFLP) (Burow and Blake, 1998), and random amplified polymorphic DNA (RAPD).

A RAPD marker makes use of the polymerase chain reaction (PCR). PCR-based markers require small amounts of DNA to be used as a template, and thus, allow early sampling and rapid DNA preparation. Large sample sizes can also be handled efficiently (Ribaut and Hoisington, 1998). A RAPD is generated through the amplification of genomic DNA by using single primers usually 10 nucleotides long and of arbitrary nucleotide sequence (Williams et al., 1990). Low stringency amplification and the short lengths of the primers make possible multiple binding sites throughout the genome. Amplification of DNA fragments, the sequences of which are unknown, occurs when two

binding sites are in close proximity (Burow and Blake, 1998). RAPDs usually behave as dominant markers, scored as the absence or presence of a particular band, and are inherited in a Mendelian fashion (Williams et al., 1990; Staub et al., 1996). Polymorphisms may be due to mutations or deletions in the primer-binding site, insertions that increase the distance between binding sites or insertions that change the size of a DNA segment without preventing its amplification (Williams et al., 1990; Burow and Blake, 1998).

In dry bean, RAPD markers are comparable to RFLPs with regard to the frequencies of polymorphisms observed (Miklas and Kelly, 1992). However, RAPD technology has the following advantages over RFLPs and other molecular marker technology: 1) specific nucleotide sequence information of primers or clones is not required to generate the polymorphisms; 2) a universal commercially available set of primers can be used for genomic analysis; 3) preliminary work, such as cloning and isolation of DNA probes and preparation of filters for hybridization, is not required; 4) the method can be automated, which allows the running of large numbers of samples simultaneously; 5) labor-intensive Southern blot hybridizations are not employed; and 6) only small quantities of DNA are needed, allowing the analysis of limited samples and eliminating extraction of large amounts of DNA (Williams et al., 1990; Burow and Blake, 1998).

The use of RAPD markers also has its disadvantages. Marker patterns from RAPD analysis are not as reliable or reproducible as those obtained from RFLP analysis, because of the low stringency of the amplification conditions used, variations in DNA quality and concentration, and optimal primer concentrations (Burow and Blake, 1998).

As is the case for any marker system relying on dominant alleles for resolution, RAPD markers cannot resolve heterozygous from homozygous loci (Williams et al., 1990). When RAPDs are used, the sequence homology of similarly-sized fragments is impossible to discern, unmapped markers are inefficient to use for genetic analysis, and clustering of markers may occur in some instances (Burow and Blake, 1998).

RAPD markers have been used to construct and align linkage maps (McClean et al., 1994 and Freyre et al., 1998), determine genetic relationships between genotypes (Beebe et al., 1995; Skroch et al., 1992), and tag single genes and QTL in several crop species, including dry beans (Bai, 1996; Miklas et al., 1995, 1996, 1998a). Most of the RAPD research in dry bean involves resistance to diseases, such as bean rust [caused by the pathogen *Uromyces appendiculatus* (Pers.:Pers.) Unger] (Jung et al., 1996), bean golden mosaic (BGM) (caused by a geminivirus) (Miklas et al., 1996), charcoal rot or ashy stem blight [*Macrophomina phaseolina* (Tassi) Goidanich] (Olaya et al., 1996), common bacterial blight (CBB) [*Xanthomonas campestris* pv. *phaseoli* (Smith) Dye] (Jung et al., 1996), and anthracnose (*Colletotrichum lindemuthianum* [(Sacc. & Magnus) Lams.-Scrib.]) (Melotto et al., 1998). Single genes control most of these resistance traits. Kelly and Miklas (1999) provide a comprehensive review of the markers, which have been identified for various resistance genes.

Jung et al. (1996) identified RAPD markers for QTL governing plant architecture and resistance to common blight and web blight [*Thanatephorus cucumeris* (A.B. Frank) Donk], using a population of recombinant inbred lines of common bean. A partial linkage map covering 545 centimorgans (cM) and including 75 of 84 markers studied was made. Miklas et al. (1996) established linkages between RAPD markers and a QTL

conditioning BGMV or CBB resistance. This study resulted in 14 RAPD markers being selectively mapped in the population. Miklas et al. (1998b) analyzed QTL for field resistance to ashy stem blight. Park et al. (1998) identified and mapped RAPD markers associated with QTL for seed size and shape.

Several authors have also identified RAPD markers linked to genes controlling various aspects of quality in crops. Examples of these traits are the milling energy requirement of barley (*Hordeum vulgare* L.) (Chalmers et al., 1993), oleic acid concentration in spring turnip rape (*Brassica rapa* L. ssp. *oleifera* DC.) (Tanhuanpää et al., 1996) and fruit ripening in tomato (*Lycopersicon esculentum* L.) (Doganlar et al., 2000). With regards to processing quality in beans, almost no work has been done using molecular markers. In a study conducted over two years and in two locations, Walters (1995) identified several RAPD markers associated with some component traits of canning quality in three populations of navy bean. The populations were screened with 390 primers. Markers were linked to VIS, TXT and WDWT of processed beans. Results of the study showed location- and population- specificity among the marker-QTL associations identified.

Selective Genotyping. Most QTL mapping experiments involve large populations, usually composed of more than 200 individuals (Paterson, 1998). Several strategies have been proposed to make use of smaller populations or to increase the efficiency of handling large ones, without sacrificing the amount and quality of the information that can be obtained. Some of these approaches are selective genotyping (Lander and Botstein, 1989; Paterson, 1998) and DNA pooling strategies (Michelmore et al., 1991; Wang and Peterson, 1994; Darvasi and Soller, 1994; Paterson, 1998).

The use of bulked segregant analysis has simplified genetic mapping by reducing the number of lines, which are initially screened for putative markers (Michelmore et al., 1991). In this method, the individuals in each phenotypic extreme as a single DNA sample or bulk (Paterson, 1998). Within each bulk, the individuals are presumably identical for a trait or genomic region of interest but are arbitrary for the others (Michelmore et al., 1991). Effectively, the two bulks differ only in the target region, and are heterozygous and monomorphic for other loci. The goal is to identify markers that distinguish the two bulks and thus presumably are linked to the target locus. These markers differ between the bulks in their presence or absence, or in the intensity of the bands observed, depending on their distance from the target locus. The putative markers are then confirmed and mapped by genotyping the entire population. This approach eliminates the need to initially screen the entire population with all possible markers. Bulked segregant analysis was originally used for single-gene traits but was also proposed to be useful for mapping QTL (Michelmore et al., 1991). Examples of simply inherited characters for which markers have been found using this approach are nematode (*Heterodera schachtii* Schm.) resistance in sugar beet (*Beta vulgaris* L.) (Heller et al., 1996) and fruit skin color in apple (*Malus* sp.) (Cheng et al., 1996).

Selective genotyping is effective for QTL that affect only one phenotype (Paterson, 1998). Using this method, a large population is generated and evaluated phenotypically, but genotyping is done only on those individuals that exhibit the most extreme phenotypes (Lander and Botstein, 1989). Since phenotypic evaluation frequently costs less than genotyping, it is more efficient to increase the number of progeny while genotyping only a subset of individuals, than to genotype the entire population. Selective

genotyping has been used to identify markers linked to various QTL such as those involved in disease resistance in common bean (Miklas et al., 1996) and tomato (Chagué et al., 1997), oleic acid concentration in spring turnip rape (*Brassica rapa* L. ssp. *oleifera* DC.) (Tanhuanpää et al., 1996), and milling energy requirements in barley (*Hordeum vulgare* L.) (Chalmers et al., 1993).

While DNA pooling methods are effective for rapidly identifying markers, several authors have observed some limitations on their applicability to QTL mapping (Darvasi and Soller, 1994; Wang and Paterson, 1994; Paterson, 1998). Although selective genotyping methods are able to detect QTL with large effects, they may not detect the majority of QTL that have small phenotypic effects (Darvasi and Soller, 1994; Wang and Paterson, 1994). Other factors such as segregation distortion and dominance may also influence the allelic composition of the DNA pools, resulting in false positive reactions and complicating the utility of these approaches (Wang and Paterson, 1994; Paterson, 1998). Wang and Paterson (1994) suggested the following to reduce the occurrence of false positives when using DNA pooling approaches: a) use parents with extreme variation for the trait of interest, b) use large populations, c) use homozygous populations such as recombinant inbred or doubled haploid lines, c) and replicate the phenotypic evaluations.

MATERIALS AND METHODS

The two recombinant inbred populations were derived from crosses between 'Montcalm' (MCM) and 'California Dark Red Kidney 82' (CDRK 82), and MCM and

'California Early Light Red Kidney' (CELRK). MCM (Figure 3), the common parent of the two populations, has a long-standing reputation in the canning industry for its desirable canning quality. Compared to MCM, CDRK 82 (Figure 4) and CELRK (Figure 5) have less appealing canning quality. The recombinant inbred lines (RILs), parents and checks for the two populations were planted in separate experiments at the Montcalm Research Farm near Stanton, Mich. in 1996, 1997, 1998 and 1999; in Perham, Minn. in 1996 and in Erie, NDak. in 1999. The details of planting were described in Study 1.

Evaluation of Canning Quality

After harvest, threshing and cleaning of the seeds, a digital moisture computer (Burrows Model 700) was used to determine percentage moisture of 250g samples of the seeds of each entry. Beans from each field plot with a fresh weight equivalent of 100 g total solids (Hosfield and Uebersax, 1980) were placed in nylon mesh bags and soaked at 21 C for 30 minutes and blanched at 88 C for 30 minutes. Two replicates of each bean sample were processed. The cold soak and blanch were done in distilled water adjusted to 100 $mg \cdot L^{-1}$ calcium ion. The soaking procedure resulted in a sample with minimum damage similar to beans soaked continuously in the high-temperature systems common throughout the U.S. canning industry (Hosfield and Uebersax, 1980). The duplicate samples of soaked and blanched beans from each field plot were placed into No. 303 (100 x 75 mm) tin cans and weighed. Soaked bean weight (SBWT), the weight (g) gained by the beans through water imbibition during soaking and blanching, was obtained for each replicate. The hydration coefficient was calculated as follows:

$$HC = \frac{SBWT}{\text{fresh weight}}$$

(Hosfield and Uebersax, 1980)

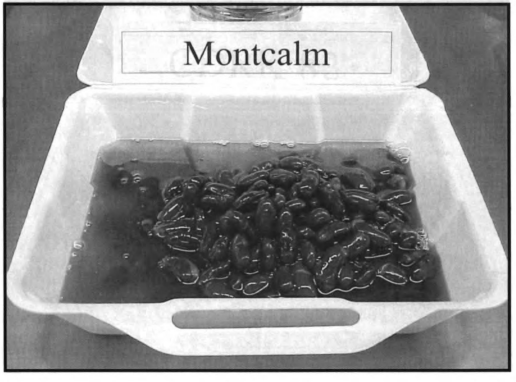


Figure 3. Processed beans of the cultivar Montcalm.

Figure 4. Processed beans of the cultivar California Dark Red Kidney 82.

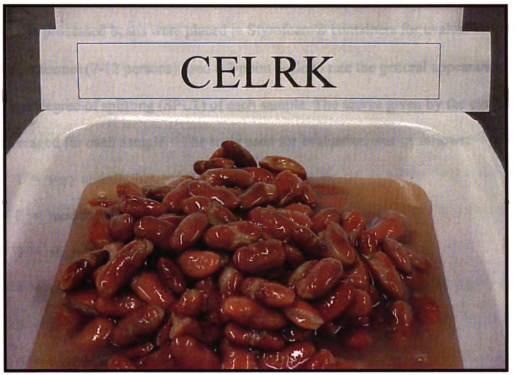


Figure 5. Processed beans of the cultivar California Early Light Red Kidney.

After weighing, the cans were filled with boiling brine (1.25 % sodium chloride, 1.57 % sucrose, 100 $mg \cdot L^{-1}$ calcium). The filled cans were exhausted in a water-filled exhaust box at 88 C for 5 minutes, sealed and cooked in a retort without agitation for 45 minutes at 116°C and 10.4 x 10 Pa (15 psi). After cooking, the cans were cooled under cold running tap water and stored inverted for a minimum of 2 weeks at room temperature.

The processed beans were placed in Styrofoam® containers for evaluation. A team of personnel (7-12 persons) used a 7-point scale to rate the general appearance (APP) and degree of splitting (SPLT) of each sample. The scores given by the evaluators were averaged for each sample. The scale used for evaluation was as follows:

1 = very undesirable

2 = moderately undesirable

3 = slightly undesirable

4 = neither desirable nor undesirable

5 = slightly desirable

6 = moderately desirable

7 = very desirable

Identification of RAPD Markers

Samples of DNA from the parents and a subset of RILs of each population were obtained from Dr. Kenneth Grafton (North Dakota State University). Seeds from the remaining RILs were planted in the greenhouse at Michigan State University. DNA from five plants of each parent and each RIL was extracted using the protocol reported by Walters et al. (1997).

Identification of putative markers was first attempted by initially screening the parents for polymorphisms. RAPD primers obtained from Operon Technologies (Alameda, CA) were screened against the three parents (MCM, CDRK 82 and CELRK) to identify those that generated polymorphic bands. The primers that amplified polymorphisms were then used to screen all the RILs in Population 1. This approach proved to be inefficient and time-consuming. To improve the efficiency of the procedure, selective genotyping was used for the rest of the study. For the latter approach, five RILs from Population 1 that had the most desirable and five RILs that had least desirable canning quality were selected. More than five lines in each DNA bulk was considered too many and, if used, may result in the bulks not representing the extremes in canning quality necessary for selective genotyping. Less than five lines were considered to result in bulks that may differ not only in canning quality but in other traits as well, which were not the interest of this study.

The choice of the five RILs for each bulk was based on the canning quality scores of the RILs in the following environments: Mich-1996, Minn-1996, Mich-1997 and Mich-1998 (Table 15). For each of these environments, the lines with the most and least desirable canning quality were determined, based on their APP and SPLT scores. The scores averaged over the four environments were also considered. The data was compared across environments to identify lines, which consistently were the most and least desirable in APP and SPLT scores. RILs 118-90, 118-89 and 118-97 were consistently in the group with the top 25% in scores for APP and SPLT in all four environments from 1996 to 1998. In addition, canned beans from each RIL were visually

Table 15. Scores for appearance of processed beans of the Population 1 RILs that were used in the DNA bulks to screen RAPD primers for polymorphism.

	Appearance Rating				
RIL	Mich 1996	Minn 1996	Mich 1997	Mich 1998	Overall[a]
Lines with desirable canning quality[b]					
118-90	6.0	6.1	6.3	6.2	6.1
118-89	4.7	3.5	4.7	4.9	4.4
118-97	4.4	4.6	4.3	4.0	4.3
118-60	4.2	4.7	4.0	4.4	4.3
118-73	4.5	4.6	4.0	3.9	4.2
Lines with undesirable canning quality[b]					
118-31	2.0	2.0	3.3	3.2	2.6
118-08	2.3	3.0	3.0	2.1	2.6
118-64	2.4	2.2	2.4	2.9	2.5
118-98	3.1	2.0	2.8	1.9	2.4
118-51	2.1	1.7	2.6	3.2	2.4
Parents					
Montcalm	3.6	3.8	4.8	4.3	4.1
CDRK 82	2.0	-	2.5	2.3	2.3
Population Mean	3.2	3.0	3.7	3.6	3.4
CV[c] (%)	18.1	20.0	14.7	24.5	19.7

[a] Overall - averaged over the four environments

[b] Canning quality rating scale: 1 = very undesirable; 4 = neither desirable nor undesirable; 7 = very desirable

[b] CV - Coefficient of variation

compared to verify that the lines chosen for the bulks represented the two extreme phenotypes in canning quality.

DNA from the five RILs with desirable canning quality was bulked for the RAPD analysis at a final concentration of 10 $ng \cdot ul^{-1}$. The same procedure was conducted with the DNA from 5 lines with undesirable canning quality. Polymerase chain reaction (PCR) amplifications of the bulked DNA were conducted in 20µl reactions containing 1X buffer (20 mM Tris-HCl, pH 8.4; 50 mM KCl), 3 mM MgCl2, 0.2 mM dNTPs, 20 ng total genomic DNA, 20 ng primer and 1 U *Taq* polymerase from Gibco BRL. The RAPDs were amplified in a Perkin Elmer Cetus DNA Thermal Cycler 480 or a Programmable Thermal Controller PTC-100 (MJ Research, Inc.). The program was for 3 cycles of 1 min at 94°C, 1 min at 35°C, 2 min at 72°C; 34 cycles of 10 s at 94°C, 20 s at 40°C, 2 min at 72°C, with a third segment extension of 1 s per cycle; and a five-min extension at 72°C. PCR products were resolved with 100-bp and 1 Kb DNA ladders from Gibco BRL on a 1.4% agarose gel on 1X TAE buffer.

Five hundred fifty-seven single decamer primers were screened, 107 of which generated markers that are part of the core linkage map reported by Freyre et al. (1998). Markers generated from the primers were labeled with 'O' (Operon) to indicate the commercial source of the primers, a letter and number indicating the kit and primer label as used by Operon Technologies, and a number indicating the molecular size (bp) of the marker band. The 557 primers were grouped into three sets. The first set of primers, 148 in number, was initially screened against the parents MCM and CDRK 82. After amplification, 12 of these primers showed polymorphic bands between the two parents. The second set, composed of 341 primers, was screened using the bulked DNA and after

amplification, 23 showed polymorphic bands. The third set, composed of 68 primers, was screened simultaneously using DNA from MCM and CDRK, and from the bulked lines; 12 of these revealed polymorphisms. A total of 47 primers revealed polymorphisms and were used to amplify DNA from each parent and the individual Population 1 RILs used in the bulks. Of these 47 primers, 17 were selected based on the segregation of the bands among the 10 lines used as bulks for canning quality traits APP and SPLT (5 with desirable and 5 with undesirable scores). Ease of scoring the bands was also a selection criterion. Population 1 was then scored for the presence or absence of marker bands for these 17 primers that appeared to exhibit polymorphism between the DNA bulks selected on the basis of canning quality. The segregation ratios of these markers in the population were determined. The markers were analyzed for linkage and for significant associations with APP and SPLT.

Population 2 was scored for the presence or absence of the marker bands that met the following criteria: a) segregation according to a 1:1 ratio, and b) either significant correlation with APP or SPLT in Population 1, or linkage with markers that were significantly associated with these traits in Population 1. Eleven markers met these criteria. Individual markers and composites of markers significantly associated with APP and SPLT were used to select lines from the second population. The canning quality scores of these selected lines were then determined.

One of the markers identified initially, OI8.1600, appeared to be identical to a RAPD marker in linkage group B8 of a core map constructed in the population BAT93 x Jalo EEP558 (Freyre et al., 1998). BAT 93, Jalo EEP558 and the parents of the kidney bean populations were amplified and resolved together in agarose gels to determine if the

markers mapped by Freyre et al. (1998) and the markers detected in the kidney bean populations were the same. Other RAPD markers in linkage group B8 were also analyzed for linkage to O18.1600 and for associations with APP and SPLT in the kidney bean populations.

To determine if the markers reported by Walters et al. (1997) to be significantly associated with canning quality in navy bean were associated with canning quality traits in kidney bean, DNA samples from the three kidney bean parents and the navy bean parents were amplified using the primers and amplification conditions reported by these authors (Walters et al., 1997). The amplification products were resolved side by side on an agarose gel to identify the markers.

Statistical Analysis and Estimation of Heritability

All data were subjected to an analysis of variance (ANOVA) appropriate to a randomized complete block design, with genotypes considered to be random, and years and environments (year-location combinations) as fixed variables. The SAS program (SAS Institute, Cary, N.C, 1998) was used for the analysis. Significance levels were set at $\alpha = 0.05$. Analyses were conducted according to the following:

Analysis 1 - separate analysis for each experiment i.e., Michigan in 1996, 1997, 1998, and 1999; Minnesota in 1996; and North Dakota in 1999.

Analysis 2 - combined data for Michigan over the years, 1996, 1997, 1998, and 1999.

Analysis 3 - combined analysis of all experiments such that years and locations were treated as environments; only the parents and RILs of each population were included in this analysis.

Box-plots of the data in Analysis 1 were constructed to provide a visual comparison of the ranges, means and median values in the different environments. Box-plots are interpreted as follows (Schabenberger, 1997):

a) mean - represented by (+)

b) median value - located by the line dissecting the box

c) first (Q_1) and third (Q_3) sample quartiles - determine the dimensions of the box. In an ordered data set, 25% of all observations are smaller and 75% are larger than Q_1; 25% are larger and 75% are smaller than the third quartile Q_3. The difference between Q_1 and Q_3 is called the inter-quartile range (IQR).

d) whiskers - represent values within 1.5 x IQR from each end of the box

e) extreme values or outliers - represented by (o) or (*). Mild outliers (o) are observations beyond the whiskers but less than 3 x IQR from the respective end of the box. Extreme outliers (*) are data more than (3 x IQR) from each end of the box.

To estimate heritability, two replications of the data from the RILs in analyses 1 were used. Heritability was estimated on a progeny mean basis (Fehr, 1987) as follows:

$$H^2 = \frac{\sigma^2_g}{\sigma^2_t} = \frac{\sigma^2_g}{\sigma^2_e / rv + \sigma^2_{gv} / v + \sigma^2_g}$$

where:
- σ^2_g = genotypic variance
- σ^2_t = total variance among RILs compared in r replications and v environments ($r = 2$, $v = 6$)
- σ^2_e = experimental error
- σ^2_{gv} = variance due to genotype x environment interactions

Confidence intervals for heritability estimates were derived according to Knapp et al. (1985). Correlations among the traits for each environment were determined using the program *proc corr* in SAS (SAS Institute, Cary, NC, 1998). Single-factor ANOVA was used to detect significant associations between each marker locus and the canning quality

traits. Chi-square tests on the segregation ratio of the putative markers were conducted for the two populations. Linkages between the markers that segregated according to a 1:1 ratio were determined using MAPMAKER (Whitehead Institute for Biomedical Research, 1992). Linkage was considered significant if the logarithm of odds (LOD) score was ≥ 4.0.

Individual markers were analyzed against the scores of Populations 1 and 2 for APP and SPLT in each environment, and for the APP and SPLT scores averaged over all environments. The SAS program *proc glm* was used, with $p = <0.05$ for acceptance of marker-trait associations. Markers also were grouped together, based on the results of the linkage analysis, and analyzed for associations with APP and SPLT. The marker composites were as follows:

A - all the markers, which individually were significantly associated with APP and SPLT or which were linked to significant markers (OY7.850, OQ14.950, OP15.1150, OAG10.1650, OA17.4000, OI8.1600, OU20.1150, OAH17.700, OG17.1300, OAN16.3000 and OH18.1000)

B - all the markers in linkage group M1 (OY7.850, OQ14.950, OP15.1150, OAG10.1650, OA17.4000, OI8.1600 and OU20.1150)

C - all the markers in linkage group M2 (OAH17.700, OG17.1300, OAN16.3000 and OH18.1000)

D - one marker each from M1 and M2 (OP15.1150 and OG17.1300)

E - flanking markers from linkage group M1-1 (OY7.850 and OU20.1150)

F - flanking markers from linkage group M1-2 (OY7.850 and OI8.1600)

G - flanking markers from linkage group M2 (OAH17.700 and OH18.1000)

The composites of markers were used to select RILs from both populations. In addition to these marker composites, two additional groups of markers, M1+G17 and M1+AN16, were tested. Group M1+G17 was composed of the seven markers in linkage group M1, and marker OG17.1300 from linkage group M2. Group M1+AN16 was composed of the M1 markers and marker OAN16.3000. The APP and SPLT means of the selected lines were determined. Putative markers, which were most effective as indicators of desirable canning quality in kidney beans, were identified.

Images in this thesis are presented in color.

RESULTS

Three components of canning quality were evaluated and analyzed for each population, as follows: hydration coefficient (HC), appearance (APP) and degree of splitting (SPLT) of the canned beans. RAPD primers were screened to identify markers associated with APP and SPLT. Insufficient data for HC was obtained for both recombinant inbred populations planted in Minn-1996. CDRK 82 was not processed in the 1996-Minn and 1999-NDak experiments due to insufficient seed. Eleven RAPD markers, in two linkage groups, were identified to be significantly associated with APP and SPLT.

Evaluation of Canning Quality

Mean squares for genotypes were significant for the three traits in both populations in all analyses (Tables 16 and 17). Years and genotype x year interactions in Analysis 2 (1996, 1997, 1998 and 1999 in Michigan) were significant for HC, APP and SPLT for both populations (Tables 16 and 17). When the locations and years were confounded and treated as environments (Analysis 3), environment effects and genotype x environment interactions were significant for the three traits in both populations (Tables 16 and 17).

Population 1 means for APP and SPLT were similar in all environments and ranged from 2.8 to 3.7 and 2.8 to 3.6 for APP and SPLT, respectively (Table 18). Means for these traits in Population 2 were similar to Population 1 (Table 19). Coefficients of variation (CV) for HC were very low (<2.0%) in both populations in all environments, indicating no variation in soaking properties among the bean samples. For both APP and SPLT, CVs were highest in Mich-1998 in both populations (Tables 18 and 19). The box

Table 16. Significance levels for main effects and interactions for canning quality traits of Population 1 entries. Data analyses were according to individual experiments, years, and environments (location and years confounded).

Source of Variation	Hydration Coefficient[ab]	Appearance[b]	Degree of Splitting[b]
	Mean squares		
Data analysis number and location-year description			
1 - Individual experiments			
Michigan 1996: Genotype	**	**	**
Minnesota 1996: Genotype	-[a]	**	**
Michigan 1997: Genotype	**	**	**
Michigan 1998: Genotype	**	**	**
Michigan 1999: Genotype	**	**	**
North Dakota 1999: Genotype	**	**	**
2 - Michigan (1996, 1997, 1998, 1999)			
Genotype	**	**	**
Year	**	**	**
Genotype x Year	**	**	**
3 - Locations and Years Confounded, and Treated as Environments			
Genotype	**	**	**
Environment	**	**	**
Genotype * Environment	**	**	**

[a] - Insufficient data for HC was obtained in Minn-1996

[b] ** - Significant at 0.05 level of significance; ns - not significant

Table 17. Significance levels for main effects and interactions for canning quality traits of Population 2 entries. Data analyses were according to individual experiments, years, and environments (location and years confounded).

Source of Variation	Hydration Coefficient[ab]	Appearance[b]	Degree of Splitting[b]
	Mean squares		
Data analysis number and location-year description			
1 - Individual experiments			
Michigan 1996: Genotype	**	**	**
Minnesota 1996: Genotype	-[a]	**	**
Michigan 1997: Genotype	**	**	**
Michigan 1998: Genotype	**	**	**
Michigan 1999: Genotype	**	**	**
North Dakota 1999: Genotype	**	**	**
2 - Michigan (1996, 1997, 1998, 1999)			
Genotype	**	**	**
Year	**	**	**
Genotype x Year	**	**	**
3 - Locations and Years Confounded, and Treated as Environments			
Genotype	**	**	**
Environment	**	**	**
Genotype * Environment	**	**	**

[a] - Insufficient data for HC was obtained in 1996-MN

[b] ** - Significant at 0.05 level of significance; ns - not significant

Table 18. Hydration coefficient and scores for appearance and degree of splitting of processed beans of Population 1 entries. Data analyses were conducted individually for each experiment (Analysis 1).

Environment	Hydration Coefficient		Appearance		Degree of Splitting	
	Mean	CV (%)[a]	Mean	CV (%)[a]	Mean	CV (%)[a]
Mich 1996	2.21	1.98	3.2	18.1	2.8	22.1
Minn 1996	-[b]	-[b]	3.0	20.0	2.6	21.6
Mich 1997	2.10	1.57	3.7	14.7	3.6	16.0
Mich 1998	2.27	1.03	3.6	24.5	3.5	25.7
Mich 1999	2.15	1.75	3.7	17.4	3.6	17.2
NDak 1999	2.20	1.18	2.8	18.5	2.9	18.9

[a] CV - coefficient of variation
[b] - Insufficient data was obtained

Table 19. Hydration coefficient and scores for appearance and degree of splitting of processed beans of Population 2 entries. Data analyses were conducted individually for each experiment (Analysis 1).

