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GENOTYPIC AND ENVIRONMENTAL VARIATION IN PROTEIN CONTENT OF FIELD PEAS

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ABSTRACT

GENOTYPIC AND ENVIRONMENTAL VARIABILITY IN PROTEIN CONTENT OF FIELD PEAS

The contributions of genotype, location, and year to variability in yield and protein content of field peas were estimated from a study of 25 genotypes grown at three locations in one year and 22 genotypes grown at one location for three years. Protein content was less variable than yield within and among locations and years. Protein content varied substantially with locations but only slightly with years.

The relationship of protein content to several other plant traits was assessed. Protein content was not correlated with height, harvest index, seed weight, or days to flower. However, it was consistently negatively correlated with yield over locations, years and a wide range of genotypes. Coefficients of determination showed that between 6 and 66% of the observed variation in protein content over three experiments was associated with variation in yield. The negative relationship diminished among F_2 populations, indicating that correlations between traits among heterogeneous populations may be misleading. Physiological explanations for the negative yield-protein content correlation were offered.

Yield and protein yield were very highly correlated, whereas protein content and protein yield were unrelated. This indicates that improved protein productivity would come only from

increased yield.

Methionine content of field peas expressed as mg met/g meal and as mg met/g protein was low and the range was very narrow, indicating insufficient scope for improvement by breeding among the genotypes tested. Protein content was positively correlated with mg met/g meal but not correlated with mg met/g protein.

Broad-sense and narrow-sense heritability estimates for protein content were low to moderate, and additive inheritance was indicated. Mg met/g protein was not heritable, indicating the need for an alternative approach to protein quality improvement.

Reported differences between smooth-seeded and wrinkle-seeded genotypes were verified and a new one added. The gene for wrinkling caused a seed-weight reduction in wrinkle-seeded compared with smooth-seeded progeny of crosses between parents of different seed shape, regardless of parental seed weight. The range in protein content among 1071 genotypes from the U.S.D.A. World Pea Collection was very narrow (22.6 to 30.9%), compared with the wide range in yield and very wide range in seed weight of the same genotypes.

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DEDICATION

This thesis is dedicated to the memory of my late father,

Alan John Jermyn.

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1. INTRODUCTION

Pisum sativum L. is a temperate-zone legume with edible seeds rich in protein. As such, it has the potential to provide much-needed protein for both humans and livestock in an increasingly protein-scarce world. The possible global lack of dietary protein has stimulated considerable research interest in the legumes whose seeds are consumed in the dry form (pulses). For peas, and pulses in general, to realize their potential in protein productivity, research emphasis must be placed on improving the dry matter and protein yield of these crops, along with improvement in the quality, digestibility, and acceptability of the protein.

The Protein Advisory Group (PAG) of the United Nations System issued guidelines for future research on legumes in Statement 22 (1973). Under the heading, "Genetic Improvement of Nutrient Composition and Digestibility", the Statement noted that the range of variability for nutritional components should be determined in each of the recommended species, and improvement made within crops where sufficient protein variability has been established, but only after it has been established that genetic changes;

(1) are possible, i.e. the component is heritable,

(2) will not adversely affect other nutritionally beneficial components, and

(3) will result in overall improvement of the total diet.

Among the legume crops, only soybeans (Glycine max (L.) Merrill) have undergone intensive breeding for yield and protein improvement and the results, on the whole, have been disappointing. Yield

increases have not kept pace with advances made in cereals, and protein content has been improved only marginally, usually at the expense of other seed components (Caldwell et al.,1973). In Western Canada, field peas were seen as a suitable alternative crop to cereals in the early 1970's when surpluses were a problem, and assumed greater importance as an alternative source of protein for livestock with the advent of high prices for imported soybean meal in 1973.

The present study is part of an ongoing program of research into all aspects of field pea production and utilization at the University of Saskatchewan, Saskatoon.

The objectives of this study were four-fold;

(1) To determine the contribution of genotype, location, season, and environment to the variability in protein content.

(2) To provide information on the relationship of protein content to other plant traits which are or may become agronomically important, and to protein quality parameters.

(3) To provide heritability estimates of protein content and protein quality.

(4) To determine the extent of genetic variability in protein content among 1,100 genotypes from the U.S.D.A. World Pea Collection.

2. LITERATURE REVIEW

Protein content of field pea seed is determined by genotype, various factors of the environment, and genotype x environment interactions. It is also influenced by the negative correlation between yield and protein content. Changes in protein content caused by any of the above factors frequently have an effect on protein quality. Consequently, a low heritability value for protein content and protein quality may be predicted.

2.1 Effect of genotype on protein content

Apart from expected phenotypic variation, genotypic factors which influence protein content include maternal influence, seed size and shape, and maturity.

2.1.1 Phenotypic effects

Various researchers have detected significant variation in protein content within pea cultivars and often attributed this to genotypic rather than phenotypic effects.

Kurnik et al.(1972) found variability within pea cultivars to the extent that they considered the cultivar as being heterozygous for protein content and quality, and suggested that selection within a cultivar could increase protein content by 2 to 3% without changing important characteristics of the cultivar. Berdyshev (1966) determined the protein content of 186 plants of the cultivar Torsdag and reported a range of 18.1 to 28.0%, but most of the plants contained 22 to 24% protein. To ascertain whether the differences were genetically based, Berdyshev grew progeny from plants of known

protein content from the extremes of the Torsdag range. There was no direct correlation between protein content of parental plants and their offspring. The lack of relationship was ascribed to "the fact that plants undergo both genetic and non-genetic changes". Nevertheless, choosing high protein plants from high protein parents enabled Berdyshev (1966) to "reinforce this characteristic and produce stable forms rich in protein." In further plant breeding work, only plants which had been selected for high protein content were used in crosses. Furedi (1970) selected high protein lines from within two commercial pea cultivars and grew them for three years. Differences among lines were apparent in favourable years, but dropped to insignificance in a year not optimal for protein accumulation. The range of protein content among lines of the wrinkle-seeded cultivar Kelvedon was approximately 25.5 to 31.0% in 1964 and 24.0 to 26.5% in 1963 and 1965. Protein content of lines from the cultivar Pauli varied from 22.0 to 25.0% and showed little change over years. Furedi (1970) commented that efficient selection could only be conducted in a favourable year when differences among lines were clearly expressed, but he did not wish to imply an over-estimation of "phenotypically positive forms."

Ali-Khan and Youngs (1973) found significant differences for protein content among plants within genotypes. The range was commonly 22 to 26% protein. These authors noted that genetic heterogeneity was probable in some genotypes, and thus considered both genetic and non-genetic differences responsible for the observed range. Differences within plants, from three different sampling

positions, were significant, but not large, i.e., 24.1%, 23.9% and 23.7% for mean protein content of peas from low, medium, and high node positions. Wolffe and Hamblin (1974) reported similar findings in Phaseolus vulgaris L. There were no differences among bean seeds within a pod, but significant differences among pods at a node, among nodes within a plant of an indeterminate cultivar where protein content decreased with ascending node position, and among plants within genotype but only for two of four genotypes tested. These authors expressed surprise that individual plants within a known homozygous cultivar would differ significantly in protein content.

Shia (1976) found highly significant differences in protein content among plants of Trapper peas grown in the field and also among plants grown in hydroponic culture. Differences in protein content of peas produced on different nodes were also significant. In general there was a decrease in protein content with ascending node number.

2.1.2 Maternal influence

Maternal influence on protein content may be illustrated by the presence of a relatively constant protein content in all seeds borne on a given maternal plant regardless of their genotype.

Maternal influence on protein content has been reported in soybeans, Glycine max L. (Singh and Hadley, 1972), Phaseolus vulgaris L. (Leleji et al. 1972), Vicia faba L. (Selim et al. 1974), and peas by Berdyshev (1966). Shia (1976) did not find significant differences between F_1 and selfed seeds borne on the same low protein parent in three crosses with high protein parents. However, he emphasized that inherent differences in protein content between

wrinkled seeds and smooth seeds borne on the same plant could confound possible maternal effects.

2.1.3 Seed shape

The differences between smooth and wrinkled pea seeds have been described recently by Kooistra (1962). Apart from the obvious seed appearance, wrinkled seeds have compound starch grains, a lower starch content, a higher percent of amylose in the starch, higher sugar content, greater water absorptive capacity, and greater water loss upon maturity than smooth seeds. Kooistra reported finding two new types of wrinkled seeds, one with smooth oval starch grains and the other with a lower starch content. In most other respects they were similar to the common type of wrinkled pea. Matthews and Whitbread (1968) indicated that the lower field emergence frequently reported for wrinkle-seeded peas relative to smooth-seeded peas, could be related to greater exudation of electrolytes leading to a greater susceptibility to Pythium ultimum. Furedi (1970) reported that "marrowfat" or wrinkle-seeded peas were slightly higher in protein content than smooth-seeded peas. He attributed the increased protein content to a slower accumulation of starch. Shia (1976) studied differences between smooth- and wrinkle-seeded F_3 progeny from crosses between low-protein, smooth-seed peas and high-protein, wrinkle-seeded peas. He found that wrinkle-seeded F_3 progeny were higher in protein content (average of 3.4%), and lower in seed yield and seed weight than corresponding smooth-seeded F_3 progeny. He also verified the starch differences as described by Kooistra (1962).

Shia considered that the higher protein content of wrinkle-seeded peas was not a pleiotropic or genetic effect, but more likely stemmed from the interaction of lower yield, lower seed weight, and lower starch content. Shia also reported significantly lower field emergence from wrinkle-seeded F_3 lines compared to smooth-seeded F_3 lines from the same cross.

