AN ABSTRACT OF THE THESIS OF

Rebecca L. McCluskey for the degree of Master of Science in Horticulture presented on March 19, 1996. Title: The Inheritance of Pod Detachment Force in Green Beans (*Phaseolus vulgaris* L.).

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The easy picking characteristic, expressed as low pod detachment force (PDF), offers a way to decrease pod damage in bush green beans mechanically harvested for processing and fresh market, and makes hand picking easier and faster. This study was undertaken to examine inheritance in a cross of two green bean cultivars, one of which is grown extensively in the Willamette Valley for processing and the other of which is unparalleled for its low PDF.

A preliminary investigation of the two parental bush bean cultivars showed that PDF of 'Easy Pick' was significantly lower than '91G' at all stages of pod maturation. The average PDF of 'Easy Pick' varied less over seasons and environments than that of '91G'. The sampling window was determined to be a week or less in duration once pods reached harvest maturity. This is important because pod detachment force changes rapidly as pods become overmature whether or not pod size changes are apparent.

Generation means analysis was used to determine the relative importance of genetic effects in the inheritance of pod detachment force in plantings made on two dates. The primary genetic effects were additive, but in Planting Two dominance effects were

also evident. Epistatic effects fit a digenic inheritance model with five parameters. Parameter estimates for the dominance and dominance x dominance genetic effects in the two planting dates were of opposite sign indicating the predominant type of non-allelic interactions are mainly of the duplicate kind. The exact nature of these effects could not be determined because the generations required for such analyses were not grown in the same year.

Estimations of heritability and response to selection were calculated from the sample variances of generation means from six generations grown in 1992, and variance component estimates from one hundred F_3 families grown in 1993. Narrow sense heritability was calculated at 59% and 54% for 1992, and 83% for 1993. The regression of F_3 progeny onto F_2 parents provided a heritability estimate of $27 \pm 4.5\%$. Selection response estimates indicated the overall F_3 mean of 13.8 ± 5.7 Newtons (N) could be reduced 2.4-4.0N from family selection in the F_3 generation.

The Inheritance of Pod Detachment Force in Green Beans (*Phaseolus vulgaris* L.)

by

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Rebecca L. McCluskey, Author

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INTRODUCTION

One way for commercial growers and processors to improve the efficiency of mechanical harvest of green beans (*Phaseolus vulgaris* L.) and decrease losses may be through development of a bean plant whose pods detach more easily from the stem.

Injury to pods from bruising and breakage has been a concern since the introduction of machine harvesters because it affects profitability for all parties involved. Growers experience losses through reduced recovery of beans from the field, either by pods being left behind on the plant or thrown out with the stems and leaves. Injury and breakage result in moisture loss and invasion of bacteria and fungi through ruptured cell walls. Not only are they susceptible to invasion by pathogens, but bruised or broken pods oxidize at the wound or break in the pod and turn dark. These events have the effect of reducing both visual eye appeal and shelf-life for the retailer, and reducing usable tonnage and storage life for the processor.

Most of the green beans grown for commercial use in the United States are mechanically harvested as immature green pods, and in Oregon are used primarily for processing. Beans are processed mainly by freezing but also by canning, dehydration, and a small percentage goes into gourmet specialty items. A mechanical harvester has metal fingers located on a rotating reel that move through the plant, detaching pods from the plant at their weakest point. This weak point may be at the stem, pedicel, or neck of the pod, depending upon environmental and genetic conditions. Pod size and age, plant size, location of pods on the plant, planting density, and reel speed of the harvester all have some effect on where and how a pod detaches.

There are genetic differences in ease of detachment. Pod wall fiber and pedicel diameter and length seem to be implicated in findings that pods from some cultivars detach with greater ease than other cultivars. Some of these cultivars have been referred to as "easy picking". About 1985, two such lines became available for trial from Ag Services Corporation of Salem, Oregon. The pods, when sampled at a harvest-ready, immature green stage, could be detached with greater ease than those of any cultivar previously reported. The pods could even be shaken from an uprooted plant. As the pods aged, stopped growing, and the final seed maturation process began, the easy picking character tended to disappear. These commercial breeding lines, AS52 and AS28 were eventually introduced as the cultivars 'Easy Pick' and 'Easy Harvest', respectively.

The present study was undertaken to describe the expression of the easy picking character in parental material and to determine the mode of inheritance. Information from the parental material was needed as a foundation for future studies, and to determine whether PDF changed significantly over the course of pod maturation. Knowledge of the mode of inheritance of the easy picking character from 'Easy Pick' may be of use to plant breeders desiring to incorporate this trait into bean lines for either processing or home garden use.

LITERATURE REVIEW

Many pod and plant characteristics have been observed and modified in the development of green bean cultivars. Breeding emphasis for pole and bush green beans was initially placed on pod quality characteristics such as shape, length, color, flavor, stringlessness, and smoothness (Silbernagel, 1986). The development and wide adoption of mechanical harvesting by the industry created new requirements for commercial green bean cultivars. Machine harvested pods were considered to be inferior in quality than hand harvested pods, due to injury and weight loss, the number of broken pods and attached stem sections. Some of the problems associated with mechanical harvest may be alleviated by easy picking characterisitics which could result in a lowered resistance to removal and subsequently less trash and damage to pods.

Background

A mechanical harvester is a self-propelled machine that has steel fingers located on rotating picking reels which strip the pods and leaves from the stems. In a study to determine the economic feasibility of machine harvest vs. hand harvest of fresh market beans, several lots of beans from four fields were sampled by Showalter (1968). The quantity of trash, immature and broken beans found in lots of machine harvested beans was double that found in lots of hand harvested beans. The removal of the extra trash and small or broken beans added to the cost of sorting and grading procedures at the packing house. Additionally, the inclusion of very small beans below the grading standards reduced the overall quality of machine harvested lots (Showalter, 1968). Even with improvements made to equipment and additional steps added to the sorting and grading process, lowered pod quality and consumer acceptance remained a concern to the industry.

Pod Anatomy

It was apparent that the cause for the damage to mechanically harvested bean pods and the degree to which they occurred needed to be addressed. The underlying reasons for loss in tonnage between the time of harvest and end use by retailers or processors were not known. Mechanically harvested beans had greater weight losses and a reduced shelf life compared to hand harvested beans. In a study done by Hoffman (1967), 49 varieties and breeding lines were compared for anatomical characteristics associated with weight loss, including hair counts, hair length, number of missing and broken hairs, and mesocarp and endocarp structural variations. Weight loss was evaluated in two seasons, and found to average 17.3% in spring and 42.2% in the fall. The number of hairs per unit area was found to be the most important factor in weight loss of snap bean pods. Hairs on snap bean pods are very fragile, breaking easily. These breaks provide channels through the epidermis allowing for a continuous moisture loss. Therefore, it is understandable that weight loss increased as the number of broken or missing hairs increased. Cellular structures, number of stoma, and hair length were not correlated with weight loss.

A comparison of the weight loss and degree of injury occurring to bean pods under different harvesting and handling methods for five cultivars noted that the degree of injury and ease of pod detachment varied with cultivar, and seemed to be related. Machine harvested pods once again lost more weight than hand-harvested pods. A single cultivar 'Sprite' was used to compare weight losses with observable pod damage. Pods broken at the neck or at the stem end of the pedicel lost less weight than pods where the pedicel was removed adjacent to the pod (Hoffman, 1971).

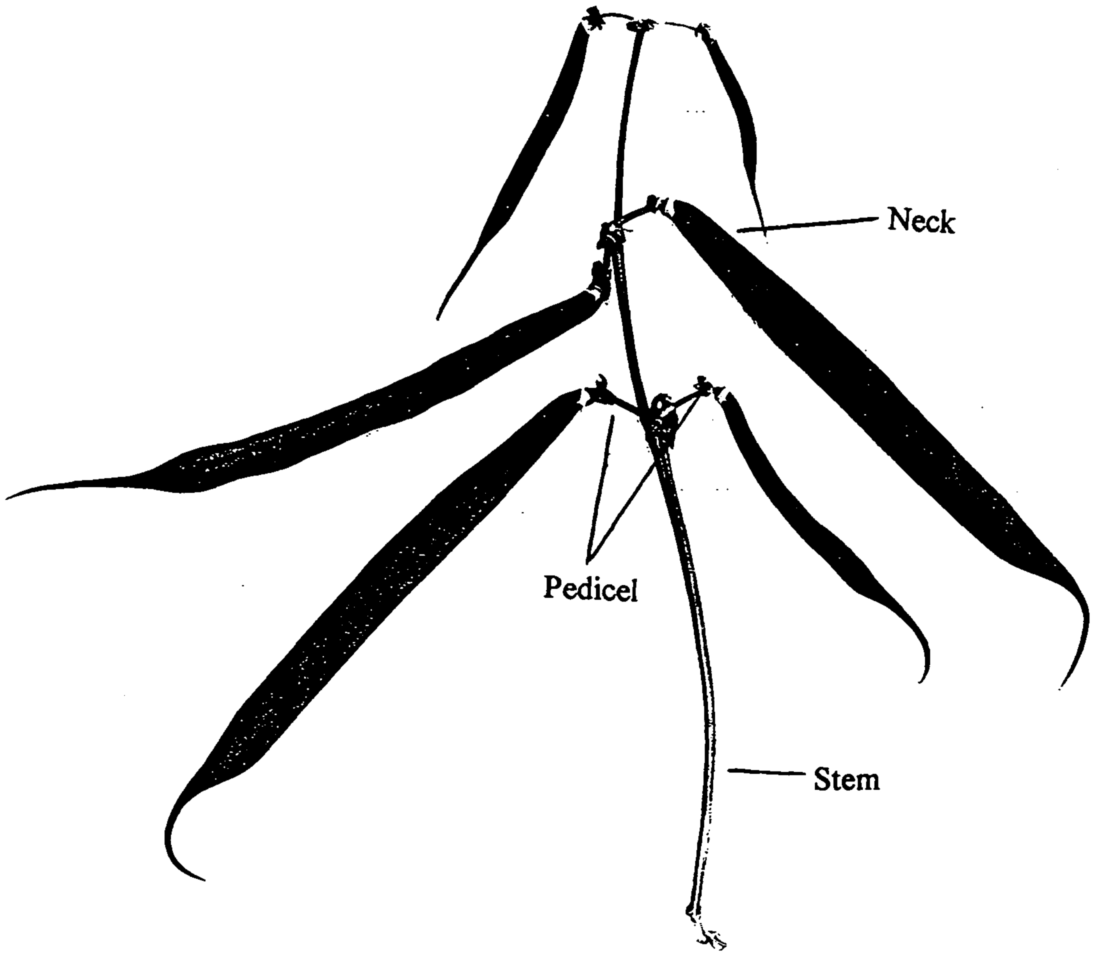

Figure 1. Cluster of green bean pods attached to stem.

Pod Detachment Characteristics

Different locations of detachment have been studied because of their influence on post-harvest grading requirements and market quality of green beans. In an examination of the points of pod detachment, Showalter (1970), found that bean pods detached from the plant stems at four locations: in the stem, between the stem and pedicel, between pod and pedicel, and in the pod (Figure 1). Pods detaching by stem breakage required hand grading to remove stem pieces and break up pod clusters; pods detaching anywhere within the pod (pod breakage) resulted in discoloration and decay. Detachment at either end of the pedicel was considered most desirable. Significant positive correlations were found between pod weight, pedicel diameter, and detachment force. In a comparison of two cultivars, 37% of the pods were broken in the cultivar with the higher pod detachment force (PDF) as compared to 18% in the variety with low PDF (Showalter, 1970). Detachment of bean pods at a natural separation layer would be useful in aiding harvesting, grading and improving quality of the harvested product.