Environment	Hydration Coefficient		Appearance		Degree of Splitting	
	Mean	CV (%)[a]	Mean	CV (%)[a]	Mean	CV (%)[a]
Mich 1996	2.24	1.61	3.4	18.4	2.8	21.5
Minn 1996	-[b]	-[b]	3.1	17.3	2.8	20.9
Mich 1997	2.19	1.37	3.7	13.7	3.7	13.2
Mich 1998	2.26	1.43	3.2	22.3	3.2	21.2
Mich 1999	2.24	1.76	3.4	17.7	3.4	18.4
NDak 1999	2.17	1.15	3.2	16.6	3.2	15.9

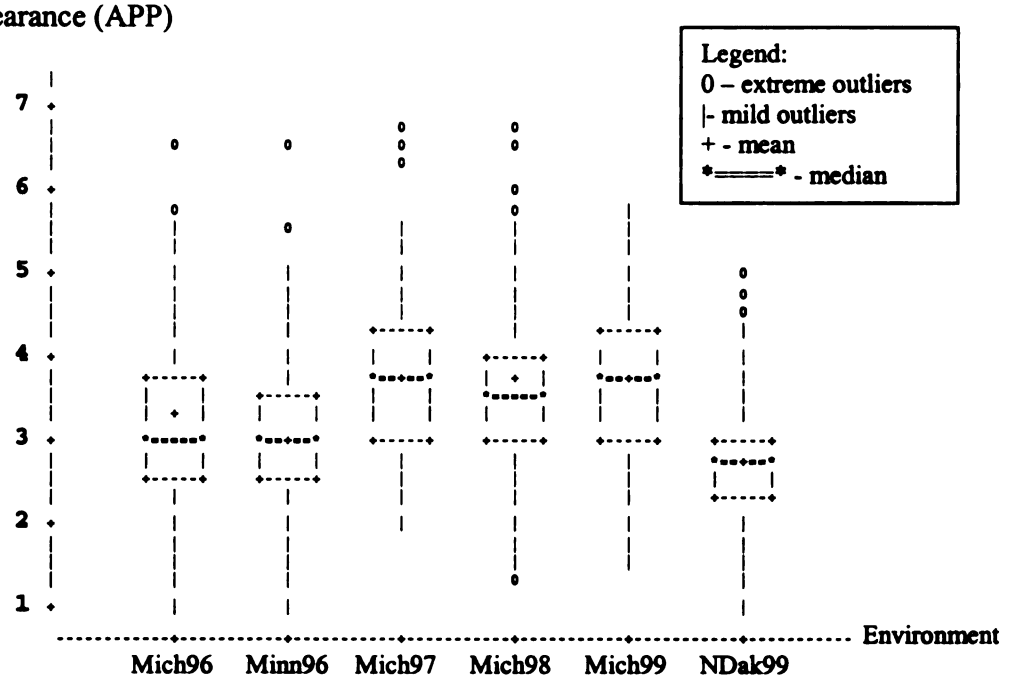
[a] CV - coefficient of variation
[b] - Insufficient data

plots in Figures 6 and 7 show several outliers for APP and SPLT scores in the two populations. These outliers are the RILs with high scores for canning quality traits.

When the Mich data for Population 1 were combined over the four years of the study (Analysis 2) (Table 20), the scores for both APP and SPLT were significantly lower in 1996 than the other three years. The box plots of data from Population 1 for 1996, 1997, 1998 and 1999 in Michigan (Figure 6) illustrates these results. There were no significant differences between the years 1997, 1998 and 1999 for APP and SPLT (Table 20). The APP and SPLT scores for 1996 were 3.1 and 2.7, respectively. For 1997, 1998 and 1999, the APP scores were similar (3.6 to 3.7) as were the SPLT scores (3.5 to 3.6). In Population 2 (Table 21), the entries planted in 1997 had significantly higher mean scores for APP and SPLT than those planted in 1996, 1998 and 1999 in Michigan (Analysis 2). For both APP and SPLT, the mean score for 1997 was 3.7. The box plots for the data from Population 2 for these four years in Michigan (Figure 7) illustrate these results.

There were significant differences between some environments for Populations 1 and 2 for HC, APP and SPLT (Tables 22 and 23). In Population 1, HC had the highest values in the Minn-1996 and Mich-1998 environments (Table 22). Both APP and SPLT scores, which ranged from 3.5 to 3.6, were highest in Mich-1997, Mich-1998 and Mich-1999, with no significant differences among these three environments. In Population 2 (Table 23), the highest scores for APP and SPLT were from the Mich-1997 environment (3.7 for both APP and SPLT), which was significantly different from the other five environments.

A. Appearance (APP)



B. Degree of Splitting (SPLT)

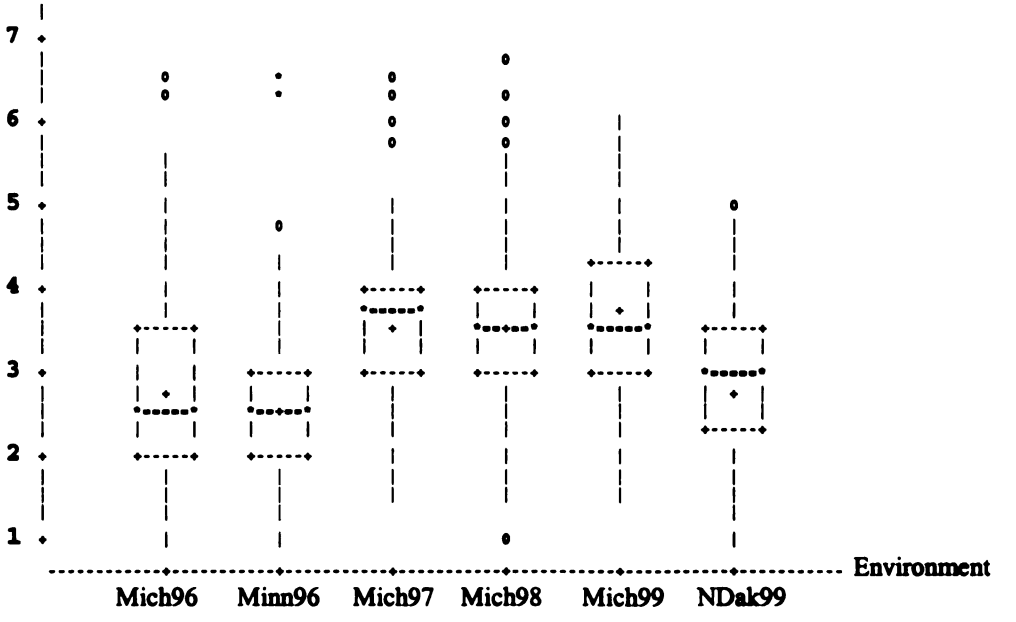
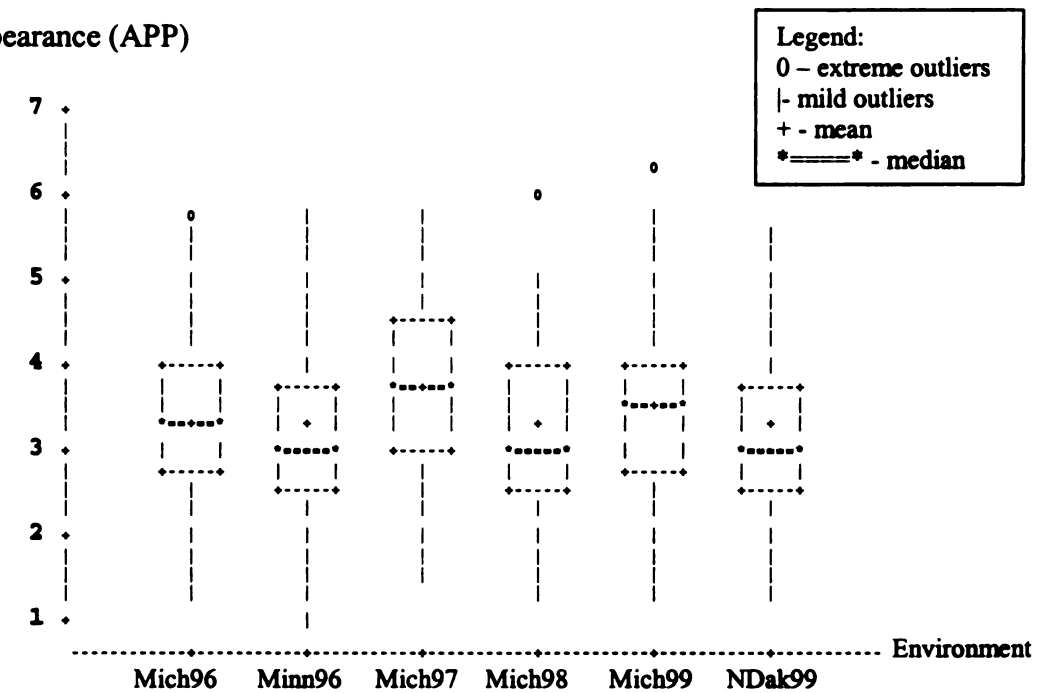


Figure 6. Data Analysis 1 - Box plots of scores for a) appearance and b) degree of splitting of processed beans of Population 1 RILs, parents and checks, planted in Michigan, Minnesota, and North Dakota from 1996 to 1999.

A. Appearance (APP)



B. Degree of Splitting (SPLT)

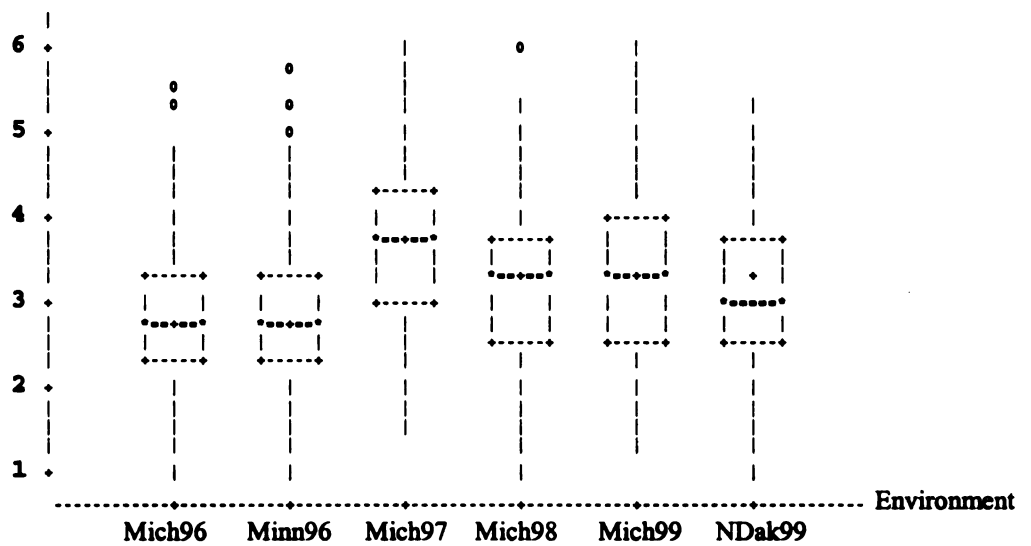


Figure 7. Data Analysis 1 - Box plots of scores for a) appearance and b) degree of splitting of processed beans of Population 2 RILs, parents and checks, planted in Michigan, Minnesota, and North Dakota from 1996 to 1999.

Table 20. Hydration coefficient and scores for appearance and degree of splitting of processed beans of Population 1 entries. Data analyses were conducted to compare individual years in Michigan (Analysis 2).

Year	Hydration Coefficient[a]		Appearance[a]		Degree of Splitting[a]	
1996	2.21	b	3.1	b	2.7	b
1997	2.10	d	3.7	a	3.6	a
1998	2.27	a	3.6	a	3.5	a
1999	2.15	c	3.7	a	3.6	a
Mean combined over years	2.18		3.5		3.4	
Coefficient of variation (%)	1.62		18.9		20.3	

[a] - Means with the same letter are not significantly different by Fisher's LSD (0.05).

Table 21. Hydration coefficient and scores for appearance and degree of splitting of processed beans of Population 2 entries. Data analyses were conducted to compare individual years in Michigan (Analysis 2).

Year	Hydration Coefficient[a]		Appearance[a]		Degree of Splitting[a]	
1996	2.24	b	3.4	b	2.8	d
1997	2.19	c	3.7	a	3.7	a
1998	2.26	a	3.2	c	3.2	c
1999	2.24	b	3.4	b	3.4	b
Mean combined over years	2.23		3.4		3.3	
Coefficient of variation (%)	1.57		18.2		18.4	

[a] - Means with the same letter are not significantly different by Fisher's LSD (0.05).

Table 22. Hydration coefficient and scores for appearance and degree of splitting of processed beans of Population 1 parents and RILs grown in Michigan, Minnesota and North Dakota from 1996 to 1999. Analyses were conducted to compare year-location combinations, treated as environments (Analysis 3).

Environment	Hydration Coefficient[a]		Appearance[a]		Degree of Splitting[a]	
Mich (1996)	2.20	b	3.1	b	2.7	bc
Minn (1996)	2.27	a	3.0	b	2.6	c
Mich (1997)	2.10	e	3.6	a	3.5	a
Mich (1998)	2.27	a	3.6	a	3.5	a
Mich (1999)	2.15	d	3.6	a	3.6	a
NDak (1999)	2.19	c	2.7	c	2.8	b
Mean combined over environments	2.19		3.3		3.1	
Coefficient of variation (%)	1.50		19.2		20.6	

[a] - Means with the same letter are not significantly different by Fisher's LSD (0.05)

Table 23. Hydration coefficient and scores for appearance and degree of splitting of processed beans of Population 2 parents and RILs grown in Michigan, Minnesota and North Dakota from 1996 to 1999. Analyses were conducted to compare year-location combinations, treated as environments (Analysis 3).

Environment	Hydration Coefficient[a]		Appearance[a]		Degree of Splitting[a]	
Mich (1996)	2.24	c	3.4	b	2.8	d
Minn (1996)	2.28	a	3.2	c	2.8	d
Mich (1997)	2.19	d	3.7	a	3.7	a
Mich (1998)	2.26	b	3.2	c	3.2	c
Mich (1999)	2.24	c	3.5	b	3.4	b
NDak (1999)	2.17	e	3.1	c	3.2	c
Mean combined over environments	2.22		3.3		3.2	
Coefficient of variation (%)	1.51		17.9		18.5	

[a] - Means with the same letter are not significantly different by Fisher's LSD (0.05)

RILs with high APP and SPLT scores in Populations 1 and 2. CDRK 82, one of the parents of Population 1, was not processed and canned in two environments, Minn-1996 and NDak-1999, due to insufficient seed. In the other four environments, CDRK 82, planted with Population 1, had undesirable APP scores (2.0 to 2.8) (Table 24). The SPLT scores of CDRK in these four environments ranged from 1.5 to 2.6. MCM had APP scores of 2.6 to 4.8 and SPLT scores of 3.4 to 4.9. In the four environments where both parents were evaluated, large differences were not observed between the mean scores of the RILs and the mean scores of the parents, either for APP or SPLT (Table 24). In each environment, the RILs with the ten highest scores for APP in Population 1 were identified (Appendix Tables A.5 and A.6). The mean APP and SPLT scores of these 10 RILs were higher than the mean scores of the parents in all of the environments (Table 24). Except for Mich-1997, the mean APP and scores of the 10 RILs were also higher than the mean scores of MCM, the parent with the more desirable canning quality. Furthermore, the mean APP and SPLT scores of these 10 RILs were higher than or comparable to the mean scores of the check varieties in all the environments.

In Population 1, one RIL, 118-90 (Figure 8), consistently had the highest score among the RILs for both APP and SPLT in all six environments (Table 24; Appendix Tables A.5 and A.6). The scores for RIL 118-90 had ranged from slightly to moderately desirable (APP = 4.6 to 6.3; SPLT = 4.6 to 6.5). The canned beans from this RIL were generally intact, had few splits, and the color of the cooked beans was judged acceptable for the market class. For comparison, RIL 118-51, a line with undesirable canning quality is shown in Figure 9. RIL 118-51 showed numerous split beans, sloughed seed coats and pieces of cotyledon in the brine. Except for Mich-1997 and NDak-1999,

Table 24. Scores for appearance and degree of splitting of processed beans of Population 1 parents and RILs that appeared in the ten highest scoring group of RILs in three and six individual experiments with the mean scores of the experiment, all all the RILs, the 10 highest scoring RILs, the parents, and the checks.

	Environment											
	Mich 1996		Minn 1996		Mich 1997		Mich 1998		Mich 1999		NDak 1999	
	Canning quality trait scores[c]											
Accession	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT
RIL that was common to the group with the 10 highest APP and SPLT scores in all six environments												
118-90	**6.0**	6.3	**6.1**	6.4	**6.3**	6.2	**6.2**	6.5	**5.7**	5.8	**4.6**	4.5
RILs that were common to the group with the 10 highest APP and SPLT scores in three of the six environments[b]												
118-05	**3.9**	4.1	-[b]	-[b]	**4.6**	4.2	-[b]	-[b]	-[b]	-[b]	**4.3**	4.1
118-09	**4.6**	4.4	-[b]	-[b]	**4.7**	4.6	-[b]	-[b]	**4.4**	4.4	-[b]	
118-66	-[b]	-[b]	-[b]	-[b]	-[b]		**4.6**	4.7	**4.7**	4.5	**3.5**	3.4
118-89	**4.7**	4.4	-[b]	-[b]	**4.7**	4.8	**4.9**	5.1	-[b]	-[b]	-[b]	-[b]
118-93	-[b]	-[b]	**3.9**	3.2	**4.5**	4.1	-[b]	-[b]	-[b]	-[b]	**3.8**	4.0
118-95	**4.2**	3.6	**4.3**	3.5	-[b]	-[b]	-[b]	-[b]	**4.8**	4.7	-[b]	-[b]
118-97	**4.4**	4.2	**4.6**	3.8	-[b]	-[b]	-[b]	-[b]	**4.8**	4.6	-[b]	-[b]
Parents of Population 1												
CDRK 82[a]	**2.0**	1.5	-[a]	-[a]	**2.5**	2.5	**2.3**	2.5	**2.8**	2.6	-[a]	-[a]
Montcalm	**3.6**	3.4	**3.8**	3.4	**4.8**	4.9	**4.3**	4.3	**4.1**	3.9	**3.6**	3.6

continued ...

Table 24. Continuation.

	Environment											
	Mich 1996		Minn 1996		Mich 1997		Mich 1998		Mich 1999		NDak 1999	
	Canning quality trait scores[e]											
Accession	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT
Means of the experiment, checks, parents, all 75 RILs in the population and the 10 highest scoring RILs, and values for LSD and CV												
Experiment mean	**3.2**	2.8	**3.0**	2.6	**3.7**	3.6	**3.6**	3.5	**3.7**	3.6	**2.8**	2.9
Check varieties	**4.4**	4.3	-[c]		**4.8**	4.7	**4.4**	4.4	**4.7**	4.9	**4.0**	4.2
Parents	**2.8**	2.5	-[d]		**3.7**	3.7	**3.3**	3.4	**3.4**	3.3	-[d]	
All RILs	**3.1**	2.7	**3.1**	2.6	**3.6**	3.5	**3.6**	3.5	**3.6**	3.6	**2.7**	2.8
Best RILs	**4.5**	4.2	**4.5**	4.0	**4.8**	4.6	**5.0**	4.9	**4.8**	4.6	**3.7**	3.7
LSD (0.05)	**1.1**	1.2	**1.3**	1.2	**1.1**	1.1	**1.9**	1.8	**1.3**	1.2	**1.1**	1.1
CV (%)	**18.1**	22.1	**20.0**	21.6	**14.7**	16.0	**24.5**	25.7	**17.4**	17.2	**19.5**	18.9

[a] CDRK 82 (California Dark Red Kidney 82) - not processed and canned in Minn-1996 and NDak-1999 due to insufficient seed samples.

[b] Only APP and SPLT scores in the environments where the RILs were among the group of lines with the 10 highest scores are shown.

[c] Not all the checks were planted in each environment; those not planted are indicated by (-)

[d] No mean scores for APP and SPLT are reported, since CDRK 82 was not canned in these environments due to insufficient seed samples

[e] Values in **bold type** are for APP

Figure 8. Processed beans of recombinant inbred line 118-90, from a cross between Montcalm and California Dark Red Kidney 82.

Figure 9. Processed beans of Population 1 recombinant inbred line 118-51, from a cross between Montcalm and California Dark Red Kidney 82.

RIL 118-90 had a higher score for both APP and SPLT than the parents and checks (Appendix Tables A.5 and A.6).

In addition to RIL 118-90, several RILs were among the 10 RILs with the highest APP scores in more than one environment. Seven RILs had high APP scores in three environments, with scores ranging from 3.5 to 4.9 (Table 24). Of these seven, two RILs 118-09 and 118-89, were among the 10 highest scoring RILs for APP and SPLT in Michigan over three years. RIL 118-09 had APP scores ranging from 4.4 to 4.7 and SPLT scores ranging from 4.4 to 4.6. RIL 118-89 had APP scores ranging from 4.7 to 4.9 and SPLT scores ranging from 4.4 to 5.1. APP ratings for the five other RILs, 118-05 (3.9 - 4.6), 118-66 (3.5 - 4.7), 118-93 (3.8 - 4.5), 118-95 (4.2 - 4.8), and 118-97 (4.4 - 4.8) were among the 10 highest scoring RILs in three different year-location combinations. In most of the environments, the lines with the 10 highest APP scores in more than two environments were comparable to or better than MCM (Table 24). The APP and SPLT scores of all the RILs and the parents of Population 1, and the checks in each environment and averaged across all six environments are shown in Appendix Tables A.5 and A.6. In each environment, one or more RILs had higher scores for both APP and SPLT than the best check variety.

In Population 2, CELRK had higher APP and SPLT scores than MCM, in Mich-1997 and in NDak-1999 (Table 25). MCM is generally known to have a more desirable canning quality than CELRK. In all environments, the parents had higher mean scores for APP and SPLT than the RILs. These differences were significant only for Michigan in 1997. The mean APP and SPLT scores of the 10 RILs with the highest scores for APP and SPLT were higher than the mid-parent scores in all environments except in

Table 25. Scores for appearance and degree of splitting of processed beans of Population 2 RILs that appeared in the ten highest scoring group of RILs in three, four and five individual experiments with the mean scores of the experiment, all RILs, the 10 highest scoring RILs, the parents, and the checks.

		Environment											
		Mich 1996		Minn 1996		Mich 1997		Mich 1998		Mich 1999		NDak 1999	
Accession		Canning quality trait scores[e]											
		APP	SPLT	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT
RILs that were common to the group with the 10 highest APP and SPLT scores in five of the six environments[c]													
119-34	Dark red	**5.6**	5.2	**5.2**	4.5	**5.1**	4.8	-[c]	-[c]	**5.9**	5.7	**4.5**	4.7
RILs that were common to the group with the 10 highest APP and SPLT scores in four of the six environments[c]													
119-20	Light red	**4.6**	4.3	-[c]	-[c]	**4.8**	4.9	**4.4**	4.2	**4.4**	4.2	-[c]	-[c]
119-33	Light red	**4.2**	3.7	**4.5**	4.3	**5.2**	5.5	-[c]	-[c]	**5.0**	4.9	-[c]	-[c]
119-69	Dark red	-[c]	-[c]	**4.8**	4.3	**4.7**	4.2	-[c]	-[c]	**4.6**	4.2	**5.5**	5.3
119-72	Light red	**4.7**	4.0	**4.6**	4.4	-[c]	-[c]	-[c]	-[c]	**5.2**	5.3	**4.5**	5.0
119-78	Light red	**5.7**	5.4	-[c]	-[c]	**5.0**	5.3	**4.1**	4.1	-[c]	-[c]	**4.3**	4.6
RILs that were common to the group with the 10 highest APP and SPLT scores in three of the six environments[c]													
119-67	Dark red	-[c]	-[c]	-[c]	-[c]	**4.6**	4.1	**4.1**	4.0	**5.0**	4.7	-[c]	-[c]

continued...

Table 25. Continuation.

Accession		Environment: Mich 1996		Minn 1996		Mich 1997		Mich 1998		Mich 1999		NDak 1999	
		Canning quality trait scores[c]											
		APP	SPLT	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT	**APP**	SPLT
Parents of Population 2													
CELRK[b]	Light red	**3.2**	2.5	**2.6**	2.2	**5.2**	5.0	**2.7**	2.8	**3.6**	3.2	**4.9**	4.9
Montcalm	Dark red	**4.1**	3.4	**3.8**	3.2	**4.7**	4.7	**4.9**	4.7	**4.4**	4.2	**3.2**	3.2
Means of the experiment, checks, parents, all 73 RILs in the population and the 10 highest scoring RILs, and values for LSD and CV													
Experiment mean		**3.4**	2.8	**3.1**	2.8	**3.7**	3.7	**3.2**	3.2	**3.4**	3.4	**3.2**	3.2
Check varieties		**3.1**	2.5	**2.7**	2.3	**4.0**	4.1	**3.6**	3.7	**3.0**	2.8	**3.4**	3.6
Parents		**3.6**	3.0	**3.2**	2.7	**5.0**	4.8	**3.8**	3.8	**4.0**	3.7	**4.0**	4.0
All RILs[d]		**3.4**	2.8	**3.1**	2.8	**3.7**	3.7	**3.2**	3.2	**3.4**	3.4	**3.2**	3.2
Highest scoring RILs		**4.6**	4.2	**4.7**	4.3	**4.9**	4.7	**4.2**	4.2	**5.0**	4.8	**4.6**	4.6
LSD (0.05)		**1.2**	1.2	**1.1**	1.2	**1.0**	1.0	**1.4**	1.4	**1.2**	1.2	**1.1**	1.1
CV (%)		**18.4**	21.5	**17.3**	20.9	**13.7**	13.2	**22.3**	21.2	**17.7**	18.4	**16.6**	15.9

[a] Non-commercial seed color: a mixture of dark and light red

[b] CELRK - California Early Light Red Kidney

[c] - Only the scores in those environments where the RILs entries were among the ten highest scoring RILs are shown.

[d] 3 RILs were not processed and canned in North Dakota in 1999 due to insufficient seed samples

[e] Values in **bold type** are for APP

Mich-1997. Except for the Minn-1996 environment, the differences were non-significant. Furthermore, the 10 RILs with the highest APP and SPLT scores had significantly higher mean scores than the check varieties in all environments except for Mich-1997 and Mich-1998.

Seven RILs in Population 2 were among the 10 lines with the highest APP scores in more than two environments (Table 25). Three of these RILs had the seed color and seed appearance of dark red kidney beans while four RILs belonged to the light red kidney bean market class. Of these seven RILs, RIL 119-34 (a dark red kidney bean) was in the group with the 10 highest APP scores in five of the six environments, with scores ranging from 4.5 to 5.9. Five RILs were among the lines with high APP scores in four environments. Among these lines, RIL 119-20 (a light red kidney line) was among the 10 RILs with the most desirable canning quality in Michigan in all four years of testing, but was not among the 10 highest scoring RILs for APP in Minnesota or North Dakota. RIL 119-33 was in the group of 10 RILs with high APP scores in Michigan in 1996, 1997 and 1999, and in Minnesota in 1996; RIL 119-78 was in the group in Michigan from 1996 to 1998, and in North Dakota in 1999. RIL 119-69 was among the 10 highest scoring RILs for APP scores in 1997 and 1999 in Michigan, in 1996 in Minnesota and in North Dakota in 1999. RIL 119-72 also was common to the group in four environments: Mich-1996, Mich-1999, Minn-1996 and NDak-1999. For comparison, MCM had APP scores beans ranging from 3.2 to 4.9 (Table 25). The APP and SPLT scores of these and the rest of the RILs, along with the parents and check varieties, ranked from highest to lowest APP score, are shown in Appendix Tables A.7 and A.8.

Heritability estimates and coefficients of correlation between traits. The ANOVA tables from which the variance components estimates were calculated from mean squares for APP and SPLT are presented in Appendix Tables A.13 to A.16. The narrow-sense heritability estimates for APP and SPLT were similar in both populations and were approaching high value (~0.9) (Table 26). For Population 1, the heritability estimates were 0.83 and 0.84 for APP and SPLT, respectively. For Population 2, APP and SPLT had a heritability of 0.85 (Table 26).

Table 26. Heritability estimates for appearance and degree of splitting of processed beans in Populations 1 and 2, using data from all environments combined.