2.1.4 Seed size

Davies (1975) showed that differences in seed size were correlated with cell number and cell weight. He demonstrated maternal effects for seed weight, cell number, and dry weight per cell. However, he reported that wet weight per cell was primarily determined by the genotype of the seed. Unfortunately, Davies used wrinkle-seeded genotypes as the maternal parent in crosses with smooth-seeded genotypes and found that the F_1 seed (smooth) differed in water uptake capacity from selfed seed (wrinkled) due to the r_b gene as described by Kooistra (1962), and not necessarily to intrinsic control as suggested by Davies. A more definite system of control for wet weight per cell would have come from reciprocal crosses between two smooth- or two wrinkle-seeded parents. In a related study, Davies and Brewster (1975) found that large seeds have more RNA per cell, primarily rRNA, than small seeds. However, in reciprocal crosses, RNA per cell was determined by the maternal parent. This maternal control of RNA negated a difference in RNA due to seed shape as smooth and wrinkled seeds on wrinkle-seeded maternal plants had similar levels of RNA.

Weickel et al. (1963) measured protein content as percent

of fresh and dry weight of Alaska and Perfection peas in relation to size and maturity at the freezing/canning stage. They reported that protein content was generally greater in large peas on a fresh weight basis, but less on a dry weight basis than in smaller peas. However, since size was really a reflection of physiological age of the seeds, the results were not separable from effects of maturity on protein content. Gottschalk et al. (1975) found no correlation between seed weight and protein content of 148 pea mutants. Ali-Khan and Youngs (1973) found a non-significant negative correlation (r= -.12) between protein content and seed weight in 10 cultivars.

2.1.5 Maturity

Weickel et al. (1963) reported that in peas harvested at the canning stage, protein content was generally greater in larger fresh peas than in smaller, i.e. less mature peas. Protein content of fresh peas was greater on a wet weight basis at advanced maturity than in earlier maturity. Furedi (1970) measured protein content of three canning pea cultivars at three stages of seed maturity; soft, semi-hard, and hard. With increasing maturity (hardness) protein content as percent of dry matter decreased from 29.00% at the first stage through 25.00% at the second stage to 24.35% at close to full maturity. Furedi remarked that the decrease in protein content is only relative to the increase in dry matter content.

Danielsson (1952) showed that,although protein content decreased almost linearly toward maturity, nitrogenous substances increased in absolute amount during the same period. Protein N and globulin N [illegible] inly during the first part of the

ripening process, while albumin N increased slowly at a constant rate. The globulin: albumin ratio decreased with time as did the vicilin : legumin ratio. These two components of globulin began synthesis at different times and increased at different rates. Millerd (1975) reported that vicilin and legumin could be detected at 9 and 10 days from flowering respectively, and the final ratio of vicilin to legumin was not constant within or between cultivars.

Pandey and Gritton (1975) grew nine pea cultivars in two years to study changes in protein content during maturation. As determined by the Kjeldahl procedure, protein decreased with increasing maturity. Protein content at the canning stage was correlated highly ($r = .91$) with protein content at the mature stage. Gritton et al. (1975) studied protein content and amino-acid composition of three pea cultivars during maturity. Protein content was highest 12 days after pollination, dropped markedly to the 18th day, and increased subsequently but did not attain the level recorded at 12 days. Changes in amino-acid levels were greatest up to 18 days after pollination. Glutamic acid, the main amino-acid of storage protein, decreased, lysine and aspartic acid increased, and S- containing amino-acids decreased slightly with maturity. Differences among the cultivars in amino-acid patterns were small. Smith (1973) showed that protein develops in parallel with RNA, and forms an increasing proportion of the total dry weight of the cotyledon. Starch accumulation was somewhat different. It was not detectable until 17 days after anthesis,

but then increased rapidly between days 20 and 35, the increase being almost entirely in starch grain size. Flinn and Pate (1968) described changes during maturation of the fruit of a "field" pea, P. arvense L. They reported differences between the field pea and earlier similar studies with "garden" peas, P. sativum L. In the field pea the phase of intensive starch synthesis was shorter, more hemicellulose was accumulated, but less sugar and starch were accumulated than in the garden pea. There was also a suggestion of differences in amino-acid metabolism between the two types.

2.2 Effect of the environment on protein content

Protein content of peas is influenced by such factors of the environment as the nitrogen supplying capacity of the soil relative to the nitrogen fixed by rhizobia, the availability of other nutrients and their interaction with climate and crop management practices. Cultivar evaluations at different locations and in different years provide an estimate of the effect of a specific environment or series of environments.

2.2.1 Effect of fertilizer application

In field experiments, Buchan (1973) showed that protein content of both the vines and the seeds of field peas increased in response to applied N fertilizer at seeding, but seed protein content was not affected by post-flowering applications of NH_4NO_3. McLean (1972), however, showed that N fertilization did not increase protein content of field peas in conditions of adequate moisture. In pot experiments, he showed that protein content was

increased by high available nitrogen and by high moisture stress. McLean also reported that protein content was increased when fertilizer was applied at rates up to 55 kg/ha of P_2O_5, but decreased at higher rates. In a greenhouse study Trevino and Murray (1975) found that applied NH_4NO_3 significantly increased protein content as well as yield. Protein content of several cultivars ranged from 23 to 31% without applied N and from 35 to 53% at the highest N level applied (200 ppm/week). However, the seed yield was extremely low at this very high N level.

2.2.2 Effect of year and location

Berdyshev (1966) reported that at one location, three genotypes varied in protein content over three years, i.e. Nemchinovsky, 22.4 to 25.6%; Alaska, 28.8% to 31.9%; and Raman, 18.0 to 19.9%. Furedi (1970) collected 95 samples of 27 genotypes at 62 locations and measured variability of protein content. The mean value was 20.7 ± 1.05%. The range in protein content over cultivars and locations was 18.0 to 23.0% and the range among cultivars only was 19.5 to 22.5%. Further data from 9 genotypes at 39 locations confirmed that intra-cultivar variation over locations was almost as large as variation among cultivars. There was a marked genotype by location interaction for protein content. Insufficient data were collected to statistically analyze the year effect, but Furedi (1970) inferred that certain genotypes could attain optimum protein levels only at a suitable location and under optimal conditions.

Ali-Khan and Youngs (1973) studied variation in protein content of peas in Canada. They recorded data from ten cultivars

for three years at one location and from 19 cultivars at four locations for one year. They reported significant differences for cultivars, locations and years and significant cultivar by location interactions. The range in protein content among cultivars was 23.1 to 28.3%, among years 25.8 to 27.4%, and among locations 24.0 to 26.3%. Variation in protein content of nine cultivars in two years at two different stages of maturity at one location was studied by Pandey and Gritton (1975). Protein content varied with cultivar, year, and maturity stage. Interactions between year and cultivar, year and maturity and cultivar and maturity were also significant.

2.2.3 Effect of nitrogen fixation

Nitrogen may be supplied to plants from the soil and by the fixation of molecular nitrogen via the root nodule symbiosis with Rhizobium in legumes. The pattern of activity of the symbiosis in peas has been recently described by La Rue and Kurz (1973). However, few reports show the effect of nitrogen fixation on seed protein content. McLean et al. (1974) reported from pot studies that in the presence of low soil nitrogen, nitrogen fixed by Rhizobium was the principal factor influencing both yield and protein content of peas. Buchan (1973) concluded that effective inoculation increased vine protein content, seed protein content, and total seed and plant protein of three cultivars grown in nitrogen deficient soil in a growth chamber. In field experiments, effective inoculation increased Century field pea nitrogenase activity, but not

yield or protein content. The soil for the latter experiments was high in nitrate, and the peas fixed a maximum of 12.6% of their total nitrogen uptake. Holl and La Rue (1975) report a value of 30% of total plant nitrogen as being usual for the contribution of the symbiont.

2.3 Effect of yield on protein content

Most reports in the literature indicate a negative relationship between yield and protein content. This relationship is widely accepted in cereals, but legume researchers have been reluctant to recognize it as an obstacle to increased protein content.

2.3.1 Cereals

In a discussion on the "bio-chemical and molecular-genetic prerequisites in the relations of plants for protein", Konarev (1973) commented that the genetic basis of protein quantity and quality in crop plants must be elucidated before it will be possible to "overcome the negative correlations widely known in agriculture between the size of the harvest and its protein wealth" (seed yield and protein content). In similar reviews on the possibilities of genetic improvement of plant protein (Oram and Brock, 1972; Johnson and Lay, 1974) the negative relationship between yield and protein content was accepted unsourced, and considered as an obstacle to increased productivity of protein.

In barley (Hordeum vulgare L.), DenHartog and Lambert (1953) found a negative correlation of -.34** between yield and protein content in 150 F_5 progenies of a malting barley cross.

However, 10% of the total F_5 population was both high in yield and satisfactory in quality. Favret et al. (1970) reported that both grain weight and test weight in barley were negatively correlated with protein content, and that since both were affected by environment, selection for increased protein should be on a protein/seed basis, as this character was more stable. Favret et al. (1970) found a high positive correlation between grain weight and N/seed in a series of lines collected in Ethiopia. This relationship was not evident among malting barleys, but they had been selected for low protein in accordance with brewing industry requirements. The data suggested that the association of N with seed size in the Ethiopian lines was related to a greater supply of raw material from maternal tissues. Zoschke (1972) showed that differences in protein content among barley cultivars were genetically determined and were maintained when nitrogen fertilizer was applied at early (pre-flowering) and late (post-flowering) stages. Those cultivars highest in protein content were also the highest in protein yield.