Abscission vs. No Abscission

At the time when snap beans are harvested, the pods are growing rapidly and there is not a developing zone of weakness for detachment (Showalter, 1969). Abscission zones develop in the leaf petioles of snap bean plants, but the pod is never released during the entire life of the plant. In contrast, there is a great deal of flower drop both pre- and post-anthesis. Studies done by Webster et al. (1986, 1987), have characterized the flowering and fruiting patterns of *Phaseolus vulgaris* L. It was observed that under controlled environmental conditions only about 18% of the total number of flowers were retained as mature pods and flowers that opened four to five days after anthesis had a much higher pod abortion rate than flowers that opened within 48 hours of anthesis. Essentially, the only fruit (pods) that develop to maturity are from the flowers that open within the first 5 days after anthesis, regardless of the length of flowering period within the plant. If the first flowers are removed, subsequent flowers to open will set and retain pods. A similar pattern has been noted in soybean (*Glycine max* L.) (Heindl and Brun, 1984, Oberholster et al. 1991), and tepary bean (*Phaseolus acutifolius* A. Gray. var *acutifolius*) (Webster and Weis, 1990). The floral abscission zone of common bean cv. 'Dark Red Kidney' was observed to be similar to that of the abscission zone of senescing leaves except that floral abscission occurs at a much accelerated rate (Webster and Chiu, 1975).

The lack of an active abscission zone in the developed pod makes the harvesting of green beans more difficult and thus more pods are lost through breakage and injury. The detachment of bean pods at a natural separation layer would aid in the harvesting, grading and quality of commercial operations. Knowledge of where pods detach during harvest and the force required to detach the pods may be useful in refining the machinery used for harvest.

Pod Detachment Force

The force required to detach bean pods has been shown to vary with genotype (Showalter, 1969; Bassett, 1973, 1976). A comparison of two cultivars, 'Provider' and 'Harvester' identified bean pods from 'Provider' as having half the PDF of 'Harvester' with an average of 2.1lbs (9.3N) as compared to 4.9lbs (21.85N) for 'Harvester'.

However, when 'Provider' was harvested after very dry weather, the PDF was almost as high as that for 'Harvester' grown with adequate moisture (Showalter, 1969). Bassett (1973) evaluated the PDF of 13 genotypes at sieve sizes two through six. He found that differences existed betweeen the genotypes at all sieve sizes. For example, within sieve size 4.0 there was a range in PDF of 0.86kg (8.43N) for cv. 'Idlelight', to 1.9kg (18.62N) for the breeding line 'B4000-1', the genotypes with the lowest and highest PDF, respectively. At sieve size 5.0, the PDF of 'B4000-1' was 1.76N (~9%) greater, whereas the PDF of 'Idlelight' was 1.42kg (13.92 N), almost 40% greater. PDF values for the cv. 'Idlelight' were lower than those of any cultivar in three previous studies (Hoffman, 1971, Showalter, 1969, Bassett, 1973).

The genetics and mode of inheritance of PDF is poorly documented. The only published material to date is a study involving the cultivars 'Harvester' and 'Idlelight', the latter being the genotype with the lowest PDF available at that time (Bassett, 1976). Crosses were made between the two parents and six generations were planted and evaluated in Florida in 1975. The average PDF for the cv. 'Idlelight' was 10.76N, higher than previously reported by Bassett (1973). The average PDF for cv. 'Harvester' was 18.10N. Narrow sense heritabilities were calculated to be 61% and the minimum number of genes was estimated to be 1.96 (Bassett, 1976). The data did not fit a simple additive - dominance model as estimated by Mather's scaling tests , nor did it fit a X^2 test for either a one factor or two factor model with X^2 values of 18.69 and 7.38 ($p < .05$), respectively. PDF of the F_1 was equal to that of the high parent, and PDF of the backcross to the high parent exceeded that of the high parent. PDF of the F_2 was nearly as high as that of the high parent. Bassett (1976) concluded that PDF was controlled by dominance of the 'Harvester' genotype, and that there were likely two major genes involved. He also commented that pods segregating for sieve size might be a confounding factor in selecting a common sieve size upon which to base observations.

Pod detachment force has also been studied in another legume, peanut (*Arachis hypogaea* L.). Peanut peg strength influences the proportion of peanut pods harvested and genotypes with increased peg strength are desirable over pegs of low strength. Loss of peanut pods in or on the soil surface as a result of mechanical harvest are a concern to peanut producers. Losses have been attributed to inherently weak or diseased pegs and damage from harvesting equipment (Thomas et al, 1977, Troeger et al, 1976). PDF was observed for 30 peanut genotypes to range from 12.1 ± 4.09N to 37.2 ± 13.08N (Thomas et al, 1983). These values are slightly higher, but generally similar to values found in green beans. Genotypes were classified into three groups having weak, moderate or strong pegs. Anatomically, the peg (gynophore) has the structure of an herbaceous stem. Differences between the groups could be related to the size and shape of vascular bundles, and degree of bundle cap lignification.. As the pod forms, the vascular bundles within the peg branch into smaller bundles over the pod surface and no abscission zone is formed between the pod and peg (Reed, 1924).

MATERIALS AND METHODS

General Cultural Methods

Greenhouse: All plants used for crossing were grown and crossed in the greenhouse from January - May, 1991 and 1992. Temperatures were maintained at approximately 20°C (day) and 15°C (night). Plants were grown in number 10 cans filled with a sterilized soil mix composed of soil, sand, peat, and pumice (1:1:1:2 v/v) which hold approximately 2 liters of soil. A complete fertilizer blend including micronutrients was incorporated into the soil mix prior to sterilization and planting. One tablespoon (about 10g) of a slow release fertilizer (Osmocote, 14 N - 6 P - 12 K) was added to each can approximately 3 weeks after planting. Five to seven seeds were sown in each can and later thinned to four plants/can. Supplemental fluorescent lighting was provided during the winter months (December through mid-February) to extend the daylength to 12 hours.

Field: Plants were field grown at the Oregon State University Vegetable Research Farm at Corvallis, Oregon in the summer months of 1991, 1992 and 1993, for seed production and to obtain the PDF measurements and other observations needed for the inheritance study. Seeds were treated with Captan 50W (fungicide) prior to being planted with a hand powered V-belt planter 4 cm deep at 3 cm intervals in rows 90 cm apart. About two weeks following emergence, plants were thinned, as needed, to 12-15 plants/m. Preplant fertilizer (12 N - 29 P - 10 K - 4S) was applied in a band directly below the rows at a rate of 600kg/ha. An insecticide drench of Lorsban 50W at a rate of 2 lb a.i./acre was applied within two days of planting. Chemical insecticides and manual weed control were scheduled as needed. Up to two inches of water was applied through overhead irrigation at 7 - 10 day intervals or as required throughout the growing season until pods were at harvest maturity.

Crossing Methodology and Plant Material

Crossing: Common beans have cleistogamous flowers, and pollination occurs just prior to flower opening. Flower buds were emasculated in the morning one day before opening. The outer petals (wings) were pulled back, the keel was opened and removed, and the stamens were uncoiled from around the pistil and gently pinched off. The stigmatic surface was examined with a magnifying glass to look for any contaminating self-pollen. Once the stigmatic surface was determined to be clean, it was dusted with pollen from a freshly opened flower from the male parent. The wing petals were then folded back over the stigma and secured with a piece of clear tape and a label identifying the cross was hung on the pedicel. Forceps were dipped in alcohol between flowers.

Parents: A preliminary study initiated 2 years prior to this research included crosses of 6 parents and provided some insight as to the nature of the easy picking character (J. R. Baggett personal communication, data not available). For this reason it was decided to focus on two parents that were of the same general type but strongly different in pod detachment force.

Two bush type green bean cultivars representing the extremes of PDF known in cultivars of this type were used as parents. 'Easy Pick', the low PDF parent, was named for its ease of pedicel detachment from the stem. It is a high quality, round-podded upright-growing cultivar with dark green pods and crinkled, dark green leaves and an immature white seed coat. It was obtained for this study from Ag Services Corporation of

Salem, Oregon and is now the property of Rogers Seed Company. The lineage from which it descended has always been and continues to be proprietary information. It has an average pod detachment force of 6N at sieve size 4.0 - 4.5, which is equivalent to a pod width of 8 - 8.75mm. This cultivar is a logical choice if one is interested in the transfer of the easy picking character into Blue Lake type bush beans. 'Easy Pick' is unique in its low pod detachment force and knowledge of the specific inheritance pattern of 'Easy Pick' might be useful to a plant breeder.

The normal or high PDF parent, 'Oregon 91G' (91G), was developed at Oregon State University (Baggett et al., 1981). This is the predominant cultivar grown for processing in the Willamette Valley. It matures about 4 - 5 days earlier and has pods slightly larger than those of 'Easy Pick'. It is extremely productive with smooth, medium green leaves and an immature green seedcoat. PDF of '91G' is on average twice that of 'Easy Pick' at a comparable sieve size. Reciprocal crosses were made between 'Easy Pick' and '91G' in the greenhouse in 1991 and 1992.

Seed production: Parent and F_1 seed was planted in June, 1991, and trueness to type was verified by visual comparison of growth habit, leaf, pod and immature seedcoat colors, and preliminary data collected. F_2 seed from F_1 plants was bulked within a plot. Reciprocals were kept separate. The F_2 seeds were planted the following summer, along with the parents, F_1, and the F_1 backcrosses to each parent. Seed from 100 F_2 plants from which pods were measured for PDF was harvested individually to provide material for F_3 families planted the following year.

Data Collection Procedures

It was observed that PDF of pods from an individual plant could be quite variable, because PDF is affected by pod age, as reflected in pod size. However, the relationship between pod age and pod size is not always a direct one, because pod size itself can be influenced by many factors such as fruit load, location on the plant, moisture stress or high temperatures during flowering and pod development. Additionally, pods on an individual plant can increase by as much as one sieve size in a single day during the optimum harvest period. The optimum time period in which to collect data is fairly short, about 3 - 5 days for an individual plant and 10 - 12 days for an entire planting. In an attempt to compensate for this variability, effort was focused on collecting as many measurements as possible on a single population in the available time frame. As noted earlier, PDF for 'Easy Pick' increases greatly as pods become overmature.

All PDF measurements and other observations were taken in the field. A plot was determined ready for PDF measurement when 50 percent of the plants had 3 - 4 pods of sieve size four. In F_2 plots, each individual plant was measured as it reached harvest maturity. After data was obtained for an individual plant, it was labeled to prevent duplicate sampling. Measurement of PDF was done with a hand held force gage (AMETEK Accu-Force Cadet) that provided a digital readout to the nearest .01kg (Figure 2). Kilograms were converted to Newtons (N) by multiplying the force gauge measurement by a conversion factor of 9.8. A special hook attachment 18 cm long with a curved end 2cm x 0.5cm was used to remove pods from the plant by hooking the pedicel and pulling straight up by hand (Figure 3). Sieve size was measured on the detached pods using a Northrup

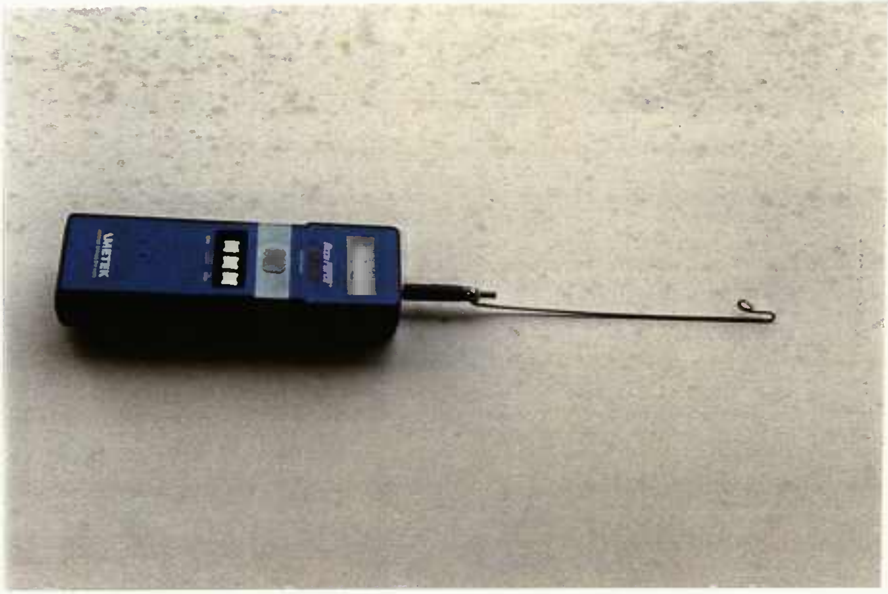

Figure 2. Hand held force gauge with specialized hook attachment used to detach pods from the bean plant.