	Appearance (CI[c])	Degree of splitting (CI[c])
Population 1	0.83 (0.75 - 0.87)	0.84 (0.76 - 0.87)
Population 2	0.85 (0.77 - 0.89)	0.85 (0.78 - 0.89)

[a] - 2 replications in 2 locations and 2 years.
[b] - 2 replications in 6 environments
[c] CI – 95% confidence interval

Pair-wise correlations among the canning quality traits - HC, APP and SPLT - and also between the canning quality traits, and yield and seed weight, are shown in Tables 27 and 28, for Populations 1 and 2, respectively. In both populations, APP and SPLT were highly correlated in each environment. Coefficients of correlation between these two traits ranged from 0.91 to 0.97. HC was positively correlated with APP in four environments in Population 1 and in five environments in Population 2; coefficients of correlation ranged from 0.24 to 0.68. HC was also correlated with SPLT in three years in

Michigan, in 1996, 1997 and 1999 in Population 1 and in five environments in Population 2; coefficients of correlation ranged from 0.34 to 0.63 (Tables 27 and 28).

In Population 1, both APP and SPLT were negatively correlated with yield in both locations in 1996, and in North Dakota in 1999 (Table 27). Coefficients of correlation between APP and yield ranged from –0.43 to –0.24, and for SPLT and yield, the coefficients ranged from –0.47 to –0.26. In Population 2, APP and yield were negatively correlated in all six environments; coefficients of correlation ranged from –0.15 to –0.50 (Table 28). SPLT and yield were negatively correlated in five environments; coefficients of correlation ranged from –0.18 to –0.55.

In Population 1, negative correlations between APP and seed weight, and between SPLT and seed weight were detected in 1996 and in 1999. Coefficients of correlation between APP and seed weight ranged from -0.37 to -0.29. For SPLT and seed weight, the coefficients ranged from -0.42 to -0.28 (Table 27). In Population 2, APP and SPLT were negatively correlated with seed weight in five environments; coefficients of correlation ranged from –0.20 to –0.37 (Table 28). Other correlations detected were between HC and seed size, and between HC and yield (Tables 27 and 28).

Identification of Putative Markers for Canning Quality Traits

The primers (OC5, OM10, ON17, OQ11, OG4, OP5, OY5, OM11, OX3, OO16, OY13, OF5, ON18, AND OAC2) that generated RAPD markers associated with canning quality traits in navy bean populations (Walters, 1995; Walters et al., 1997) were screened against the three kidney bean parents in the current study. For four primers (OC5, OQ11, OG4 and OAC2), the marker bands were not identified due to faint

Table 27. Significant correlations between canning quality traits, seed weight and yield in Population 1, planted in Michigan, Minnesota and North Dakota from 1996 to 1999.

		Environment[a]						
Trait 1	Trait 2	Mich 1996	Minn[b] 1996	Mich 1997	Mich 1998	Mich 1999	NDak 1999	Coefficient of Correlation
yield	seed weight		*	*	*		*	0.42 to 0.66
HC	seed weight		-		*			-0.38
HC	yield		-		*		*	-0.39 to -0.62
APP	yield	*	*				*	-0.24 to -0.43
APP	seed weight	*	*			*	*	-0.29 to -0.37
APP	HC	*	-	*		*	*	0.37 to 0.68
SPLT	yield	*	*				*	-0.26 to -0.47
SPLT	seed weight	*	*			*	*	-0.28 to -0.42
SPLT	HC	*	-	*		*		0.36 to 0.59
APP	SPLT	*	*	*	*	*	*	0.94 to 0.97

[a] * - Significant at level of significance = 0.05

[b] - Insufficient data was obtained for HC in 1996-MN

Table 28. Significant correlations between canning quality traits, seed weight and yield in Population 2, planted in Michigan, Minnesota and North Dakota from 1996 to 1999.

		Environment[a]						
Trait 1	Trait 2	Mich 1996	Minn[a] 1996	Mich 1997	Mich 1998	Mich 1999	NDak 1999	Coefficient of Correlation
HC	seed weight	*	-		*	*	*	-0.32 to 0.25
HC	yield	*	-			*	*	-0.21 to -0.58
APP	seed weight	*	*	*	*	*	*	-0.20 to -0.33
APP	yield	*	*	*	*	*	*	-0.15 to -0.50
APP	HC	*	-	*	*	*	*	0.24 to 0.60
SPLT	seed weight	*	*	*	*	*	*	-0.22 to -0.37
SPLT	yield	*	*		*	*	*	-0.18 to -0.55
SPLT	HC	*	-	*	*	*	*	0.34 to 0.63
APP	SPLT	*	*	*	*	*	*	0.91 to 0.97

[a] * - Significant at level of significance = 0.05

[b] - Insufficient data was obtained for HC in 1996-MN

amplification products. Twelve primers - OM10, ON17, OP5, OY4, OM11, OX3, OO16, OY13, OF5, and ON18 - did not amplify polymorphic bands in the kidney bean parents, MCM, CDRK 82 and CELRK. Primer OP5 detected a polymorphism among the kidney bean parents, but the band was faint and difficult to score in the population. No further amplifications with this primer were conducted on either Population 1 or 2.

Selective genotyping (Miklas et al., 1996) was effective in identifying markers associated with canning quality traits in the two kidney bean populations. Of the 8 markers identified initially, 4 (1.2% of 341 primers) were screened using the bulked DNA procedure. One marker (0.7% of 148 primers) was screened between the parents only. Three (4.4% of 68 primers) were screened using the parents and the bulks simultaneously. After the initial screening of the primers, the marker genotypes of the individual lines, which composed the bulks, were evaluated to determine the segregation of the marker bands among these 10 lines. This approach was less time-consuming and more efficient than if the entire population were scored immediately.

Thirteen RAPD bands - OY7.850, OQ14.950, OP15.1150, OAG10.1650, OA17.4000, OI8.1600, OU20.1150, OG17.1300, OAN16.3000, OH18.1000, OA7.2100 and OQ1700 - segregated in Population 1 according to a 1:1 ratio (Figure 10). Only these 13 bands were used for scoring the populations since the use of markers with distorted segregation ratios increases the possibility of detecting false positive polymorphism (Wang and Peterson, 1994). Eleven of these marker bands formed two linkage groups, designated M1-1 and M2-1, in Population 1. Seven markers - OQ14.950, OP15.1150, OAG10.1650, OY7.850, O18.1600, OU20.1150 and OA17.4000 - comprised linkage group M1-1, with a total map distance of 25.9 cM (Figure 11). Markers OP15.1150 and

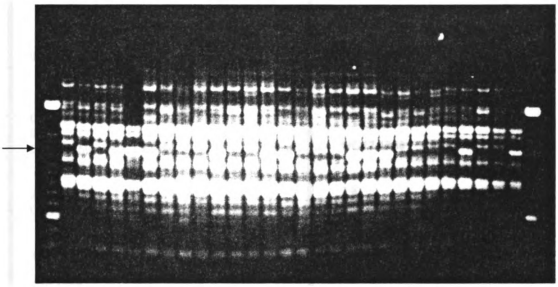


Figure 10. Amplification of primer OG17, showing marker OG17.1300, using DNA from parents and some RILs of Populations 1 and 2: Primer OG17: Lanes 1 and 30 – 100 bp ladder; 2 – MCM; 3 – CDRK 82; 4 to 9 – some RILs of Populations 1.

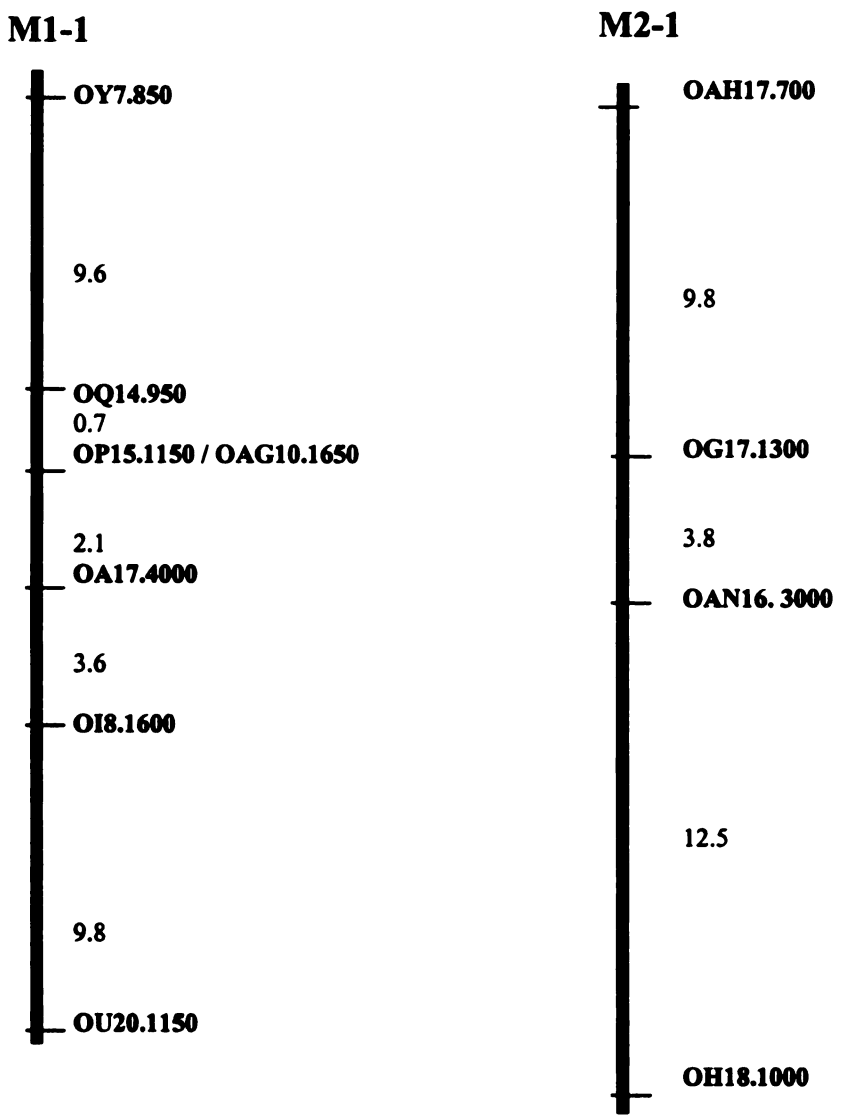


Figure 11. Linkage groups detected in Population 1 (MCM x CDRK 82). M1-1 (OY7.850, OQ14.950, OP15.1150, OAG10.1650, OA17.4000, OI8.1600, OU20.1150), total map distance = 25.9 cM; M2-1 (OAH17.700, OG17.1300, OAN16.3000, OH18.1000), total map distance = 26.1 cM.

OAG10.1650 had a map distance of 0 cM between them, indicating no recombination between these two markers in this population. Four markers - OAH17.700, G17.1300, OAN16.3000 and OH18.1000 - comprised linkage group M2-1, with a total map distance of 26.1 cM (Figure 11).

In Population 2, two linkage groups, composed of the same markers as the linkage groups in Population 1, were detected (Figure 12), designated M1-2 and M2-2. The same seven markers in M1-1 (Population 1) comprised M1-2, but were in a different order in Population 2. This map had a total map distance of only 6.5 cM. Markers U20.1150, OP15.1150 and OQ14.950 were very closely linked (map distance = 0.0 cM), and had a distance of 0.7 cM to OAG10.1650. Linkage group M2-2 (total map distance = 27.4 cM) had the same four markers in the same order as in M2-1 (Population 1).

In order to identify a possible location of the M1-1/M1-2 maps relative to the core map of the bean genome (Freyre et al., 1998), DNA samples from MCM, CDRK 82, CELRK, BAT 93 and Jalo EEP558 were amplified using the RAPD primers OI8 and U20, and resolved side by side on agarose gels (Figure 13). The results indicated that the marker I8.1500 in linkage group B8 reported by Freyre et al. (1998) might be a length polymorphism between these two lines, with BAT having a band 1500 bp long and Jalo with a slightly longer band, about 1600 bp. The band that was polymorphic among MCM, CDRK 82 and CELRK was also about 1600 bp long, indicating that marker I8.1500 reported by Freyre et al. (1998) and marker OI8.1600 found in the two kidney bean populations may be at the same locus. Marker U20.1150 was clearly the same band that was polymorphic between BAT 93 and Jalo EEP558, and among the kidney bean parents, MCM, CDRK 82 and CELRK (Figure 13).

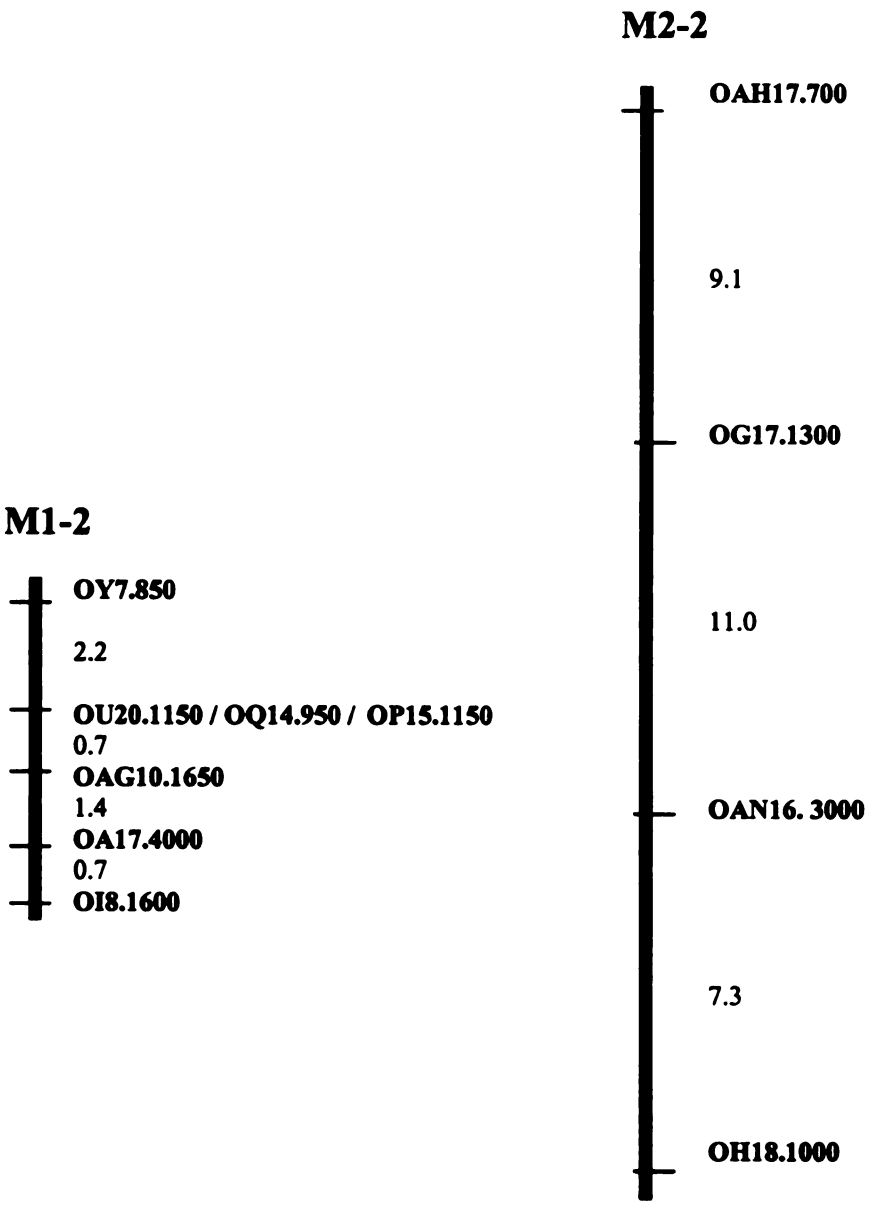


Figure 12. Linkage groups detected in Population 2 (MCM x CELRK). M1-2 (OY7.850, OQ14.950, OP15.1150, OAG10.1650, OA17.4000, OI8.1600, OU20.1150), total map distance = 6.5 cM; M2-2 (OAH17.700, OG17.1300, OAN16.3000, OH18.1000), total map distance = 27.4 cM.

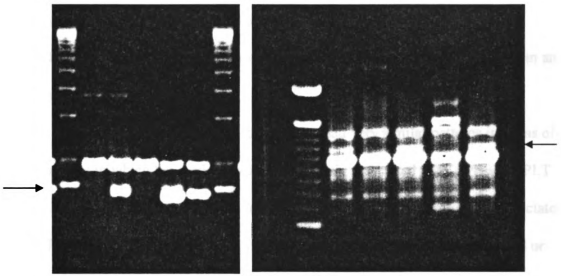


Figure 13. Amplification products of RAPD primers OI8 and OU20, showing Markers O18.1600 and OU20.1150, respectively.

a. OI8: Lanes1 and 7 –1 Kb ladder; 2 – CDRK 82; 3 – MCM; 4 – CELRK; 5 - BAT93; 6 - Jalo EEP558.

b. OU20: Lane 1 - 100 bp ladder; 2 - CDRK 82; 3 – MCM; 4 – CELRK; 5 – BAT93; 6 - Jalo EEP558.

Identification of putative RAPD markers in Population 1. Of the 13 markers that segregated at a 1:1 ratio in Population 1, nine were significantly correlated with APP and SPLT scores in at least one environment (Table 29). Among these nine markers significantly associated with canning quality traits were all the seven markers in linkage group M1-1 (Figure 11). Two markers in linkage group M2-1, OG17.1300 and OAN16.3000, were significantly associated with APP and SPLT in at least one environment. The other two markers in linkage group M2-1, OAH17.700 and OH18.1000, were not significantly associated with APP or SPLT in Population 1 in any environment.

The seven markers in linkage group M1-1 had very similar patterns in terms of the environments in which the markers were significantly associated with APP and SPLT (Table 29). Six of the seven markers in this linkage group were significantly associated with APP in 1996, 1997 and 1999 in Michigan, but not in Minn-1996, Mich-1998 or NDak-1999. Marker OU20.1150 was significantly associated with APP only in Mich-1996. For SPLT, six markers were associated with the trait in 1996, 1997 and 1999 in Michigan. Marker OY7.850 was further associated with SPLT in Mich-1998. Again, marker OU20.1150 was significantly associated with SPLT only in Mich-1996. All the markers were significantly associated with APP and SPLT scores averaged over all environments.

No pattern was observed in the M2-1 markers, OG17.1300 and OAN16.3000. Marker OG17.1300 was significantly associated with APP in Minn-1996, Mich-1999 and NDak-1999, and with SPLT in Minn-1996 and NDak-1999. Marker OAN16.3000 was significantly associated with APP in Mich-1999 and with SPLT in NDak-1999. Both

Table 29. Coefficients of determination (R^2) of RAPD markers associated with scores for appearance and degree of splitting of 75 RILs of Population 1, planted in Michigan, Minnesota, and North Dakota, from 1996 to 1999.

Markers[a]	Environment						
	Mich 1996	Minn 1996	Mich 1997	Mich 1998	Mich 1999	NDak 1999	All Env.[b]
Appearance (APP)							
Linkage group M1							
OY7.850	0.062	-	0.046	-	0.083	-	0.082
OQ14.950	0.073	-	0.079	-	0.065	-	0.068
OP15.1150	0.079	-	0.067	-	0.060	-	0.069
OAG10.1650	0.078	-	0.064	-	0.062	-	0.069
OA17.4000	0.051	-	0.031	-	0.044	-	0.039
OI8.1600	0.072	-	0.047	-	0.044	-	0.052
OU20.1150	0.043	-	-	-	-	-	0.038
Linkage group M2							
OAH17.700	-	-	-	-	-	-	-
OG17.1300	-	0.036	-	-	0.031	0.047	0.036
OAN16.3000	-	-	-	-	0.025	-	0.026
OH18.1000	-	-	-	-	-	-	-
Degree of splitting (SPLT)							
Linkage group M1							
OY7.850	0.062	-	0.037	0.029	0.074	-	0.071
OQ14.950	0.092	-	0.083	-	0.079	-	0.084
OP15.1150	0.099	-	0.066	-	0.072	-	0.083
OAG10.1650	0.099	-	0.064	-	0.073	-	0.084
OA17.4000	0.076	-	0.026	-	0.044	-	0.045
OI8.1600	0.091	-	0.044	-	0.046	-	0.058
OU20.1150	0.066	-	-	-	-	-	0.044
Linkage group M2							
OAH17.700	-	-	-	-	-	-	-
OG17.1300	-	0.056	-	-	-	0.059	0.035
OAN16.3000	-	-	-	-	-	0.044	0.027
OH18.1000	-	-	-	-	-	-	-

[a] (-) - not significant at level of significance = 0.05

[b] All Env. - APP and SPLT scores averaged over all environments

OG17.1300 and OAN16.3000 were significantly associated with APP and SPLT scores averaged over all environments.

The nine markers significantly associated with canning quality traits in Population 1 individually accounted for 2.5 to 8.3% of the variation in APP and 2.9 to 9.9% in SPLT (Table 29). Marker OY7.850 accounted for the highest amount of variation (8.2%) in APP averaged over environments, followed by OP15.1150 (6.9%) and OPAG10.1650 (6.9%). Markers OQ14.950 (8.4%) and OAG10.1650 (8.4%) accounted for the highest amount of variation in SPLT averaged over environments, followed by OP15.1150 (8.3%). The two markers in linkage group M2-1 accounted for the lowest amounts of variation in both APP and SPLT scores averaged over environments. Marker OAN16.3000 accounted for 2.6% of the variation in APP and 2.7% of the variation in SPLT, averaged over environments. Marker OG17.1300 accounted for 3.6% and 3.5% of the variation in APP and SPLT, respectively, averaged over environments (Table 29).

Tables 30 and 31 show the mean scores for APP and SPLT of all RILs in Population 1 with either the marker band present or absent. For the seven markers in linkage group M1-1 (OY7.850, OQ14.950, OP15.1150, OAG10.1650, OA17.4000, O18.1600 and OU20.1150), the allele associated with desirable APP and SPLT scores came from MCM, the parent chosen in the study for its desirable canning quality. For the two significant markers in linkage group M2-1 (OG17.1300 and OAN16.3000), the alleles associated with desirable canning quality traits were derived from CDRK 82. For each marker, the genotype of RIL 118-90, the highest scoring RIL in all environments, was consistent with the allele associated with high APP and SPLT scores, whether the allele came from MCM or CDRK 82 (Tables 30 and 31).

Table 30. Average scores for appearance of processed beans of two groups of Population 1 RILs that had the opposite alleles of the markers significantly associated with these traits, and the genotypes of the parents (Montcalm and California Dark Red Kidney 82), and RIL 118-90.

Marker	Allele[a]	Source of allele	Genotype of 118-90	Average score for appearance[bd]						
				Mich 1996	Minn 1996	Mich 1997	Mich 1998	Mich 1999	NDak 1999	All Env.[c]
OY7.850	-	**MCM**	-	**3.3**	ns	**3.8**	ns	**3.9**	ns	**3.4**
	+	CDRK 82		2.8		3.5		3.3		3.1
OQ14.950	-	**MCM**	-	**3.4**	ns	**3.9**	ns	**3.9**	ns	**3.5**
	+	CDRK 82		2.9		3.5		3.4		3.2
OP15.1150	-	**MCM**	-	**3.4**	ns	**3.9**	ns	**3.9**	ns	**3.5**
	+	CDRK 82		2.9		3.5		3.5		3.2
OAG10.1650	-	**MCM**	-	**3.4**	ns	**3.9**	ns	**3.9**	ns	**3.5**
	+	CDRK 82		2.9		3.5		3.4		3.2
OA17.4000	+	**MCM**	+	**3.3**	ns	**3.8**	ns	**3.8**	ns	**3.4**
	-	CDRK 82		2.9		3.5		3.5		3.2
OI8.1600	+	**MCM**	+	**3.3**	ns	**3.8**	ns	**3.8**	ns	**3.4**
	-	CDRK 82		2.8		3.5		3.4		3.2
OU20.1150	-	**MCM**	-	**3.3**	ns	ns	ns	ns	ns	**3.41**
	+	CDRK 82		2.9						3.19
OG17.1300	-	MCM		ns	2.9	ns	ns	3.5	2.6	3.2
	+	**CDRK 82**	+		**3.3**			**3.8**	**2.9**	**3.4**
OAN16.3000	-	MCM		ns	ns	ns	ns	3.5	ns	3.2
	+	**CDRK 82**	+					**3.8**		**3.4**

[a] Allele: (-) - marker band is absent; (+) - marker band is present

[b] ns - marker was not significant at level of significance = 0.05.

[c] All Envs. - averaged over the six environments

[d] Parent with highest score and value of highest score in each environment in **bold type.**

Table 31. Average scores for degree of splitting of processed beans of two groups of Population 1 RILs that had the opposite alleles of the markers significantly associated with these traits, and the genotypes of the parents and line 118-90.

Marker	Allele[a]	Source of allele	Genotype of 118-90	Average score for degree of splitting[bd]						
				Mich 1996	Minn 1996	Mich 1997	Mich 1998	Mich 1999	NDak 1999	All Env.[c]
OY7.850	-	**MCM**	-	**2.9**	ns	**3.7**	**3.6**	**3.8**	ns	**3.3**
	+	CDRK 82		2.4		3.4	3.3	3.3		2.9
OQ14.950	-	**MCM**	-	**3.1**	ns	**3.8**	ns	**3.9**	ns	**3.3**
	+	CDRK 82		2.4		3.3		3.3		3.0
OP15.1150	-	**MCM**	-	**3.1**	ns	**3.8**	ns	**3.8**	ns	**3.3**
	+	CDRK 82		2.4		3.4		3.4		3.0
OAG10.1650	-	**MCM**	-	**3.1**	ns	**3.8**	ns	**3.8**	ns	**3.3**
	+	CDRK 82		2.4		3.4		3.4		3.0
OA17.4000	+	**MCM**	+	**3.0**	ns	**3.7**	ns	**3.8**	ns	**3.3**
	-	CDRK 82		2.4		3.4		3.4		3.0
OI8.1600	+	**MCM**	+	**3.0**	ns	**3.7**	ns	**3.7**	ns	**3.3**
	-	CDRK 82		2.4		3.4		3.4		3.0
OU20.1150	-	**MCM**	-	**3.0**	ns	ns	ns	ns	ns	**3.3**
	+	CDRK 82		2.4						3.0
OG17.1300	-	MCM		ns	2.4	ns	ns	ns	2.7	3.0
	+	**CDRK 82**	+		**2.9**				**3.0**	**3.3**
OAN16.3000	-	MCM		ns	ns	ns	ns	ns	2.7	3.0
	+	**CDRK 82**	+						**3.0**	**3.2**

[a] Allele: (-) - marker band is absent; (+) - marker band is present

[b] ns - marker was not significant at level of significance = 0.05.

[c] All Envs. - averaged over the six environments

[d] Parent with highest score and value of highest score in each environment in **bold type**

The marker composites were not significantly associated with APP and SPLT in all the environments and reflected the environmental specificity of the individual markers (Table 32). The composites accounted for about 5 to 21% of the variation observed in both APP and SPLT. Marker composite A - all 11 markers, in both linkage groups M1 and M2 - accounted for the greatest amounts of variation in both APP (14 to 21%) and SPLT (16 to 21%), followed by marker composite B - linkage group M1 (11 to 13% for APP and 12 to 14% for SPLT). Marker composite A (all markers) was significantly associated with APP and SPLT in Michigan in all four years of the study, but was not significantly associated with the traits in either Minn-1996 or NDak-1999. Marker composite B (M1 markers) was significantly associated with APP and SPLT in Michigan in 1996, 1997 and 1999, but not in Minn-1996, Mich-1998, or NDak-1999. The markers in linkage group M2 (composite C) together accounted for 7.4% of the variation in APP and 8.2% of the variation in SPLT (Table 32). This composite was significantly associated with APP in NDak-1999, and with SPLT in Minn-1996 and NDak-1999.

The composite of one marker from each linkage group (marker composite D: OP15.1150 and OG17.1300) was significantly associated with APP and SPLT in five of the six environments, and accounted for about 6 to 11% of the variation in APP, and 7 to 13% in SPLT (Table 32). The different flanking markers in M1-1 (Population 1) - composite E: OY7.850 and OU20.1150 - and M1-2 (Population 2) - composite F: OY.850 and OI8.1600 - accounted for about the same amounts of variation (5 to 9% for APP and SPLT), and were significant in the same environments. The flanking markers of linkage group M2 - composite G: OAH17.700 and OH18.1000 - were not significantly associated with canning quality traits in any environment.