Haunold et al. (1962) cited several reports of a negative yield-protein relationship in wheat (Triticum aestivum L.). They grew four cultivars of wheat, Wichita, Commanche, Atlas 50, and Atlas 66. The first two are hard red winter (HRW) wheats and the latter two soft red winter (SRW) wheats. Plants of the HRW cultivars low in protein produced more grain than high-protein plants, whereas the SRW cultivars had highest yields at intermediate protein levels. In one year, protein-yield relationships were small, negative and significant for the two HRW cultivars and non-

significant for the two SRW cultivars. In the following year, the correlations were somewhat higher for Commanche (HRW) and Atlas 66 (SRW). Atlas 66 showed consistently higher protein content than the other cultivars in different environments and different years. The yield-protein curves for the two Atlas derivatives suggested a threshold for protein, i.e. yield and protein were positively correlated up to the threshold and then negatively correlated at higher yield levels. Negative correlations were strongest in the second year when available nitrogen was lacking. Haunold et al. (1962) suggested that these genotypes could not express their protein threshold under limiting nitrogen conditions.

Bhatia (1975) analyzed the relationships between protein and yield components in 21 spring wheat cultivars of diverse origin selected for high and low protein content, and excluding genotypes with shrivelled seeds. Protein content was highly negatively correlated with yield ($r = -.84^{**}$), grain number ($r = -.81^{**}$) and harvest index ($r = -.71^{**}$). Protein per grain was positively correlated with seed weight and negatively correlated with seed number. Protein yield was positively correlated with seed yield ($r = +.84^{**}$), grain weight ($r = +50^{*}$), grain number ($r = +.91^{*}$) and harvest index ($+.59^{**}$). Bhatia (1975) considered that protein yield/unit area provided the best criterion for making early generation selection for improving protein productivity.

Pepe and Heiner (1975) reported that, among 126 F_5 lines from a cross between two semi-dwarf wheat cultivars, height was not correlated with either yield or protein content. There was a highly significant inverse relationship between yield and protein

content (r= -.61**). This was not due to an association of either character with height, but rather due to a probable source limitation. Despite the negative relationship, lines existed which were almost equal in yield to a standard cultivar Era, and had higher percent protein in the grain.

Gomez and DeDatta (1975) analyzed yield and protein data for two cultivars of rice, Oryza sativa L., IR8 and IR480-5-9 grown at several locations over the years 1968-72. Protein content ranged from 4.8 to 12.1% in IR8 and from 6.4 to 17.4% in IR480-5-9. Major effects on variability came from season, location, nitrogen fertilizer, water supply and weed control. Yield and protein content were positively related up to a threshold value of protein characteristic for each genotype and negatively related beyond that point. The threshold values were 8.5% protein for IR8 and 10.3% protein for IR480-5-9 and were relatively stable from year to year.

Crook and Casady (1974) reported a negative correlation (r= -.42**) between yield and protein content among 40 sorghum (Sorghum vulgare L hybrids and their parents. Protein was also negatively correlated with days to 50% bloom, height, leaf area, panicles per plant, and test weight.

Spilde et al. (1974) regressed protein on yield of five interspecific crosses in oats, Avena spp. Linear regression coefficients were negative and significant in all crosses. Standard partial regression coefficients also showed that protein was significantly negatively correlated with yield.

2.3.2 Legumes

2.3.2.1 Glycine max (L.) Merrill

Johnson et al. (1955) studied genotypic and phenotypic correlations between 24 traits in two populations of F_3 lines of soybean. The phenotypic and genotypic correlations between yield and protein content were r= -.08 and -.12 respectively, in population I and r= -.33 and -.64 respectively, in population II. These authors commented that selection for increased protein content would be limited by negative correlations of protein with yield and shattering resistance. Smith and Weber (1968) studied mass selection for protein content in soybeans by use of specific gravity selection. They reported phenotypic correlations between protein content and density of r= 0.48**, 0.57**, and 0.60** in three populations. The higher protein content was also associated with lower oil content. Yield was independent of density, but no direct relationship between yield and protein was recorded. In six F_4 populations of soybeans Shannon et al. (1972) reported that yield-protein correlations were significantly negative in only two populations, and one was small enough (r= -.28*) that it was not considered a barrier to selecting high-protein, high-yielding strains. In three populations, there was no association, and in one there was a significant, positive correlation (r= +.61**) between yield and protein. Lines with the highest percent protein and the highest protein per unit area were obtained from the population derived from crossing two high protein parents. However, these high protein parents were not much lower in yield than currently grown cultivars and had been previously selected for good agronomic characteristics. Hartwig and Hinson (1972) produced BC_1 and BC_2 lines from a cross between a productive high-oil cultivar and a lower yielding, but high protein, breeding line. Selection on the basis of oil was effective in obtaining

populations different in protein content. Yield and protein content were negatively correlated in both populations, but significantly so only in the BC_1 population. The most productive line in the BC_2 population was similar to the high yielding parent and had 10% higher protein. Thus, after two backcrosses, it was possible to isolate a line combining favorable yield and increased protein content.

2.3.2.2 Phaseolus sp.

Tandon et al. (1957) measured the effect of year and location on yield, protein content and several food quality parameters in 25 cultivars of beans, Phaseolus vulgaris L. Yield and nitrogen content were strongly negatively correlated (r= -.635**) as was yield with lysine, niacin, and thiamine. Rutger (1970) reported correlations of r= -.23 and r= -.36 between yield and protein content in dry beans, Phaseolus sp. but these were non-significant. Leleji et al. (1972) estimated heritability of crude protein content in beans and measured the relationship between yield and protein in F_2 and F_3 progenies from crosses between high and low protein lines. Yield and crude protein content were negatively correlated in three of four populations (r= -.446**, -.287*, -.044, -.220*). However, protein yield/plant and seed yield/plant were highly correlated in all crosses (r= .964**, .724**, .961**, .831**). Leleji et al. (1972) considered that although yield and protein content were negatively related, enough variation occurred to select plants that combined relatively high yields with relatively high percent crude protein. However, highest total protein yield was

best achieved with high yielding lines. Kelly and Bliss (1975) reported a low negative correlation (r= -.30*) between seed yield and protein content among 65 F_4 families of a cross in beans. The authors commented that although negative, the relationship was low enough to allow for increased protein content within genotypes that produced substantial yields, and further suggested that selection for high yielding families should be practised first and selection subsequently made within these families for high protein content.

2.3.2.3 *Vigna sp.*

Bliss *et al.* (1973) grew 11 cultivars of *Vigna unguiculata* (L) Walp. at three locations under short-day and long-day environments. Yield and protein content showed only a small negative correlation (r = -.14).

2.3.2.4 *Cicer sp.*

Sandhu *et al.* (1974) assayed seeds of 33 chickpea, *Cicer arietinum* L., genotypes for total protein and sulphur content. They reported a highly significant negative phenotypic correlation (r= -.57**) between protein content and 100-seed weight. Small, shrivelled and sometimes unfilled seeds were high in percent protein. Thus, protein weight per seed was considered more meaningful as a selection criterion for a protein improvement breeding program. Protein weight per seed was positively correlated with 100-seed weight (r= +.83**) and sulphur as percent of protein (r= +.49**). However, 100-seed weight was not related to yield so that the yield-protein relationship could not be directly assessed.

2.3.2.5 *Vicia faba*

Munck *et al.* (1973) selected for low and high crude protein

content in Vicia faba for three consecutive years in three populations. All populations responded to selection and seed size and other yield parameters were not significantly influenced by selection for protein in either direction. Bond (1975) stated that in 19 separate cultivar trials with Vicia faba in the United Kingdom only two showed a negative yield-protein relationship.

2.3.2.6 Pisum

Neklyndov and Antonova (1973) reported that protein content of pea seeds in F_1 to F_4 populations was not correlated strongly with protein in the vegetative parts, nor with earliness or yield. Selection for protein within a genotype was not successful.

Furedi (1970) noted the importance of yield in determining protein content but observed "in spite of the apparent negative correlation between seed yield and protein content it is probable that these two characters can be combined. Appropriate source material may be derived from a collection comprising a wide range of lines, or from a segregating population."

Among F_3 and F_4 progenies of four crosses of peas, Pandey and Gritton (1975) found that yield and protein content were significantly negatively correlated in progenies from one cross only. Since the values were low ($r = -.34^{**}$ and $-.35^{**}$ in F_3 and F_4, respectively), the relationship was not seen as a barrier to increasing both components simultaneously. The cross in question was between a wrinkle-seeded and a smooth-seeded parent. A negative yield-protein relationship was inferred indirectly by Pandey and Gritton (1975). When they discussed the fact that F_1 pea hybrids had

protein levels below their parents, they also noted that F_1's exhibited heterosis for seed yield, and these produced a greater yield of protein than parents. Ali-Khan and Youngs (1973) reported that the correlation between yield and protein content of 10 genotypes grown in three seasons was non-significant (r= +.57). In F_3 populations from crosses between high and low protein parents, Shia (1976) found that protein content was positively correlated with protein weight/seed (r= +.43** to +.59**), and protein weight/seed was positively correlated with 100-seed weight (r= +.89** to +.91**). Thus, protein weight/seed was primarily a function of seed weight. Seed weight was unrelated to protein content. Protein content was negatively correlated with seed yield/row (r= -.26* to -.57**). Shia concluded that these correlations were low enough to permit combination of high values of both traits. In fact there were F_3 lines which combined above average yield and protein. Protein yield and seed yield were highly positively correlated (r= +.95** to +.99**), both on a per row and a per plant basis.