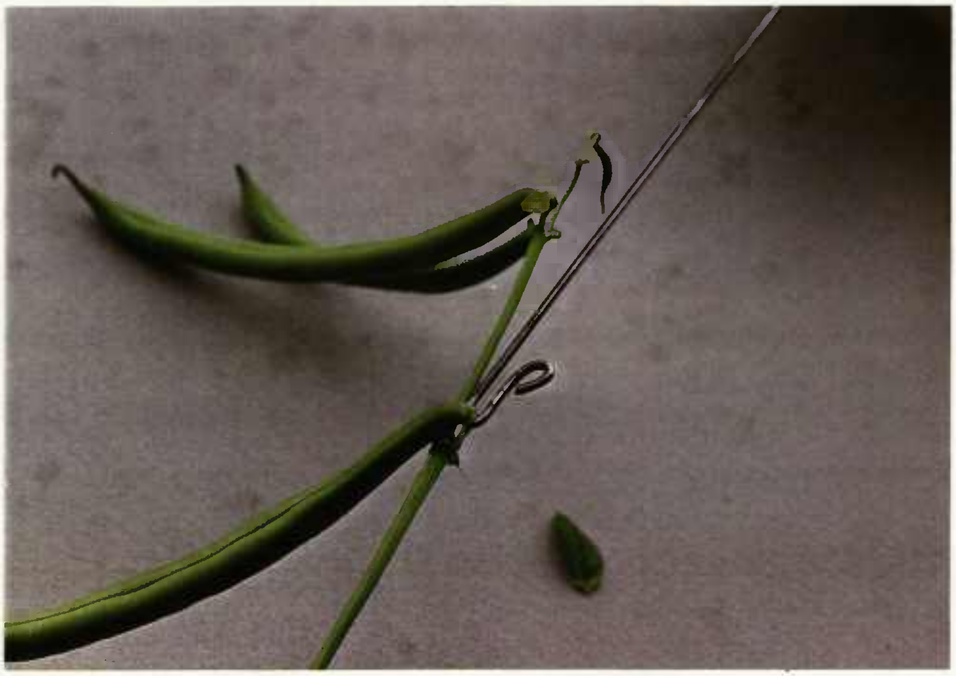

Figure 3. Illustration of the technique used for sampling pods for PDF using the specialized hook attachment on the force gauge.

King raw product bean and pea gauge. With this, pod width (in cross-section parallel to the suture) is measured in increments as follows: Sieve size 1 = 5 - 6mm; 2 = 6 - 7mm; 3 = 7 - 8mm; 4 = 8 - 9.5mm; 5 = 9.5 - 10.5mm; 6 = 10.5 - 12.0mm; 7 = >12.0mm (Anonymous, 1953). Seed length was measured to the nearest mm with a ruler.

Description of the Field Experiments

General Chronology

The sequence of events in this project were as follows:

Summer 1991 F_1's and parents planted in the field.

Winter 1991-Spring 1992 Additional crosses and backcrosses made.

Summer 1992 Parent study characterizing PDF

Summer 1992 Evaluation of parents and progeny generations (F_1, F_2, and reciprocal backcrosses) for genetic analysis.

Summer 1993 F_3 families and parents evaluated in the field.

Parental Characterization

A preliminary study of the parents 'Easy Pick' and '91G' was conducted to compare the changes in PDF as pods matured and note any other distinguishing features that may be related to PDF changes. Plants used in this study were taken from a replicated yield trial planted in a randomized complete block design. Plants were spaced 4 - 5 cm in plots 3 m long in rows 90 cm apart. Sampling was done every other day for a 14 day period. Each sampling day included measuring all pods of sieve 0.5 (<sieve size 1.0) to 7 from four plants in four blocks for a total of sixteen plants per parent per day. PDF

and sieve size were recorded for each pod. The measuring period covered both pre-and post-harvest maturity in order to measure pods at both extremes. Analysis of variance was used to test the differences between the parents and the parent by day interaction.

Inheritance Study

The F_1 of 'Easy Pick' x '91G' was grown in the field during the summer of 1991 to provide F_2 seed for future study. The following summer, parents, F_1, F_2, and F_1 backcrosses were planted on two dates, June 3 and June 16, 1992. Plot size varied with generation, the backcross plots being approximately 1m long, F_1 and parent plots 3m long and F_2 plots 4m long. The number of plants measured per plot were 6, 15, 15, and 25, respectively. There were four plots of each backcross and two each of the other generations in each block. A randomized complete block design with four blocks was used, a block consisting of all generations and their reciprocals. Data collected from Planting One included PDF, sieve size, seed length at harvest and immature seedcoat color (ISC). A complete data set for Planting Two included PDF, sieve size and ISC, but not seed length.

Reciprocal populations were pooled for the F_1, F_2, and backcross generations after the Waller-Duncan mean separation t test showed no differences. Populations were homogeneous with the exception of one backcross to '91G' in the first planting and two of the four backcrosses to '91G' in the second planting. These inconsistent data from the backcrosses may have been the result of the relatively low number of plants (6) per backcross plot. There were clear delineations among all generations when means of pooled reciprocals were tested. To determine whether the two plantings could be analyzed as one experiment, homogeneity of variance was tested with an F test using error variances from analysis of variance (Snedecor and Cochran, 1967).

Genetic effects were estimated using Cavalli's joint scaling test procedure as described by Mather and Jinks (1982). The scaling test procedure was extended to include digenic interactions as indicated by Rowe and Alexander (1980). A weighted least squares method was used to estimate the genetic parameters since there were unequal number of plants contributing to each mean. Generation means were weighted by the inverse of the squared standard error for that generation. Least squares generation means and the coefficients of genetic effects were used to obtain perfect fit estimates for an analysis of generation means (Tables 1 and 2). The formulae of Jinks and Jones (Mather and Jinks, 1982), were also used to obtain perfect fit estimates of the genetic effects for a comparison of the two methods (Table 3). Estimates of the genetic effects and expected generation means were identical for the two methods other than rounding errors.

A X^2 test was used to test the fit of the least squares means to those expected for the simple additive - dominance model. The perfect fit model with only 5 parameters was also tested with a X^2 test. T tests were used to test for significance of the individual estimates of the 6 parameters estimated by the perfect fit model. It was not feasible to use a X^2 test to determine the fit of the full digenic model because six parameters were estimated from six generations, leaving zero degrees of freedom. Correlation coefficients were calculated to test for a relationship between PDF and sieve size, seed length, and ISC.

Table 1. Least squares generation means of pod detachment force from 'Easy Pick' x '91G' crosses in two plantings in 1992.

	Planting One		Planting Two	
Generation[z]	n[y]	LS Mean ± s.e.[x]	n	LS Mean ± s.e.
91G	59	15.39 ± .43	61	13.62 ± .40
BC'	86	12.46 ± .41	93	14.57 ± .40
F_1	98	11.07 ± .36	108	13.50 ± .33
F_2	196	11.78 ± .21	200	11.43 ± .21
BC	97	8.04 ± .40	87	10.06 ± .39
EZP	60	6.19 ± .42	62	5.86 ± .41

[z]BC' = Backcross to 91G, BC = backcross to Easy Pick.
[y] n = Number of plants from which pods were measured.
[x]LS Mean = Ordinary least squares mean.

Table 2. Coefficients of genetic effects used in the analysis of 6 generation means.

	Genetic Effects[z]					
Generation[y]	m	a	d	aa	ad	dd
91G	1	1	0	1	0	0
BC'	1	0.5	0.5	0.25	0.25	0.25
F_1	1	0	1	0	0	1
F_2	1	0	0.5	0	0	0.25
BC	1	-0.5	0.5	0.25	-0.25	0.25
EZP	1	-1	0	1	0	0

[z]Genetic effects are as follows: m (mean), a (additive), d (dominance), aa (additive x additive), ad (additive x dominance), dd (dominance x dominance).
[y]BC' = Backcross to 91G, BC = backcross to Easy Pick.

Table 3. Formulae for perfect fit estimates of parameters used to fit a digenic inheritance model using generation means[Z].

$m = .5P_1 + .5P_2 + 4F_2 - 2B_1 - 2B_2$

$a = .5P_1 - .5P_2$

$d = 6B_1 + 6B_2 - 8F_2 - F_1 - 1.5P_1 + 1.5P_2$

$aa = 2B_1 + 2B_2 - 4F_2$

$ad = 2B_1 - P_1 - 2B_2 + P_2$

$dd = P_1 + P_2 + 2F_1 + 4F_2 - 4B_1 - 4B_2$

[Z] Where m (mean), a (additive), d (dominance), aa (additive x additive), ad (additive x dominance), dd (dominance x dominance) are equivalent to Mather's m, d, h, i, j, l, respectively.

Heritability Estimates

Heritability estimates were calculated by three different methods. Estimations of broad and narrow sense heritability were calculated from data collected in 1992 using variances estimated from standard deviations of observed means of six generations per planting date (Stoskopf et al., Ch. 4, 1993). Estimations of narrow sense heritability were calculated from data collected in 1993 using variance component estimates from F_3 families and parent-progeny regression.

Seed for F_3 families was harvested from individual F_2 plants in September 1992, and 100 F_3 families were planted as single plots on 3 dates in June 1993. One pod per plant was measured for PDF, sieve size, and ISC. Data were collected from 7 plants per plot as a plot reached harvest maturity, for a total of 21 plants per family.

Estimations of narrow sense heritability between and within F_3 families were calculated on balanced data using both individual plant and plot mean data with the GLM and VARCOMP procedures of SAS (SAS Institute, 1988) for analysis of variance. The restricted maximum likelihood (reml) method was specified.

Narrow sense heritability was also estimated by regressing the F_3 family means onto F_2 parental values following the method described by Hallauer and Miranda (1981). Response to selection in the F_3 generation was also estimated. Selection differential (i) was calculated for n = 100 families and n = 700 individual plants using a SAS program provided by Dr. Steven J. Knapp (Appendix 1).

RESULTS AND DISCUSSION

Parent Characterization

Comparison of PDF measured on seven days over a 14-day period shows that at each sampling day there were differences between '91G' and 'Easy Pick'. In addition to the significant differences between the two cultivars there was a significant day effect (p = .0001), and a significant parents x days interaction (p = .01) (Table 4). The magnitude of mean square error for the interaction is small in comparison of the magnitude of error for either parents or days, suggesting that while statistically significant, the interaction effects were small relative to the individual effects of either parents or days.

Table 4. Analysis of variance for PDF and sieve size for the parental cultivars 'Easy Pick' and '91G', across 7 sampling days using plant means.

		Mean Squares	
Source of Variation	df	PDF	Sieve
Block	3	1.00	0.31*
Parent	1	1007.47****	6.51****
Day	6	51.31****	11.94****
Parent x Day	6	3.86**	0.12
Error	39	1.21	0.10

*, **, **** Significant at p = 0.05, 0.01, and 0.0001 by F-tests.