Table 32. Coefficients of determination (R^2) for composites of RAPD markers significantly associated wth scores for appearance and degree of splitting of processed beans of 75 RILs of Population 1, planted in Michigan, Minnesota, and North Dakota from 1996 to 1999.

Trait and Environment	Marker Composites [ab]						
	A	B	C	D	E	F	G
Appearance							
Mich 1996	0.170	0.125	-	0.089	0.071	0.087	-
Minn 1996	-	-	-	0.059	-	-	-
Mich 1997	0.144	0.115	-	0.071	0.051	0.059	-
Mich 1998	0.172	-	-	-	-	-	-
Mich 1999	0.176	0.113	-	0.098	0.088	0.090	-
NDak 1999	-	-	0.074	0.061	-	-	-
Overall[c]	0.211	0.132	0.080	0.113	0.082	0.089	-
Degree of splitting							
Mich 1996	0.178	0.124	-	0.114	0.087	0.101	-
Minn 1996	-	-	0.075	0.082	-	-	-
Mich 1997	0.156	0.134	-	0.069	0.045	0.052	-
Mich 1998	0.174	-	-	-	-	-	-
Mich 1999	0.170	0.123	-	0.100	0.076	0.082	-
NDak 1999	-	-	0.082	0.077	-	-	-
Overall[c]	0.212	0.136	0.074	0.126	0.075	0.085	-

[a]Marker composites:

A - all markers (OY7.850, OQ14.950, OP15.1150, OAG19.650, OA17.4000, OI8.1600, OU20.1150, OAH17.700, OG17.1300, OAN16.3000 and OH18.1000).

B - markers in linkage group M1 (OY7.850, OQ14.950, OP15.1150, OAG10.1650, OA17.4000, OI8.1600, and OU20.1150)

C - markers in linkage group M2 (OAH17.700, OG17.1300, OAN16.3000 and OH18.1000)

D - one marker each from M1 and M2 (OP15.1150 and OG17.1300)

E - flanking markers from linkage group M1-1 (OY7.850 and OU20.1150)

F - flanking markers from linkage group M1-2 (OY7.850 and OI8.1600)

G - flanking markers from linkage group M2 (OAH17.700 and OH18.1000)

[b] (-) - not significant at level of significance = 0.05.

[c] Overall - APP and SPLT scores averaged over all environments

The marker groups were used to select RILs from Population 1 to test their ability to select lines with desirable canning quality (Table 33). Seven lines had the 11 marker alleles associated with desirable canning quality and were selected using marker composite A. The average scores for APP and SPLT of these selected lines were 3.5 and 3.3, respectively, averaged over all environments. For comparison, the population means were 3.3 and 3.1 for APP and SPLT, respectively. The individual lines selected using composite A are shown in Table 34. Selection using the markers in linkage group M1 (composite B) resulted in 30 lines, with an average score of 3.4 for APP and 3.3 for SPLT, averaged over environments (not shown). Selection with the markers in linkage group M2 (composite C) resulted in fewer lines (17), which had lower average scores for APP (3.4) and SPLT (3.2), averaged over environments (not shown).

Using one marker each from the two linkage groups (composite D) - OP15.1150 from M1, and OG17.1300 from M2 - resulted in 12 selected RILs (Table 33). These selections had average scores for APP and SPLT of 3.7 and 3.6, respectively, which were higher than the population means. The individual lines and their APP and SPLT scores are shown in Table 34. Selection using the flanking markers in M1 (composites E and F) resulted in a similar number of lines, 31 for composite E and 33 for composite F (individual lines not shown). The average APP and SPLT scores of these selections were equal to or higher than the population mean by 0.1 unit. Selection using the flanking markers in linkage group M2 resulted in 18 selected RILs, which had average APP and SPLT scores equal to the population means (individual lines not shown).

Selection using group M1+G17 (linkage group M1 and marker OG17.1300) resulted in 11 RILs, which had average APP and SPLT scores of 3.7 and 3.6, respectively

Table 33. Mean scores for appearance and degree of splitting of processed beans of Population 1 RILs selected using groups of markers, analyzed per year-location combination.

Environment	Parent		Population	Marker Groups[ab]								
	MCM	CDRK	mean	A	B	C	D	E	F	G	M1+G17	M1+AN16
		82		(7)	(30)	(17)	(12)	(31)	(33)	(18)	(11)	(10)
	---------- Mean score for appearance of parents and selected RILs ----------											
Mich 1996	3.6	2.0	3.1	3.7	3.4	3.2	3.7	3.4	3.4	3.2	3.7	3.8
Minn 1996	3.8	-	3.1	3.2	3.2	3.0	3.5	3.2	3.2	3.0	3.5	3.6
Mich 1997	4.8	2.5	3.6	3.9	3.8	3.7	4.1	3.8	3.8	3.7	4.1	4.1
Mich 1998	4.3	2.3	3.6	3.4	3.6	3.7	3.7	3.6	3.6	3.7	3.7	3.8
Mich 1999	4.1	2.8	3.6	3.8	3.8	3.8	4.1	3.9	3.9	3.7	4.0	4.1
NDak 1999	3.6	-	2.7	3.0	2.7	2.8	3.1	2.8	2.7	2.7	3.1	3.2
Overall[a]	4.0	2.4	3.3	3.5	3.4	3.4	3.7	3.4	3.4	3.3	3.7	3.8
	---------- Mean score for degree of splitting of parents and selected RILs ----------											
Mich 1996	3.4	1.5	2.7	3.4	3.1	2.8	3.5	3.1	3.0	2.8	3.5	3.6
Minn 1996	3.4	-	2.6	2.7	2.7	2.6	3.1	2.7	2.7	2.6	3.1	3.2
Mich 1997	4.9	2.5	3.5	3.7	3.7	3.6	3.9	3.7	3.7	3.5	4.0	3.9
Mich 1998	4.3	2.5	3.5	3.2	3.5	3.5	3.6	3.6	3.5	3.5	3.6	3.7
Mich 1999	3.9	2.6	3.6	3.7	3.8	3.6	4.0	3.8	3.8	3.6	3.9	4.0
NDak 1999	3.6	-	2.8	3.1	2.8	2.9	3.2	2.9	2.9	2.8	3.3	3.3
Overall[a]	3.9	2.3	3.1	3.3	3.3	3.2	3.6	3.3	3.3	3.1	3.6	3.6

[a]Marker composites:

A - all markers
B - markers in linkage group M1
C - markers in linkage group M2
D - one marker each from M1 and M2 (OP15.1150 and OG17.1300)
E - flanking markers from linkage group M1-1 (OY7.850 and OU20.1150)
F - flanking markers from linkage group M1-2 (OY7.850 and OI8.1600)
G - flanking markers from linkage group M2 (OAH17.700 and OH18.1000)

[b] Overall - APP and SPLT scores averaged over all environments

(Table 33). The individual RILs selected are shown in Table 34. Selection using group M1+AN16 (linkage group M1 and marker OAN16.3000) resulted in 10 RILs, which had average APP and SPLT scores of 3.8 and 3.6, respectively. These 10 RILs are shown in Table 34. Both groups M1+G17 and M1+AN16 resulted in RILs with APP and SPLT scores higher than the population means for these traits.

Table 34. Average scores for appearance and degree of splitting of processed beans of RILs of Population 1 that were selected using marker composites composites A and D, and M1+G17 (linkage group M1 and OG17.1300), and M1+AN16 linkage group M1 and OAN16.3000).

Accession	Trait and overall scores[a]		Marker Composite			
	APP	SPLT	A	D	M1+G17	M1+AN16
118-05	3.9	3.6	*	*	*	*
118-09	3.8	3.7	*	*	*	*
118-21	3.7	3.6		*	*	*
118-22	3.4	3.2	*	*	*	*
118-42	3.2	3.1	*	*	*	*
118-49	3.4	3.2		*	*	
118-63	3.4	3.3		*		
118-72	3.6	3.4	*		*	*
118-81	2.8	2.8	*		*	*
118-90	5.8	5.9		*	*	*
118-94	3.4	3.3		*	*	*
118-95	3.9	3.6	*		*	*
Population Mean	3.3	3.1				

[a] Overall Scores -averaged over environments

Based on the number of lines selected, and the APP and SPLT scores of these selected RILs, the best marker subsets for identifying RILs with desirable canning quality were D, M1+G17, and M1+AN16. These subsets permitted the selection of 12 (average APP = 3.7), 11 (average APP = 3.7), and 10 lines (average APP = 3.8) with desirable

canning quality, respectively (Table 33). The lines selected using these sets of markers had average scores higher than the population means for both APP and SPLT in all environments. Seven RILs were common to the groups of RILs selected using these 3 marker subsets (Table 34). Marker subsets M1+G17 and M1+AN16 permitted the selection of an RIL with less than desirable canning quality - RIL 118-81, which had an average APP and SPLT score of 2.8 (Table 34). This RIL was not selected using marker composite D. Marker subsets M1+G17 and M1+AN16 also permitted the selection of 2 RILs, which had desirable canning quality scores but which were not selected using marker composite D. These 2 RILs were 118-72 (average APP = 3.6) and 118-95 (average APP = 3.9). The three marker subsets - D, M1+G17 and M1+AN16 - permitted the selection of RIL 118-90, which had consistently desirable canning quality traits across environments (average APP = 5.8).

Verification of putative RAPD markers in Population 2. In Population 2, only the markers in linkage group M2 - OAH17.700, OG17.1300, OAN16.3000 and OH18.1000 - were significantly associated with APP and SPLT (Table 35). Two markers - OAH17.700 and OH18.1000 - were not significantly associated with APP and SPLT in Population 1 (Table 29), but were significantly associated with these traits in Population 2 (Table 34). In general, the markers in linkage group M2 accounted for larger amounts of variation in Population 2 than any marker in Population 1.

Marker OG17.1300 was significantly associated with APP and SPLT in Minn-1996 and NDak-1999. In NDak-1999, OG17.1300 accounted for about 14% of the variation in APP and SPLT, the largest amounts of variation accounted for by any individual marker in both populations. Markers OAN16.3000 and OH18.1000 were

significantly associated with APP and SPLT only in NDak-1999. Marker OAN16.3000 accounted for about 6% of the variation in APP and SPLT, while marker OH18.1000 accounted for 7 to 8% of the variation in the traits. Markers OG17.1300, OAN16.3000 and OH18.1000 were significantly associated with APP and SPLT scores, averaged over all environments, and accounted for 3 to 4% of the variation in these traits.

Table 35. Coefficients of determination (R^2) for RAPD markers in linkage group M2 that were significantly associated with scores for appearance and degree of splitting of 73 RILs of Population 2, planted in Michigan, Minnesota, and North Dakota from 1996 to 1999[a].

Trait and M2 Markers[b]	Environment						
	Mich 1996	Minn 1996	Mich 1997	Mich 1998	Mich 1999	NDak 1999	All Env.[c]
	Values of R^2						
Appearance (APP)							
OAH17.700	-	-	-	-	-	0.097	-
OG17.1300	-	0.041	-	-	-	0.140	0.044
OAN16.3000	-	-	-	-	-	0.060	0.033
OH18.1000	-	-	-	-	-	0.081	0.032
Degree of splitting (SPLT)							
OAH17.700	-	0.044	-	-	-	0.097	-
OG17.1300	-	0.046	-	-	-	0.142	0.042
OAN16.3000	-	-	-	-	-	0.063	0.036
OH18.1000	-	-	-	-	-	0.067	0.029

[a] M1 markers were not significantly associated with APP and SPLT in Population 2.
[b] (-) - not significant at level of significance = 0.05.
[c] Overall - APP and SPLT averaged over all environments

For the markers significantly associated with canning quality traits in Population 2, the alleles associated with high APP and SPLT scores were derived from CELRK (Table 36). The difference in the average APP and SPLT scores of the RILs with either

Table 36. Average scores for appearance and degree of splitting of processed beans of two groups of Population 2 RILs that had the opposite alleles of the markers significantly associated with these traits, and the genotypes of the parents, Montcalm and California Early Light Red Kidney).

Trait and Marker[a]	Allele[b]	Source of allele	Average score for appearance (APP)[c]						
			Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[d]
Appearance									
OAH17.700	-	MCM	ns	ns	ns	ns	ns	2.9	ns
	+	**CELRK**						**3.5**	
OG17.1300	-	MCM	ns	3.0	ns	ns	ns	2.8	3.2
	+	**CELRK**		**3.4**				**3.5**	**3.5**
OAN16.3000	-	MCM	ns	ns	ns	ns	ns	3.0	3.2
	+	**CELRK**						**3.4**	**3.5**
OH18.1000	+	MCM	ns	ns	ns	ns	ns	2.9	3.2
	-	**CELRK**						**3.5**	**3.5**
Degree of splitting									
OAH17.700	-	MCM	ns	2.7	ns	ns	ns	3.0	ns
	+	**CELRK**		**3.1**				**3.6**	
OG17.1300	-	MCM	ns	2.6	ns	ns	ns	2.9	3.1
	+	**CELRK**		**3.1**				**3.6**	**3.4**
OAN16.3000	-	MCM	ns	ns	ns	ns	ns	3.0	3.1
	+	**CELRK**						**3.5**	**3.4**
OH18.1000	+	MCM	ns	ns	ns	ns	ns	3.0	3.1
	-	**CELRK**						**3.5**	**3.3**

[a] Markers in linkage group M1 were not significantly associated with APP and SPLT in Population 2.

[b] Allele: (-) - marker band is absent; (+) - marker band is present

[c] ns - markers was not significant at level of significance = 0.05.

[d] Overall - averaged over the six environments

marker allele was as much as 0.7 units, in the case of the alleles of marker OG17.1300, for APP in NDak-1999.

Only the marker composites with markers from linkage group M2 - composites A, C, D and G - had significant associations with APP and SPLT (Table 37), as expected from the associations of the individual markers with the canning quality traits. Marker composites B, E and F were not significant in any environment. Marker composite B was composed of the markers in linkage group M1 while composites E and F were of the flanking markers in M1. Marker composites A (all the markers together) and C (markers in linkage group M2) - was significantly associated with APP and SPLT only in NDak-1999. In this environment, marker composite A accounted for 22% and 24% of the variation in APP and SPLT, respectively, while composite C accounted for about 16% of the variation in APP and SPLT.

Marker composite D (OP15.1150 and OG17.1300) was significantly associated with APP and SPLT in Minn-1996 and NDak-1999, and with scores averaged over environments (Table 37). This composite accounted for 5 to 17% of the variation in the traits. Marker composite G (flanking markers in linkage group M2, OAH17.700 and OH18.1000) was significantly associated with APP in Mich-1998 and NDak-1999, and with SPLT in Minn-1996 and NDak-1999.

When the composites were used to select RILs in Population 2 (Table 38), the results were similar those in Population 1. Based on the number of RILs selected and the average overall scores of the selected RILs, the best composites for selecting RILs with desirable canning quality were composites D, M1+G17 and M1+AN16. Marker composite D resulted in the selection of 13 RILs, which had average overall scores of 3.6

Table 37. Coefficients of determination (R^2) of composites for RAPD markers significantly associated with scores for appearance and degree of splitting of processed beans of 73 RILs of Population 2, planted in Michigan, Minnesota, and North Dakota from 1996 to 1999.

Trait and Environment	Marker Composites[a,b]						
	A	B	C	D	E	F	G
Appearance							
Mich 1996	-	-	-	-	-	-	-
Minn 1996	-	-	-	0.050	-	-	-
Mich 1997	-	-	-	-	-	-	-
Mich 1998	-	-	-	-	-	-	0.043
Mich 1999	-	-	-	-	-	-	-
NDak 1999	0.223	-	0.160	0.174	-	-	0.121
Overall[c]	-	-	-	0.053	-	-	-
Degree of splitting							
Mich 1996	-	-	-	-	-	-	-
Minn 1996	-	-	-	0.057	-	-	0.047
Mich 1997	-	-	-	-	-	-	-
Mich 1998	-	-	-	-	-	-	-
Mich 1999	-	-	-	-	-	-	-
NDak 1999	0.244	-	0.158	0.182	-	-	0.119
Overall[c]	-	-	-	0.056	-	-	-

[a]Marker composites:

A - all markers (OY7.850, OQ14.950, OP15.1150, OAG19.650, OA17.4000, OI8.1600, OU20.1150, OAH17.700, OG17.1300, OAN16.3000 and OH18.1000).

B - markers in linkage group M1 (OY7.850, OQ14.950, OP15.1150, OAG10.1650, OA17.4000, OI8.1600, and OU20.1150)

C - markers in linkage group M2 (OAH17.700, OG17.1300, OAN16.3000 and OH18.1000)

D - one marker each from M1 and M2 (OP15.1150 and OG17.1300)

E - flanking markers from linkage group M1-1 (OY7.850 and OU20.1150)

F - flanking markers from linkage group M1-2 (OY7.850 and OI8.1600)

G - flanking markers from linkage group M2 (OAH17.700 and OH18.1000)

[b] (-) - not significant at level of significance = 0.05.

[c] Overall - APP and SPLT scores averaged over all environments

Table 38. Mean scores for appearance and degree of splitting of processed beans of Population 2 RILs selected using groups of markers, analyzed per year-location combination.

Trait and Environment	Population MCM	CELRK	mean	Marker Groups[ab] A (5)	B (38)	C (16)	D (13)	E (40)	F (39)	G (20)	M1+G17 (12)	M1+AN16 (10)
Mean score for appearance of selected RILs												
Mich 1996	4.1	3.2	3.4	3.5	3.4	3.3	3.7	3.4	3.4	3.4	3.8	3.5
Minn 1996	3.8	2.6	3.2	3.4	3.2	3.3	3.4	3.2	3.2	3.4	3.5	3.4
Mich 1997	4.7	5.2	3.7	3.8	3.8	3.6	3.9	3.7	3.7	3.6	3.9	3.8
Mich 1998	4.9	2.7	3.2	2.8	3.1	3.4	3.0	3.1	3.1	3.4	3.0	3.1
Mich 1999	4.4	3.6	3.4	3.6	3.5	3.5	3.7	3.5	3.5	3.5	3.8	3.5
NDak 1999	3.2	4.9	3.1	4.2	3.2	3.6	3.7	3.2	3.2	3.6	3.8	3.6
Overall[u]	4.2	3.7	3.3	3.5	3.4	3.4	3.6	3.3	3.3	3.5	3.6	3.5
Mean score for degree of splitting of selected RILs												
Mich 1996	3.4	2.5	2.8	3.0	2.8	2.7	3.1	2.8	2.8	2.8	3.2	3.0
Minn 1996	3.2	2.2	2.8	3.3	2.9	3.0	3.2	2.8	2.9	3.1	3.2	3.1
Mich 1997	4.7	5.0	3.7	3.7	3.8	3.6	3.9	3.7	3.7	3.7	3.9	3.7
Mich 1998	4.7	2.8	3.2	2.9	3.1	3.4	3.0	3.1	3.1	3.5	3.0	3.1
Mich 1999	4.2	3.2	3.4	3.4	3.5	3.4	3.6	3.4	3.4	3.4	3.7	3.4
NDak 1999	3.2	4.9	3.1	4.2	3.2	3.7	3.8	3.2	3.2	3.7	3.8	3.6
Overall[u]	3.9	3.4	3.2	3.3	3.2	3.3	3.4	3.2	3.2	3.4	3.5	3.3

[a]Marker composites:
A - all markers
B - markers in linkage group M1
C - markers in linkage group M2
D - one marker each from M1 and M2 (OP15.1150 and OG17.1300)
E - flanking markers from linkage group M1-1 (OY7.850 and OU20.1150)
F - flanking markers from linkage group M1-2 (OY7.850 and OI8.1600)
G - flanking markers from linkage group M2 (OAH17.700 and OH18.1000)

[b] Overall - APP and SPLT scores averaged over all environments

and 3.4 for APP and SPLT, respectively. Marker composite M1+G17 resulted in 12 selected RILs, with average overall scores of 3.6 and 3.5 for APP and SPLT, respectively. Marker composite M1+AN16 resulted in 10 selections, with average overall scores of 3.5 and 3.3 for APP and SPLT, respectively. The average overall scores for the RILs selected using these marker composites were higher than the population means for APP (3.3) and SPLT (3.2).

The RILs selected using composites A, D, M1+G17 and M1+AN16 are shown in Table 39. Nine RILs were commonly selected using D, M1+G17 and M1+AN16. Two of these, RIL 119-45 and RIL 119-94 had less than desirable APP and SPLT scores. The other RILs, including those not commonly selected using these composites, had desirable APP and SPLT scores. Composites D and M1+G17 permitted the selection of RILs with desirable canning quality traits, which were not selected using composite M1+AN16.

Table 39. Average scores for appearance and degree of splitting of processed beans selected using marker composites A and D, and M1+G17 (linkage group M1 and OG17.1300), and M1+AN16 (linkage group M1 and OAN16.3000).

Accession	Trait and Overall Scores[a]		Marker Composite			
	APP	SPLT	A	D	M1+G17	M1+AN16
119-14	3.8	3.7		*	*	
119-36	2.8	2.6		*		
119-42	3.6	3.6		*	*	*
119-45	2.9	2.7				*
119-53	2.5	2.3	*	*	*	*
119-54	3.4	3.2		*	*	*
119-55	3.3	3.2		*	*	
119-64	3.2	3.1	*	*	*	*
119-65	3.7	3.4		*	*	*
119-69	4.5	4.0	*	*	*	*
119-71	3.7	3.3		*	*	*
119-72	4.5	4.5		*	*	
119-78	4.6	4.6	*	*	*	*
119-94	2.8	2.6	*	*	*	*

[a] Overall Scores -averaged over environments

DISCUSSION

Breeding programs for kidney beans and other dry bean market classes must consider consumer preferences for canning quality, in addition to yield and other agronomic characteristics. Although desirable canning quality traits are important, bean producers do not accept varieties solely for these characteristics. In the same way, high-yielding breeding lines are also subject to the strict requirements for canning quality sought by processors and consumers. Thus, in addition to the yield potential of RILs comprising Populations 1 and 2, which were evaluated in this study, canning quality of these RILs must be evaluated concurrently.

The significant negative correlations detected in the two populations, between the canning quality traits (APP and SPLT) and seed weight complicate breeding for these traits simultaneously. These findings are in agreement with Forney et al. (1990) who found significant correlations in kidney beans between large seeds and splitting during processing. The negative correlations observed among canning quality traits, yield and seed size have important implications in breeding for these traits. Breeders must devise strategies to select for these traits simultaneously. Considering each trait separately may lead to the improvement of one at the expense of the other two. In breeding for canning quality, for example, the breeder must ensure that seed size and quality are not altered beyond acceptable limits. Since seed size in dry bean is subject to a federal grade restriction by the USDA Agricultural Marketing Service, seed size for the market class is an important criterion for the acceptance or rejection of a cultivar by the bean industry.

Canning quality of two kidney bean recombinant inbred populations

Although several factors influencing the appearance of canned beans - such as brine clarity and the amount of starch in the brine and on the surface of beans, the degree of clumping, and seed color, size and shape - are considered in evaluating the acceptability of canned kidney beans, the degree of splitting of the beans also plays a large role in acceptance or rejection of a sample (Lu and Chang, 1996; Forney et al., 1990). The causes of splitting during processing are not known, although factors such as genotype, condition of the seed at harvest, storage practices and processing methods may affect the trait. The positive correlations between HC- a measure of how well a bean hydrates during soaking – and APP and SPLT indicate the importance of factors that affect water imbibition during processing. These factors, which include the physiology of the seed coat and cotyledons, affect the degree of splitting of the beans and thus overal quality. The high positive correlations between APP and SPLT indicate that a single rating will suffice to evaluate the canning quality of kidney bean lines. The use of APP alone will include perceptions of the degree of splitting of the beans and other traits that affect the appearance of the processed beans.

In both Populations 1 and 2, first-order interactions (genotype x year and genotype x environment) were significant for APP and SPLT, indicating that either a change in the ranking of the genotypes or the degree of the differences between them occurred. Some RILs in both populations had consistently desirable canning quality across years and year-location combinations (environments). The significance of these interactions may therefore indicate a change in the degree of differences among the genotypes rather than a possibility that the performance of a line may differ drastically

from one environment to another. Moderate to high estimates of heritability for APP and SPLT indicate that selection should be effective in developing lines with desirable canning quality. Walters et al. (1997) reported heritability estimates in navy bean of 0.48 to 0.78 for the components of canning quality – visual appeal (VIS), texture (TXT) and washed drained mass (WDWT).

The significant effects of the environment on canning quality traits in this study were expected, based on experiments conducted by others over a span of 20 years (Ghaderi et al., 1980; Hosfield and Uebersax, 1990; Hosfield et al., 1984b; Walters et al., 1997). What allometrically correlated plant characteristics and developmental aspects of the seed that accounted for variable canning quality responses to a range of physical environments are present unknown. However, the results from studies in grain crops (Borojevic and Williams, 1982; Wych et al., 1982) suggested that stresses induced by the environment during seed development had large effects on seed characteristics. In the Michigan environments, seasonal temperature and rainfall patterns (not shown) conducive to a stress environment prevailed at times during the seed development period in some of the years during which the experiment was conducted.

Location effects including the presence of foliar pathogens on the experimental materials may also have contributed to stress influences on seed development. The climate prevailing at harvest (not shown) is an additional factor that may have influenced the results of this study. Cool and wet climatic conditions at harvest may also have a negative effect on canning quality. Seeds with high moisture content at harvest are often discolored and sprouted and must be removed to ensure that the sample falls into a marketable grade. Moreover, marketable beans high in moisture have high respiration

rates (Gonzales et al., 1982; Kays et al., 1980). High respiration rates of beans indicate that major metabolic pathways in the seeds are activated (Kays et al., 1980), which could lead to physico-chemical changes affecting canning quality.

Sufficient variability in canning quality was observed among RILs in both populations to select individual RILs that scored as high as, or better than, commercially accepted varieties used as checks for canning quality traits. The RILs, 118-90 and 119-34, and the others with consistently desirable APP scores show potential for use as sources of genes for desirable canning quality. However, these two RILs had significantly lower yields than the checks. RIL 118-90 had an average yield of 1657 $kg \cdot ha^{-1}$ over the six environments, and was among the lowest yielding entries (Appendix Table A.1). Line 119-34 was likewise one of the lowest yielding lines, with a yield of 1983 $kg \cdot ha^{-1}$ averaged over all environments (Appendix Table A.3). The seed weights of both lines were within the range of 50-60 per 100 seeds (Appendix Tables 2 and 4), which is considered acceptable for the kidney bean (Adams and Bedford, 1975), although line 118-90 is at the low end of this range. The low yields of these two RILs, which both had desirable canning quality, offer further evidence for the negative correlation between yield and APP. Although RIL 118-90 and RIL 119-34 are both low yielding, these lines merit consideration for further testing in a dry bean breeding program. In crosses with high yielding genotypes, one would strive to "capture" the genes for desirable canning quality carried by these RILs, and combine them with genes for yield from the high-yielding parents.

Deshpande et al. (1984) foresaw an increased demand for canned beans, due to their availability as easy-to-prepare or ready-to-eat food. This demand is not likely to

decrease, with the increased interest in convenience and fast food. The contribution of beans to human nutrition as an alternative protein source will also serve to encourage its consumption, especially among those who choose a vegetarian diet. An increased demand for kidney bean varieties with desirable canning quality should follow an increased consumption of beans of this market class. The identification of genotypes with superior canning quality represents continuing efforts to meet these demands. Improved understanding of the inheritance of the trait and the effect of the environment and genotype x environment interactions serve to broaden the information on which breeding approaches for the trait are based.

RAPD markers for canning quality traits in kidney bean

An important factor in applying selective genotyping in identifying markers is the choice of lines to include in the bulks. The composition of the bulks must be such that the extreme phenotypes are represented and that the bulks differ as much as possible only in the genomic region or regions of interest. For example, in the case of the bean traits under consideration in this study, five RILs were selected based on their desirable APP and SPLT scores in four environments. Five other RILs were selected to comprise the bulk with undesirable canning quality traits. The choice of RILs for the bulks is especially important when the contrasting phenotypes differ by degrees, as in this study. Unlike single-gene traits, quantitative traits cannot be categorized into discrete groups that differ markedly in their phenotypes. Variation is continuous, with slight differences between genotypes commonly indistinguishable. Significant environmental effects also cause the differences between genotypes to differ from one environment to another. Thus, in addition to the performance of a line relative to the others, the consistency of

that line's performance across environments should be considered. The number of lines included in the bulk is also an important consideration and is affected by the size of the population under study. A balance must be achieved between having too many and too few lines in the bulks. Including too many lines in each bulk will increase the similarity between the bulked DNA, thus making it harder to identify genomic regions that distinguish one from the other. Using too few lines will increase the number of genomic regions in which the bulks differ; some of these regions may not be at all involved in the trait of interest.