2.4 Relationship between protein content and protein quality

Munck et al. (1973) reported that as crude protein increased the concentration of essential amino-acids decreased in both barley and faba beans. In faba beans, the sulphur containing amino-acids contributed almost nothing when protein content was increased by selection. Arginine was the largest contributor to the increase. Munck et al. (1973) questioned the wisdom of selecting for crude protein content in view of such evidence.

In Phaseolus. Adams (1973) recorded correlations between

nitrogen and methionine, nitrogen and cystine, nitrogen and cystine plus methionine of -.73*, -.84**, and -.84**, respectively, among 8 genotypes. As protein content increased above about 21%, the protein became progressively poorer in quality. Adams further commented that, since it costs the plant more energy to produce low quality protein than carbohydrate, increased protein acts as a yield depressant.

Royes (1973) grew Cajanus cajan on nutrient deficient soils and supplemented with ammonium sulphate. Contrary to his expectations, supplementation decreased methionine as a percent of protein from 0.86% to 0.50%. There was a preferential uptake of nitrate ions compared to sulphate ions.

Bajaj (1972) evaluated 21 pea genotypes and found that protein efficiency ratio, as determined by rat growth, was correlated with total N, extractable N, globulin content and albumin content (r= 0.42, 0.02, 0.32 and 0.77, respectively).

The high correlation with albumin content was due to the higher concentration of lysine and sulphur-amino-acids in the albumin fraction compared to the globulin fraction. She thus concluded that crude protein or nitrogen was of dubious value in indicating biological value of peas.

Sandhu et al. (1974) measured total sulphur content in 33 genotypes of chickpeas and found that percent protein was negatively correlated (r= -.76**) with sulphur as percent of protein. However, since sulphur as percent of protein was correlated with protein weight/seed (r= +.49**) and since Sandhu et al. had recommended selecting for the latter, improvement in sulphur as percent of protein would follow.

Bliss et al. (1973) found a correlation of (r= +.51, not significant) between methionine as percent of protein and protein content of Vigna. However, the genotypic correlation was higher (r= +.63) and significant. Similarly, Kelly and Bliss (1975) found that available methionine as percent of protein was positively correlated with protein content (r= +.33*) in Phaseolus.

Vogel et al. (1973) found that among 12,613 common wheats from the U.S.D.A. World Wheat Collection, lysine percent and protein content were highly correlated (r= +.94). Thus, lysine percent was more an indicator of protein content than quality. Lysine as percent of protein was considered to be a better indicator of quality. It was negatively correlated with protein content up to 15%, and above that, the effect of increased protein on lysine was negligible.

2.5 Heritability of protein content and quality

Thorne and Fehr (1970) made 2- and 3-way crosses between adapted and exotic strains of soybeans. Broad-sense heritability of protein content, based on parent-progeny regression, ranged from 81.0% to 95.9%. As indicated by these values, population means did not differ greatly from mid-parent values. Additive effects were more important than non-additive effects. Shannon et al. (1972) reported similar high values for broad sense heritability of protein content in soybeans, i.e. 81-96%. Values were calculated for F_2-derived F_4 populations. The values may have been inflated by the growing of different generations in different years as well as variance components estimated from material not under

study.

Leleji et al. (1972) evaluated F_1's, F_2's and F_3's from crosses between 5 lines of Phaseolus vulgaris L. They found that all progeny means were between the parental means, but tended toward the lower parent. Protein content was maternally determined in F_1. Broad sense heritability estimates ranged from 30.7% to 63.7% while narrow sense heritability was 20.1% among backcross progenies and 12.0% among single cross progenies, based on F_3/F_2 regression. Thus, there was low additive genetic variance for protein content. Kelly and Bliss (1975) made three crosses between 4 strains of Phaseolus vulgaris L. They grew and analyzed F_1, F_2, BCP_1, BCP_2, F_3, and F_4 generations. Narrow sense heritability, based on F_3/F_2 and F_4/F_3 regression, for protein content was 63 to 79% and 32 to 61%, respectively; for percent available methionine as percent of protein was 81 to 85% and 51 to 81% respectively. These narrow sense heritability estimates were larger than broad sense heritability estimates for the same populations calculated by variance component analysis. There was partial dominance for both expressions of available methionine.

Romero et al. (1975) subjected 4 strains of Phaseolus vulgaris L. to electrophoretic analysis of the G_1 globulin fraction and showed that the two strains high in methionine content had a 3-subunit structure, while the two strains low in methionine had a 2-subunit structure. F_1 progeny were intermediate in banding and as the F_2 showed a Mendelian segregation pattern consistent with a system

controlled by a single gene.

Bliss et al. (1973) grew 9 cultivars of cowpea at three locations under two daylength regimes and calculated broad sense heritability by variance component analysis. The heritability estimates for protein content, methionine content and methionine as percent of protein were 29%, 54% and 46%, respectively. Tryptophan and cystine contents were less heritable than methionine.

Singh and Singh (1973) studied a 7-parent diallel and obtained a narrow sense heritability estimate of 73.48% for protein content in mung beans, Vigna radiata (L.) Wilczek. Although both additive and non-additive components were important, general combining ability for protein content was higher than specific combining ability.

Broad sense heritability for protein content in chickpeas was 70% calculated from variance components of 33 genotypes grown in 2 years by Sandhu et al. (1974). Broad sense heritability for protein per seed, percent sulphur, and sulphur as percent of protein was 70%, 64% and 51%, respectively. Mean values for each genotype were based on the mean of three single plants.

Selim et al. (1974) made crosses between high and low protein lines of Vicia faba L. They analyzed protein content of 5 plants at random from each F_3 population. Maternal inheritance was noted. High protein was found to be incompletely dominant and controlled by either 1 or 2 pairs of genes showing both additive and multiplicative gene action. Heritability was estimated at between 62.11 and 79.58%.

In peas, Pandey and Gritton (1976) made 4 crosses between

high and low protein lines and found that the mean of F_2 and F_2-derived progeny was lower than the higher parent and tended toward the lower parent. Narrow sense heritability for yield was lower than for protein. Observed gain from selection for high protein was less than predicted whereas the observed decrease from selection for low protein was greater than expected.

Shia (1976) made three crosses between high-protein, wrinkle-seeded lines and low-protein, smooth-seeded lines. Narrow sense heritability estimates for protein content based on F_3/F_2 regression, ranged from 56 to 68%. However, when F_3 progenies were divided into homozygous smooth or homozygous wrinkled, narrow sense heritability estimates decreased substantially and were not statistically significant. Shia concluded that protein content was a character of essentially low heritability.

2.6 Summary of literature

Protein content is a highly variable, weakly inherited character negatively correlated with yield and quality in both cereal and legume food crop species. Variation due to location, year, season, and soil condition has been documented, as has variation within genotypes among and within environments. Considerable single plant variation is common, leading to suggestions that selection on a single plant basis could lead to improvements in protein content, usually without evidence that the observed variation was genetic.

The effect of nitrogen supply on protein content in legumes is variable and not well defined due to the interacting effects of symbiotically supplied and externally available nitrogenous compounds. There is no reported consistent effect of seed size on protein percent, but it is axiomatic that larger seeds contain more protein and in one legume crop protein per seed was considered the most valuable selection criterion.

Yield and protein content were consistently negatively related in almost all the crop species documented, with the exception of Vicia faba L. However, the magnitude of the relationship was generally low to moderate, allowing most authors to conclude that both yield and protein content could be combined. Most reports though, concluded that either protein or yield could be increased while holding the other at an average level, or above average levels of both could be achieved. In rice and wheat, evidence for a threshold level of protein was presented, i.e. up to a certain level, protein and yield may increase together, but beyond that

level or 'threshold' they are negatively related.

Reports show conflicting evidence on the relationship between protein content and protein quality. In legumes sulphur bearing amino-acids are the first limiting, and unfortunately, it is often these amino-acids which do not increase when protein content increases, resulting in a greater content of nutritionally poorer protein.

There are relatively few estimates of heritability of protein content in legumes, and some of these recorded are of little use to breeders in that they are estimated in the broad sense. Still others were derived from data which could be used only with great caution due to very limited populations and sample size. Nevertheless, protein content is low to moderately heritable, with the possible exception of protein in soybeans, and additive variance is the major genetic variance component.

3. MATERIALS AND METHODS

This research program was divided into five major experiments: a genotype by environment study involving 25 pea genotypes grown in three environments in which both plot and single plant data were collected; a study of the changes in protein content and starch content in pea seeds with advancing maturity; a study of heritability of protein content and other metric traits based on 21 F_2 populations and their parents; a study of the effect of seed shape on seed weight; a study of genotypic variability for protein content and other metric traits involving 1071 genotypes from the U.S.D.A. World Pea Collection grown in replicated lattices at one location.

3.1 Genotype by environment study

3.1.1 Plant material

Twenty-five genotypes, representing a wide range of protein contents, were selected from approximately 40 genotypes with sufficient seed available to plant a large plot multi-location trial. The genotypes included three currently licensed cultivars as well as a number of breeding lines from the Agriculture Canada cooking-pea breeding program based at Morden, Manitoba, and diverse genotypes from the U.S.D.A. world collection. Two of the genotypes were wrinkle-seeded.