Values presented here are averages for all pods measured on a specific day for each genotype. 'Easy Pick' PDF values remained fairly constant for days 2, 4, and 6, but increased at each sampling day thereafter as pods became overmature. In contrast, '91G' PDF values increased for all but sampling day 6 (Figure 4). The field was irrigated on the evening of day 5 and this may have produced the aberration one can see in the graph of '91G' PDF on day 6.

Sieve size of 'Easy Pick' increased steadily over the sampling period as the within plant pod distribution shifted to larger pods. The same pattern was seen in '91G' pods with the exception of days 8 and 10 where '91G' sieve size remained constant (Figure 5). An examination of PDF and sieve size shows both PDF and sieve changed little in '91G' between days 8 and 10 (Figure 5). The difference in mean PDF between the two genotypes was tested using t tests and found to be significant for each sampling day regardless of pod age or size (Table 5).

Further examination of the parental material included data from the two inheritance study plantings. Frequency distributions in these two plantings show a wider range of PDF values for '91G' than for 'Easy Pick' (Figure 6). Depending upon planting date, 55% to 61% of the 'Easy Pick' pods measured for PDF were in the 3 - 6 PDF range and 38% to 36% were in the 6 - 9 PDF range. This accounted for 93% to 97% of all measurements recorded on a total of 121 plants between both planting dates. On planting dates one and two, '91G' had 42% and 45% of the pods concentrated in the 12 - 15 PDF range, with 15% and 29% in the 9 - 12 PDF range, and another 25% and 19% in the 15 - 18 PDF range. The remaining 7% to 18% PDF observations fell into the extreme categories of 6 - 9 and 21 - 24 N. It is likely that this variability affected heritability estimates as the calculations for environmental variance were 56% larger for '91G' than the variance of 'Easy Pick'. In all three of the plantings which were examined, 'Easy Pick' consistently had less variability in PDF values than '91G'. This trend carried through in data collected in 1993 as well, with the standard deviation of '91G' (± 4.56), being twice that of 'Easy Pick' (± 2.02) for PDF observations made on a similar number of pods.

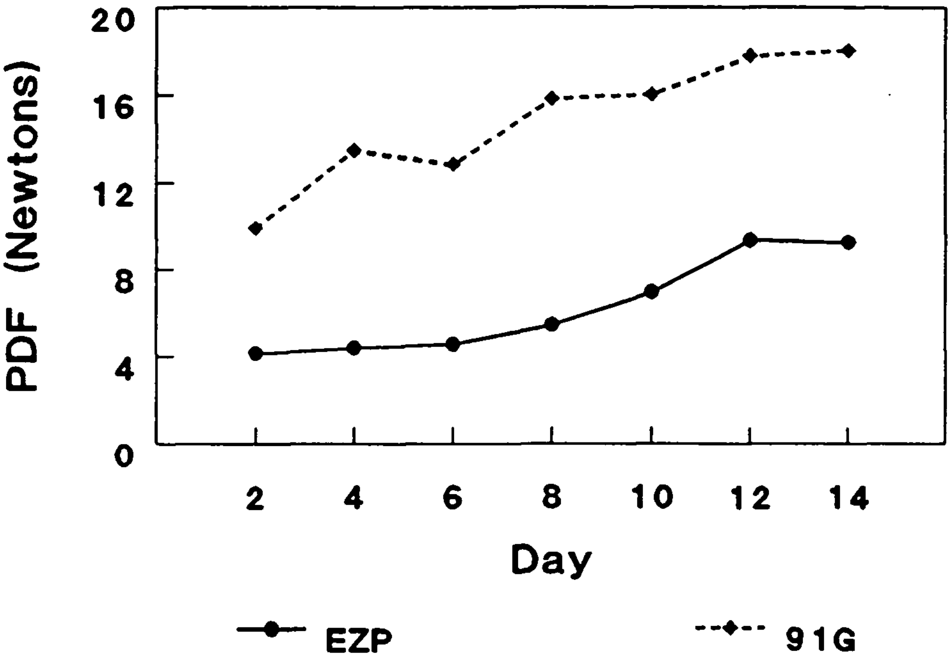

Figure 4. Changes in pod detachment force of 'Easy Pick' and '91G' sampled over a 14-day period (August 18 - September 1, 1992).

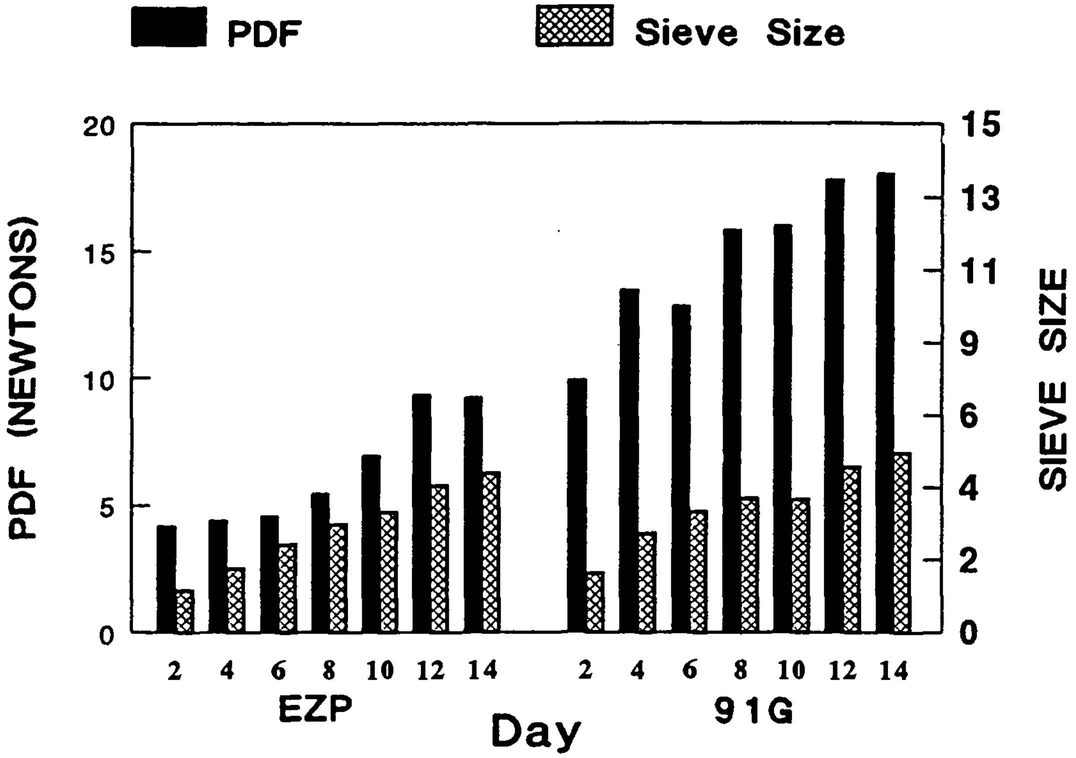

Figure 5. Comparison of pod detachment force with changes in sieve size of 'Easy Pick' and '91G' sampled over a 14-day period (Aug.18 - Sept 1, 1992).

Table 5. Pod detachment force (N) and sieve size of 'Easy Pick' and '91G' over 14 days (1992)[Z].

Day	Parent	n[Y]	PDF (N)	Sieve
2	Easy Pick	239	4.17 ± 1.59	1.22 ± .99
	91G	238	9.92 ± 5.54***	1.72 ± 1.16***
4	Easy Pick	199	4.41 ± 1.72	1.88 ± 1.23
	91G	231	13.49 ± 5.52***	2.91 ± 1.30***
6	Easy Pick	193	4.59 ± 2.15	2.58 ± 1.28
	91G	178	12.86 ± 5.55***	3.55 ± 1.40***
8	Easy Pick	190	5.46 ± 3.11	3.17 ± 1.38
	91G	213	15.83 ± 6.66***	3.94 ± 1.48***
10	Easy Pick	212	6.97 ± 4.61	3.52 ± 1.27
	91G	197	16.03 ± 7.13***	3.92 ± 1.75**
12	Easy Pick	223	9.36 ± 6.74	4.33 ± 1.37
	91G	201	17.77 ± 7.63***	4.86 + 1.54***
14	Easy Pick	201	9.25 ± 5.53	4.70 ± 1.24
	91G	179	18.04 ± 7.56***	5.30 ± 1.55***

[Z] Data presented are means ± standard deviation.
[Y] n = Total number of pods of all sizes from 16 plants per day.
, ** Refers to significance at p = .05 and .001 between cultivars within each day, by one-tailed t test, respectively.

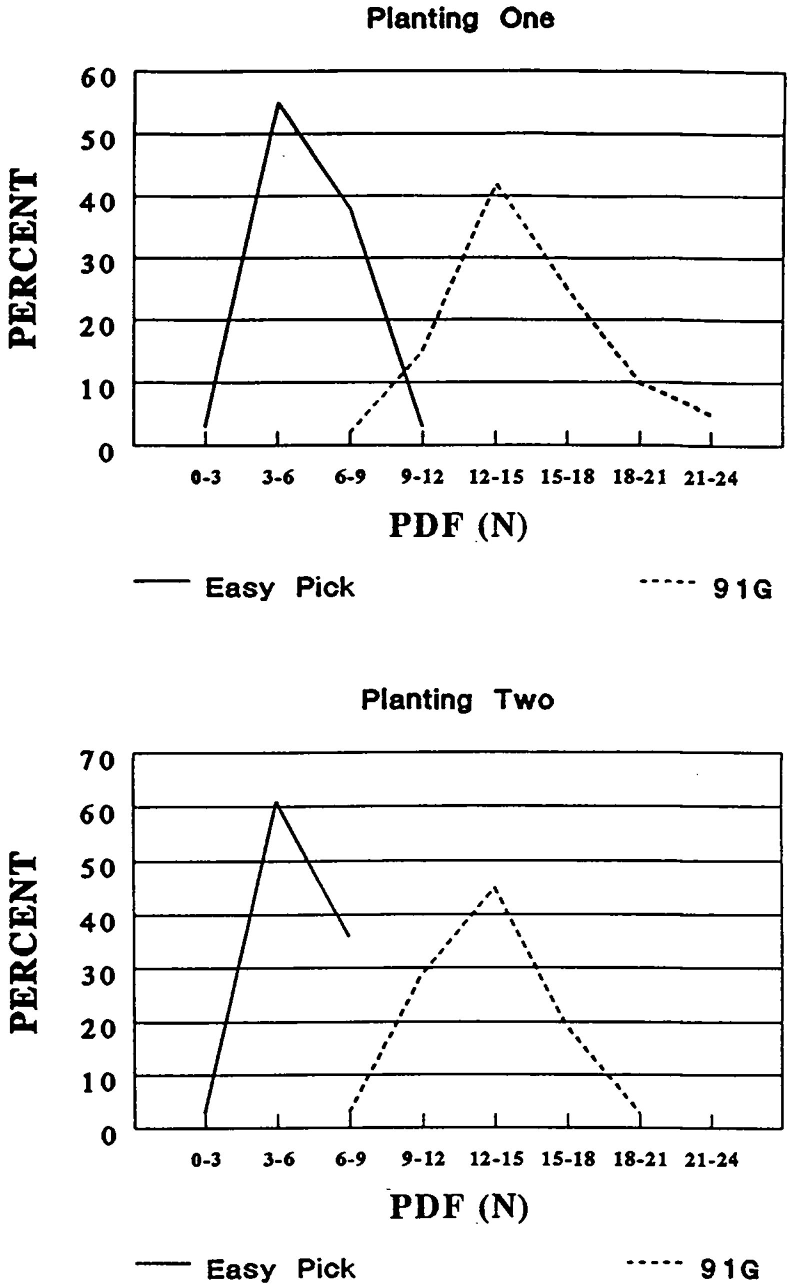

Figure 6. Pod detachment force frequency distribution of 'Easy Pick' and '91G' in (a.) Planting One and (b.) Planting Two. Classes represent the percentage of plants from which pods were measured.