In this study, 5 lines from Population 1, which comprised of 73 RILs, were deemed as just the right number of lines for each bulk. RILs with APP and SPLT scores at both ends of the 7-point scale, representing the most and least desirable phenotypes, were identified in each of the four environments. The consistency of the lines' scores across environments was considered. The quality of the canned beans of the lines was verified visually. In this last step, such as in the evaluation of most quantitative traits, some degree of judgment was left to personal discretion regarding the choice of the lines. The choices for the two bulks used in this study were thus based on three criteria: APP and SPLT scores in four environments, consistency of the scores across these environments and visual evaluation.

Eleven markers, which as a group accounted for a moderate but significant amount of variation, were identified in the two kidney bean populations. The low number of markers identified for canning quality traits may be due to several factors, such as low levels of polymorphism between the parental lines detected by the RAPD markers, and the incidence of many QTL with small effects on the trait which could not

be detected. Interactions between genes (epistasis), and genotype x environment interactions (Paterson et al., 1991), which were significant in this study, may also be contributing factors. Another primary obstacle in marker identification, particularly for quantitative traits, is the precision of phenotypic evaluation (Luby and Shaw[1]), which in turn is affected by the degree to which the genetic effects are confounded by genotype x environment interactions. Unless care is taken in assessing the phenotype and ensuring sufficient population sizes, the observed degree of correlation between the trait and a marker in any population may not accurately reflect the actual degree of linkage. This, in turn, ultimately affects the genetic efficiency of using MAS to improve the trait (Luby and Shaw[1]).

The eleven markers, in two linkage groups, associated with canning quality traits indicate the presence of at least two QTLs, which influence canning quality traits in kidney bean. The first linkage group, M1 (OY7.850, OQ14.950, OP15.1150, OAG10.1650, OA17.4000, OI8.1600 and OU20.1150), was putatively located on linkage group B8 in the core map for *P. vulgaris* (Freyre et al., 1998), based on the amplification products of OI8.1600/1500 and OU20.1150 (Figure 10). The exact orientation of this linkage group on the core map cannot be determined because of the different location of the marker U20.1150 in the maps generated from the two populations, M1-1 and M1-2 from Populations 1 and 2, respectively (Figures 11 and 12). Based on the order of the markers in Population 1 (M1-1) (Figure 11), the linkage group M1 is at the lower half of linkage group B8 of the core map (Freyre et al., 1998). Based on the order of the markers in Population 2 (M1-2) (Figure 12), M1 is at the center portion of B8 (Freyre et al.,

[1] Luby and Shaw. Unpublished manuscript. Does marker-assisted selection make dollars and sense in a fruit breeding program?

1998). The difference in the order of the markers in the two maps may be due to a translocation involving the segment with marker U20.1150, which occurred in one population but not in the other, or simply heterogeneity within the lines. Genes of known function that are located on B8 are lipoxygenase (Adam-Blondon et al., 1994) and glutamine synthetase (Nodari et al., 1993). Additional markers and populations with a higher degree of inbreeding are needed to precisely determine the location of the M1 linkage group on the B8 of the core map, and to map the location of linkage group M2.

Linkage group M1-1 also has a greater total distance and fewer markers clustered together (no recombination) than M1-2. These differences may be due to more points of recombination in this region of the genome in Population 1 than in Population 2. Greater similarities may exist between the parents of Population 1 (both dark red kidney bean) than between those of Population 2 (one light red and one dark red kidney bean), thus facilitating greater crossing over at this region.

QTL involved in canning quality may be within or near the region of the kidney bean genome represented by linkage group M1. Except for marker U20.1150, the position of a particular marker on the linkage group does not seem to affect the amount of variation associated with that marker (Table 29). The QTL may thus be within the M1 region, but since the physical map distance covered by M1 is not known, the possibility that the linked QTL resides outside the region cannot be excluded. Furthermore, if more than one QTL is located at this region, one (or more) QTL may be within M1 and others may be near the region. In either case, the QTL appear to be more adjacent to the markers other than U20.1150, which accounted for less variation than the other markers and was significantly associated with APP and SPLT in fewer environments (Table 29).

If QTL reside within the region of the M1 marker group, then the markers in the center of the map have a greater potential for use in marker-assisted selection (MAS) for canning quality traits, than the flanking markers. A map distance of 10 cM or less between a marker and the QTL of interest aids in increasing gain from selection using that marker (Paran et al., 1991; Kennard et al., 1994; Timmerman et al., 1994). A marker that is closely linked to the QTL or gene of interest facilitates faster improvement of the trait during MAS than one in which there is a high degree of recombination with the gene. The three markers at the center of M1, OP15.1150, OAG10.1650, and OA17.4000, have a total map distance of less than 10 cM in both populations.

Since it is not known whether the QTL is located exactly at the position of the M1 markers, the genotype of the QTL cannot be known with certainty (Paterson et al., 1991). However, the source of these marker alleles is MCM, and the probability that the associated QTL is also derived from MCM is high. The use of MCM as a source of genes for the improvement of canning quality in kidney bean breeding programs seems justified by the results of this study. These linked markers, as a group, are associated with a significant amount of variation in the APP and SPLT traits in canned beans in Population 1 - 11.3 to 13.6% (Table 32).

The M1 markers segregated in a similar fashion in Population 2, which was derived from a cross between a light red (CELRK) and a dark red kidney bean (MCM). Even though MCM was a common parent in the two populations and presumably the source of genes for the desirable canning quality traits in Population 1, the M1 markers did not account for any significant variation observed in Population 2. Walters et al. (1997) reported population-specific markers in navy beans. Some of the population-

specific markers reported in the Walters et al. (1997) study were monomorphic in all but one of the three populations of navy beans studied; hence, the non-significant effects in the other two populations. The small population sizes evaluated by Walters et al. (1997) may have contributed to the population-specificity of the markers. In the current study, the number of RILs in each population was more than two times that used in the Walters et al. (1997) study. The eight putative markers in Population 1 of this study were also polymorphic in Population 2 and did not deviate significantly from a 1:1 segregation ratio. Segregation and similar linkage phases between the marker and the QTL are important if markers identified in one population are to be useful in another (Dudley, 1993).

The second group of markers, linkage group M2 (OAH17.1300, OG17.1300, OAN16.3000 and OH18.1000), were significantly associated with canning quality traits in both the dark red and light red kidney bean populations, and were not derived from MCM (30, 31 and 36). Genotypes with undesirable canning quality are generally not considered as sources of genes for improving canning quality traits. However, other studies have shown that poor performing genotypes such as wild crop relatives, which are rarely used in the improvement of quantitative traits, may in fact be used to improve quality. Examples are QTL from the phenotypically inferior wild rice relative, *Oryza rufipogon* used to improve grain yield in cultivated rice (Xiao et al., 1998), and QTL from unadapted tomato germplasm used to improve color and soluble solids in cultivated tomato (Tanksley and Nelson, 1996).

In the current study, CDRK 82 and CELRK appeared to transmit the QTL detected by the markers in linkage group M2, which were significant in Populations 1

and 2. Considering that the markers in M1 were not significant in both populations, the two undesirable canning parents (CDRK 82 and CELRK) would not be likely to have the same alleles for desirable canning quality at the loci represented by M2. Instead, alleles, which do not contribute to the acceptability of canned beans, may be present in MCM at the loci represented by M2. In some environments, MCM may exhibit average or even undesirable canning quality because of the expression of these alleles. The substitution of these alleles with others, even those from a variety with generally undesirable canning quality, as may have occurred in these two populations, may improve canning quality. The loss of these MCM alleles for undesirable canning quality traits is more important than the source of the substituted alleles in promoting desirable canning quality. This finding may explain the results of the experiments in Michigan in 1997 and in North Dakota in 1999 in which MCM had lower than expected scores for APP and SPLT of canned beans. In fact, CELRK, which was expected to manifest low APP and SPLT scores (~3.0), had higher scores for these traits than MCM in these environments.

The QTL linked to the M2 are apparently more sensitive to environmental effects than are the markers in M1. In Populations 1 and 2, OG17.1300 was significant in both Minn-1996 and NDak-1999 for APP and SPLT but was significant only for APP in Population 1 in Mich-1999. Also in Population 1, marker OAN16.3000 was significant only for APP in Mich-1999 and for SPLT in NDak-1999. In Population 2, this marker was significant for APP and SPLT in NDak-1999. The other two markers, OAH17.700 and OH18.1000, show similar patterns of environment-specificity.

Unlike at the M1 region, only one QTL for canning quality may exist at the region represented by M2. The flanking markers, OAH17.700 and OH18.1000, were

significantly associated with the APP and SPLT only in Population 1. The markers at the center, however, were significant in both populations. These central markers - OG17.1300 and OAN16.3000 - thus appear to have more potential for MAS than the flanking markers.

Since the two populations used in this study had a common parent, and dark red and light red kidney beans are closely related market classes (Ghaderi et al., 1982), markers common to both populations were expected to be found. This result was observed only for the M2 markers, which were derived from the parent other than MCM. The QTL detected by M2 markers in Population 1 (dark red x dark red) were also important in Population 2 (dark red x light red) (Tables 29 and 35). For the M1 markers, however, this result was not observed. Several hypotheses are possible to explain these results. Although the same QTL may be present in light red kidney bean RILs at the M1 region, these QTL may not be as important in the regulation of canning quality in this market class as are other regions of the genome, such as the M2 region. This conclusion is supported by the usefulness of the M1 markers in selecting lines with desirable canning quality in Population 2, even though the markers did not account for significant variation in this population. Other regions of the genome may have larger effects on APP and SPLT in light red kidney bean. Other marker systems that generate higher degrees of polymorphism than RAPD markers may be able to identify these QTL. Other dark red kidney bean populations derived from MCM should also be investigated with regards to the segregation of M1 markers and their effects on canning quality traits in those populations.

Another explanation may be that the genome of both the light red and dark red kidney bean has not been fully characterized. Additional markers may indicate that the M1 region may be similarly important in Population 2. Still another possible explanation for the lack of significant associations between markers and QTL in Population 2 may be epistatic interactions between QTL, which masks their effect on APP and SPLT of light red kidney beans (Dudley, 1993). Greater variability of the data in Population may also have an effect in the identification of markers in this population. Further research is needed to verify these hypotheses.

The use of only one marker for each linkage group may be all that's required to effectively select for desirable canning quality in these populations. Based on the results of the selection experiments on Populations 1 and 2, and considering the efficiency of using the least number of markers possible, the best set of markers to use appear to be one marker from each linkage group, particularly markers OP15.1150 and OG17.1300 (marker composite D). Marker OP15.1150 has a distance of 0.0 cM from OAG10.950 in Population 1, and from OQ14.950 and OU20.1150 in Population 2. Selecting for this marker, therefore, increases the possibility that the other three markers will also be selected, whether in Population 1 or Population 2. Marker OP15.1150 accounted for a relatively large amount of variation for APP and SPLT in Population 1, indicating either close linkage with a QTL with minor effects on canning quality or more distant linkage with a QTL, which has a large effect. Marker OG17.1300 accounted for the largest amount of variation in APP and SPLT in either population - 14% in NDak-1999 in Population 2 (Table 35). The use of these two markers to select for RILs with canning quality resulted in similar numbers of RILs with similar average APP and SPLT scores in

the two populations (Tables 33 and 38). These results indicate that the two markers were equally effective in selecting for canning quality in the two populations.

The heritability of the trait under selection and the proportion of additive variance explained by a marker are factors that affect the efficiency of using MAS in improving a quantitative trait (Luby and Shaw[2]). Miklas et al. (1995) suggested that for a marker to be useful, it should account for variation as much as or more than the heritability of the trait. In this study, the heritabilities for APP and SPLT are more than the variation accounted for by any of the markers individually or by any composite of markers. The stability of marker-QTL associations over environments is also another factor to consider (Miklas et al., 1995). Environmental-specificity was observed in some of the marker-QTL associations. Although the markers reported here have been shown to be effective in selecting for desirable canning quality in these two populations, their use in other populations needs evaluation, particularly in populations in which MCM is not a parent. In such populations, the markers identified in this study may be useful in indicating a genotype's potential for desirable canning quality, even before seed production, and in reducing the number of crosses needed to evaluate the trait (Dudley, 1993). The markers could also be useful in reducing the number of lines to be planted, harvested, and evaluated using conventional canning methods, saving considerable time and resources.

The QTL detected in this study offer important insights into markers, which may be useful in breeding for canning quality in kidney bean. For example, QTL for desirable canning quality traits may be present in the genomes of varieties showing undesirable canning quality. Further investigations using other DNA marker systems on both dark

[2] Luby and Shaw. Unpublished manuscript. Does marker-assisted selection make dollars and sense in a fruit breeding program?

red and light red kidney beans may shed more light on the genes responsible for canning quality in these two kidney bean market classes.

In addition to the QTL detected here, other QTL responsible for a larger amount of variation may be present in other regions of the genome. Likewise, additional minor genes, each with a small effect, may be present. Further investigations with other marker systems, such as AFLPs, and using other approaches may be useful to detect other genes influencing canning quality, further define the linkage map presented here, and fine-map the location of the QTL relative to known genes or markers in linkage group B8. Additional markers associated with either a few QTL with major effects or of numerous QTL with minor effects need to be identified if MAS for canning quality in beans is to be feasible. Mapping strategies that utilize saturated maps of the bean genome might prove productive in identifying these additional markers. The presence of a low level of polymorphism due to a narrow genetic base is another concern in using RAPDs. Marker systems that generate a higher degree of polymorphism than RAPDs may allow the identification of additional loci that were not detected here.

APPENDIX

Table A.1. Yields (kgs.ha^{-1}) of 75 RILs and the parents of Population 1, and check varieties, planted in Michigan, Minnesota and North Dakota in 1996, 19997, 1998 and 1999.

	Yield (kgs.ha^{-1}) in each environment						
Accession[a]	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-82	3533	3181	3119	3268	3811	2093	3168
118-84	3670	2517	2727	2731	3604	2508	2960
K86012 (Isles)[d]	3392	-	2975	2712	3631	1912	2924
118-46	3391	2986	3240	2330	3209	2383	2923
118-33	2864	2801	3342	3014	2979	2133	2855
118-12	2737	2989	2857	2492	3553	2325	2826
118-55	3045	2377	3480	2566	3397	1957	2804
118-39	2810	3438	1833	2557	3298	2642	2763
118-68	2965	2449	3080	2291	3762	2010	2759
K90122 (Lassen/Isabella/Montcalm)[d]	2730	-	-	-	-	-	2730
118-51	2686	2403	2088	2793	3759	2478	2701
K93201 (Montcalm/37-16)[d]	-	-	2684	-	-	-	2684
118-93	3126	2563	2072	2829	3633	1856	2680
118-100	2958	2496	2557	3038	2893	2087	2671
118-31	3171	2280	2299	3016	3353	1891	2668
118-98	2205	2758	2438	2837	3674	1968	2647
118-63	2378	2087	3131	3018	3145	2085	2641
K97309 (Red Hawk / K93644)[d]	-	-	-	3461	3356	1082	2633
118-29	2706	2615	2771	2506	3448	1649	2616
118-19	2837	2330	2549	2857	3333	1755	2610
118-27	2810	2550	2304	2658	3206	2110	2606
118-15	2024	2574	2770	2655	3515	2066	2601
118-35	2219	3250	1926	2507	3132	2524	2593

continued...

Table A.1. Yields (kgs.ha^{-1}) continued...

Accession[a]	Yield (kgs.ha^{-1}) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-11	2655	2953	2299	2170	3398	2070	2591
118-49	2140	1893	2865	3199	3550	1879	2588
118-74	2508	2701	2200	2492	3099	2502	2584
118-24	2925	2854	1953	2316	3805	1576	2571
118-89	1969	3108	1869	2410	3508	2559	2570
118-71	2772	2636	1783	2622	3555	1985	2559
118-95	2559	2271	3173	2641	2990	1652	2548
118-22	2675	2359	2878	2491	3233	1645	2547
118-47	2678	2414	2360	2584	2985	2194	2536
Montcalm[c]	2790	2499	1381	2649	3713	2159	2532
118-97	2583	2360	2636	2709	3229	1670	2531
118-25	2957	2785	1206	2720	3552	1903	2521
118-01	2698	2040	2400	2550	3126	2115	2488
118-38	3008	2469	1789	2282	3498	1867	2486
118-09	2361	2194	2238	2811	3242	1974	2470
118-88	2499	2707	2103	2587	3255	1658	2468
118-08	1931	2541	2560	2934	2632	2103	2450
118-16	3036	2396	2041	2206	2720	2248	2441
118-62	3181	2208	1396	2538	3488	1821	2439
118-37	2797	1889	1861	2630	3402	1966	2424
118-13	2540	1713	2693	3312	3054	1211	2421
118-64	2939	2111	1457	2724	3203	2035	2412
118-66	2725	1416	2402	2698	3804	1397	2407

continued...

Table A.1. Yields (kgs.ha^{-1}) continued...

Accession[a]	Yield (kgs.ha^{-1}) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-67	2761	2713	1828	2261	3016	1778	2393
118-85	2626	2184	2179	2759	2740	1781	2378
118-75	2577	2697	1553	2448	2931	2060	2378
Red Hawk[d]	2096	-	1919	3101	3596	1168	2376
118-94	2131	1761	3153	2480	3730	966	2370
118-18	2060	2681	2160	2418	2998	1862	2363
118-65	2931	1709	2215	2890	3598	812	2359
118-04	2792	1583	2254	2323	3236	1918	2351
118-23	2615	2361	1736	2242	3062	2055	2345
118-05	2649	2250	2308	3042	3034	602	2314
118-48	2515	2094	1649	2750	2992	1857	2309
118-72	2440	1517	3206	2526	2926	1128	2291
118-45	2254	2604	1423	2664	2813	1924	2280
K94202 (Sacramento / I89021)[d]	1967	-	2525	-	-	-	2246
118-41	2796	1069	2994	2808	3221	459	2225
118-60	2447	1292	2916	2745	3248	672	2220
118-81	1692	2379	2078	2404	2891	1795	2206
118-32	2655	1313	2701	2568	3171	785	2199
118-06	2511	1387	2032	2943	3219	926	2170
118-30	2608	956	3209	2404	2804	992	2162
118-69	3081	1748	2113	2230	2822	960	2159
118-43	2524	640	2534	2449	3465	1219	2138
118-73	2439	1267	2575	2079	3593	876	2138

continued...

Table A.1. Yields (kgs.ha^{-1}) continued...

Accession[a]	Yield (kgs.ha^{-1}) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-61	2215	1928	2410	2271	3003	983	2135
118-42	2383	1697	2438	2903	2624	731	2129
118-07	2285	1593	1908	2839	3104	996	2121
118-44	2378	2164	1532	2531	3211	826	2107
K97305 (Red Hawk / Drake)[d]	-	-	-	2696	2775	815	2095
118-50	2399	1349	3072	2300	3151	291	2094
118-17	2523	931	2586	2474	2709	1233	2076
118-99	2038	1375	2400	2109	2821	1562	2051
CDRK 82[c]	2613	1273	2715	2670	2875	99	2041
118-21	2948	530	2984	1901	2815	910	2015
118-92	2972	1420	2151	2399	2735	342	2003
118-90	2766	1026	1808	2116	2584	828	1855
118-70	2187	1240	1609	1848	2990	1027	1817
118-36	2133	789	1695	2547	1899	1358	1737
118-76	1651	939	1626	2188	2839	471	1619
Mean	2615	2107	2345	2602	3197	1590	
Coefficient of variation (%)	21.1	23.5	19.9	13.7	11.6	18.4	

[a] - Accessions were arranged according to descending overall yield (averaged over all environments)

[b]Overall - averaged over environments

[c] - Parents of the population

[d] - Check varieties

Table A.2. Seed weights (g.100^{-1} seed) of 75 RILs and the parents of Population 1, and check varieties, planted in Michigan, Minnesota and North Dakota in 1996, 1997, 1998 and 1999.

Accession[a]	Seed weight (g.100 seed^{-1}) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-84	63.4	64.8	64.7	62.9	72.4	52.1	63.4
118-12	63.0	57.5	72.6	62.9	72.1	51.5	63.3
K93201 (Montcalm/37-16)[d]	-	-	62.9	-	-	-	62.9
118-01	60.3	57.9	68.3	60.9	70.1	51.0	61.4
118-27	60.1	64.0	61.7	63.6	68.9	48.9	61.2
118-97	60.4	56.8	70.0	60.0	65.0	48.2	60.0
K86012 (Isles)[d]	65.5	-	60.2	63.2	70.3	50.0	59.9
118-62	60.9	60.7	57.0	60.6	68.6	49.2	59.5
118-82	60.2	62.0	75.3	52.8	62.3	44.1	59.5
118-29	59.5	58.2	73.8	59.4	62.5	43.3	59.5
118-37	62.9	59.1	53.9	62.3	69.1	49.2	59.4
118-48	58.7	54.3	63.1	63.0	66.6	49.7	59.2
118-68	61.0	58.5	60.5	59.0	66.4	49.6	59.2
118-07	63.3	53.9	63.2	62.6	64.1	46.1	58.9
118-70	60.6	55.1	55.6	62.8	69.2	48.2	58.6
118-11	60.4	55.8	57.7	59.8	69.6	47.4	58.4
118-55	58.6	55.6	72.7	56.1	64.5	43.0	58.4
118-95	56.6	58.5	68.8	58.5	62.8	43.3	58.1
118-23	55.5	59.3	61.9	60.6	65.5	44.4	57.9
118-35	52.9	56.8	66.1	56.9	61.6	52.3	57.8
118-100	57.8	56.0	59.6	59.7	65.9	47.4	57.7
118-44	58.0	59.3	50.2	65.6	65.4	47.6	57.7
118-51	55.6	55.7	59.3	63.8	65.6	46.0	57.7

continued...

Table A.2. Seed weights (g.100^{-1} seed) continued...

Accession[a]	Seed weight (g.100 seed^{-1}) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-13	59.4	49.8	69.7	60.8	65.1	41.2	57.7
118-04	52.4	47.1	66.1	60.3	70.2	49.9	57.6
118-09	53.3	54.7	67.0	60.4	61.2	49.0	57.6
118-47	57.7	55.9	63.5	60.5	62.6	45.0	57.5
118-24	61.2	58.5	58.0	58.6	63.9	44.8	57.5
118-42	57.5	52.4	68.7	60.9	62.7	42.3	57.4
118-15	56.3	54.0	67.4	57.7	63.0	45.7	57.4
118-98	54.4	53.5	64.0	59.7	64.3	47.5	57.2
118-39	57.6	57.7	54.9	58.6	64.4	50.2	57.2
118-08	50.6	49.9	59.3	62.7	69.9	50.6	57.2
118-18	56.2	58.7	60.8	57.9	63.2	45.7	57.1
118-25	58.9	57.5	55.1	58.2	65.4	47.4	57.1
118-88	57.6	55.5	58.4	61.4	65.4	44.1	57.1
118-99	57.7	54.7	61.0	58.0	65.4	45.5	57.1
118-63	55.5	57.4	59.6	58.8	63.4	47.0	57.0
118-46	57.2	56.8	66.1	54.7	61.1	45.0	56.8
118-16	57.5	54.5	59.4	55.3	66.2	46.3	56.5
118-72	52.4	50.0	74.7	57.5	61.1	43.6	56.5
118-05	61.8	63.4	65.1	56.0	56.9	35.8	56.5
Montcalm[c]	55.1	57.2	58.4	57.9	62.8	47.5	56.5
118-89	56.2	57.6	53.6	57.4	64.5	48.6	56.3
118-21	58.5	44.7	68.8	58.2	65.5	42.0	56.3
118-49	53.9	51.5	71.8	56.8	60.8	42.8	56.2

continued...

Table A.2. Seed weights (g.100^{-1} seed) continued...

Accession[a]	Seed weight (g.100 seed^{-1}) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-17	56.5	48.7	70.8	56.6	61.7	43.1	56.2
118-92	59.2	51.9	60.3	57.9	63.3	44.2	56.1
118-31	57.8	55.7	57.3	57.5	62.9	44.8	56.0
118-38	55.8	55.7	60.0	55.3	63.3	45.6	56.0
118-30	56.0	49.4	68.5	56.6	61.4	43.0	55.8
118-61	55.4	52.3	60.4	55.4	63.2	47.7	55.7
118-85	53.8	56.0	63.7	55.2	63.2	42.3	55.7
118-22	52.1	52.7	73.2	56.3	58.0	41.4	55.6
118-69	59.9	50.1	60.6	56.3	63.7	43.2	55.6
K97309 (Red Hawk / K93644)[d]	-	-	-	64.3	61.2	41.4	55.6
118-67	55.9	54.3	60.4	56.6	61.3	43.8	55.4
118-60	54.7	47.6	64.5	59.6	61.3	44.6	55.4
118-93	57.1	56.9	47.0	60.7	65.5	44.9	55.4
118-74	53.3	58.1	52.4	57.5	61.6	47.1	55.0
118-19	59.9	59.8	67.4	53.4	60.6	27.8	54.8
118-06	56.4	48.2	61.4	56.3	66.5	40.1	54.8
K97305 (Red Hawk / Drake)[d]	-	-	-	58.3	65.4	40.7	54.8
118-33	53.3	57.1	49.5	61.7	61.0	45.3	54.6
118-50	53.7	46.5	67.3	55.7	59.4	43.6	54.4
CDRK 82[c]	57.8	49.1	54.2	55.6	65.7	42.1	54.1
118-41	54.5	44.0	71.0	56.0	57.3	41.6	54.1
118-94	49.5	47.6	71.6	57.5	56.9	38.4	53.6
118-73	55.6	36.3	66.7	54.6	62.3	44.9	53.4

continued...

Table A.2. Seed weights (g.100^{-1} seed) continued...

Accession[a]	Seed weight (g.100 seed^{-1}) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-76	49.7	49.5	56.5	57.4	61.8	45.3	53.4
118-64	54.5	49.3	49.7	54.5	62.9	49.2	53.3
118-81	48.9	53.6	53.5	57.6	61.0	45.4	53.3
K94202 (Sacramento / I89021)[d]	49.8	-	56.8	-	-	-	53.3
118-66	51.0	50.7	65.4	52.8	57.6	39.8	52.9
118-32	56.1	45.6	58.7	54.9	60.0	41.7	52.8
118-43	56.3	44.3	53.9	57.4	61.3	43.1	52.7
Red Hawk[d]	47.1		59.5	61.2	55.9	39.5	52.6
118-71	53.2	51.5	57.5	53.3	58.0	41.4	52.5
118-65	54.2	45.5	65.9	51.7	56.7	37.7	52.0
118-45	47.5	54.4	54.6	52.7	58.2	43.3	51.8
118-75	52.8	52.0	50.2	51.8	58.0	44.2	51.5
118-90	50.9	43.2	60.3	50.7	61.0	42.3	51.4
118-36	50.4	45.6	55.2	58.6	55.8	41.7	51.2
K90122 (Lassen/Isabella/Montcalm)[d]	50.4	-	-	-	-	-	50.4
Mean	56.23	53.75	61.93	58.21	63.37	44.89	
Coefficient of variation (%)	6.12	7.72	4.81	4.63	3.49	7.42	

[a] - Accessions were arranged according to descending overall yield (averaged over all environments)

[b]Overall - averaged over environments

[c] - Parents of the population

[d] - Check varieties

Table A.3. Yields (kgs.ha^{-1}) of 73 RILs and the parents of Population 2, and check varieties, planted in Michigan, Minnesota and North Dakota in 1996, 19997, 1998 and 1999.