3.1.2 Experimental layout

The experimental design was a 25-genotype randomized complete block design (RCBD) with four replications at three sites in Saskatchewan, namely Saskatoon, Nipawin, and Bellevue. At Saskatoon and Nipawin identically sized plots of a check variety Trapper were sown between each treatment plot. The plots consisted

of four rows 4.8m long, 30cm apart, with 90cm between plots. Seeding rate was 135 seeds/row to give an estimated 85 seeds/m^2. Seeding was by a cone seeder with shoe-type openers with commercial pea inoculant (Nitragin Co.) applied at seeding. No fertilizer was used. Initial weed control was by pre-plant incorporated herbicide (Treflan) and later the experimental area was kept weedfree by cultivation and hand-hoeing. Seeding dates were May 20 and 21, and June 1, 1974, for Saskatoon, Nipawin, and Bellevue, respectively. Seeding was delayed by heavier than usual spring rainfall, particularly at Bellevue. The soil types for the 1974 locations were: Saskatoon - Elstow clay loam, Bellevue - Blaine Lake silt loam, Nipawin - Nipawin loam. The experiment was located on a free-draining sandy knoll on this soil series.

The 1974 season was shorter and cooler than average. There was no prolonged period of moisture stress. At Bellevue, the growing season was particularly cool and moist, resulting in delayed flowering and maturity of the indeterminate genotypes.

Data for 1973 were obtained from 22 common genotypes grown in a 40-genotype RCBD under the same conditions as described above without covariate plots. In 1975 the 25 genotypes were seeded on May 14 in a 4-replicate RCBD as described above, also without covariate plots. Three replicates were used for the genotype x environment study while the fourth was used for a maturity study (section 3.2.2).

3.1.3 Data collection and analysis

At Saskatoon and Nipawin, five single plants per plot from each genotype were randomly taken from the inside two rows at maturity prior to harvest, and the whole above-ground portion of the

a 50mg sub-sample was analyzed for protein content by the micro-Kjeldahl method (A.O.A.C., 1970).

Yield, protein content and height were determined for each plot of the check variety Trapper and the mean value of the two adjacent check plots was used as covariate for each genotype value.

3.2 Effect of stage of maturity on protein content

3.2.1 Plant material

Seed of the 25 genotypes used in the previous study was available for one location in 1975.

3.2.2 Experimental layout

The genotypes were seeded on May 14 as described in section 3.1.2.

3.2.3 Data collection and analysis

Three replicates were harvested at maturity on August 21. The seed was dried, cleaned, weighed, and a 15g sample taken for analysis of protein content by infra-red reflectance spectroscopy (Neotec Grain Quality Analyzer). The data were analyzed as a three-replicate RCBD.

The fourth replicate was sub-divided into four 1m plots which were harvested at four intervals from pod-filling to maturity (July 21 and 28, August 7 and 21). At each harvest two two-row samples 1m long from each genotype were cut and the peas were shelled by hand. The fresh peas were weighed, immediately dried for 72 hours as described previously and then reweighed. A 15g sub-sample was ground in a cyclone mill (Udy Analyzer Co. model MS.) to pass through a 40- mesh sieve. Protein content was determined by the micro-Kjeldahl method and starch content was determined by polarimetry (A.O.A.C., 1970).

plant bagged, dried, and the haulm and seeds of each plant separated before weighing. The following single plant characters were measured: seed weight, haulm weight, harvest index (calculated from seed weight/seed+haulm weight, expressed as a percentage), seed protein content, haulm protein content, protein weight per haulm and total protein weight per plant. The values expressed were means of 5 single plants. Single plant data were recorded only at Saskatoon and Nipawin due to the aforementioned seasonal abnormalities at Bellevue.

Height was measured at cessation of flowering and was taken as the mean distance from the ground level to the uppermost node of five random plants from the inner two rows when the plant was pulled erect. Height was expressed to the nearest 5cm. Height was not recorded at Bellevue because many of the genotypes did not cease flowering before the harvest.

Each plot was harvested with a modified Hege model 125 combine and the seed was bagged, dried for 72h, cleaned and weighed to the nearest gram. Unless otherwise stated all drying in this and subsequent studies was in a hot-air grain drying cabinet for 72h.

For protein analysis on the plot samples, a 15g sub-sample was ground in a mill (Udy Analyzer Co. cyclone model MS.) to pass through a 40-mesh sieve. Protein was determined by infra-red reflectance spectroscopy (Neotec Grain Quality Analyzer). Seed from each individual plant was ground in a Culatti micro-mill to pass through a 1mm sieve and a 280mg sample analyzed for protein content by the Udy (1971) method. Single plant haulms could not be individually ground, so the five haulms from each plot were combined and ground in a laboratory-size mill (Wiley, model no. 4). From each bulk sample

3.3 Heritability of agronomic traits, protein content and methionine content

3.3.1 Plant material

Sufficient seed for a replicated experiment was available from 21 F_2 bulk populations of crosses between higher protein genotypes from the U.S.D.A. World Pea Collection and lower protein adapted genotypes. The crosses were made in 1972 and the F_1 seed grown in the field of 1973. Ten of the populations were segregating for seed shape.

3.3.2 Experimental layout

The 21 F_2 bulk populations and their 19 common parents were seeded in a 2-replicate RCBD with 2 row plots 3.05m long and 30cm between rows. Plots were 90cm apart. Seeding rate was 85 seeds per row. The seeds were dusted with a fungicide (Captan) prior to seeding and then sown with commercial pea inoculum (Nitragin Co.) and without fertilizer on May 14, 1975.

These genotypes all became infected with Erysiphe polygoni in late July and were sprayed with sulphur on July 25 and 30 as described in section 3.5.2.

3.3.3 Data collection and analysis

Date of first open flower was recorded during the growing period. All genotypes were harvested at full maturity on August 30 by a modified Hege model 125 plot combine. The seed was dried, cleaned, weighed and a 15g sample ground in a cyclone mill (Udy Analyzer Co.) for protein determination by infra-red reflectance spectroscopy. Duplicate 200-seed lots were used to determine seed weight.

Methionine content of the pea meal was determined by the method of Finlayson and McKenzie (1976) with the following modifications: the meal was reacted with cyanogen bromide (10% w/v) in 50% formic acid. The column used was 2-3mm internal diameter by 40 cm Pyrex glass packed with Poropak QS (100-120 mesh) and operated at 160C. Methyl isobutyl ketone was used as an internal standard.

3.4 Effect of seed shape on seed weight

3.4.1 Plant material

Progeny of 10 crosses segregating for seed shape (from section 4.3) were separated on the basis of seed shape, weighed, and screened into four sizes by screens with hole diameters of 18, 16, 14, and 12/64". Parental seed weight was determined. A Chi-square test for independence of seed shape and seed size was performed.

3.5 Genotypic variation in field peas

3.5.1 Plant material

In 1971, 1452 genotypes from the U.S.D.A. World Pea Collection were grown in single unreplicated rows at Saskatoon (Slinkard, unpublished report). Approximately 150 of these either germinated poorly or yielded poorly so that insufficient seed was available for seeding in 1975. Thus, the sample of 1071 genotypes taken was not random in the strictest sense, but was a random sample of genotypes that had produced more than 350 mature seeds in 1971, and thus were at least slightly adapted to the Saskatoon environment. It is probable that at least some of the genotypes were not pure. Plants showing gross morphological differences and differences in flower colour from the rest of the plot were removed prior to harvest.

3.5.2 Experimental layout

Eighty-five seeds per row were packeted and dusted with approximately 0.5g of a fungicide (Captan). Each plot consisted ot two rows 3.05m long and 30cm apart. Plots were 90cm apart. The genotypes were randomly grouped into 17 eight by eight lattices with two replicates per lattice. The genotypes were seeded as described previously with commercial pea inoculum (Nitragin Co.) and without fertilizer at Saskatoon on May 12, 13, and 14, 1975. In the hot, dry weather of late July most of the genotypes became infected with powdery mildew, Erysiphe polygoni. Consequently, they were sprayed with elemental sulphur at a rate of approximately 2kg/ha suspended in 400 l of water. Liquid detergent was added to aid suspension of the powder. All plots were sprayed on July 19, 25, and 30. Since infection was widespread and relatively uniform no attempt was made to rate the genotypes for reaction to the disease.

3.5.3 Data collection and analysis

In all but three of the lattices, the genotypes were fully mature and the plants totally senescent by August 3. The other three lattices were in a hollow in the field where higher soil moisture delayed senescence and maturity until the end of August. Harvesting commenced on August 3 and continued on August 4, 6, 14, 21, 28 and 30. The sporadic timing of harvest was due to rain and subsequent cool weather not allowing sufficient drying to enable harvest by combine. Although the harvesting was sporadic, at each harvest date only whole lattices were completed. The seed was dried, cleaned and weighed. Fifteen gram sub-samples were ground in a

cyclone mill (Udy Analyzer Co.) and analyzed for protein content by infra-red reflectance spectroscopy (Neotec Grain Quality Analyzer). Duplicate 200-seed lots were used to determine seed weight.

3.6 The nitrogen-to-protein factor

The value 6.25 as the nitrogen-to-protein factor is still in common usage despite the acknowledged errors inherent in its calculation (Jones, 1941; Tkachuk, 1969). Holt (1976) concluded from a study of amino-acid and non-protein nitrogen constituents of legume seeds that the value of 5.7 more accurately reflected the true nitrogen-to-protein ratio in those crops.

However, 6.25 was retained in the present study since the dye-binding method and the infra-red reflectance spectroscopy method of determining protein content were calibrated on the basis of that factor. All protein content values reported in this thesis are in effect crude protein content values and their use is thereby limited to comparative purposes.