Inheritance Study

The responses observed between the two plantings is indicative of a quantitatiave pattern of inheritance. The variation in the phenotypic expression of PDF, and lack of segregation into discrete classes by the progeny do not support a qualitative mode of inheritance. The continuous nature of the phenotypic expression of the easy pick character can be seen even within the two inbred parents and especially within the F_1 and F_2 generations (Table 6 and Table 7). In both plantings, the F_1 and F_2 follow a normal distribution curve (Figure 7 and Figure 8). If the expression of the character were affected by only one or a few genes with little environmental effect, one would expect the distribution of the parents and progeny to fall into a few discrete classes rather than having such a distinct a bell shaped distribution.

In earlier studies, it had been noted that PDF seemed to be affected by environment (Showalter, 1969). Observations from the present study would also suggest that there is a genotype by environment response, as is indicated by the variation of the F_1, F_2, and backcrosses between the two plantings. Plantings One and Two were from the same plant material, differing only by planting date and location on the farm. The areas on the farm in which they were planted differed in soil texture and previous use history, the first site being very sandy and the second site having a much higher clay content. Additionally, growing conditions were quite different as the second planting went through a period of very warm temperatures which affected pod maturation. At very high temperatures bean pod seed size can increase faster than sieve size, resulting in a pod that is undersized yet overmature.

Table 6. Frequency distribution of plants for pod detachment force in Planting One.

Planting One

	PDF Class (Newtons)								
Generation	0-3	3-6	6-9	9-12	12-15	15-18	18-21	21-24	Total[z]
EZP	2	33	23	2	0	0	0	0	60
BC_1	1	20	47	19	9	1	0	0	97
F_1	0	3	25	36	28	5	0	1	98
F_2	0	12	35	59	54	27	8	1	196
BC_2	0	0	10	25	41	7	2	1	86
91G	0	0	1	9	25	15	6	3	59

[z]Represents the number of plants from which pods were measured. Classification based on means of 3 pod measurements per plant.

Table 7. Frequency distribution of plants for pod detachment force in Planting Two.

Planting Two

	PDF Class (Newtons)								
Generation	0-3	3-6	6-9	9-12	12-15	15-18	18-21	21-24	Total[z]
EZP	2	37	22	0	0	0	0	0	61
BC_1	0	25	27	23	13	4	1	0	93
F_1	0	0	6	38	41	18	5	0	108
F_2	0	9	43	67	57	13	9	2	200
BC_2	0	0	3	26	35	20	3	0	87
91G	0	0	2	18	28	12	2	0	62

[z]Represents the number of plants from which pods were measured. Classification based on means of 3 pod measurements per plant.

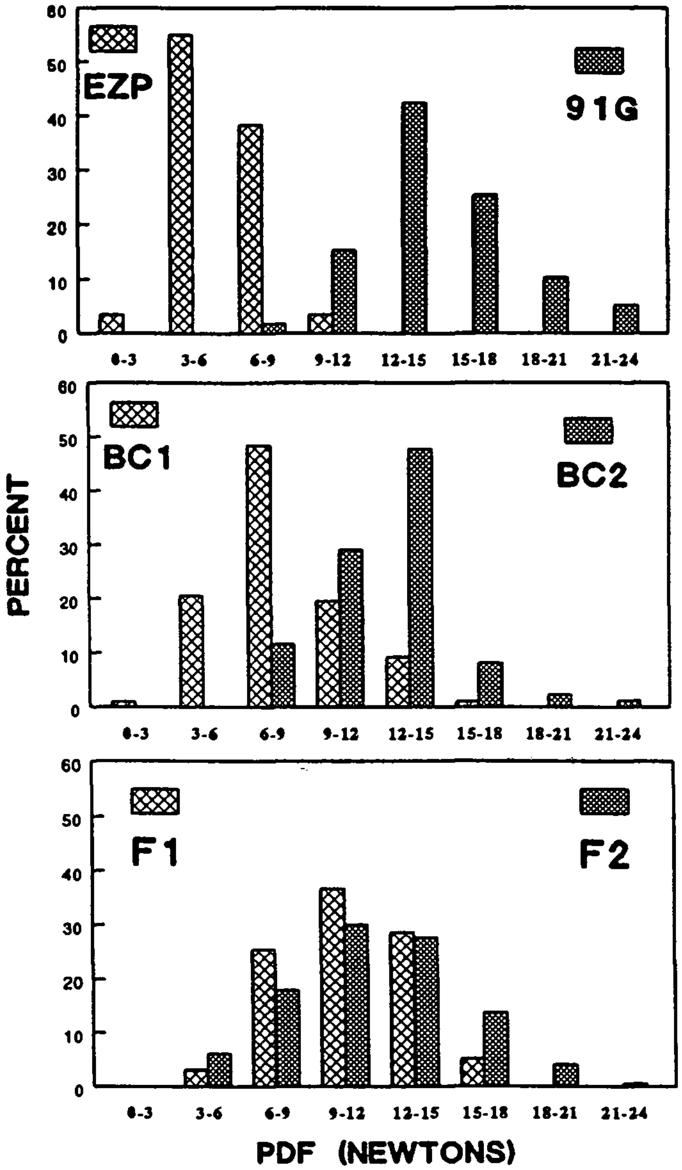

Figure 7. Frequency distribution for pod detachment force as a percentage of the total number of plants in each generation from which data was obtained in Planting One.

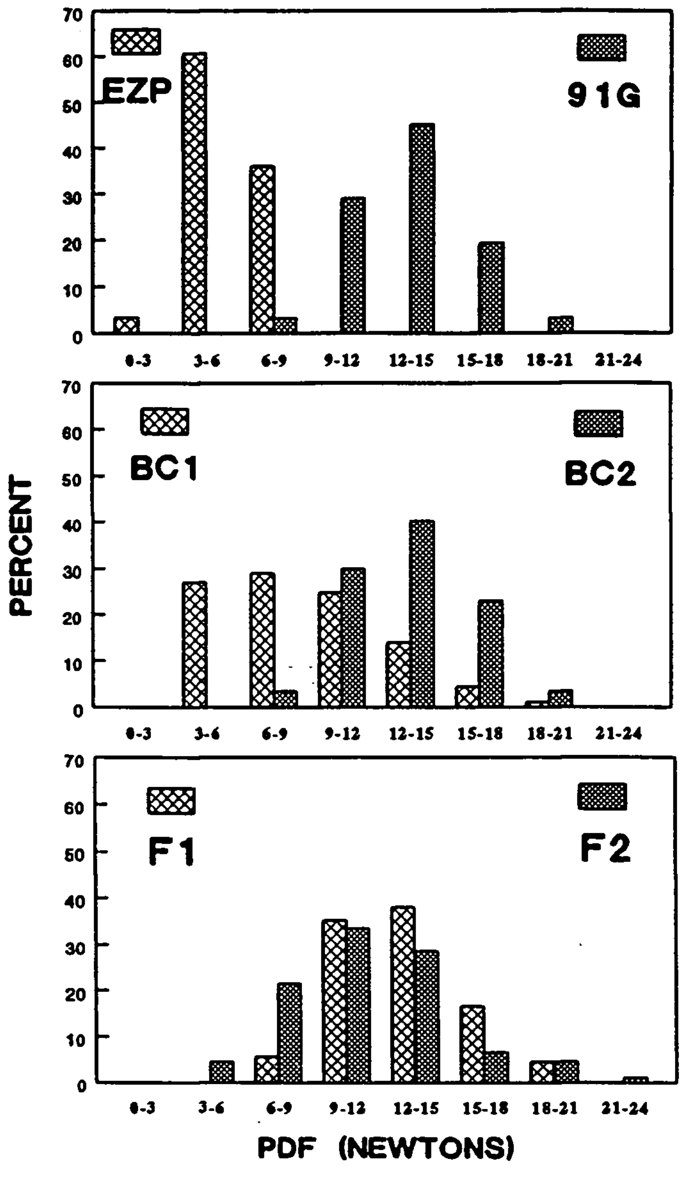

Figure 8. Frequency distribution for pod detachment force as a percentage of the total number of plants in each generation from which data was obtained in Planting Two.

Although a two-tailed F test provided an F statistic of 1.062 (p value $\alpha_{.05}$ = 1.107), the two plantings were visually different enough that they were not combined. This was supported by a graphical plotting of generation means (Figure 9 and Figure 10). In Planting One, the backcross to the low parent had a mean value that was halfway between the low parent and the F_1 mean. The backcross to the high parent had a mean value midpoint between the F_1 and the high parent. The F_2 mean was intermediate between the F_1 and backcross to the high parent (Figure 9). This response is typical when genetic effects are primarily additive. In contrast, the '91G' parent, F_1, and backcross to '91G' generation means were similar in Planting Two, indicating the expression of dominance effects towards high PDF (Figure 10).

Showalter (1970) observed that PDF values nearly doubled in the cv 'Provider' when the plants were exposed to drought stress suggesting that environment seems to have a large effect on the expression of the easy pick character. The change in the amount of dominance exhibited both graphically and with the joint scaling tests is a good example of genotype x environment interaction. This type of interaction might also make the inheritance pattern appear to involve more genes than are actually involved.

A generation means analysis was performed on the data from each planting date to estimate genetic effects. Genetic effects were estimated by Cavalli's joint scaling test for a simple additive - dominance model and extended to include a digenic model. Results from the joint scaling test for a simple additive - dominance model were consistent with visual examination of the data. This test estimates the mean (m), additive (d), and dominance (h) genetic effects. In Planting One, estimates of additive genetic effects were highly

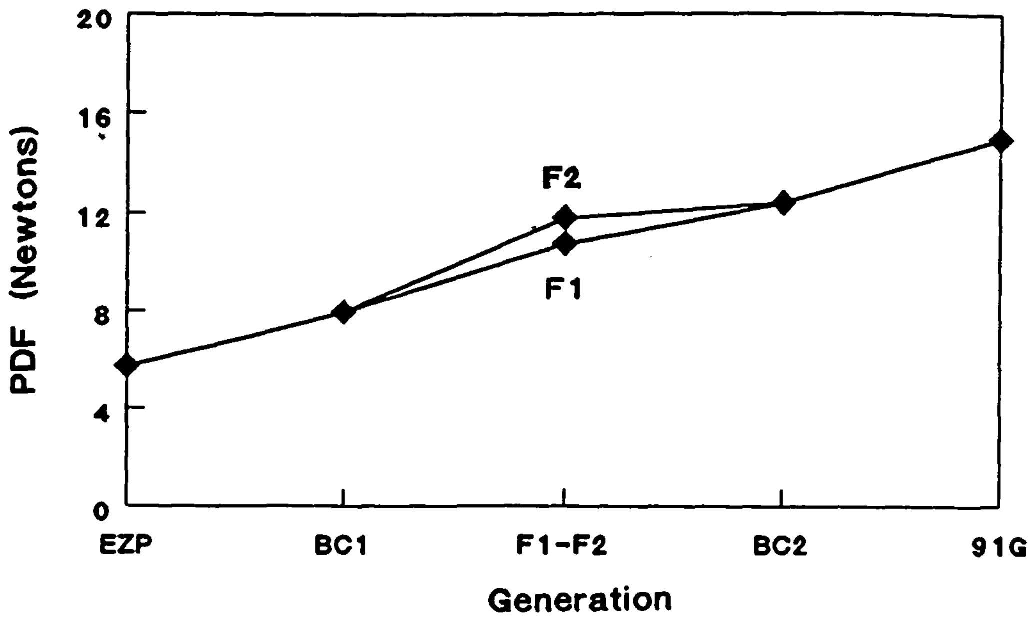

Figure 9. Planting One. Generation means of pod detachment force of parents, F_1, F_2, and backcrosses to each parent planted June 2, 1992.