Accession[a]	Seed type	Yield (kgs.ha^{-1}) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
K94515 (K89829 / K88401)[d]	Light red	3861	-	-	-	-	-	3861
Isles[d]	Light red	4364	2955	-	-	-	-	3660
Chinook[d]	Light red	4138	1493	2942	-	-	-	3540
K94601 (Chinook 2000)[d]	Light red	4507		2053	2925	4709	2376	3314
119-70	Light red	3514	3245	2313	3312	4342	1761	3081
119-79	Light red	4621	2683	1910	2612	4265	2337	3071
119-32	Dark red	3542	3069	2213	3248	3991	2293	3059
119-21	Light red	3076	3191	2536	3176	4086	2274	3056
119-17	Light red	3514	2581	2842	3128	4153	1932	3025
119-01	Light red	3525	3118	2508	3232	3828	1921	3022
119-88	Light red	3729	2456	2170	2950	3961	2746	3002
119-60	Non-commercial	3605	3076	1552	3088	3971	2532	2971
119-39	Light red	3716	2921	2452	2964	3578	2104	2956
119-89	Dark red	3681	2195	2811	2907	4077	2060	2955
119-65	Light red	3628	3162	2122	2733	3649	2313	2934
119-61	Light red	3440	3110	2934	2704	3512	1826	2921
119-56	Non-commercial	3553	3154	2131	2757	3683	2144	2904
119-19	Light red	4038	2872	1300	2494	3919	2548	2862
119-73	Light red	3131	2357	2725	2552	4270	2035	2845
119-15	Non-commercial	2878	2827	2998	3046	3278	1997	2837
119-105	Light red	4267	2751	2320	2807	3096	1702	2824
119-27	Dark red	3165	2329	2857	2965	3660	1896	2812
119-50	Light red	3801	3006	1826	2715	3160	2294	2800

continued...

Table A.3. Yields (kgs.ha^{-1}) continued...

Accession[a]	Seed color	Yield (kgs.ha^{-1}) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
119-03	Non-commercial	3731	2478	2351	2865	3565	1779	2795
119-75	Dark red	2960	2749	2672	2634	3594	2147	2793
119-51	Light red	3093	2734	1856	2924	3589	2533	2788
119-59	Light red	3532	2759	2101	2591	3520	2179	2780
119-20	Light red	3070	2676	1904	2888	3779	2264	2764
119-80	Light red	3968	2694	1770	2448	3643	2050	2762
119-74	Non-commercial	3677	1820	2584	2599	3206	2664	2758
119-31	Light red	3828	2821	2255	2858	3150	1490	2734
119-28	Dark red	3069	2639	1896	3035	3593	2014	2708
119-02	Dark red	3608	2529	1693	3133	3716	1550	2705
119-57	Dark red	3532	2426	2526	2879	3600	1233	2699
119-64	Light red	4149	1516	2385	2796	3525	1799	2695
119-40	Light red	2888	2540	1954	2913	3674	2069	2673
119-38	Light red	3431	2706	2449	2875	3025	1523	2668
119-76	Dark red	3309	2650	1983	2807	3614	1636	2666
Montcalm[c]	Dark red	3578	2120	1580	2610	3563	2546	2666
119-96	Dark red	3245	2910	1463	2479	4034	1841	2662
119-35	Dark red	3394	2622	2522	2960	2868	1526	2649
119-33	Light red	3914	2595	2303	2592	2895	1582	2647
K93654 (Chinook / CELRK)[d]	Light red	2992	-	2283	-	-	-	2637
119-67	Dark red	3194	2724	1710	2697	3253	2209	2631
119-43	Light red	3826	3000	1650	2175	3222	1835	2618
119-78	Light red	3232	2031	2688	2466	4115	1093	2604
119-14	Light red	3004	2260	2461	2854	3293	1679	2592

continued...

Table A.3. Yields (kgs.ha^{-1}) continued...

Accession[a]	Seed color	Yield (kgs.ha^{-1}) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
119-10	Dark red	3616	2939	1750	2778	3548	867	2583
119-54	Dark red	3393	2187	1926	2710	3546	1719	2580
Red Hawk[d]	Dark red	3151	-	1992	-	-	-	2571
119-101	Light red	3312	2806	1642	2448	2986	2232	2571
119-58	Light red	2793	1913	2300	2616	4121	1646	2565
119-94	Light red	3244	2629	2223	2555	3907	798	2559
119-44	Non-commercial	3112	2565	2256	2236	3456	1702	2554
CELRK[c]	Light red	3823	1964	2610	3242	3214	436	2548
K97503 (Red Hawk / CELRK)[d]	Light red	-	-	-	2306	3637	1664	2535
119-98	Dark red	3517	1819	2706	2897	3853	330	2520
K97504 (Red Hawk / Foxfire)[d]	Light red	-	-	-	2293	3261	1960	2504
119-36	Dark red	3344	2355	2955	2880	2869	588	2498
119-42	Light red	3144	1955	2495	2946	3673	635	2475
119-104	Dark red	3694	3170	2028	2619	2906	393	2468
119-45	Dark red	2664	2173	2408	2982	3251	1318	2466
119-83	Non-commercial	2668	1692	2727	2677	3605	1407	2463
119-55	Dark red	3053	2192	2358	2943	3487	720	2459
119-71	Dark red	3283	1568	2890	3102	3012	628	2414
119-81	Non-commercial	2922	2222	2534	2001	3358	1436	2412
119-93	Dark red	2790	3003	1659	2037	3322	1598	2402
119-72	Light red	3282	2342	1944	2559	3698	568	2399
119-106	Light red	3399	1581	2348	3057	3293	314	2332
K93621 (CELRK/Chinook)[d]	Light red	-	-	-	2596	3371	1029	2332
119-95	Dark red	2364	2337	2566	3298	2964	243	2295

continued...

Table A.3. Yields (kgs.ha^{-1}) continued...

Accession[a]	Seed color[b]	Yield (kgs.ha^{-1}) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[c]
119-69	Dark red	2925	2008	2416	2369	3512	494	2287
119-86	Light red	2474	2726	2020	1773	2889	1704	2264
119-97	Dark red	3330	1314	1849	2954	3389	700	2256
K93629 (CELRK/Chinook)[d]	Light red	-	-	1537	2591	3439	701	2244
119-30	Non-commercial	2899	1867	2061	2473	3454	620	2229
119-09	Dark red	3038	1385	2196	2626	3314	793	2225
119-85	Dark red	3111	2611	903	2412	2871	1163	2178
119-48	Light red	2945	1138	2747	2705	2669	446	2108
119-49	Light red	2923	1585	2677	2537	2352	435	2085
119-47	Non-commercial	2884	2602	2159	1741	2323	739	2075
119-77	Dark red	3288	1670	1387	2108	3176	485	2019
119-34	Dark red	2330	2117	1976	2271	2684	522	1983
119-53	Non-commercial	2908	1349	1548	2556	2904	340	1934
119-46	Light red	2968	1076	1357	2395	3199	512	1918
K93653 (Chinook / CELRK)[d]	Light red	-	-	2421	2874	3073	545	-
Mean		3359	2414	2199	2711	3467	1491	
Coefficient of variation (%)		17	18	16	17	14	21	

[a] - Accessions were arranged according to descending overall yield (averaged over all environments)

[b] Overall - averaged over environments

[c] - Parents of the population

[d] - Check varieties

Table A.4. Seed weights (g.100^{-1} seed) of 73 RILs and the parents of Population 2, and check varieties, planted in Michigan, Minnesota and North Dakota in 1996, 1997, 1998 and 1999.

Accession[a]	Seed type	Seed weight (g.100 seed^{-1}) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
119-58	Light red	70.1	62.6	75.1	71.2	71.8	54.7	67.6
119-38	Light red	66.7	66.7	71.2	69.8	66.3	53.0	65.6
Isles[d]	Light red	66.5	62.7	-	-	-	-	64.6
119-59	Light red	65.6	69.7	56.1	62.7	76.7	56.0	64.5
119-19	Light red	65.6	60.1	75.2	59.3	69.5	56.0	64.3
119-79	Light red	69.9	64.4	60.4	62.2	74.7	54.1	64.3
119-105	Light red	72.1	63.2	63.1	59.6	71.2	54.3	63.9
119-40	Light red	66.2	65.5	62.9	61.9	72.3	53.9	63.8
119-61	Light red	65.2	65.8	66.7	67.9	63.2	51.9	63.5
119-50	Light red	65.9	67.4	57.1	59.3	72.8	56.6	63.2
119-39	Light red	68.5	64.2	65.7	59.4	68.9	52.2	63.1
119-33	Light red	67.9	59.5	62.8	63.7	70.6	54.1	63.1
119-88	Light red	68.9	65.3	60.0	61.6	70.0	51.7	62.9
Chinook[d]	Light red	53.6	50.2	72.2	-	-	-	62.9
119-20	Light red	66.8	63.0	65.9	60.8	68.0	51.3	62.7
119-51	Light red	60.6	62.9	68.9	58.2	69.4	54.0	62.3
119-93	Dark red	60.5	67.3	63.9	64.0	63.3	51.7	61.8
119-17	Light red	62.5	60.9	68.9	63.9	65.9	48.4	61.7
119-80	Light red	64.5	61.3	63.0	58.6	70.1	51.5	61.5
119-65	Light red	65.9	64.0	59.2	60.8	65.7	50.5	61.0
119-101	Light red	61.2	59.9	62.8	59.6	67.9	54.0	60.9
K94515 (K89829 / K88401)[d]	Light red	60.8	-	-	-	-	-	60.8
119-76	Dark red	65.7	62.3	64.6	63.4	60.2	47.6	60.6

continued...

Table A.4. Seed weights (g.100^{-1} seed) continued...

Accession[a]	Seed type	Seed weight (g.100 seed^{-1}) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
119-77	Dark red	64.3	57.0	66.6	65.5	62.5	47.9	60.6
119-64	Light red	64.2	49.0	63.4	59.0	71.4	56.7	60.6
119-21	Light red	61.2	61.0	66.9	61.1	63.1	50.2	60.6
119-34	Dark red	63.1	58.7	66.4	65.4	63.2	46.4	60.5
119-01	Light red	60.3	56.5	67.5	55.5	70.8	52.0	60.4
119-28	Dark red	62.1	60.1	63.8	60.5	65.5	50.1	60.4
119-43	Light red	67.1	66.3	57.5	57.3	67.2	46.1	60.3
119-55	Dark red	63.7	59.2	62.8	69.5	59.2	45.6	60.0
119-03	Non-commercial	62.4	60.9	68.5	57.4	62.3	48.3	60.0
119-02	Dark red	61.5	57.6	59.8	65.2	64.6	49.9	59.8
119-42	Light red	62.0	57.1	66.5	64.8	63.9	44.1	59.7
119-31	Light red	59.4	54.5	77.6	53.3	67.1	46.0	59.7
119-15	Non-commercial	60.8	56.8	68.5	58.9	64.0	48.2	59.5
119-14	Light red	63.0	60.9	58.1	62.6	60.2	51.9	59.5
119-94	Light red	63.7	61.0	61.2	65.3	63.0	42.6	59.5
119-60	Non-commercial	62.2	64.1	59.1	56.5	64.3	49.9	59.3
119-69	Dark red	62.7	56.4	74.8	60.6	57.6	44.0	59.3
119-10	Dark red	64.2	65.3	64.9	57.3	59.8	44.5	59.3
119-36	Dark red	62.9	54.8	69.5	59.4	67.8	39.9	59.0
119-85	Dark red	61.6	61.0	59.1	64.1	59.6	48.7	59.0
119-32	Dark red	61.3	57.5	64.5	58.5	63.6	48.5	59.0
119-27	Dark red	60.1	59.2	64.2	59.1	64.2	46.8	58.9
119-74	Non-commercial	58.7	50.3	60.6	57.2	70.5	56.2	58.9
119-49	Light red	63.8	53.0	66.5	63.8	61.9	44.3	58.9

continued...

Table A.4. Seed weights (g.100^{-1} seed) continued...

Accession[a]	Seed type	Seed weight (g.100 seed^{-1}) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
Montcalm[c]	Dark red	62.8	56.0	69.0	56.3	61.9	46.9	58.8
119-57	Dark red	60.9	56.5	66.8	57.8	64.7	46.2	58.8
CELRK[c]	Light red	64.0	57.2	61.6	64.5	60.9	44.2	58.7
K93654 (Chinook / CELRK)[d]	Light red	60.8	-	56.4	-	-	-	58.6
119-48	Light red	62.4	61.7	64.6	61.1	62.0	38.7	58.4
119-73	Light red	63.1	58.5	60.7	58.2	63.2	46.3	58.3
119-35	Dark red	61.9	52.5	65.6	59.9	62.2	46.6	58.1
119-56	Non-commercial	62.0	46.2	67.2	54.1	67.0	51.2	58.0
119-104	Dark red	68.1	66.7	61.4	53.8	58.2	39.2	57.9
119-45	Dark red	57.6	55.1	68.9	57.5	61.6	46.5	57.9
119-72	Light red	64.0	57.6	50.7	60.9	64.7	48.4	57.7
K93621 (CELRK/Chinook)[d]	Light red	-	-	-	58.8	65.8	48.2	57.6
119-67	Dark red	58.1	58.6	65.4	56.2	60.9	45.7	57.5
Red Hawk[d]	Dark red	53.9	-	60.9	-	-	-	57.4
119-70	Light red	58.5	57.7	66.2	55.3	62.6	43.9	57.4
119-47	Non-commercial	56.6	59.1	67.5	59.6	57.8	43.6	57.4
119-75	Dark red	58.0	51.1	66.9	57.8	62.0	47.1	57.1
119-81	Non-commercial	55.4	57.8	66.0	58.8	57.6	47.2	57.1
119-86	Light red	56.6	57.1	64.3	58.2	57.9	48.0	57.0
119-78	Light red	60.6	52.6	61.3	54.6	64.1	47.6	56.8
119-89	Dark red	58.3	54.5	64.2	56.5	60.2	46.6	56.7
119-97	Dark red	63.2	47.8	68.1	66.8	59.6	34.2	56.6
119-98	Dark red	56.3	51.7	69.3	60.1	57.5	44.2	56.5
K94601 (Chinook 2000)[e]	Light red	57.8	-	67.1	52.8	58.9	44.8	56.3

continued...

Table A.4. Seed weights (g.100^{-1} seed) continued...

Accession[a]	Seed type	Seed weight (g.100 seed^{-1}) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
119-106	Light red	63.6	46.9	66.2	56.4	61.7	42.5	56.2
119-96	Dark red	61.3	56.5	57.2	55.0	59.5	47.2	56.1
119-46	Light red	57.3	51.6	59.3	65.6	60.2	42.3	56.0
119-09	Dark red	60.3	50.6	61.3	59.1	59.9	41.5	55.4
119-54	Dark red	55.4	54.5	65.0	59.7	53.1	43.8	55.3
119-30	Non-commercial	59.0	49.9	65.2	54.3	62.5	39.9	55.1
119-95	Dark red	55.7	53.1	67.8	53.6	54.4	43.9	54.8
K97503 (Red Hawk / CELRK)[d]	Light red	-	-	-	52.9	64.6	46.6	54.7
119-53	Non-commercial	57.1	50.0	60.3	60.0	56.5	40.5	54.1
119-83	Non-commercial	55.8	52.9	60.9	56.8	54.7	42.8	54.0
119-71	Dark red	56.4	45.1	65.0	54.5	55.4	43.1	53.3
K97504 (Red Hawk / Foxfire)[d]	Light red	-	-	-	45.5	64.3	48.1	52.6
K93629 (CELRK/Chinook)[d]	Light red	-	-	53.0	52.8	58.6	44.6	52.0
119-44	Non-commercial	52.3	51.5	64.4	51.3	46.4	40.6	51.1
K93653 (Chinook / CELRK)[d]	Light red	-	-	66.4	55.4	58.7	43.5	-
Mean		61.9	58.1	64.4	59.5	63.4	47.6	
Coefficient of variation		4.4	6.1	5.8	4.7	3.3	6.7	

[a] - Accessions were arranged according to descending overall seed weight (averaged over all environments)

[b] Overall - averaged over environments

[c] - Parents of the population

[d] - Check varieties

Table A.5. Scores for appearance of processed beans from 75 RILs and the parents of Population 1, and check varieties, planted in Michigan, Minnesota and North Dakota from 1996 to 1999.

Accession[a]	Scores for appearance (APP) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-90	6.0	6.1	6.3	6.2	5.7	4.6	5.8
Redhawk[d]	5.7	-	6.6	4.9	5.3	4.6	5.4
K90122 (Lassen/Isabella/Montcalm)[d]	5.0	-	-	-	-	-	5.0
K97305 (Redhawk / Drake)[d]	-	-	-	4.6	4.8	4.8	4.8
118-97	4.4	4.6	4.3	4.0	4.8	2.6	4.1
118-60	4.2	4.7	4.0	4.4	3.8	3.2	4.0
Montcalm[c]	3.6	3.8	4.8	4.3	4.1	3.6	4.0
K94202 (SAC / I89021)[d]	3.8	-	4.2	-	-	-	4.0
118-89	4.7	3.5	4.7	4.9	3.2	2.9	4.0
K97309 (Redhawk / K93644)[d]	-	-	-	3.9	4.5	3.4	3.9
118-95	4.2	4.3	4.1	3.2	4.8	3.0	3.9
118-73	4.5	4.6	4.0	3.9	3.9	2.8	3.9
K93201 (Montcalm / 37-16)[d]	-	-	3.9	-	-	-	3.9
118-05	3.9	3.6	4.6	3.2	3.8	4.3	3.9
118-18	4.0	3.6	4.7	3.9	4.1	2.8	3.8
K86012 (Isles)[d]	3.4	-	4.4	4.1	4.2	3.1	3.8
118-66	3.2	3.2	3.7	4.6	4.7	3.5	3.8
118-13	3.3	4.3	4.2	4.2	4.1	2.8	3.8
118-93	2.8	3.9	4.5	3.8	4.1	3.8	3.8
118-09	4.6	3.5	4.7	3.3	4.4	2.2	3.8
118-82	3.5	3.3	4.5	3.9	4.6	2.9	3.8
118-41	3.5	4.8	3.6	2.9	5.1	2.4	3.7
118-21	3.9	3.6	3.5	3.9	4.0	3.3	3.7

continued...

Table A.5. Scores for appearance (APP) continued...

Accession[a]	Scores for appearance (APP) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-07	2.5	3.7	4.1	4.0	4.2	3.7	3.7
118-24	3.7	2.5	3.8	5.1	3.9	2.9	3.6
118-72	3.6	3.5	3.5	3.2	4.7	3.3	3.6
118-88	3.4	3.4	4.7	3.8	3.6	2.9	3.6
118-38	3.8	3.5	3.9	3.9	4.3	2.1	3.6
118-23	3.6	2.6	4.3	4.6	3.8	2.8	3.6
118-71	3.4	2.5	3.9	4.9	3.7	2.9	3.5
118-35	3.4	2.7	3.6	3.9	4.6	2.5	3.4
118-04	2.5	3.4	3.1	4.7	4.2	2.9	3.4
118-22	3.1	3.2	2.9	4.8	2.9	3.8	3.4
118-63	3.5	3.2	3.9	2.9	4.3	2.8	3.4
118-65	2.4	3.3	3.6	4.0	4.1	3.3	3.4
118-94	2.3	3.7	4.0	3.5	4.1	2.9	3.4
118-29	3.8	2.4	4.7	3.2	4.1	2.4	3.4
118-37	3.4	3.6	4.3	3.7	3.2	2.4	3.4
118-49	3.2	2.8	4.3	3.5	3.7	2.9	3.4
118-32	2.6	4.0	3.2	3.0	4.2	3.3	3.4
118-76	4.4	2.9	2.2	3.4	4.1	3.3	3.4
118-43	2.9	3.9	3.3	2.7	4.1	3.3	3.3
118-68	3.1	2.9	4.3	4.0	3.4	2.4	3.3
118-84	3.3	2.8	3.6	4.8	3.1	2.5	3.3
118-62	2.8	2.5	4.1	4.1	3.5	2.9	3.3
118-17	2.9	3.1	3.2	4.1	3.5	2.9	3.3

continued...

Table A.5. Scores for appearance (APP) continued...

Accession[a]	Scores for appearance (APP) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-15	3.9	3.5	3.9	2.3	3.8	2.4	3.3
118-50	3.3	3.5	3.0	3.4	3.2	3.3	3.3
118-30	2.1	3.1	3.9	3.9	3.4	3.2	3.3
118-44	2.8	3.1	4.4	3.2	4.0	2.1	3.3
118-36	2.8	3.0	3.2	3.7	3.8	3.0	3.2
118-100	2.7	3.2	3.5	3.2	4.4	2.4	3.2
118-01	3.7	2.7	3.9	2.9	3.5	2.6	3.2
118-42	3.1	2.6	3.6	3.4	4.1	2.5	3.2
118-69	2.9	3.4	3.2	3.5	3.8	2.5	3.2
118-75	3.5	2.2	3.4	3.7	4.2	2.0	3.2
118-47	2.6	2.3	3.6	3.3	3.7	3.2	3.1
118-12	3.3	2.6	3.9	3.2	3.1	2.8	3.1
118-70	3.0	2.5	3.2	4.2	3.8	1.9	3.1
118-06	3.2	3.4	2.3	3.7	3.1	3.0	3.1
118-74	2.5	1.4	3.4	5.2	4.0	2.1	3.1
118-92	2.7	3.1	2.7	2.9	4.3	2.8	3.1
118-45	2.8	3.3	3.1	3.2	3.2	2.9	3.1
118-99	3.2	2.7	3.0	3.1	3.1	3.1	3.0
118-85	2.5	2.7	3.7	3.4	3.7	2.1	3.0
118-25	2.5	2.5	4.1	3.7	2.9	2.3	3.0
118-67	2.6	2.1	3.5	3.2	4.2	2.0	2.9
118-55	1.7	2.5	3.3	3.8	2.7	3.3	2.9
118-48	2.3	2.5	3.5	2.8	3.3	2.6	2.8

continued...

Table A.5. Scores for appearance (APP) continued...

Accession[a]	Scores for appearance (APP) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-61	2.5	3.2	3.2	2.6	2.8	2.7	2.8
118-81	3.3	2.3	3.9	2.9	2.1	2.4	2.8
118-39	2.2	3.2	3.8	2.3	2.8	2.2	2.7
118-46	2.3	2.3	3.5	3.4	2.7	2.1	2.7
118-33	2.5	2.8	3.1	3.0	2.8	2.0	2.7
118-11	3.0	2.3	2.7	3.3	2.1	2.0	2.6
118-19	1.5	1.8	2.6	4.1	2.9	2.4	2.5
118-16	2.3	3.0	2.6	2.7	2.6	1.9	2.5
118-27	2.3	1.8	3.1	3.1	2.4	2.3	2.5
118-98	3.1	2.0	2.8	1.9	2.7	2.3	2.5
118-08	2.3	3.0	3.0	2.1	2.6	1.6	2.4
CDRK 82[c]	2.0	-	2.5	2.3	2.8	-	2.4
118-31	2.0	2.0	3.3	3.2	1.9	2.1	2.4
118-64	2.4	2.2	2.4	2.9	2.9	1.3	2.4
118-51	2.1	1.7	2.6	3.2	2.0	1.4	2.2
Mean	3.2	3.0	3.7	3.6	3.7	2.8	
Coefficient of variation	18.1	20.0	14.7	24.5	17.4	18.5	

[a] - Accessions were arranged according to descending overall scores for appearance (averaged over all environments)

[b]Overall - averaged over environments

[c] - Parents of the population

[d] - Check varieties

Table A.6. Scores for degree of splitting of processed beans from 75 RILs and the parents of Population 1, and check varieties planted in Michigan, Minnesota and North Dakota from 1996 to 1999.

Accession[a]	Scores for degree of splitting (SPLT) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-90	6.3	6.4	6.2	6.5	5.8	4.5	5.9
Redhawk[d]	5.3	-	6.3	4.8	5.0	4.6	5.2
K97305 (Redhawk / Drake)[d]	-	-	-	4.7	5.5	5.1	5.1
K90122 (Lassen/Isabella/Montcalm)[d]	5.0	-	-	-	-	-	5.0
K97309 (Redhawk / K93644)[d]	-	-	-	4.1	5.3	3.9	4.4
K93201 (Montcalm / 37-16)[d]	-	-	4.1	-	-	-	4.1
118-60	3.4	4.4	4.2	3.9	4.2	3.5	3.9
Montcalm[c]	3.4	3.4	4.9	4.3	3.9	3.6	3.9
K94202 (SAC / I89021)[d]	3.5	-	4.3	-	-	-	3.9
118-89	4.4	3.1	4.8	5.1	3.2	2.8	3.9
118-97	4.2	3.8	4.0	3.8	4.6	2.7	3.8
118-73	4.0	4.0	3.9	4.2	3.9	2.6	3.8
118-09	4.4	3.1	4.6	3.2	4.4	2.5	3.7
K86012 (Isles)[d]	3.5	-	4.1	4.1	3.8	3.1	3.7
118-05	4.1	2.9	4.2	2.8	4.0	4.1	3.7
118-66	3.0	3.1	3.5	4.7	4.5	3.4	3.7
118-13	3.1	3.6	4.0	4.1	4.0	3.0	3.6
118-93	2.5	3.2	4.1	3.8	4.2	4.0	3.6
118-95	3.6	3.5	3.7	3.0	4.7	3.4	3.6
118-82	2.8	2.6	4.4	3.8	4.5	3.6	3.6
118-21	3.8	3.0	3.6	3.9	3.9	3.5	3.6
118-38	3.6	3.0	3.8	4.1	4.5	2.4	3.6
118-41	3.0	4.0	3.7	2.9	5.0	2.7	3.5

continued...

Table A.6. Scores for degree of splitting (SPLT) continued...

Accession[a]	Scores for degree of splitting (SPLT) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-18	3.5	2.8	4.5	3.4	4.1	2.9	3.5
118-07	2.0	3.1	4.2	3.7	4.4	3.6	3.5
118-23	3.4	2.2	4.6	4.2	3.7	2.9	3.5
118-65	2.3	2.8	3.6	3.9	4.7	3.6	3.5
118-24	3.4	1.9	3.7	5.1	3.5	3.1	3.4
118-29	3.4	2.4	4.6	3.2	4.2	2.6	3.4
118-71	2.7	2.0	4.1	5.0	3.7	2.9	3.4
118-88	3.1	2.7	4.4	3.5	3.5	3.0	3.4
118-72	3.0	3.2	3.3	3.1	4.4	3.2	3.4
118-63	2.9	2.9	3.8	3.0	4.4	3.0	3.3
118-37	2.9	3.1	4.6	3.6	3.2	2.7	3.3
118-36	2.4	3.3	3.2	3.6	3.6	3.7	3.3
118-94	2.3	3.2	3.8	3.5	3.8	3.2	3.3
118-44	2.3	2.8	4.5	3.3	4.0	2.4	3.2
118-43	2.3	3.5	3.2	2.7	4.2	3.4	3.2
118-17	2.5	3.0	3.1	4.0	3.5	3.1	3.2
118-32	2.1	3.3	3.2	3.2	4.3	3.1	3.2
118-49	2.6	2.5	4.1	3.3	3.7	2.9	3.2
118-22	2.6	2.8	2.6	4.4	2.9	3.6	3.2
118-76	3.9	2.3	2.1	3.3	3.9	3.4	3.2
118-15	4.1	2.7	3.8	2.2	3.5	2.6	3.1
118-04	1.6	3.0	2.8	4.5	4.0	2.9	3.1
118-30	1.5	2.8	3.8	3.9	3.3	3.4	3.1

continued...

Table A.6. Scores for degree of splitting (SPLT) continued...

Accession[a]	Scores for degree of splitting (SPLT) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-01	3.9	2.4	3.7	2.9	3.4	2.5	3.1
118-62	2.4	2.0	4.0	3.8	3.5	3.1	3.1
118-68	2.8	2.5	4.0	3.8	3.2	2.4	3.1
118-69	2.5	3.3	3.2	3.3	3.6	2.7	3.1
118-50	2.6	2.8	2.9	3.4	3.5	3.4	3.1
118-42	3.2	2.2	3.6	3.1	3.6	2.7	3.1
118-84	2.5	2.4	3.3	4.6	3.1	2.4	3.1
118-75	3.2	1.8	3.5	3.8	4.0	1.9	3.0
118-74	2.4	1.4	3.4	5.1	3.7	2.1	3.0
118-35	2.6	1.9	3.4	3.5	4.1	2.4	3.0
118-06	2.8	3.2	1.9	3.3	3.1	3.6	3.0
118-45	2.7	2.7	3.1	3.0	3.3	3.0	3.0
118-85	2.2	2.2	4.0	3.6	3.5	2.2	3.0
118-92	2.2	3.0	2.6	3.0	4.0	3.0	3.0
118-100	2.2	2.4	3.2	3.2	4.3	2.4	2.9
118-70	2.7	1.7	3.1	4.3	3.8	2.0	2.9
118-47	2.3	1.8	3.5	3.1	3.4	3.5	2.9
118-99	2.8	2.3	2.8	3.0	3.0	3.1	2.8
118-67	1.8	1.8	3.6	3.1	4.2	2.3	2.8
118-81	3.0	2.0	4.0	3.1	2.1	2.6	2.8
118-25	2.0	2.0	3.7	3.7	2.8	2.6	2.8
118-12	2.5	2.1	3.8	2.7	2.8	2.6	2.7
118-39	1.6	3.0	3.8	2.2	3.2	2.6	2.7

continued...