4. RESULTS

4.1 Genotype by environment study

This experiment was designed to provide information on the relative contributions of genotypes, locations, years, and local environment to variability of protein content in accordance with Objective 1 (see Introduction) and also to provide information on the relationship of protein content to other plant traits under Objective 2.

4.1.1 Analysis of variance for 1974 data from Saskatoon, Nipawin and Bellevue

Bartlett's test for homogeneity of error variance showed that a combined analysis of the 1974 data on seed yield and protein content from Saskatoon, Nipawin and Bellevue was statistically valid. The combined analysis shows that locations, replicates within locations, and the genotype location interaction were significant (p= .01) for both yield and protein content (Table 4.1).

Table 4.1 Analysis of variance for yield and protein content of 25 pea genotypes grown at three locations in 1974

Source	d.f.	Yield M.S.	Protein content M.S.
Locations	2	12,129,388**	524.7**
Genotypes	24	389,114	37.5**
Replicates/location	9	212,304**	31.3**
Genotype x location	48	447,469**	6.5**
Error	216	55,801	2.1
Total	299		

** Significant at the .01 level

The relative yield of each genotype was similar at Saskatoon and Nipawin, but differed greatly at Bellevue (Table 4.2). For example,

Table 4.2 Mean yield (g /plot) of 25 pea genotypes grown at three locations in 1974

Genotype	Saskatoon	Nipawin	2-location mean	Bellevue	3-location mean
MP 761	2153	1651	1902	1598	1801
Triumph	2214	1619	1917	1486	1773
MP 790	2141	1624	1883	1538	1768
MP 712	2116	1556	1836	1624	1765
MP 789	2085	1272	1678	1890	1749
P.I. 269812	2010	1456	1733	1681	1716
W 718	1911	1401	1656	1832	1714
Trojan	2111	1656	1742	1495	1660
W703	1947	1324	1636	1733	1668
Century	1819	1665	1742	1495	1660
MP 702	2028	1937	1983	967	1644
Petit Pois	1843	1680	1762	1235	1586
P.I. 356885	2135	1538	1837	1079	1584
MP 783	1994	1533	1763	1202	1576
P.I. 356837	2073	1472	1773	1175	1573
Trapper	1941	1603	1772	1169	1571
P.I. 356834	2002	1377	1690	1279	1552
Dashaway	2199	1585	1892	831	1538
P.I. 356846	1925	1473	1699	1187	1528
MP 39	2320	2012	2166	124	1485
Lincoln	1656	1237	1447	1531	1474
Palouse	1444	1219	1332	1752	1472
P.I. 324705	1725	1706	1716	345	1259
P.I. 357001	1876	1344	1610	529	1249
P.I. 206790	1219	841	1031	1105	1055
Mean	1955	1511	1734	1269	1578
L.S.D.(.05)	391	343	249	292	190
C.V.	13.7%	15.6%	14.6%	15.8%	15.6%

MP 39, the highest yielding genotype at both Saskatoon and Nipawin, was the lowest yielding genotype at Bellevue with a yield approximately 1/10 of the location mean. Similarly, Lincoln and Palouse ranked 23rd and 24th, respectively, at both Saskatoon and Nipawin, but shifted to 10th and 4th, respectively, at Bellevue. Thus, the significant genotype x location interaction for yield was apparently due to the widely divergent results from Bellevue.

Considerable local variability was indicated by the significant mean square for replicates within locations and the high coefficient of variation (C.V.) for yield of 15.6%. The range for yield over the three locations was from 1269 to 1955 g/plot which was almost as great as the range of the 25 genotypes, i.e. 1055 to 1801 g/plot (Table 4.2).

Genotype means for protein content are presented in Table 4.3. The location with the highest protein content (Bellevue) was lowest in yield. However, the location with the lowest protein content (Nipawin) was not the highest in yield. In general, within a location, genotypes that were high yielding had low protein content, and low yielding genotypes tended to have high protein content. The range of protein content among locations was 22.6 to 27.1%, almost as large as the range among genotypes, 22.4 to 28.9%. Exclusion of the Bellevue location increased the range among genotypes only marginally (.3%), but lowered the level of that range from 22.4-28.9% to 21.3-28.1%.

4.1.2 Analysis of variance for 1974 data from Saskatoon and Nipawin

Due to the divergent results from Bellevue, data from this location were deleted and the remaining data reanalyzed.

Table 4.3 Mean protein content (%) of 25 pea genotypes grown at three locations in 1974

Genotype	Saskatoon	Nipawin	2-location mean	Bellevue	3-location mean
P.I. 206790	29.3	26.8	28.1	30.7	28.9
P.I. 357001	27.1	27.6	27.4	31.2	28.6
P.I. 324705	27.1	25.3	26.3	31.6	28.0
Lincoln	26.9	25.5	26.2	28.6	27.0
P.I. 356846	26.7	22.5	24.6	29.2	26.1
W 703	26.3	22.9	24.6	26.9	25.3
P.I. 356834	24.8	23.6	24.3	27.2	25.2
P.I. 356837	24.6	22.3	23.5	27.9	24.9
Petit Pois	25.1	21.2	23.2	28.3	24.9
Trojan	24.0	22.6	23.3	27.7	24.8
Trapper	24.3	21.5	22.9	28.7	24.8
P.I. 269812	25.1	23.0	24.1	25.9	24.7
MP 39	22.2	20.4	21.3	30.6	24.4
W 718	25.7	21.4	23.6	25.5	24.2
MP 790	22.9	23.4	23.2	26.0	24.1
P.I. 356885	22.5	22.2	22.4	26.7	23.8
Dashaway	23.1	20.9	22.0	27.1	23.7
Palouse	24.4	21.9	23.2	24.9	23.7
MP 783	24.8	21.1	23.0	25.4	23.7
Century	24.1	22.2	23.2	24.6	23.6
MP 702	23.8	20.8	22.3	26.0	23.5
Triumph	24.0	19.8	21.9	26.2	23.3
MP 789	22.4	21.2	22.0	23.8	22.6
MP 761	22.4	21.4	22.0	23.8	22.6
MP 712	23.0	21.4	22.2	22.8	22.4
Mean	24.7	22.6	23.6	27.1	24.8
L.S.D.(.05)	2.15	2.34	1.52	1.79	1.16
C.V.	5.9%	7.1%	6.5%	4.5%	5.8%

As expected, the results of the analyses of variance for yield and protein content were as described in section 4.1.1, with the exception that the genotype x location interaction was not significant (Table 4.4). Thus for both of these traits, the geno-

Table 4.4 Analysis of variance for yield, protein content and height of 25 pea genotypes grown at Saskatoon and Nipawin in 1974

Source	d.f.	Yield M.S.	Protein content M.S.	Height M.S.
Locations	1	9,871,392**	232.4**	2628**
Genotypes	24	394,364**	24.3**	3240**
Replicates/locations	6	290,107**	43.7**	871**
Genotype x location	24	74,875	3.6	228
Error	144	63,632	2.3	218
Total	199			

** Significant at the .01 level

types performed similarly at each location, and deletion of data from the Bellevue location removed all significant genotype x location effects.

For height there were significant differences (p= .01) among genotypes, locations, and replicates within locations (Table 4.4). The genotype x location interaction was not significant. Thus, the factors which produced differences between the two locations affected all genotypes in a similar manner. Most genotypes yielded less, had a lower protein content, and were shorter at Nipawin than at Saskatoon. The C.V. for height (15.6%) was of the same magnitude as that for yield, and the significant differences (p= .01) among replicates within locations indicated that replicates were effective in controlling local variability. Protein content was less subject to environmental variation than either yield or height as indicated by the lower C.V.

Mean performance of all genotypes at a location has been frequently used as an estimator of that environment (Finlay and

Wilkinson, 1963; Eberhart and Russell, 1966). Thus, the test site used at Nipawin in 1974 was a less favorable environment than the Saskatoon test site for the growth of field peas, and the absence of a significant genotype x location interaction indicated that the difference between locations was not in season length or drought stress, to which one or more of the genotypes might have responded differentially. The Nipawin site was, therefore, less productive. In future discussion, productivity will be referred to as fertility, without inferring measured soil fertility.

4.1.3. Analysis of variance for single plant traits

At both Saskatoon and Nipawin the following single plant traits were measured; seed protein content, haulm protein content, yield/plant, protein weight/plant, haulm protein weight/plant, and harvest index. All traits measured on a single plant basis were analyzed for each location separately due to heterogeneity of error variance.

Mean square values for genotypes are presented in Table 4.5. At Saskatoon there were significant differences ($p=.01$) among genotypes for seed protein content, seed yield/plant, total protein weight/plant, and harvest index, but not for haulm protein content or haulm protein weight/plant. Haulm protein weight/plant, total protein weight/plant and seed yield/plant had high C.V.'s, indicating that individual plant data were extremely variable and unreliable.