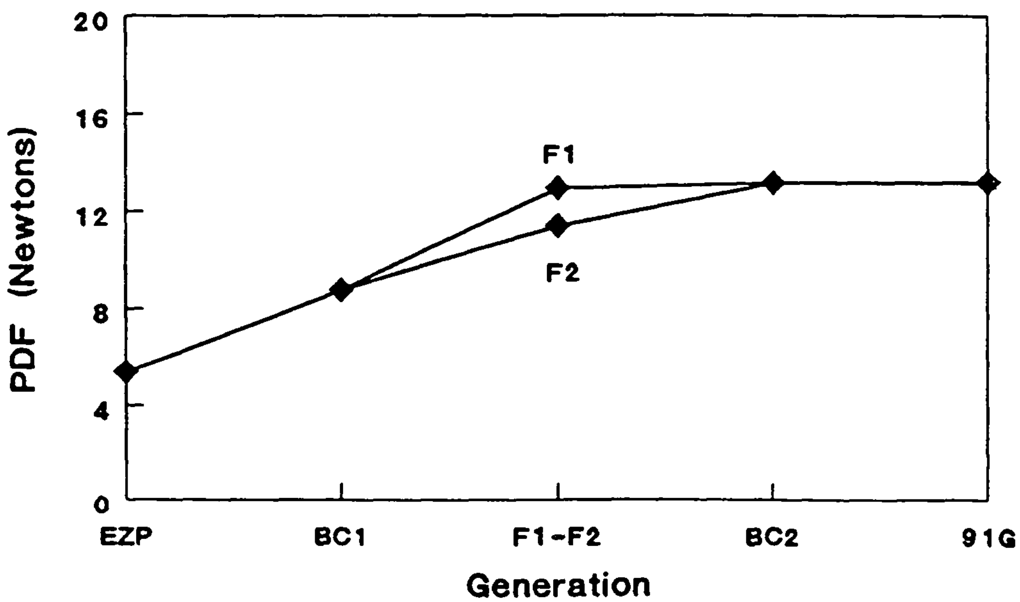

Figure 10. Planting Two. Generation means of pod detachment force of parents , F_1, F_2, and backcrosses to each parent planted June 16, 1992.

significant at $p = .05$ but estimates of dominance effects were not significant. Both additive and dominance genetic effects were significant at $p = .05$ in Planting Two.

Although additive and dominance effects were significant, a X^2 test for fit to the additive - dominance inheritance model with three degrees of freedom indicated that this model was not appropriate for either planting. A model testing for digenic interactions was tried, and perfect fit estimates for digenic interaction effects were significant for all but the additive x dominance effects in Plantings One and Two, and the dominance x dominance genetic effects in Planting Two (Table 8). A five parameter model was fit by omitting the non-significant additive - dominance parameter. This had two advantages: improved precision of estimates of the remaining parameters, and second, it allowed a X^2 goodness of fit test with one degree of freedom for the five parameter model (Table 8).

The X^2 goodness of fit test indicated that a digenic inheritance model with five parameters fit the data from both plantings better than either the digenic model with six parameters or the simple additive - dominance inheritance model. In Planting One, genetic effects were significant at $p = .05$, and simple additive genetic effects were highly significant at $p = .01$. This would indicate that epistatic effects are small relative to additive genetic effects. Epistatic effects were not significant in Planting Two when a five parameter model was tested, yet the X^2 test indicated a better fit to this digenic inheritance model than to a simple additive - dominance model. Again, additive effects are the predominant genetic effects with minimal dominance and interaction effects being expressed. Overall, the two plantings responded in a similar fashion with the exception of

Table 8. Five and six parameter perfect fit estimates of the additive, dominance and digenic interaction effects for the inheritance of pod detachment force in two plantings in 1992.

Genetic effect[z]	Six Parameters	Five Parameters	Six Parameters	Five Parameters
	Planting One		Planting Two	
m	16.93 ± 1.46	16.92 ± 1.46	6.22 ± 1.43	6.24 ±1.43
a	4.62 ± .32***	4.56 ± .27***	3.79 ± .31**	4.01 ± .26***
d	-14.73 ± 3.96*	-14.70 ± 3.96*	13.58 ± 3.88***	13.52 ± 3.88*
aa	-6.14 ± 1.43***	-6.13 ± 1.43*	3.52 ± 1.40*	3.50 ± 1.40^{ns}
ad	-0.42 ± 1.37^{ns}	------	1.43 ± 1.35^{ns}	------
dd	8.87 ± 2.62***	8.85 ± 2.62*	-6.30 ± 2.56^{ns}	-6.26 ± 2.56^{ns}
$X^2_{(1)}$	------	.08	------	.98

[z]Genetic effects are: m (mean), a (additive), d (dominance), aa (additive x additive), ad (additive x dominance), dd (dominance x dominance).
X^2 = Chi square.
*, **, ***, ns Significant at or below .05, .01, .001, or nonsignificant by two-tailed t test using 4 and 5 degrees of freedom for the five and six parameter models, respectively.

degree of epistatic expression. This would suggest that while additive genetic effects predominate, environment can enhance the expression of non-allelic interactions.

An interesting point to note is that the signs of four of the six parameters were exactly opposite in the two plantings. For example, in Planting One, the dominance, additive x additive, additive x dominance genetic effects were all negative, while in Planting Two the estimates for these effects were of equal magnitude but were positive. According to Mather and Jinks (1982), interactions in which dominance and dominance x dominance genetic effects have opposite signs is an indication that the predominant type of interactions are mainly of the duplicate epistatic kind. When these parameters have the same sign, the interactions are generally of a complementary epistatic kind. In both plantings the signs were opposite, indicating the former type of non-allelic interaction.

Correlation coefficients were calculated from Planting One data only because this had the more complete set of measurements. Correlation coefficients between PDF , sieve size, seed length, and immature seed color were significant in the F_2 and parental generations only (Table 9). All correlations were positive. The correlation of seed length with PDF appears to be slightly greater than the correlation of sieve size with PDF. This is because seed size is a better indicator of pod age than sieve size. There is a high positive correlation between sieve size and seed length (r = .50 - .75 depending on generation), which could lead to the assumption that in most cases, measurements of either trait should be a good indicator of pod age. Two generations segregated for immature seed color (ISC), the F_2 and backcross to 'Easy Pick'. Correlation of pod detachment force to immature seed color in the F_2 generation was significant but very weak. The results indicate a trend of increasing PDF with green ISC which is the seed coat color of '91G', and immature green color is dominant over white (Baggett, 1984).

Table 9. Correlation coefficient (r) of pod detachment force to sieve size, seed length, and immature seed coat color in Planting One.

Generation[z]	n[y]	PDF & Sieve[x]	PDF & Seed length	PDF & ISC	Sieve & Seed length
P'	59	.18	.25*	---	.74***
B'	86	.07	.14	---	.59***
F1	98	.02	.15	---	.56***
F2	196	.18**	.34***	.12*	.58***
B	97	.16	.08	-.04	.50***
P	60	.04	.25*	---	.70***

[z]Based on mean of 3 pods/plant. P' = 91G, B' = BC to 91G, p = Easy Pick, B = BC to Easy Pick
[y]n = Total number of plants sampled.
[x] Immature seed color has a value of 1 = white or 2 = green.
*,**,*** Significant at p = 0.1, 0.05, 0.001.

Heritability

Heritability estimates from the 1992 plantings resulted in a negative estimate for dominance variance in Planting One and a very small estimate for dominance variance in Planting Two (Table 10). Using zero as a value for dominance variance in Planting One, broad sense heritability, h^2_B, was estimated to be 58.8% and 55.9%, respectively, for plantings one and two. Narrow sense estimates, h^2_N, were quite high at 58.8% and 54.5%, respectively. This would indicate a relatively high proportion of the heritability is due to additive genetic effects and selection for low PDF would likely be effective.

Table 10. Estimates of the variance comonents used in calculating heritability for two plantings in 1992.

	Variance Component			Heritability Estimate	
	V_a	V_d	V_e	h^2_B	h^2_N
Planting One	11.39	-6.41 (= 0)	7.98	58.8%	58.8%
Planting Two	6.75	0.18	5.46	55.9%	54.5%

V_a = Additive genetic variance = $2VF_2 - (VB_1 + VB_2)$.
V_d = Variance due to dominance effects = $(VB_1 + VB_2) - VF_2 - (VP_1 + VP_2 + VF_1)/3$.
V_e = Variation due to environmental effects = $(VP_1 + VP_2 + VF_1)/3$.
h^2_B = Broad sense heritability = $(V_a + V_d)/(V_a + V_d + V_e)$.
h^2_N = Narrow sense heritability = $V_a/(V_a + V_d + V_e)$.

The heritability estimates calculated from the variance components of 100 F_3 families in 1993 pertain to only one environment and one year. The heritability estimates resulting from parent-progeny regression represent data from two years. A more reliable estimate of heritability would require data from several locations or years to observe performance over multiple environments. Estimates using the variance component procedures were similar whether calculations were based on individual plants or plot means therefore only results based on individual plant data are presented here.

A random effects linear model was used to define the analysis of variance of balanced data:

$$y_{ij} = \mu + g_i + b_j + gb_{ij} + e_{ijk}$$

where μ = mean, g_i = variation due to families or lines, b_j = variation due to blocks, gb_{ij} is the family x block interaction and is equivalent to the error variance between families, and e_{ijk} is the within family error variance (Table 11).

Block, family, and block x family genetic effects are all considered random in this model. The between family variance is equal to the covariance among families, and as such is an estimate of the total additive genetic variance, assuming epistasis and dominance are negligible.

Table 11. Method used for analysis of variance of 100 F_3 families evaluated in a randomized complete block design in one location and one year using individual plants within a plot rather than plot means.

Source of Variation[Z]	Degrees of Freedom	Mean Squares[Y]	Expected Mean Squares[X]
Block	2 = 3 - 1	MS_b	$\sigma^2_w + s\sigma^2_{gb} + sg\sigma^2_b$
Line	99 = 100 - 1	MS_g	$\sigma^2_w + s\sigma^2_{gb} + sb\sigma^2_g$
Block x Line	198 = (3 - 1)(100 - 1)	MS_{bg}	$\sigma^2_w + s\sigma^2_{gb}$
Error	1800 = (3)(100)(7 - 1)	MS_w	$\sigma^2_w = \sigma^2_{s:gb}$
Total	2099 = (7)(3)(100) - 1		

[Z] Block x line = error between families; Error = variation within families.
[Y] $_{b, g, bg,}$ and $_w$ represent the effects of blocks, families, blocks * family, and within family error, respectively; σ^2 refers to the variance effect.
[X] s, b and g refer to the number of plants within a plot, blocks, and families, respectively.

The test statistic for the hypothesis $H_o : \sigma^2_g = 0$, or that there are no differences between F_3 families, is an F-statistic. (Table 12). The F test statistic of 5.87 was highly significant, confirming that genetic differences in pod detachment force between families did exist (Table 13). The between-family heritability was quite high, 83%, while heritability based on individual plants (from which single pod measurements were taken) was only 23% (Table 14). Heritability estimated by regression of the F_3 family means onto F_2 parental PDF values was 27 ± 4.5%, and is similar to the heritability estimate based on individual F_3 plants (Figure 11). Since

Table 12. F tests for the analysis of variance of 100 F_3 families evaluated in a randomized complete block design in one location and one year where blocks and lines are random effects, determined by equating mean squares and solving for the components.