Table A.6. Scores for degree of splitting (SPLT) continued...

Accession[a]	Scores for degree of splitting (SPLT) in each environment						
	Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
118-48	1.9	2.5	3.2	2.4	3.4	2.7	2.7
118-61	2.1	2.6	3.0	2.6	2.6	2.9	2.6
118-33	2.0	2.4	3.0	2.7	2.7	2.1	2.5
118-11	2.8	1.9	2.8	3.2	2.0	2.1	2.5
118-27	1.9	1.7	3.4	3.0	2.4	2.3	2.4
118-46	1.8	1.6	3.5	3.0	2.5	2.1	2.4
118-55	1.5	1.7	2.6	3.5	2.3	2.9	2.4
118-19	1.3	1.4	2.4	3.9	2.7	2.2	2.3
118-16	1.8	2.4	2.6	2.6	2.6	1.9	2.3
CDRK 82[c]	1.5	-	2.5	2.5	2.6	-	2.3
118-98	3.0	1.5	2.6	1.8	2.4	2.3	2.3
118-08	1.5	2.8	2.7	2.1	2.3	1.6	2.2
118-64	1.8	2.1	2.2	2.6	2.8	1.3	2.1
118-31	1.3	1.6	2.9	2.8	1.9	2.1	2.1
118-51	1.5	1.6	2.5	3.0	1.9	1.6	2.0
Mean	2.8	2.6	3.6	3.5	3.6	2.9	
Coefficient of variation	22.1	21.6	16.0	25.7	17.2	18.9	

[a] - Accessions were arranged according to descending overall scores for appearance (averaged over all environments)

[b]Overall - averaged over environments

[c] - Parents of the population

[d] - Check varieties

Table A.7. Scores for appearance of processed beans from 73 RILs and the parents of Population 2, and check varieties, planted in Michigan, Minnesota and North Dakota from 1996 to 1999.

Accession[a]	Seed Type	Scores for appearance (APP) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
119-34	Dark red	5.6	5.2	5.1	3.6	5.9	4.5	5.0
Redhawk[d]	Dark red	5.2	-	4.6	-	-	3.4	4.9
119-78	Light red	5.7	4.1	5.0	4.1	4.2	4.3	4.6
119-69	Dark red	4.2	4.8	4.7	3.8	4.6	5.5	4.6
119-106	Light red	4.7	5.5	4.4	3.9	4.3	-	4.5
119-72	Light red	4.7	4.6	4.3	3.6	5.2	4.5	4.5
119-33	Light red	4.2	4.5	5.2	3.3	5.0	4.1	4.4
119-20	Light red	4.6	3.8	4.8	4.4	4.4	3.4	4.2
119-95	Dark red	4.1	4.4	3.9	3.6	5.1	-	4.2
Montcalm[c]	Dark red	4.1	3.8	4.7	4.9	4.4	3.2	4.2
119-73	Light red	4.3	3.4	4.2	3.6	4.1	5.0	4.1
119-85	Dark red	3.6	3.4	5.1	3.3	5.0	3.8	4.0
119-77	Dark red	4.2	4.5	4.3	3.9	4.2	3.1	4.0
119-21	Light red	3.8	4.3	4.5	3.3	3.9	4.2	4.0
K93629 (CELRK/Chinook)[d]	Light red	-	-	4.9	4.4	2.6	4.1	4.0
119-61	Light red	3.6	3.9	4.8	3.6	4.3	3.4	3.9
119-67	Dark red	4.0	2.5	4.6	4.1	5.0	3.4	3.9
119-43	Light red	3.8	2.3	4.4	4.4	5.0	3.4	3.9
K93621 (CELRK/Chinook)[d]	Light red	-	-	-	4.4	3.4	-	3.9
119-49	Light red	3.9	4.1	4.1	2.4	4.3	4.4	3.8
119-14	Light red	4.2	4.0	4.1	3.4	3.8	3.6	3.8
119-86	Light red	3.5	3.7	3.5	3.4	4.4	4.1	3.8
K97504 (Redhawk / Foxfire)[d]	Light red	-	-	-	4.2	3.1	4.1	3.8

continued...

Table A.7. Scores for appearance (APP) continued...

Accession[a]	Seed Type	Scores for appearance (APP) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
K93654 (Chinook / CELRK)[d]	Light red	3.3	-	4.2	-	-	-	3.7
119-71	Dark red	3.5	3.8	3.9	3.6	3.5	4.0	3.7
CELRK[c]	Light red	3.2	2.6	5.2	2.7	3.6	4.9	3.7
119-39	Light red	3.9	3.1	4.0	3.3	4.4	3.4	3.7
119-65	Light red	4.3	3.4	3.6	4.4	3.6	2.6	3.7
119-80	Light red	3.7	3.4	3.8	3.8	3.9	3.3	3.7
119-46	Light red	3.9	3.9	4.5	2.2	4.4	3.1	3.6
119-10	Dark red	3.5	3.3	3.9	3.5	4.0	3.3	3.6
119-42	Light red	3.6	4.2	3.8	2.3	3.8	3.8	3.6
119-59	Light red	4.3	3.7	3.1	3.8	3.1	3.3	3.6
K93653 (Chinook / CELRK)[d]	Light red	-	-	3.5	3.4	3.6	4.0	3.6
119-76	Dark red	3.5	3.6	4.2	2.5	4.2	3.3	3.5
119-09	Dark red	3.2	3.1	4.3	4.0	3.2	3.3	3.5
119-96	Dark red	3.3	3.4	4.1	2.8	4.3	2.9	3.5
119-27	Dark red	3.9	2.7	4.3	3.4	3.6	2.9	3.4
119-70	Light red	3.7	3.1	3.7	2.7	4.0	3.6	3.4
119-74	Non-commercial	3.5	4.9	5.2	3.7	1.7	1.7	3.4
119-88	Light red	3.0	3.5	3.7	3.1	4.0	3.3	3.4
119-54	Dark red	3.5	3.2	4.7	2.6	3.5	2.8	3.4
119-30	Non-commercial	2.8	4.1	2.7	4.8	2.0	3.9	3.4
Isles[d]	Light red	3.9	2.8	-	-	-	-	3.3
119-104	Dark red	2.5	1.9	2.3	3.9	4.8	4.5	3.3
119-55	Dark red	3.9	2.2	3.9	2.0	4.1	3.6	3.3

continued...

Table A.7. Scores for appearance (APP) continued...

Accession[a]	Seed Type	Scores for appearance (APP) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
119-47	Non-commercial	3.2	2.4	4.3	3.4	3.7	2.8	3.3
119-48	Light red	3.1	3.2	4.0	1.9	3.1	4.1	3.2
119-75	Dark red	3.0	3.2	3.5	3.3	3.7	2.5	3.2
119-64	Light red	3.2	3.1	3.4	3.5	2.9	2.9	3.2
119-19	Light red	3.9	2.5	3.3	4.0	2.4	2.9	3.1
119-98	Dark red	2.9	3.7	3.6	1.8	2.6	4.4	3.1
119-50	Light red	3.1	3.2	3.6	3.3	2.5	3.1	3.1
119-32	Dark red	3.0	2.6	3.8	4.1	3.2	2.2	3.1
119-81	Non-commercial	3.0	2.6	3.2	3.0	3.5	3.6	3.1
119-93	Dark red	3.4	2.4	4.0	3.0	3.7	2.0	3.1
119-31	Light red	3.1	2.9	3.7	3.1	2.5	3.2	3.1
119-40	Light red	4.0	2.9	3.9	2.8	2.5	2.4	3.1
119-57	Dark red	2.9	3.0	3.8	3.2	1.9	3.4	3.0
119-02	Dark red	3.4	3.2	3.2	2.3	3.2	2.9	3.0
119-28	Dark red	3.1	3.2	2.8	3.9	2.8	2.1	3.0
K97503 (Redhawk / CELRK)[d]	Light red	-	-	-	2.8	2.9	3.1	3.0
119-35	Dark red	2.7	2.5	2.4	3.3	3.8	3.0	2.9
119-83	Non-commercial	2.9	2.7	2.3	3.4	3.3	3.1	2.9
119-38	Light red	3.1	1.8	3.7	2.1	4.1	2.7	2.9
119-89	Dark red	2.8	3.2	4.0	2.5	2.8	1.9	2.9
119-45	Dark red	2.7	2.3	2.9	3.6	3.1	2.6	2.9
119-97	Dark red	2.1	3.8	3.3	2.0	2.9	3.1	2.9
119-101	Light red	2.8	2.5	3.2	3.9	2.4	2.2	2.8

continued...

Table A.7. Scores for appearance (APP) continued...

Accession[a]	Seed Type	Scores for appearance (APP) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
Chinook[d]	Light red	2.2	-	3.4	-	-	-	2.8
119-94	Light red	2.6	2.5	3.2	1.2	2.7	4.6	2.8
119-36	Dark red	2.6	2.6	2.9	2.8	2.3	3.6	2.8
119-17	Light red	3.2	2.8	3.5	1.8	2.6	2.8	2.8
119-79	Light red	2.9	2.9	2.9	3.0	2.4	2.3	2.7
119-51	Light red	3.1	1.2	3.1	3.9	2.7	2.2	2.7
119-58	Light red	3.0	3.0	3.0	1.8	2.7	2.4	2.7
119-105	Light red	2.5	2.3	3.2	2.6	2.7	2.3	2.6
K94601 (Chinook 2000)[d]	Light red	2.2		3.7	2.6	2.2	2.1	2.5
119-53	Non-commercial	2.1	2.6	2.8	1.5	3.5	-	2.5
119-60	Non-commercial	2.5	2.0	2.1	4.0	2.2	2.0	2.5
119-01	Light red	2.3	2.9	2.3	3.0	1.6	2.5	2.4
K94515 (K89829 / K88401)[d]	Light red	2.2	2.6	-	-	-	-	2.4
119-44	Non-commercial	2.5	2.0	2.6	3.2	2.0	1.8	2.3
119-56	Non-commercial	2.3	1.8	1.7	3.7	1.7	2.0	2.2
119-03	Non-commercial	2.4	1.3	1.7	2.2	1.5	1.3	1.7
119-15	Non-commercial	2.1	1.2	1.9	2.0	1.5	1.4	1.7
Mean		3.4	3.1	3.7	3.2	3.4	3.2	
Coefficient of variation		18.4	17.3	13.7	22.3	17.7	16.6	

[a] - Accessions were arranged according to descending overall scores for appearance (averaged over all environments)

[b]Overall - averaged over environments

[c] - Parents of the population

[d] - Check varieties

Table A.8. Scores for degree of splitting of processed beans from 73 RILs and the parents of Population 2, and check varieties, planted in Michigan, Minnesota and North Dakota from 1996 to 1999.

Accession[a]	Seed Type	Scores for degree of splitting (SPLT) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
119-34	Dark red	5.2	4.5	4.8	3.5	5.7	4.7	4.8
119-78	Light red	5.4	3.9	5.3	4.1	4.0	4.6	4.6
119-72	Light red	4.0	4.4	4.7	3.7	5.3	5.0	4.5
Redhawk[d]	Dark red	4.4	-	4.6	-	-	3.6	4.5
119-106	Light red	4.0	5.5	4.7	3.7	4.3	-	4.4
119-33	Light red	3.7	4.3	5.5	3.3	4.9	4.0	4.3
K93629 (CALELRK/Chinook)[de]	Light red	-	-	5.4	4.3	2.5	4.4	4.2
119-69	Dark red	3.4	4.3	4.2	3.7	4.2	5.3	4.1
119-95	Dark red	3.4	4.4	4.0	3.6	5.0	-	4.1
119-20	Light red	4.3	3.5	4.9	4.2	4.2	3.3	4.1
119-73	Light red	4.1	3.3	4.0	3.6	4.0	4.9	4.0
119-61	Light red	4.1	3.8	4.7	3.7	4.1	3.4	4.0
Montcalm[cd]	Dark red	3.4	3.2	4.7	4.7	4.2	3.2	3.9
119-21	Light red	3.6	3.9	4.4	3.4	4.0	4.1	3.9
119-77	Dark red	3.7	4.0	4.2	3.7	4.3	3.2	3.9
K97504 (Redhawk / Foxfire)[d]	Light red	-	-	-	4.3	2.9	4.3	3.8
119-49	Light red	3.3	3.8	4.6	2.4	4.3	4.4	3.8
K93621 (CALELRK/Chinook)[de]	Light red	-	-	-	4.3	3.3	-	3.8
119-85	Dark red	3.1	3.1	4.6	3.2	4.8	3.9	3.8
119-86	Light red	3.0	3.7	3.9	3.5	4.1	4.0	3.7
119-43	Light red	3.3	2.2	4.2	4.5	4.6	3.3	3.7
119-14	Light red	3.7	3.5	4.2	3.3	4.0	3.3	3.7
119-42	Light red	3.5	3.9	3.8	2.5	3.8	4.2	3.6

continued...

Table A.8. Scores for degree of splitting (SPLT) continued...

Accession[a]	Seed Type	Scores for degree of splitting (SPLT) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
K93653 (Chinook / CELRK)[d]	Light red	-	-	3.4	3.4	3.5	4.1	3.6
119-67	Dark red	3.3	2.0	4.1	4.0	4.7	3.4	3.6
K93654 (Chinook / CELRK)[d]	Light red	2.8	-	4.4	-	-	-	3.6
119-46	Light red	3.4	3.7	4.5	2.2	4.4	3.3	3.6
119-39	Light red	3.1	2.8	3.8	3.3	4.5	3.3	3.5
119-65	Light red	3.7	3.0	3.7	4.2	3.5	2.6	3.4
119-30	Non-commercial	2.4	4.0	3.0	5.0	2.0	4.2	3.4
119-80	Light red	3.0	3.0	3.8	3.7	3.9	3.1	3.4
CELRK[cd]	Light red	2.5	2.2	5.0	2.8	3.2	4.9	3.4
119-88	Light red	2.8	3.2	3.9	3.1	4.1	3.3	3.4
119-10	Dark red	2.8	2.8	3.8	3.7	3.9	3.3	3.4
119-59	Light red	3.7	3.4	3.5	3.6	3.0	2.9	3.4
119-96	Dark red	3.2	2.9	3.9	2.9	4.1	3.0	3.3
119-70	Light red	3.1	3.1	3.6	2.7	3.9	3.6	3.3
119-71	Dark red	2.6	3.0	3.7	3.4	3.3	3.8	3.3
119-09	Dark red	2.6	2.6	4.1	4.1	2.9	3.4	3.3
119-83	Non-commercial	2.0	2.5	4.1	3.5	4.2	3.5	3.3
119-76	Dark red	2.9	3.1	4.0	2.6	3.8	3.2	3.3
119-47	Non-commercial	2.8	2.1	3.8	3.5	4.0	3.6	3.3
119-74	Non-commercial	3.0	4.5	4.5	3.8	1.7	1.7	3.2
119-54	Dark red	2.9	2.7	4.7	2.8	3.4	2.7	3.2
119-55	Dark red	3.1	2.0	3.7	2.4	3.9	4.0	3.2
119-64	Light red	2.8	3.4	3.3	3.7	2.8	2.9	3.1

continued...

Table A.8. Scores for degree of splitting (SPLT) continued...

Accession[a]	Seed Type	Scores for degree of splitting (SPLT) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
119-104	Dark red	1.7	1.3	2.4	4.2	4.6	4.7	3.1
119-27	Dark red	3.1	2.0	4.1	3.3	3.5	2.8	3.1
119-48	Light red	2.4	2.8	4.1	1.9	3.0	4.4	3.1
119-75	Dark red	2.5	2.7	3.5	3.3	3.8	2.5	3.0
119-19	Light red	3.4	2.4	3.3	3.9	2.2	2.9	3.0
K97503 (Redhawk / CELRK)[d]	Light red	-	-	-	3.0	2.7	3.1	3.0
119-81	Non-commercial	2.4	1.9	3.2	3.1	3.4	3.8	3.0
119-40	Light red	3.8	2.5	3.6	2.9	2.4	2.6	3.0
119-35	Dark red	2.0	2.4	2.9	3.3	3.8	3.3	2.9
119-50	Light red	2.4	3.0	3.6	3.2	2.4	3.0	2.9
119-57	Dark red	2.3	2.4	3.7	3.3	2.1	3.7	2.9
119-28	Dark red	2.4	3.0	3.0	3.8	2.9	2.4	2.9
119-32	Dark red	2.2	2.3	3.7	3.9	3.0	2.4	2.9
119-31	Light red	2.4	2.6	3.5	2.9	2.7	3.1	2.9
119-98	Dark red	2.0	3.2	3.5	2.0	2.3	4.1	2.9
119-93	Dark red	2.7	2.1	4.3	2.9	3.3	1.8	2.9
119-02	Dark red	2.7	2.4	3.5	2.2	3.1	2.9	2.8
119-45	Dark red	2.2	2.0	3.0	3.5	3.1	2.4	2.7
119-101	Light red	2.4	2.0	3.0	3.7	2.5	2.4	2.7
119-97	Dark red	1.5	3.2	3.3	2.1	2.6	3.1	2.7
119-17	Light red	2.4	2.4	3.8	1.9	2.4	2.9	2.6
119-89	Dark red	1.9	2.8	3.8	2.5	2.8	2.1	2.6
Isles[d]	Light red	3.1	2.2	-	-	-	-	2.6

continued...

Table A.8. Scores for degree of splitting (SPLT) continued...

Accession[a]	Seed Type	Scores for degree of splitting (SPLT) in each environment						
		Mich-1996	Minn-1996	Mich-1997	Mich-1998	Mich-1999	NDak-1999	Overall[b]
119-38	Light red	2.3	1.3	3.5	2.1	3.8	2.5	2.6
119-94	Light red	2.2	2.3	2.9	1.2	2.6	4.4	2.6
119-36	Dark red	1.9	2.2	3.0	2.8	2.2	3.4	2.6
119-51	Light red	2.4	1.2	3.4	3.7	2.8	1.9	2.6
119-58	Light red	2.2	2.9	2.9	2.0	2.8	2.5	2.5
119-79	Light red	2.2	2.8	2.7	2.8	2.5	2.1	2.5
Chinook[d]	Light red	1.6	-	3.4	-	-	-	2.5
K94601 (Chinook 2000)[d]	Light red	1.8	-	3.6	2.7	2.1	2.0	2.4
119-105	Light red	2.1	1.7	3.1	2.7	2.6	2.4	2.4
119-53	Non-commercial	1.3	2.6	2.8	1.6	3.5	-	2.3
119-60	Non-commercial	1.7	1.4	2.6	3.9	2.2	2.1	2.3
119-01	Light red	1.9	2.2	2.1	2.9	1.7	2.6	2.2
119-56	Non-commercial	1.8	1.3	2.3	4.1	1.7	1.9	2.2
119-44	Non-commercial	1.9	1.5	2.5	3.3	2.0	1.6	2.1
K94515 (K89829 / K88401)[d]	Light red	1.6	2.4	-	-	-	-	2.0
119-15	Non-commercial	1.8	1.1	2.1	2.0	1.5	1.4	1.6
119-03	Non-commercial	1.9	1.1	1.8	2.2	1.5	1.2	1.6
Mean		2.8	2.8	3.7	3.2	3.4	3.2	
Coefficient of variation		21.5	20.9	13.2	21.2	18.4	15.9	

[a] - Accessions were arranged according to descending overall scores for appearance (averaged over all environments)

[b] Overall - averaged over environments

[c] - Parents of the population

[d] - Check varieties

Table A.9. ANOVA for yield ($kg \cdot ha^{-1}$) of 2 replications of Population 1, planted in six environments in Michigan, Minnesota and North Dakota from 1996 to 1999, used to estimate heritability.

Source	Df	Expected Mean Squares	Mean Squares
Environment, G	$v-1$		41652120
Rep, R	$(r-1)\,v$		2971499
Genotype, G	$g-1$	$\sigma^2 + 1.99\,\sigma^2_{gv} + 11.95\,\sigma^2_g$	1050286
G x E	$(g-1)(v-1)$	$\sigma^2 + 1.99\,\sigma^2_{gv}$	397258
Error	$v\,(g-1)(r-1)$	σ^2	186815

Table A.10. ANOVA for seed weight ($g \cdot 100^{-1}$) of 2 replications of Population 1, planted in six environments in Michigan, Minnesota and North Dakota from 1996 to 1999, used to estimate heritability.

Source	Df	Expected Mean Squares	Mean Squares
Environment, V	$v-1$		6650.8
Rep, R	$(r-1)\,v$		74.5
Genotype, G	$g-1$	$\sigma^2 + 1.99\,\sigma^2_{gv} + 11.95\,\sigma^2_g$	83.6
G x E	$(g-1)(v-1)$	$\sigma^2 + 1.99\,\sigma^2_{gv}$	35.3
Error	$v\,(g-1)(r-1)$	σ^2	10.3

Table A.11. ANOVA for yield ($kg \cdot ha^{-1}$) of 2 replications of Population 2, planted in six environments in Michigan, Minnesota and North Dakota from 1996 to 1999, used to estimate heritability.

Source	Df	Expected Mean Squares	Mean Squares
Environment, V	$v-1$		74795711
Rep, R	$(r-1)\,v$		2806308
Genotype, G	$g-1$	$\sigma^2 + 2.00\,\sigma^2_{gv} + 11.98\,\sigma^2_g$	1085626
G x E	$(g-1)(v-1)$	$\sigma^2 + 2.00\,\sigma^2_{gv}$	407105
Error	$v\,(g-1)(r-1)$	σ^2	183115

Table A.12. ANOVA for seed weight ($g \cdot 100^{-1}$) of 2 replications of Population 2, planted in six environments in Michigan, Minnesota and North Dakota from 1996 to 1999, used to estimate heritability.

Source	Df	Expected Mean Squares	Mean Squares
Environment, V	$v-1$		5482.2
Rep, R	$(r-1)\,v$		81.9
Genotype, G	$g-1$	$\sigma^2 + 2.00\,\sigma^2_{gv} + 11.98\,\sigma^2_g$	111.7
G x E	$(g-1)(v-1)$	$\sigma^2 + 2.00\,\sigma^2_{gv}$	34.1
Error	$v\,(g-1)(r-1)$	σ^2	9.6

Table A.13. ANOVA for scores on appearance (APP) of processed beans of 2 replications of Population 1, planted in six environments in Michigan, Minnesota and North Dakota from 1996 to 1999, used to estimate heritability.

Source	Df	Expected Mean Squares	Mean Squares
Environment, V	$v-1$		22.4907248
Rep, R	$(r-1)\,v$		1.9878034
Genotype, G	$g-1$	$\sigma^2 + 1.96\,\sigma^2_{gv} + 11.75\,\sigma^2_g$	3.4476766
G x E	$(g-1)(v-1)$	$\sigma^2 + 1.97\,\sigma^2_{gv}$	0.5986469
Error	$v\,(g-1)(r-1)$	σ^2	0.4029635

Table A.14. ANOVA for scores on degree of splitting (SPLT) of processed beans of 2 replications of Population 1, planted in six environments in Michigan, Minnesota and North Dakota from 1996 to 1999, used to estimate heritability.

Source	Df	Expected Mean Squares	Mean Squares
Environment, V	$v-1$		29.8749153
Rep, R	$(r-1)\,v$		3.8871539
Genotype, G	$g-1$	$\sigma^2 + 1.96\,\sigma^2_{gv} + 11.75\,\sigma^2_g$	3.8115691
G x E	$(g-1)(v-1)$	$\sigma^2 + 1.97\,\sigma^2_{gv}$	0.6354538
Error	$v\,(g-1)(r-1)$	σ^2	0.4188847

Table A.15. ANOVA for scores on appearance (APP) of processed beans of 2 replications of Population 2, planted in six environments in Michigan, Minnesota and North Dakota from 1996 to 1999, used to estimate heritability.

Source	Df	Expected Mean Squares	Mean Squares
Environment, V	$v-1$		5.7590902
Rep, R	$(r-1)\,v$		2.1265000
Genotype, G	$g-1$	$\sigma^2 + 1.96\,\sigma^2_{gv} + 11.70\,\sigma^2_g$	4.9363941
G x E	$(g-1)(v-1)$	$\sigma^2 + 1.98\,\sigma^2_{gv}$	0.7669883
Error	$v\,(g-1)(r-1)$	σ^2	0.3543357

Table A.16. ANOVA for scores on degree of splitting (SPLT) of processed beans of 2 replications of Population 2, planted in six year-location combinations in Michigan, Minnesota and North Dakota from 1996 to 1999, used to estimate heritability.

Source	Df	Expected Mean Squares	Mean Squares
Environment, V	$v-1$		16.8613975
Rep, R	$(r-1)\,v$		1.6999876
Genotype, G	$g-1$	$\sigma^2 + 1.96\,\sigma^2_{gv} + 11.70\,\sigma^2_g$	4.9774993
G x E	$(g-1)(v-1)$	$\sigma^2 + 1.98\,\sigma^2_{gv}$	0.7503643
Error	$v\,(g-1)(r-1)$	σ^2	0.3404407

LITERATURE CITED

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ADAM-BLONDON, A.F., M. Sevignac, and M. Dron. 1994. A genetic map of common bean to localize specific resistance genes against anthracnose. *Genome.* 37: 915-924.

ADAMS, M.W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean, *Phaseolus vulgaris*. *Crop Sci.* 7(5): 505-510.

ADAMS, M.W. and C.L. Bedford. 1975. Breeding food legumes for improved processing and consumer acceptance properties. In: M. Milner (ed.). Nutritional Improvement of Food Legumes by Breeding. John Wiley and Sons, N.Y. pp. 299-304.

ALLARD, R.W. and A.D. Bradshaw. 1964. Implications of genotype-environmental interactions in applied plant breeding. *Crop Sci.* 4: 503-508.

AL-MUKHTAR, F.A. and D.P. Coyne. 1981. Inheritance and association of flower, ovule, seed, pod, and maturity characters in dry edible beans (*Phaseolus vulgaris* L.). *J. Amer. Soc. Hort. Sci.* 106 (6): 713-719.

BAI, Y., T.E. Michaels and K.P. Pauls. 1996. Identification of RAPD markers linked to bacterial blight resistance genes in *Phaseolus vulgaris* L. *Ann. Rep. Bean Improvement Cooperative.* 39: 164-165.

BEAVER, J.S., C.V. Paniagua, D.P. Coyne, and G.F. Freytag. 1985. Yield stability of dry bean genotypes in the Dominican Republic. *Crop Sci.* 25(6): 923-926.

BEEBE, S.E., I. Ochoa, P. Skroch, J. Nienhuis and J. Tivang. 1995. Genetic diversity among common bean breeding lines developed for Central America. *Crop Sci.* 35: 1178-1183.

BOROJEVIC, S. and W.A. Williams. 1982. Genotype x environment interactions for leaf area parameters and yield components and their effects on wheat yields. *Crop Sci.* 22: 1020- 1025.

BOTSTEIN, D., R.L. White, M. Skolnick and R.W. Davis. Construction of a genetic linkage map in man using restriction fragment length polymorphisms. *Am. J. Hum. Genet.* 32: 314-. as cited by M.D. Burow and T.K. Blake. 1998. Molecular tools for the study of complex traits. In: Molecular dissection of complex traits. A.H. Paterson (ed.). New York: CRC Press. pp. 13-29.

BUROW, M.D. and T.K. Blake. 1998. Molecular tools for the study of complex traits. In: Molecular dissection of complex traits. A.H. Paterson (ed.). New York: CRC Press. pp. 13-29.

CATELL, R.B. 1965a. Factor analysis: An introduction to essentials. I. The purpose and underlying models. *Biometrics*. 21: 190-215. as cited by G.L. Hosfield, A. Ghaderi and M.A. Uebersax. 1984. A factor analysis of yield and sensory and physico-chemical data from tests used to measure culinary quality in dry edible beans. *Can. J. Plant Sci.* 64: 285-293.