There were significant differences ($p= .01$) among genotypes for all traits at Nipawin (Table 4.5). Although the locations could not be compared statistically, the location means for each

Table 4.5 Mean squares for genotypes, means and coefficients of variation for six plant traits of 25 pea genotypes grown at Saskatoon and Nipawin in 1974

Character	Saskatoon			Nipawin		
	M.S. for genotypes	$\bar{X}$	C.V.	M.S. for genotypes	$\bar{X}$	C.V.
Seed protein content/plant	8.34**	24.2%	4.5	9.16**	19.4%	8.6
Haulm protein content	345.95	8.37%	21.8	2.32**	5.89%	17.3
Harvest index	92.16**	50.6%	8.0	44.07**	51.1%	5.7
Seed yield/plant	5113.52**	8.45g	50.0	453.03**	5.86g	25.0
Total protein wt/plant	2.73**	2.78g	53.5	36.33**	1.46g	27.3
Haulm protein wt/plant	1.63	.71g	70.7	2.47**	.32g	33.1

** Significant at the .01 level

trait indicated that all single plant traits were lower at Nipawin than at Saskatoon, with the exception of harvest index. This is in agreement with the results for yield, protein content, and height reported in section 4.1.2. Single plant protein content and seed yield/plant were, respectively, 19.8% and 30.7%, lower at Nipawin than at Saskatoon. Thus, the greater reduction in yield compared with protein content noted earlier on a plot basis was evident on a single plant basis, except that both were reduced more substantially than on a plot basis. Haulm protein content was reduced 29.6%, indicating that under reduced fertility haulm protein may have been transferred to the seed, or alternatively, less protein was accumulated in the haulm. Although it was not possible to discern which is the more likely from this study, it did serve to indicate that under reduced fertility, protein content in the seed was affected less than protein content of the leaves and stem. There was a substantial reduction (47%) in total protein weight/plant at the less fertile location, which reflected the decreased weight of both seed and haulm, as well as decreased protein content of both seed and haulm.

Although the location effect was significant ($p = .01$) for some of the observed traits, it is noteworthy that the mean value for harvest index changed only very slightly (Table 4.5). Thus, the effect of reduced soil fertility was manifest equally on the vegetative and reproductive parts of the plant. Reasonable stability of harvest index was indicated, but the fertility differential may not have been sufficient to induce changes in this trait.

4.1.4 Analysis of variance for data from three years at Saskatoon

In order to gauge the effect of season on the expression of yield and protein content among genotypes, additional data were obtained (Slinkard, unpublished report) on 22 genotypes grown at Saskatoon in 1973, and which were also included in the 1974 and 1975 nurseries at Saskatoon. Since the 1975 test had only three replicates, one replicate was removed at random from the other tests. Bartlett's test for homogeneity of error variance showed that the 22 genotypes over 3 years could be analyzed together. The separate season analyses of variance for yield and protein content are given in Table 4.6 and mean values for each genotype are given in Table 4.7 . There were significant differences

Table 4.6 Analyses of variance for yield and protein content of 22 pea genotypes grown for three years at Saskatoon

		Yield M.S.			Protein content M.S.		
Source	d.f.	1973	1974	1975	1973	1974	1975
Replicates	2	14874.5	55630.0	22668.0	0.12	13.72**	1.14
Genotypes	21	**228624.9****	297614.4**	**160721.1****	7.97**	11.11**	4.65**
Error	42	23868.8	56718.4	48060.8	.81	**2.52**	1.21
Total	65						

** **Significant at the .01 level**

(p= .01) among genotypes for both yield and protein content in each season. There were no differences in yield among replicates in any of the seasons. The C.V!s. for yield were similar and moderate, while those for protein content were low but slightly more variable over seasons. Thus local environmental variability was similar over the

Table 4.7 Mean yield and protein content of 22 genotypes grown for three years at Saskatoon

Genotype	Yield. g/plot				Protein content. %			
	1973	1974	1975	Mean	1973	1974	1975	Mean
MP 39	1560	2449	2259	2089	24.6	22.1	22.9	23.2
MP 761	2029	2139	2084	2084	22.1	22.2	23.0	22.4
MP 712	1593	2435	2098	2042	24.5	22.9	22.4	23.2
MP 702	1949	2187	1889	2008	23.9	23.9	22.9	23.5
MP 789	1596	2138	2145	1959	23.9	23.5	22.4	23.3
Trojan	1701	2145	1862	1903	25.0	23.9	25.4	24.8
Dashaway	1324	2277	1812	1804	23.9	23.2	23.0	23.4
Triumph	1342	2243	1821	1802	22.7	24.3	22.3	23.1
P.I.357001	1578	1946	1862	1795	26.9	27.5	25.6	26.7
P.I.356837	1545	2179	1612	1779	24.9	25.0	24.7	24.8
P.I.269812	1339	1974	2003	1772	24.0	24.7	23.5	24.1
P.I.356834	1655	2100	1555	1770	24.9	24.7	23.5	24.1
Trapper	1424	2028	1814	1755	25.2	24.3	23.6	24.4
P.I.356846	1536	2056	1593	1728	24.6	27.1	25.3	25.7
W 703	1280	1847	2054	1727	24.5	25.7	23.7	24.6
Petit Pois	1229	1840	2024	1698	24.6	25.1	24.3	24.6
W 718	1292	1990	1752	1678	24.3	25.5	23.7	24.5
Century	1188	1838	2005	1677	24.4	24.9	23.7	24.3
P.I.324705	1292	1803	1526	1540	27.6	27.0	26.6	27.1
Palouse	1289	1349	1519	1386	24.5	24.7	23.0	24.1
Lincoln	1005	1549	1483	1346	28.4	26.9	25.0	26.8
P.I.206790	843	1178	1429	1150	28.7	30.3	26.7	28.5
Mean	1436	1986	1827	1749	24.9	25.0	24.0	24.6
S.D.	276	315	242	422	1.6	1.9	1.3	1.5
C.V.	10.8%	12.0%	11.9%	11.9%	3.6%	6.3%	4.6%	5.0%

three seasons at one location. There were significant differences (p= .01) among replicates for protein content only in 1974.

The combined analysis of variance is given in Table 4.8.

Table 4.8 Combined analysis of variance for yield and protein content of 22 pea genotypes grown at Saskatoon for three years

Source	d.f.	Yield M.S.	Protein content M.S.
Years	2	5288414**	20.4**
Genotypes	21	501307**	20.5**
Replicates/years	6	25161	5.0**
Genotype x year	42	100308**	1.8
Error	126	43529	1.5
Total	197		

** Significant at the .01 level

There were significant differences (p= .01) among genotypes and years, for both yield and protein content, among replicates within years for protein content and the genotype x year interaction was significant (p= .01) for yield. Mean yield was highest in 1974, followed by a reduction of 8% in 1975 and a further reduction of 23% in 1973 (Table 4.7) when a drought in late July and August hastened maturity (Slinkard, unpublished report). Although the genotype x year interaction was significant (p= .01) for yield, most of the genotypes performed similarly in the three seasons. The low-yielding, wrinkle-seeded genotypes P.I.206790 and Lincoln, and the smooth-seeded Palouse were always the lowest three. Similarly, MP39 and MP761 were highest in two out of three and one out of three seasons, respectively, and were the two highest yielding genotypes over all seasons. The relatively low yield of Lincoln and P.I.206790 in 1974 undoubtedly contributed largely to the genotype x year interaction.

Mean protein content did not differ between 1973 and 1974, but the mean for 1975 was significantly lower($p = .05$) than the previous two years, although the difference was only one percentage point (Table 4.7). In the absence of any genotype x year interaction, the genotypes performed similarly relative to one another over the three seasons. In each year, P.I. 206790 had the highest protein content, ranging from 26.7% in 1975 to 30.4% in 1974. That range was the widest of any genotype. Another high-protein genotype, Lincoln, had a range of 3.4% protein. All other genotypes showed a range of less than 2.5% protein over the three seasons. Among genotypes, the range was least in 1975 (4.4% protein), when mean protein content was lowest. In 1973 and 1974 the ranges were 6.6% and 8.1%, respectively. The narrower range in 1975 was due to the lower protein content of P.I. 206790. The range in protein content among genotypes based on the three-year mean was 6.1% protein, or a difference between highest and lowest of 27%. Thus, the range among genotypes and seasons was narrow (6.1% and 1.0%, respectively) and the range of the most variable genotype was 3.7%.

4.1.5 Analysis of covariance for within-location variability

The analysis of covariance may be used to increase precision and to clarify the nature of treatment effects when the assumption is made that some pre-existing factor will have an influence on the outcome of applied treatment effects (Snedecor and Cochran, 1967). As previously mentioned (Materials and Methods), check plots of the licensed cultivar Trapper were seeded between each treatment plot at Saskatoon and Nipawin in 1974 to obtain

information on the within-location variation due to gradients or micro-environmental differences in soil fertility or moisture supply. The mean value of the two Trapper plots adjacent to each treatment plot was used as the covariate for yield, plot protein content, and height. The value for plot protein content was also used as the covariate for single plant protein content. Although yield, plot protein content, and height were homogeneous for error variance over the two locations, covariance was restricted to separate locations on the premise that variation at one location was entirely unrelated to variation at the other and thus best kept separate even at the expense of reduced degrees of freedom.

The analyses of covariance for yield, plot protein content, single plant protein content and height are shown in Table 4.9. All regressions, except that for height at Nipawin, were significant ($p = .01$) and covariance resulted in a considerable reduction in error mean square, particularly at Nipawin. Adjusted F values for genotypes were higher than unadjusted F values except for height at Nipawin. Adjusted F values for replicates were reduced in most instances, and lost significance for single plant protein content at both locations.