Source of Variation	Mean Squares[Z]	F test[Y]	Expected mean squares
Block	MS_b	MS_b/MS_{bg}	$[\sigma^2_w + s\sigma^2_{bg} + sg\sigma^2_b] / [\sigma^2_w + s\sigma^2_{bg}] = sg\sigma^2_b$
Line	MS_g	MS_g/MS_{bg}	$[\sigma^2_w + s\sigma^2_{bg} + sb\sigma^2_g] / [\sigma^2_w + s\sigma^2_{bg}] = sb\sigma^2_g$
Line x Block	MS_{bg}	MS_{bg}/MS_w	$[\sigma^2_w + s\sigma^2_{bg}] / [\sigma^2_w] = s\sigma^2_{bg}$
Error	MS_w		

[Z] $_{b, g, bg}$ and $_w$ represent the effects of blocks, families, block * family interaction, and error within families, respectively.
[Y] s, b, g, and bg refer to the number of plants within a plot, blocks, families, block * family interactions, respectively.

Table 13. Analysis of variance for 100 F_3 families evaluated in one year and one location in a randomized complete block design where all effects are random.

Source of Variation	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	299	29714.5654	99.3798	4.54	0.0001
Block ($\sigma^2 b$)	2	6372.5164	3186.2582	106.50	0.0001
Family ($\sigma^2 g$)	99	17418.3323	175.9428	5.88	0.0001
Family x Block ($\sigma^2 e$)	198	5923.7166	29.9178	1.37	0.01
Error (σ^2 w)	1796	39296.7435	21.8801		
Corrected Total	2095	69011.3089			

R-Square	C.V.
0.430575	33.92240

Table 14. a. Estimates of genetic variability between and within F_3 families using restricted maximum likelihood variance components estimation procedure for 100 families evaluated in a randomized complete block design with balanced data in one location and one year. b. Restricted maximum likelihood variance component estimates. The numbers in bold were used as estimates of the genetic variances.

A. Genetic estimates:	Estimate	Variance Components[z]
Genetic variance (σ^2_G)	6.95	σ^2_G
Error variance		
Between family (σ^2_{GB})	1.15	σ^2_{GB}
Within family (σ^2_W)	21.88	σ^2_W
Phenotypic variance (σ^2_P)		
Between family	8.38	$(\sigma^2_W / sb) + (\sigma^2_{GB} / b) + \sigma^2_G$
Within family	29.98	$\sigma^2_W + \sigma^2_{GB} + \sigma^2_G$
Heritability (σ^2_G / σ^2_P)		
Between family	0.83	
Within family	0.23	

[z] s = no. of plants within a plot and b = no. of blocks.

B. Example of Reml Variance Component Estimates:

Iteration	Objective	Family (σ^2_G)	Block (σ^2_B)	Family x Block (σ^2_{GB})	Error (σ^2_W)
0	6742.30833	6.97977	4.53902	1.14103	21.88115
1	6742.30735	6.95125	4.51578	1.15093	21.87946
2	6742.30735	**6.95125**	**4.51578**	**1.15093**	**21.87946**

this estimate is based on the relationship of progeny means to the observed parental PDF, it may be more reliable than estimates based on variance components.

Standardized selection differentials (R), were calculated for both F_2 and F_3 generations using the formula $R = k(c)(h^2)(p^2)^{1/2}$ where k is the selection differential, c is the gamete control factor (=1), h^2 is the estimated heritability and p^2 is the phenotypic variance (Appendix 1). Selection of the top 10% of F_2 plants could result in a lowering of the PDF by 4.27 and 3.17N, from a mean of 11.76 ± 3.60 and 11.39 ± 3.52N, for plantings One and Two, respectively. The 100 F_2 plants used as parents for the F_3 generation are representative of the range of PDF values found in the F_2 generation, and had a mean of 11.80N.

Standardized selection differentials for the F_3 generation were calculated based on n = 100 families and n = 700 individuals for between and within family selection response, respectively. Predicted gains from selecting 5% and 10% of families with the lowest PDF using a heritability estimate of 83% would potentially reduce pod detachment force by 4.78 and 3.97 N, respectively, from an overall mean of 13.79 ± 5.74 N. If one were to select individual plants from a population of 700 plants, equivalent to the number of plants in each block or planting date in this case, the gains from selecting 6% and 10%, or 40 and 70 individuals, for low PDF are 2.48 and 2.11N. Reduction in PDF based on a heritability of 27% from parent-progeny regression estimates is predicted to be 2.44 - 2.94N, similar to the predicted gains made by individual plant selection in the F_3 generation. Gains would be achieved through selecting entire families followed by selecting the best individuals within the best F_3 families since the total genetic variability between families is

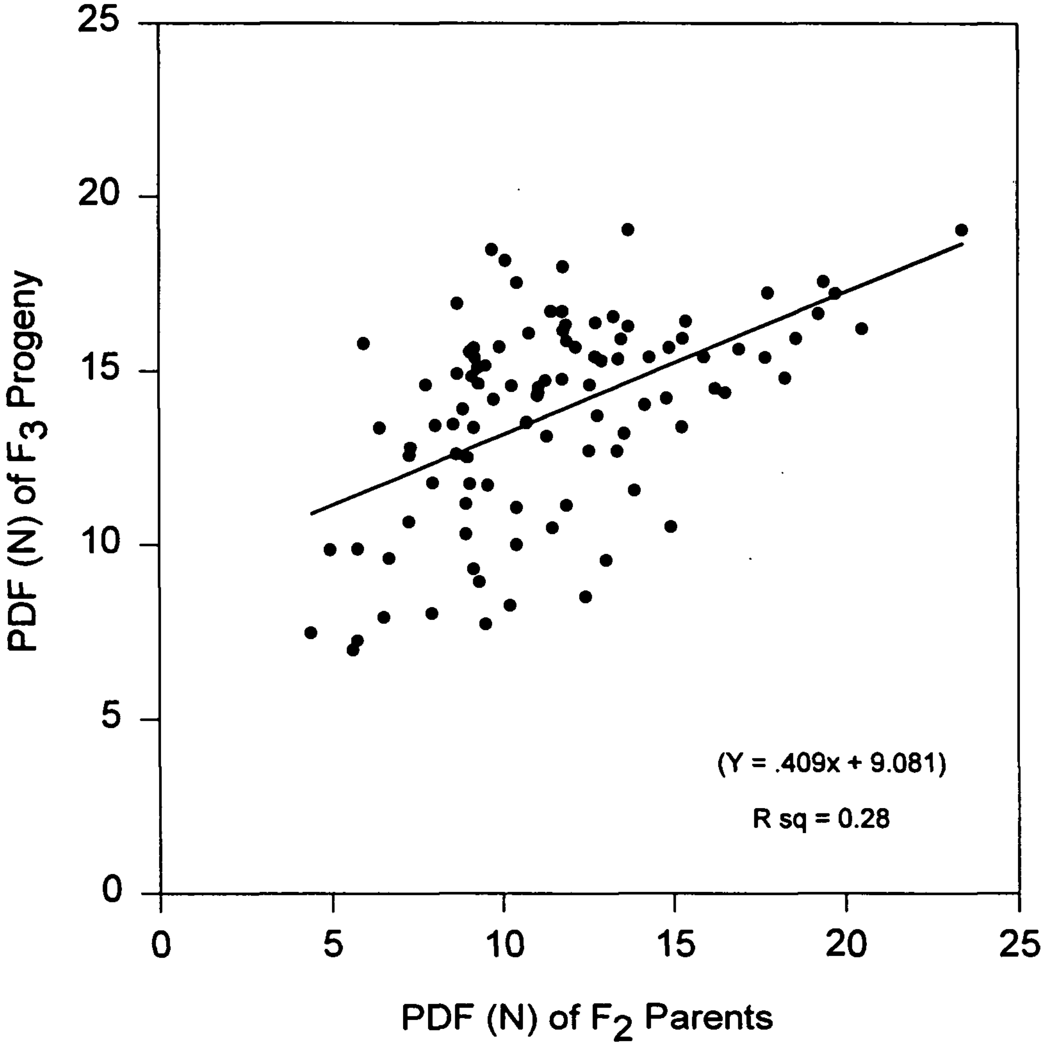

Figure 11. F_3 progeny grown in 1993 regressed onto F_2 parents grown in 1992.

twice that of the additive genetic variance within families. This strategy would take full advantage of additive genetic effects both within- and between-families.

GENERAL DISCUSSION

Pod detachment force was studied in a cross of 'Easy Pick' and '91G, and conclusions regarding the inheritance of pod detachment force only apply to the material used in this study. To determine if these results apply to a wider array of genotypes one would need to include measurements from several crosses and from more than one environment or year. As mentioned previously, additional data has been collected but was not available for inclusion in this study. The intent was to combine the studies on pod detachment force for publication at the completion of this project.

The parental study cleared the way for a better understanding of sampling variability within the two parents, and provided valuable information as to optimal sampling time. Values for 'Easy Pick' varied little across all plantings, averaging 5.41 ± 1.42N in 1992 to 6.11 ± 2.02N in 1993. Average PDF in '91G' from the same plantings was 13.21 ± 2.53N and 16.42 ± 4.56N, respectively. Values obtained in 1993 are slightly higher, which is possibly due to environmental influence on the expression of the character.

In the two-week period during which pods were sampled, it was evident that pod age as much as pod size affected pod detachment force. Within a sampling day, PDF remained fairly consistent up to sieve size 5.0 for the first week, and greatly increased thereafter. Pod detachment force increased overall after day 8, indicating that one week was the maximum sampling period allowable within a homogeneous group of plants. Regardless of pod size, pod detachment force of 'Easy Pick' was always significantly less than '91G' on a given sampling day. Based on these results, it appears that sampling in all other plantings was done within the appropriate time frame needed to minimize the effects of pod age on pod detachment force.

It must be recognized that inherent differences in days to maturity exist between cultivars, and the parents used in this study were no exception. The pods of '91G' mature about one week earlier than 'Easy Pick' and are slightly larger at harvest maturity. Measurements recorded in the parental study were taken on the same days, and therefore adjustments might be required to make a more accurate comparison of PDF at the true sieve potential. Since 'Easy Pick' has a slightly smaller pod, a better comparison might be to compare pods of sieve size 3 of 'Easy Pick' to pods of sieve size 4 of '91G'. This would increase the differences in PDF between the two. If one were to base PDF on maturity factor such as days after first bloom, then one would need to compare PDF of 'Easy Pick' recorded approximately one week after measurements of '91G'. An examination of Figure 1 indicates that differences between the two would still be detectable. Recognizing that progeny are also segregating for pod shape, pod size, and days to maturity in addition to PDF, it was necessary to make a decision as to when the best time to collect data might be. Based on the differences between parents, an assumption was made that measurements for PDF based on a common sieve size of 4.0 for all progeny would average out the effects that other segregating factors may have.

The expression of the easy pick character did not fit tidily into discrete classes but followed a continuous distribution, indicative of a a pattern of quantitative inheritance. The primary genetic effects in the cross between 'Easy Pick' and '91G' were additive for both plantings. Perfect fit estimates also indicated the presence of dominance, additive x additive, and dominance x dominance interaction effects in Planting One. Digenic interaction effects were non-significant in Planting Two after the fitting of a five parameter model gave a perfect fit, but simple dominance effects were significant.

These results do not agree with the manner of inheritance of pod detachment force previously reported (Bassett, 1976). Working with cultivars that are unrelated to the cultivars used in ths study, Bassett determined that the easy pick character was the result of dominance genetic effects contributed by the high parent, 'Harvester', and estimated the number of genes controlling the expression to be two. Data from Planting Two in this study more closely resembles the pattern of inheritance seen in Bassett's study. However, the data from Planting One clearly indicate an additive mode of inheritance. Bassett estimated a narrow sense heritability of 61%, which is similar to the estimates derived from variance components in the present study. Results from both studies suggest that low pod detachment force could successfully be transferred to other snap bean lines, including '91G'.