CATELL, R.B. 1965b. Factor analysis: An introduction to essentials. II. The role of factor analysis in research. *Biometrics*. 21: 405-435. as cited by G.L. Hosfield, A. Ghaderi and M.A. Uebersax. 1984. A factor analysis of yield and sensory and physico-chemical data from tests used to measure culinary quality in dry edible beans. *Can. J. Plant Sci.* 64: 285-293.

CHAGUÉ, V., J.C. Mercier, M. Guénard, A. de Courcel and F. Vedel. 1997. Identification of RAPD markers linked to a locus involved in quantitative resistance to TYLCV in tomato by bulked segregant analysis. *Theor. Appl. Genet.* 95: 671-677.

CHALMERS, K.J., U.M. Barua, C.A. Hackett, W.T.B. Thomas, R. Waugh and W. Powell. 1993. Identification of RAPD markers linked to genetic factors controlling the milling energy requirement of barley. *Theor. Appl. Genet.* 87(3): 314-420.

CHENG, F.S., N.F. Weeden and S.K. Brown. 1996. Identification of co-dominant RAPD markers tightly linked to fruit skin color in apple. *Theor. Appl. Genet.* 93: 222-227.

COCHRAN, W.G. and G.M. Cox. 1968 Experimental Designs. 2nd. Edition. New York: John Wiley & Sons, Inc. 611 p.

COPELAND, L.O., and M.H. Erdmann. 1977. Montcalm and Mecosta: Halo blight tolerant kidney bean varieties for Michigan. *MSU Cooperative Extension Service Bull. 957 No. 81.*

COYNE, D.P. 1968. Correlation, heritability and selection of yield components in field beans, *Phaseolus vulgaris* L. *Proc. Am. Soc. Hortic. Sci.* 93: 388-396.

DARVASI, A. and M. Soller. 1994. Selective DNA pooling for determination of linkage between a molecular marker and a quantitative trait locus. *Genetics*. 138: 1365-1373.

DESHPANDE, S.S., S.K. Sathe and D.K. Salunkhe. 1984. Dry beans of *Phaseolus*: A review. Part 3. Processing. *CRC Crit. Rev. Food Science and Nutrition.* 21 (2): 137-195.

DOGANLAR, S., S.D. Tanksley and M.A. Mutschler. 2000. Identification and molecular mapping of loci controlling fruit ripening time in tomato. *Theor. Appl. Genet.* 100(2): 249-255.

DRAKE, S.R. and B.K. Kinman. 1984. Canned dry bean quality as influenced by high temperature short time (HTST) steam blanching. *J. Food Science.* 49(5): 1318-1320.

DUDLEY, J.V. 1993. Molecular markers in plant improvement: manipulation of genes affecting quantitative traits. *Crop Sci.* 33: 660-668.

EATHINGTON, S.R., J.W. Dudley and G.K. Rufener II. 1997. Usefulness of marker-QTL associations in early generation selection. *Crop Sci.* 37: 1686-1693.

EDWARDS, K., C. Johnstone, and C. Thompson. 1991. A simple and rapid method for the preparation of plant genomic DNA for PCR analysis. *Nuc. Acids Res.* 19(6):1349.

ELIA, F.M., G.L. Hosfield, J.D. Kelly and M.A. Uebersax. 1997. Genetic analysis and interrelationships between traits for cooking time, water absorption, and protein and tannin content of Andean dry beans. *J. Amer. Soc. Hort. Sci.* 122 (4): 512-518.

FEHR, W.R. 1987. Principles of Cultivar Development. Vol. 1: Theory and Technique. New York: Macmillan Publishing Company. 536 p.

FORNEY, A.K., D.E. Halseth and W.C. Kelly. 1990. Quality of canned "Ruddy" kidney beans as influenced by planting date, harvest time and length of storage before canning. *J. Amer. Soc. Hort. Sci.* 115(6): 1051-1054.

FRANCO, M.C., S.T.A. Cassini, F.C. Montrazzi, S.M. Tsai and C. Vieira. 1998. RAPD analysis of common bean (*Phaseolus vulgaris* L.) cultivars and evaluation of common bacterial blight (CBB) and wild fire (WF) resistance. *Ann. Rep. Bean Improvement Cooperative.* 41: 143-144.

FREEMAN, G.H. 1973. Statistical methods for the analysis of genotype-environment interactions. *Heredity.* 31: 339-354.

FREYRE, R., P.W. Skroch, V. Geffroy, A.-F. Adam-Blondon, A. Shirmohamadali, W.C. Johnson, V. Llaca, R.O. Nodari, P.A. Pereira, S.-M. Tsai, J. Tohme, M. Dron, J. Nienhuis, C.E. Vallejos and P. Gepts. 1998. Towards an integrated linkage map

of common bean. 4. Development of a core linkage map and alignment of RFLP maps. *Thero. Appl. Genet.* 97:847-856.

GABRIEL, O. 1971. Locating enzymes on gels. *Methods in Enzymology.* 22: 578- . as cited by M.D. Burow and T.K. Blake. Molecular tools for the study of complex traits. In: Molecular dissection of complex traits. A.H. Paterson (ed.). New York: CRC Press. pp. 13-29.

GHADERI, A., G. Varner and W. Adams. 1980. Adaptability of dry bean classes and varieties to Michigan. *Mich. Dry Bean Digest.* 5(3): 12-14.

GHADERI, A., M.W. Adams and A.W. Saettler. 1982. Environmental response patterns in commercial classes of common bean (*Phaseolus vulgaris* L.). *Theor. Appl. Genet.* 63: 17-22.

GHADERI, A., G.L. Hosfield, M.S. 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.

GONZALES, A.R., K.M. Edwards, and D.B. Marx. 1982. Storage and processing quality of beans (*Phaseolus vulgaris* L.) harvested at the semi-dry stage. *J. Amer. Soc. Hort. Sci.* 107 (1): 82-86.

GOTTLIEB, L.D. 1982. Conservation and duplication of isozymes in plants. *Science.* 216: 373-380.

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.

HAWTIN, G.C., K.O. Rachie and J.M. Green. 1977. Breeding strategy for the nutritional improvement of pulses. In: Nutritional Standards and Methods of Evaluation for Food Legume Breeders. J.H. Hulse, K.O. Rachie and L.W. Billingsley (eds.) Ottawa: IDRC. 100 p.

HEIL, J.R., M.J. McCarthy and M. Özilgen. 1992. Parameters for predicting canning quality of dry kidney beans. *J. Sci. Food Agric.* 60(4): 519-523.

HELENTJARIS, T., T.M. Slocum, S. Wright, A. Schaefer and J. Nienhuis. 1986. Construction of genetic linkage maps in maize and tomato using restriction fragment length polymorphisms. *Theor. Appl. Genet.* 72: 761-769.

HELLER, R., J. Schondelmaier, G. Steinrücken and C. Jung. 1996. Genetic localization of four genes for nematode (*Heterodera schachtii* Schm.) resistance in sugar beet (*Beta vulgaris* L.). *Theor. Appl. Genet.* 92(8): 991-997.

HILL, J. 1975. Genotype-environment interactions – a challenge for plant breeding. *J. Agric. Sci., Camb.* 85: 477-493.

HOFF, J.E. and P.E. Nelson. 1965. An investigation of accelerated water-uptake in dry pea beans. *Res. Prog. Rept. 211.* Agric. Expt. Station. Purdue University, West Lafayette, Indiana.

HOSFIELD, G.L. 1991. Genetic control of production and food quality factors in dry bean. *Food Technology.* 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. Culinary quality in dry bean: can it be improved?. *Ann. Rep. Bean Improvement Cooperative.* 33: 17-18.

HOSFIELD, G.L., A. Ghaderi and M.A. Uebersax. 1984a. A factor analysis of yield and sensory and physico-chemical data from tests used to measure culinary quality in dry edible beans. *Can. J. Plant Sci.* 64: 285-293.

HOSFIELD, G.L., M.A. Uebersax and T.G. Isleib. 1984b. Seasonal and genotypic effects on yield and physico-chemical seed characteristics related to food quality in dry, edible beans. *J. Am. Soc. Hort. Sci.* 109:182-189.

HOSFIELD, G.L., J.D. Kelly, M.J. Silbernagel, J.R. Stavely, M.W. Adams, M.A. Uebersax and G.V. Varner. 1995. Eight small-red dry bean germplasm lines with upright architecture, narrow profile, and short vine growth habit. *HortScience.* 30(7): 1479-1482.

JOHNSON, E., P.N. Miklas and J.R. Stavely. 1994. The potential of coupling and repulsion phase RAPD markers for indirect selection of rust resistant progeny in common bean. *Ann. Rep Bean Improvement Cooperative.* 37: 81-82.

JUNEK, J.J., W.A. Sistrunk and M.B. Neely. 1980. Influence of processing methodology on quality attributes of canned dry beans. *J. Food Sci.* 45:821-824. as cited by W. Lu and K.C. Chang. 1996. Correlations between chemical composition and canning quality attributes of navy bean (*Phaseolus vulgaris* L.). *Cereal Chemistry.* 73 (6): 785-787.

JUNG, G., D.P. Coyne, P.W. Skroch, J. Nienhuis, E. Arnaud-Santana, J. Bokosi, H.M. Ariyarathne, J.R. Steadman, J.S. Beaver and S.M. Kaeppler. 1996. Molecular markers associated with plant architecture and resistance to common blight, web blight, and rust in common beans. *J. Amer. Soc. Hort. Sci.* 121(5): 794-803.

KAYS, S.J., J.W. Williams and D.R. Davis. 1980. Harvest of dry beans in the pre-dry stage of development: effect on yield and processed quality product. *J. Amer. Soc. Hort. Sci.* 105 (1): 15-17.

KELLY, J.D. and P.N. Miklas. 1998. The role of RAPD markers in breeding for disease resistance in common bean. *Molecular Breeding.* 4: 1-11.

KELLY, J.D. and P.N. Miklas. 1999. Marker-assisted selection. In: Common bean improvement in the twenty-first century. vol. 7: Developments in plant breeding. S.P. Singh (ed.). London: Kluwer Academic Publishers. pp. 93-123.

KELLY, J.D., J.M. Kolkman and K. Schneider. 1998. Breeding for yield in dry bean (*Phaseolus vulgaris* L.). *Euphytica.* 102: 343-356.

KELLY, J.D., K.A. Scheiner and J.M. Kolkman. 1999. Breeding to improve yield. In: Common bean improvement in the twenty-first century. S.P. Singh (Ed.). Kluwer Academic Publishers, Netherlands. pp. 185-222.

KENNARD, W.C., K. Poetter, A. Dijkhuizen, V. Meglic, J. Staub and M. Harvey. 1994. Linkages among RFLP, RAPD, isozyme, disease resistance, and morphological markers in narrow and wide crosses of cucumber. *Theor. Appl. Genet.* 89:42-48. as cited by J.E. Staub and F.C. Serquen. 1995. Genetic markers, map construction and their application in plant breeding. *HortScience.* 31 (5): 729-740.

KIM, J. 1975. Factor analysis. In SPSS: Statistical package for the social sciences. New York: McGraw-Hill, Inc. pp. 468-514. as cited by G.L. Hosfield, A. Ghaderi and M.A. Uebersax. 1984. A factor analysis of yield and sensory and physico-chemical data from tests used to measure culinary quality in dry edible beans. *Can. J. Plant Sci.* 64: 285-293.

KNAPP, S.J., W.W. Stroup, and W.M. Ross. Exact confidence intervals for heritability on a progeny mean basis. *Crop Sci.* 25: 192-194.

KNAPP, S.J. 1998. Marker-assisted selection as a strategy for increasing the probability of selecting superior genotypes. *Crop Sci.* 38: 1164-1174.

KON, S. and D. W. Sanshuck. 1981. Phytate content and its effect on cooking quality of beans. *J. Food Processing and Preservation.* 5(3): 169-178.

LANDER, E.S. and D. Botstein. 1989. Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. *Genetics.* 121: 185-199.

LEAKEY, C.L.A. 1988. Genotypic and phenotypic markers in common bean. In: P. Gepts (ed.). Genetic Resources of *Phaseolus* beans. Kluwer Academic Publishers, Boston. p. 245-327.

LU, W. and K.C. Chang. 1996. Correlations between chemical composition and canning quality attributes of navy bean (*Phaseolus vulgaris* L.). *Cereal Chemistry.* 73 (6): 785-787.

LU, W., K.C. Chang, K.F. Grafton and P.B. Schwarz. 1996. Correlations between physical properties and canning quality attributes of navy bean (*Phaseolus vulgaris* L.). *Cereal Chemistry.* 73(6): 788-790.

McCLEAN, P., J. Ewing, M. Lince and K. Grafton. 1994. Development of a RAPD map of *Phaseolus vulgaris* L. *Ann. Rep. Bean Improvement Cooperative.* 37: 79-80.

MEINERS, C.R., N.L. Derise, H.C. Lau, S.J. Ritchey and E.W. Murphy. 1976. Proximate composition and yield of raw and cooked mature dry legumes. *J. Agric. Food Chem.* 24:1122. as cited by S.K. Sathe, S.S. Despande and D.K. Salunkhe. 1984. Dry beans of *Phaseolus*: A review. Part 1. Chemical composition: proteins. *CRC Crit. Rev. Food Sci. Nutr.* 20: 1-46.

MELOTTO, M., R.A. Young and J.D. Kelly. 1998. Marker-assisted dissection of genes conditioning resistance to anthracnose. *Ann. Rep. Bean Improvement Cooperative.* 41: 9-10.

MICHELMORE, R.W., I. Paran and R.V. Kesseli. 1991. Identification of markers linked to disease-resistance genes by bulked segregant analysis: a rapid method to detect markers in specific genomic regions by using segregating populations. *Proc. Natl. Acad. Sci. USA.* 88: 9828-9832.

MIKLAS, P. and J. Kelly. 1992. Identifying bean DNA polymorphisms using the polymerase chain reaction. *Ann. Rep. Bean Improvement Cooperative.* 35: 21-22.

MIKLAS, P., E. Johnson, and J. Beaver. 1995. RAPD markers for QTLs expressing BGMV resistance in dry bean. *Ann. Rep. Bean Improvement Cooperative.* 38: 111-112.

MIKLAS, P., E. Johnson, V. Stone, J.S. Beaver, C. Montoya and M. Zapata. 1996. Selective mapping of QTL conditioning disease resistance in common bean. *Crop Sci.* 36: 1344-1351.

MIKLAS, P.N., R. Delorme, V. Stone, C.A. Urrea, J.S. Beaver and J.R. Steadman. 1998. A RAPD map of disease resistance traits in common bean. *Ann. Rep. Bean Improvement Cooperative.* 41:93-94.

MIKLAS, P.N., V. Stone, C.A. Urrea, E. Johnson and J.S. Beaver. 1998. Inheritance and QTL analysis of field resistance to ashy stem blight in common bean. *Crop Sci.* 38: 916-921.

NIENHUIS, J. and S.P. Singh. 1985. Combining ability analyses and relationships among yield, yield components and architectural traits in dry bean. *Crop Sci.* 26 (1): 21-27.

NIENHUIS, J. and S.P. Singh. 1988. Genetics of seed yield and its components in common bean (*Phaseolus vulgaris* L.) of Middle-American origin, I. Genetic variance, heritability and expected response from selection. *Plant Breeding.* 101: 155-163.

NODARI, R.O., S.M. Tsai, R.L. Gilbertson, and P. Gepts. 1993. Towards an integrated linkage map of common bean. 2. Development of an RFLP-based linkage map. *Theor. Appl. Genet.* 85: 513-520.

NORDSTROM, C.L. and W.A. Sistrunk. 1977. Effect of type of bean, soak time, canning media, and storage time on quality attributes and nutritional value of canned dry beans. *J. Food Sci.* 42: 797–800.

NORDSTROM, C.L. and W.A. Sistrunk. 1979. Effect of type of bean, moisture level, blanch treatment and storage time on quality attributes and nutrients of canned dry beans. *J. Food Sci.* 44: 392-395. as cited by W. Lu and K.C. Chang. 1996. Correlations between chemical composition and canning quality attributes of navy bean (*Phaseolus vulgaris* L.). *Cereal Chemistry.* 73 (6): 785-787.

OGWAL, M.O. and D.R. Davis. 1994. Rapid rehydration methods for dried beans. *J. Food Science.* 59(3):611-612, 654.

OLAYA, G., G.S. Abawi and N.F. Weeden. 1996. Inheritance of the resistance to *Macrophomina phaseolina* and identification of RAPD markers linked to resistance genes in beans. *Phytopathology.* 86(6): 674-679.

OSBORN, T.C., D.C. Alexander and J.F. Fobes. 1987. Identification of restriction fragment length polymorphisms linked to genes controlling soluble solids content in tomato. *Theor. Appl. Genet.* 73: 350-356.

PARAN, I., R. Kesseli and R. Michelmore. 1991. Identification of RFLP and RAPD markers linked to downy mildew resistance genes in lettuce using near-isogenic lines. *Genome.* 34: 1021-1027. as cited by J.E. Staub and F.C. Serquen. 1995. Genetic markers, map construction and their application in plant breeding. *HortScience.* 31 (5): 729-740.

PARK, S.O., D.P. Coyne, G. Jung, E. Arnaud-Santana and H. Ariyarathne. 1998. Detection and mapping of RAPD markers associated with QTL affecting seed size and shape in common bean. *Ann. Rep. Bean Improvement Cooperative.* 41: 147-148.

PATERSON, A.H. 1995. Molecular dissection of quantitative traits: progress and prospects. *Genome Research.* 5: 321-333.

PATERSON, A.H. 1998. Of blending, beans, and bristles: The foundations of QTL mapping. In: Molecular dissection of complex traits. A.H. Paterson (ed.). New York: CRC Press. pp. 1-10.

QUAST, D.G. and S.D. da Silva. 1977. Temperature dependence of hydration rate and effect of hydration on the cooking rate of dry legumes. *J. Food Sci.* 42: 1299-1303.

RANALLI, P., G. Ruaro and P. Del Re. 1991. Response to selection for seed yield in bean (*Phaseolus vulgaris*). *Euphytica.* 57 (2): 117-123.

RIBAUT, J-M. and D. Hoisington. 1998. Marker-assisted selection: new tools and strategies. *Trends in Plant Science.* 3 (6): 236-239.

RUENGSAKULRACH, S., N. Srisuma, M.A. Uebersax, G.L. Hosfield and L.G. Occeña. Early generation screening of navy bean breeding lines by canning quality assessment and pasting characteristics of bean flour. *J. Food Quality.* 17: 321-333.

SARAFI, A. 1978. A yield-component selection experiment involving American and Iranian cultivars of the common bean. *Crop Sci.* 18 (1): 5-7.

SATHE, S.K., S.S. Despande and D.K. Salunkhe. 1984. Dry beans of *Phaseolus*: A review. Part 1. Chemical composition: proteins. *CRC Crit. Rev. Food Sci. Nutr.* 20: 1-46.

SAX, K. 1923. The association of size differences with seed coat pattern and pigmentation in *Phaseolus vulgaris*. *Genetics.* 8: 552-560.

SCHABENBERGER, O. 1997. Statistics for Biologists I. Course pack for STS/CSS 464, Section I: for Crop and Soil Sciences Majors. Fall Semester 1997. Michigan State University, East Lansing, MI.

SCULLY, B.T., D.H. Wallace and D.R. Viands. 1991. Heritability and correlation of biomass, growth rates, harvest index, and phenology to the yield of common beans. *J. Amer. Soc. Hort.Sci.* 116 (1): 127.130.

SHELLIE-DESSERT, K.C. and F.A. Bliss. 1991. Genetic improvement of food quality factors. In: Common beans: Research for crop improvement. A.van Schoonhoven and O. Voysest (eds.). CIAT: CAP International. pp. 649-677.

SIMMONDS, N.W. 1979. Principles of crop improvement. New York: Longman, Inc. 408 pp.

SINGH, S.P., H. Teran, A. Molina and J.A. Gutierrez. 1991. Genetics of seed yield and its components in common beans (*Phaseolus vulgaris* L.) of Andean origin. *Plant Breeding*. 107 (3): 254-257.

SINGH, S.P. and C.A. Urrea. 1995. Inter- and intraracial hybridization and selection for seed yield in early generations of common bean, *Phaseolus vulgaris* L. *Euphytica*. 81 (2) 131-137.

SKROCH, P.W., J.B. dos Santos and J. Nienhuis. 1992. Genetic relationships among *Phaseolus vulgaris* genotypes based on RAPD marker data. *Ann. Rep. Bean Improvement Cooperative*. 35: 23-24.

SKROCH, P., G. Jung, J. Nienhuis and D. Coyne. 1996. Integration of RAPD marker linkage maps and comparative mapping of QTL for disease resistance in common bean. *Ann. Rep. Bean Improvement Cooperative*. 39: 48-49.

STAUB, J.E., F.C. Serquen and M. Gupta. 1996. Genetic markers, map construction and their application in plant breeding. *HortScience*. 31(5): 729-740.

STUBER, C.W. and M.D. Edwards. 1986. Genotypic selection for improvement of quantitative traits in corn using molecular marker loci. 1986. *Proc. 41st Annual Corn and Sorghum Research Conf., Am. Seed Trade Assoc.* 41: 40-83. as cited by J.V. Dudley. Molecular markers in plant improvement: manipulation of genes affecting quantitative traits. *Crop Sci.* 33: 660-668.

TANHUANPÄÄ, P.K., J.P. Vilkki and H.J. Vilkki. 1996. Mapping of a QTL for oleic acid concentration in spring turnip rape (*Brassica rapa* ssp. *oleifera*). *Theor. Appl. Genet.* 92(8): 952-956.

TANKSLEY, S.D. and J.C. Nelson. 1996. Advanced backcross QTL: a method for the simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines. *Theor. App. Genet* 92: 899-909.

TIMMERMAN, G.M., T.J. Frew, N.F. Weeden, A.L. Miller and D.S. Goulden. 1994. Linkage analysis of *er-1*, a recessive *Pisum sativum* gene for resistance to powdery mildew fungus (*Erysiphe pisi* D.C.). *Theor. Appl. Genet.* 88: 1050-1055. as cited by J.E. Staub and F.C. Serquen. 1995. Genetic markers, map construction and their application in plant breeding. *HortScience*. 31 (5): 729-740.

UEBERSAX, M.A. 1972. Effects of storage and processing parameters on quality attributes of processed navy beans. M.S. Thesis, Michigan State University.

UEBERSAX, M.A. and C.L. Bedford. 1980. Navy bean processing: effect of storage and soaking methods on quality of canned beans. *Mich. State Univ. Agr. Expt. Sta., E. Lansing Res. Rpt.* 410.

UEBERSAX, M.A. 1985. Quality aspects of moisture, soaking and blanching in dry bean processing. In: Proc. of Tech. Conf. on Dry Bean Research. San Francisco, February 13, Food Processors Institute, Washington D.C. p. 7. as cited by K.L. Wiese and E.R. Jackson. 1993. Changes in thermal process time (B_b) for baked beans based on water hardness and fill temperature. *J. Food Protection*. 56(7): 608-611.

UEBERSAX, M.A., S. Ruengsakulrach and L.G. Occena. 1991. Strategies for processing dry beans. *Food Technol.* 45:104. as cited by M.O. Ogwal and D.R. Davis. 1994. Rapid rehydration methods for dried beans. *J. Food Science*. 59(3): 611-612, 654.

USDA (United States Department of Agriculture). 1982. The United States standards for beans. Federal Grain Inspection Service. U.S. Department of Agriculture. 16 p. as cited by O. Voysest and M. Dessert. 1991. *Bean cultivars: Classes and commercial seed types*. In: Common beans: Research for crop improvement. A. van Schoonhoven and O. Voysest (eds.). CAB International: CIAT. pp.119-162.

USDA-NASS (United States Department of Agriculture – National Agricultural Statistics Service). 2000. Agricultural statistics 2000. U.S. Government Printing Office, Washington. at http://www.usda.gov/nass/pubs/agstats.htm.

USDA-NASS (United States Department of Agriculture – National Agricultural Statistics Service) and Michigan Department of Agriculture. 2000. Michigan Agricultural Statistics 1998-1999. at http://www.mda.state.mi.us/mass/stats00/Crops00.htm.

USDA-NASS (United States Department of Agriculture – National Agricultural Statistics Service) and Minnesota Department of Agriculture. 2000. Minnesota Agricultural Statistics 2000. at http://www.nass.usda.gov/mn.

USDA-NASS (United States Department of Agriculture – National Agricultural Statistics Service) and North Dakota Department of Agriculture. 2000. North Dakota Agricultural Statistics 2000. at http://www.nass.usda.gov/nd.

VAN BUREN, J., M. Bourne, D. Downing, D. Queale, E. Chase and S. Comstock. 1986. Processing factors influencing splitting and other quality characteristics of canned kidney beans. *J. Food Science*. 51(5): 1228-1230.

WALTERS, K.J. 1995. Identification of RAPD markers associated with canning quality in navy beans. M.S. thesis. Michigan State University.

WALTERS, K.J., G.L. Hosfield, M.A. Uebersax and J.D. Kelly. 1997. Navy bean canning quality: correlations, heritability estimates, and randomly amplified polymorphic DNA markers associated with component traits. *J. Amer. Soc. Hort. Sci.* 122(3): 338 - 343.

WANG, C.C.R. and S.K.C. Chang. 1988. Effect of selected canning methods on trypsin inhibitor activity, sterilization value, and firmness of canned beans. *J. Agric. Food Chem.* 36: 1015-1018.

WANG, C.R., K.C. Chang and K. Grafton. 1988. Canning quality evaluation of pinto and navy beans. *J. Food Science.* 53 (3): 772-776.

WANG, G.L. and A.H. Paterson. 1994. Assessment of DNA pooling strategies for mapping of QTLs. *Theor. Appl. Genet.* 88: 355-361.

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.

WEEDEN, N.F., M. Timmerman, M. Hermmat, B.E. Kneen and M.S. Lodhi. 1992. Inheritance and repeatability of RAPD markers. In: J. Nienhuis (ed.). Proc. Symp. Applications of RAPD Technology in Plant Breeding, 12-17. Nov. 1992. Minneapolis, MN. as cited by J.E. Staub and F.C. Serquen. 1995. Genetic markers, map construction and their application in plant breeding. *HortScience.* 31 (5): 729-740.

WELSH, W., W. Bushuk, W. Roca and S.P. Singh. 1995. Characterization of agronomic traits and markers of recombinant inbred lines from intra- and interracial populations of *Phaseolus vulgaris* L. *Theor. Appl. Genet.* 91 (1) 169-177.

WIESE, K.L. and E.R. Jackson. 1993. Changes in thermal process time (B_b) for baked beans based on water hardness and fill temperature. *J. Food Protection.* 56(7): 608-611.

WILLIAMS, J.G.K., A.R. Kubelik, K.J. Livak, J.A. Rafalski and S.V. Tingey. 1990. DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. *Nucleic Acids Research.* 18 (22): 6531-6535.

WYCH, R.D., R.L. McGraw, and D.D. Stuthman. Genotype x year interaction for length and rate of grain filling in oats. *Crop Sci.* 22: 1025-1028.

XIAO, J., J. Li, S. Grandillo, S.N. Ahn, L. Yuan, S.D. Tankley and S.R. McCouch. 1998. Identification of trait-improving quantitative trait loci alleles from a wild rice relative, *Oryza rufipogon*. *Genetics*. 150: 899-909.

YAN, W. and D.H. Wallace. 1995. Breeding for negatively associated traits. *Plant Breeding Reviews*. 13: 141-177.

YOUNG, R.A. and J.D. Kelly. 1996. Gene pyramiding using marker assisted selection for stable resistance to bean anthracnose. *Ann. Rep. Bean Improvement Cooperative*. 39: 57-58.

ZIMMERMAN, M.J.O., A.A. Rosielle and J.G. Waines. 1984a. Heritabilities of grain yield of common bean in sole crop and intercrop with maize. *Crop Sci.* 24(4): 641-644.

ZIMMERMAN, M.J.O., A.A. Rosielle, J.G. Waines and K.W. Foster. 1984b. A heritability and correlation study of grain yield, yield components, and harvest index of common bean in sole crop and intercrop. *Field Crops Res.* 9: 109-118.

ZIMMERMAN, M.J.O., A.A. Rosielle, K.W. Foster and J.G. Waines. 1985. Gene action for grain yield and harvest index of common bean grown as sole crop and in intercrop with maize. *Field Crops Res.* 12(4): 319-329.