The calculation of perfect fit estimates can be influenced by the interaction of many genes having varying degrees of cancellation of positive and negative effects. This cancellation can subsequently influence the calculated additive and dominance effects, and may be why the two different studies, Bassett's (1976) and the present one, are able to come to such different conclusions about the mode of inheritance of the easy pick trait, yet estimate similar heritabilities.

It should be pointed out that the parental material used in Bassett's study (1976), had higher average PDF values overall than the material used in the present study.

However, in both his study and the present one, the PDF of pods from the high parent was almost double that of pods from the low parent. A screening study for PDF was carried out at Oregon State University in the mid 1980s and included the cultivars 'Idlelight', 'Easy Pick', and '91G' as well as several other genotypes. PDF was observed at three sieve sizes over a four week period in the same planting. In this earlier study the PDF of pods from 'Idlelight' at sieve sizes three and four was intermediate between that of 'Easy Pick' and '91G', tending more toward '91G'. It is firmly believed that the 'Easy Pick' germplasm is unique in its low PDF, and has a lower PDF than 'Idlelight', the low parent used in Bassett's study.

The heritability of a character is the proportion of the phenotypic variance which is due to genetic effects. The effectiveness of selecting for a specific character within a genetically variable population will depend upon the level of heritability, i.e. a character with high heritability will be expressed in a predictable manner in the progeny.

Heritability estimates calculated from variance components are based on second order statistics which involve the partitioning of observed phenotypic variation into genetic and environmental components. If the genetic variation is large relative to the environmental variation, then heritability will be high. Heritability estimates calculated from parent-progeny regression are based on observed parental and progeny PDF values and their relationship to one another.

Certain assumptions have to be satisfied for heritability estimates to be accurate, otherwise the estimates are biased upwards. These assumptions, such as growing progeny in more than one environment, random selection of parents, and random mating of progeny, were not met because the F_3 progeny were grown from selfed parents in one year in one location, and the F_2 were also grown in only one year. Keeping this in mind, one should interpret the heritability estimates cautiously knowing that they are probably biased. In spite of this bias, data from the F_3 lines indicate that the inheritance of the easy pick character is controlled predominantly by additive genetic effects. This is in agreement with conclusions drawn from the generation means analysis, which was based on data collected from two plantings grown in the previous year.

The degree to which a character is inherited can influence the choice of selection procedure used by the plant breeder. One of the principal uses of heritability estimates is to determine which selection method would optimize character improvement and predict genetic advance (Poehlman and Sleper, 1995).

Genetic gain within one cycle of selecting the best 10% of F_2 plants or F_3 families was predicted using the observed variance and heritability estimates of the quantitative character under investigation. Selection response and genetic gain should be favorable with the high degree of additive genetic effects seen in both 1992 and 1993. A decrease in PDF of 3.72N (4.27 + 3.17 / 2) was predicted from selecting among the lowest F_2 plants. A decrease in PDF of 3.97N was predicted from selecting among the lowest F_3 families (when $h^2 = 83\%$), or 2.44N (when $h^2 = 27\%$). This should be interpreted cautiously as only 27 out of 100 F_3 families had a lower mean PDF than their F_2 parent with an observed reduction in PDF of 1.94N. Progeny were not taken beyond the F_3 generation to test F_3 selection response predictions.

SUMMARY

The parental material used in this study was significantly different in pod detachment force at all stages of pod size. In two years of study, 'Easy Pick' consistently exhibited less variability than '91G'. The effective sampling period was determined to be about ± 3 - 4 days within the optimal harvest period.

The continuous distribution and amount of variability seen in the parents and progeny indicate that the expression of the easy picking character is under multigenic control and influenced by the environment. The primary genetic effects were additive although some dominance and digenic interaction genetic effects were also detected. Parameter estimates of dominance and dominance x dominance genetic effects were of opposite sign, suggesting duplicate epistatic effects. The exact nature of the epistatic effects could not be determined because the generations required for such analyses were not available.

Heritability estimates also indicated that the mode of inheritance is predominantly additive and selection for the character should be effective. However, since there were no progeny recovered with pod detachment force as low as 'Easy Pick', but several F_3 progeny had PDF higher than '91G' these results should be interpreted cautiously. Predicted selection response suggests that gains will be made from individual selection in the F_2 as well as family and individual selection in the F_3 progeny.

The information presented here should be useful in determining breeding and selection strategies for low pod detachment force should the green bean processing

industry feel it would be to their advantage to have easy-picking bean lines suitable for mechanical harvest.

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APPENDICES

Appendix 1. Standardized selection differential for family and individual selection in the F_3 generation.

Family Selection

j = number selected and n = number of lines evaluated

J	N	P	K
1	100	0.01	2.479
2	100	0.02	2.314
3	100	0.03	2.184
4	100	0.04	2.078
5	100	0.05	1.988
6	100	0.06	1.908
7	100	0.07	1.836
8	100	0.08	1.770
9	100	0.09	1.709
10	100	0.10	1.652

Individual Plant Selection Within a Family

j=number selected and n=number of plants evaluated

J	N	P	K
10	700	0.014	2.519
20	700	0.029	2.265
30	700	0.043	2.096
40	700	0.057	1.965
50	700	0.071	1.856
60	700	0.086	1.760
70	700	0.100	1.675

Formula for using the selection differential to select top 1 - 10 families or top 10 - 70 individuals in the F_3 generation:

$$R = k\,(c)(h^2)(p^2)^{1/2}$$

where k is the selection differential, c is the gamete control factor, h^2 is heritability estimate, and p^2 is phenotypic variance. C is equal to 1 when intermating is done between selected female and male parents.

Appendix 2. Observed generation means of Planting One for pod detachment force (PDF), sieve size, and seed length in 1992.[Z]

		PDF	Sieve Size	Seed length
Generation[Y]	n	Mean ± s.d.	Mean ± s.d.	Mean ± s.d.
EZP	60	5.75 ± 1.88 a	3.7 ± .41 ab	6.7 ± .51 c
B_1	97	7.93 ± 2.67 b	3.8 ± .44 abc	6.3 ±.51 ab
F_1	98	10.72 ± 3.03 c	3.8 ± .38 c	6.2 ± .45 ab
F_2	196	11.76 ± 3.60 d	3.7 ± .35 a	6.3 ± .56 b
B_2	86	12.39 ± 2.72 d	3.8 ± .44 bc	6.1 ± .47 a
91G	59	14.94 ± 3.35 e	3.8 ± .37 abc	6.4 ± .53 b
MSD		.82	.12	.01

Appendix 3. Observed generation means of Planting Two for pod detachment force (PDF) and sieve size in 1992[Z].

		PDF	Sieve Size
Generation	n	Mean ± s.d	Mean ± s.d
EZP	61	5.41 ± 1.42 a	4.47 ± .27 b
BC_1	93	8.76 ± 3.53 b	4.47 ± .28 b
F_1	108	12.96 ± 2.82 d	4.22 ± .30 a
F_2	200	11.39 ± 3.52 c	4.46 ± .35 b
BC_2	87	13.19 ± 2.36 d	4.46 ± .39 b
91G	62	13.21 ± 2.53 d	4.70 ± .40 c
MSD		.79	.09

[Z] Mean separation by Waller-Duncan k-ratio t test, k-ratio = 100.
[Y] EZP = Easy Pick, B_1 = BC to Easy Pick, B_2 = BC to 91G.

Appendix 4. **Pod detachment force and percentage of pods in each size class in 'Easy Pick' snap bean from August 18-September 1, 1992.**

Sampling Day		Sieve Size														n^z
		0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	
2	pdf	3.62	4.36	5.12	4.54	4.58	5.01	6.74	5.78	4.85						239
	%	52.7	12.6	5.8	13.8	4.6	5.4	2.1	2.1	0.8						
4	pdf	4.29	4.56	4.58	4.47	4.62	3.77	3.80	4.26	5.46	9.21					199
	%	27.6	12.1	9.0	14.6	10.6	11.0	5.5	5.5	3.0	1.0					
6	pdf	4.35	4.45	4.21	4.16	4.11	4.90	4.40	4.38	6.82	7.57	2.45				192
	%	11.4	7.8	7.8	14.6	12.0	11.4	13.5	12.5	5.7	2.6	0.5				
8	pdf	3.48	5.23	4.79	4.51	5.08	5.49	4.79	5.83	5.45	7.68	10.51	7.45			190
	%	9.5	3.2	4.2	8.4	8.4	13.2	11.0	20.5	11.0	6.3	3.7	0.5			
10	pdf	5.34	4.04	4.71	5.87	4.92	4.80	4.63	6.98	8.23	11.22	12.03	17.10			222
	%	1.8	4.1	4.5	7.6	5.4	13.1	11.7	18.9	9.9	12.6	5.0	5.4			
12	pdf	6.04	5.60	6.37	6.45	5.19	4.51	6.67	6.41	7.73	11.31	12.79	14.88	19.21	18.52	223
	%	1.3	2.7	0.9	4.0	5.8	4.5	6.3	18.4	10.8	22.0	9.4	10.8	0.4	2.7	
14	pdf	--	4.80	6.14	4.13	3.57	4.71	6.76	6.19	7.34	10.05	12.45	12.84	--	12.63	201
	%		1.0	1.5	3.5	3.5	5.5	2.5	11.4	13.4	21.9	16.9	15.4	0	3.5	

^{z}n = Total number of pods per sampling day from 16 plants were used to calculate mean and percent.

Appendix 5. Pod detachment force and percentage of pods in each size class in 'Oregon 91G' snap bean from August 18-September 1, 1992.

Sampling Day		Sieve Size 0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	n[z]
2	pdf	5.88	8.61	11.80	11.75	13.37	13.48	15.47	16.16	16.37						223
	%	34.1	12.1	4.9	15.7	7.6	15.7	4.5	4.5	0.9						
4	pdf	7.29	9.32	10.48	10.55	11.62	14.70	15.56	16.91	16.87	20.56	13.35				231
	%	10.4	3.0	3.9	12.1	14.7	13.0	12.6	14.7	9.5	3.9	2.2				
6	pdf	6.76	8.28	11.54	10.00	8.82	11.50	12.65	12.39	16.62	15.97	18.26	19.40	13.33		178
	%	7.9	2.2	2.2	2.8	7.3	16.8	10.1	15.7	12.4	15.2	6.2	0.6	0.6		
8	pdf	5.80	9.80	12.09	10.33	10.61	13.32	13.79	16.48	18.66	20.08	17.86	17.28	14.70	18.36	213
	%	6.1	1.9	2.3	3.8	4.7	8.9	5.6	16.4	18.3	16.4	9.4	4.2	0.5	1.4	
10	pdf	9.06	11.24	10.76	10.24	12.06	13.30	16.32	18.03	17.67	18.87	17.79	20.98	18.23	20.57	197
	%	7.6	4.1	3.0	5.6	5.1	9.1	3.0	10.2	11.7	17.2	11.2	8.1	0.5	3.6	
12	pdf	8.69	7.90	11.96	11.97	10.61	14.90	13.62	13.25	17.58	17.87	18.57	21.56	--	23.63	201
	%	1.5	2.5	1.0	4.5	4.0	3.5	3.5	5.0	4.0	21.9	20.4	18.4	0	9.9	
14	pdf	--	10.88	5.19	10.31	13.78	10.92	13.35	13.58	15.63	13.47	20.26	21.29	9.51	22.62	179
	%	0	0.6	0.6	5.0	3.4	4.5	2.2	7.8	6.7	10.0	12.8	17.3	1.1	27.9	

[z]n = Total number of pods per sampling day from 16 plants were used to calculate mean and percent.