Thus,the overall effect of covariance analysis was to increase precision by reducing error variance. Replicate variance and genotype variance was also reduced. Adjustment was greatest

Table 4.9 Analysis of covariance for yield, plot protein content, single plant protein content and height of 25 genotypes grown at Saskatoon and Nipawin in 1974

		Saskatoon				Nipawin			
Yield	d.f.	M.S.	F	MS'	F	M.S.	F	MS'	F
Genotypes	24	240693	3.35**	246860	4.22**	228543	4.12**	192917	6.06**
Replicates	3	238741	3.32**	119672	2.05	341477	6.16**	112513	3.54*
Error	72	71854		58487		55408		31817	
reduction				18.6%				42.6%	
b				.503**				.866**	
Plot protein content									
Genotypes	24	12.78	6.00**	12.27	6.93*	15.20	5.89**	12.47	7.79**
Replicates	3	14.16	6.65**	4.91	2.77*	73.45	28.47**	35.74	22.34**
Error	72	2.13		1.77		2.58		1.60	
reduction				16.9%				38.0%	
b				.539**				.803**	
Single plant protein content									
Genotypes	24	8.67	6.52**	8.34	6.95**	10.05	2.73**	9.16	3.31**
Replicates	3	6.30	4.74**	2.33	1.94	23.33	6.34**	4.56	1.65
Error	72	1.33		1.20		3.68		2.77	
reduction				9.8%				2.47%	
b				.338**				.782**	
Height									
Genotypes	24	1705	7.02**	1702	7.63**	1762	9.13**	1775	9.29**
Replicates	3	216	.89	232	1.04	1526	7.91**	671	3.51*
Error	72	243		223		193		191	
reduction				8.2%				-	
b				.363*				.208 n.s.	

MS'- adjusted mean squares, with 71 degrees of freedom in the error term

* and ** Significant at the .05 and .01 level of F, respectively

for yield, and decreased through plot protein content and single plant protein content to height, for which covariance was not significant at Nipawin. Least significant differences (.05) for yield and plot protein content at Saskatoon were reduced from 391 to 352 and from 2.05 to 1.95, respectively. The corresponding reductions in L.S.D. (.05) at Nipawin were from 343 to 260 g/plot, and from 2.34 to 1.85% for yield and plot protein content, respectively.

4.1.6 Simple correlations among traits

Simple correlations between the traits measured in this study were made in an effort to identify the traits strongly related to protein content. Results would provide an indication of the effect of a change in protein content on other traits and likewise the effect on protein content of a shift in one of the other traits. Mean values for yield, protein content, and single plant protein content at both locations were adjusted by covariance before calculation of the correlation coefficients.

Correlation coefficients were calculated separately for each location, despite the statistical validity of combining locations where correlations were homogeneous, because correlations between traits may be considered biological phenomena and thus subject to interaction with locations. Phenotypic correlations among yield, plot protein content, single plant protein content, haulm protein content, harvest index, height, seed yield/plant, protein weight/plant, and haulm protein weight/plant for both locations are given in Table 4.10. Genotypic correlations between yield and protein content were calculated for both locations, and were higher than the corresponding phenotypic correlations (-1.01 and -.697 for

Table 4.10 Simple correlation coefficients among nine plant traits of 25 genotypes grown at Saskatoon and Nipawin in 1974

Trait	Location	Plot protein	Single plant protein	Haulm protein	Harvest index	Height	Seed yield/ plant	Protein wt/plant	Haulm protein wt/plant
Yield	S'toon	-.811**	-.779**	-.209	.009	.103	-.522**	-.643**	-.620**
	Nip.	-.690**	-.683**	-.049	-.087	-.009	-.309	-.506**	-.241
Plot protein	S'toon		.846**	.358	-.177	.034	.119	.284	.345
	Nip.		.844**	.249	-.002	.199	.135	.480*	.302
Single plant protein	S'toon			.318	-.087	-.212	.271	.410*	.381
	Nip.			.284	-.087	.204	.153	.538**	.399*
Haulm protein	S'toon				-.266	.081	-.080	.035	.260
	Nip.				-.214	.304	-.467*	-.128	.295
Harvest index	S'toon					-.744**	-.458*	.281	-.155
	Nip.					-.799**	.248	-.045	-.571**
Height	S'toon						-.504*	-.406*	-.64
	Nip.						-.281	.013	.450*
Seed yield/ plant	S'toon							.969**	.758**
	Nip.							.859**	.455*
Protein weight/ plant	S'toon								.877**
	Nip.								.755**

* and ** Significant at the .05 and .01 level, respectively

Saskatoon and Nipawin, respectively), but since no valid test of significance is available for genotypic correlations, they were not included in the analysis.

4.1.6.1. Yield and single plant traits

Yield was significantly ($p = .01$) negatively related to single plant protein content, and protein weight/plant at both locations, and negatively related to yield/plant and haulm protein weight/plant at Saskatoon. Correlations of yield with haulm protein content and harvest index were low and not significant. Height and yield were not correlated at either location, indicating that one of these traits may be independently manipulated without affecting the other.

4.1.6.2 Plot protein content and single plant traits

Correlations between plot protein content and single plant traits were similar at both locations. Plot protein content was significantly positively correlated ($p = .01$) with single plant protein content at both locations. Single plant protein content was generally lower than plot protein content, but the genotypes were similar with respect to both traits. At Nipawin, plot protein content was significantly positively correlated ($p = .05$) with total protein weight/plant. The correlation coefficient was positive, but lower and non-significant at Saskatoon. The correlation coefficients between plot protein content and haulm protein content were low, positive and non-significant.

4.1.6.3 Single plant traits

Single plant protein content was significantly, positively

correlated with protein weight/plant at both locations (p= .05 at Saskatoon; p= .01 at Nipawin) and with haulm protein weight/plant only at Nipawin (p= .05). Thus, single plant protein content behaves similarily to plot protein content. Likewise, the correlation coefficent between single plant protein content and haulm protein content was positive, but low and non-significant. The relationship between single plant protein content and protein weight/plant (r= .410* and .538** for Saskatoon and Nipawin, respectively) indicated that seed protein content has a closer relationship to protein weight/plant than does haulm protein content (r= .035 and -.128 for Saskatoon and Nipawin, respectively).

Haulm protein content was not significantly correlated with any other trait except seed yield/plant at Nipawin, where the relationship was negative. Harvest index was highly negatively correlated (p= .01) with height at both locations (r=-.744** and -.799** for Saskatoon and Nipawin, respectively) and with haulm protein weight/plant (r= -.571**) at Nipawin. Harvest index was negatively correlated (p= .05) with seed yield/plant only at Saskatoon. The low to moderate values for r were unexpected in view of the fact that seed yield/plant is one of the two components of harvest index. However, the high correlation with height indicated that the proportion of vegetative dry matter was the more important of the two in determining harvest index.

Height was negatively correlated (p= .05) with both seed yield/plant and protein weight/plant at Saskatoon. At Saskatoon, shorter genotypes were generally higher yielding on a single plant basis. The same trend was apparent at Nipawin, but the correlation

was not significant. Height was correlated (p= .05) with haulm protein weight/plant at Nipawin but no such relationship existed at Saskatoon.

Seed yield/plant was positively correlated (p= .01) with protein weight/plant and haulm protein weight/plant at both locations. Since haulm protein weight/plant is a component of protein weight/plant and is positively correlated (p= .01) with protein weight/plant, this latter correlation is not surprising.

4.1.6.4 Yield and protein content

Yield and protein content were negatively correlated (p= .01) among 25 genotypes at three locations in 1974, as well as among 22 genotypes grown at Saskatoon for three consecutive years. (Tables 4.11 a and b). Coefficients of determination indicated that between one third and two thirds of the observed variation in protein content was related to variation in yield. Since yield and protein content were not strongly correlated with the other single plant traits, there was no indication of a spurious correlation of both traits to a third. From the traits measured, there was no indication of the reason for a negative correlation.

4.1.7 Variance component analysis

If a random model for analysis is assumed, it is possible to apportion total variance into main effects and interactions which comprise the model as follows:

$$y_{ijk} = u + a_i + b_j + c_k + ab_{ij} + e_{ijk}$$

where y_{ijk} = the phenotypic value of the i^{th} genotype at the j^{th} location (or year) in the k^{th} replicate

Table 4.11.a Correlation coefficients between yield and protein content of 25 pea genotypes grown at three locations in 1974

	Saskatoon	Nipawin	Bellevue
r_2	-.811**	-.690**	-.759**
r^2 (%)	65.8	47.6	57.6

Table 4.11.b Correlation coefficients between yield and protein content of 22 pea genotypes grown in three consecutive years at Saskatoon.

	1973	1974	1975
r_2	-.582**	-.746**	-.603**
r^2 (%)	33.9	55.6	36.4

** Significant at the .01 level

u = the population general mean

a_i = the effect of the i^{th} genotype

b_j = the effect of the j^{th} location (or year)

c_k = the effect of the k^{th} replicate

ab_{ij} = the effect of the i^{th} genotype at the j^{th} location (or year)

and e_{ijk} = the environmental effect peculiar to the i^{th} genotype in the k^{th} replicate of the j^{th} location (or year)

The models assumed for the variance component analysis of the two-location and three-location, and the three-year analyses were of the above type, with the assumptions made that location x replicate and genotype x replicate interactions were non-existent and therefore included into replicate within location and error effects, respectively. The third order interaction was taken as the error term. The variance due to each component for both yield and protein content as calculated from the analyses of variance is shown in Tables 4.12 a,b and c.

The genotypic variance for yield was negative, for which the best estimate is zero (Comstock and Robinson, 1955). This may be partly explained by the large genotype x location and error variances which are subtracted in calculation of the genotypic variance. There was much greater genotype x location variance for yield (64% of the total) than for protein co ntent (19%). Variance due to genotype, was just slightly greater than error variance. In contrast to yield, the genotype x location interaction for protein content was only approximately 2/5 of the size of the genotypic component.

Table 4.12a Variance components for yield and protein content of 25 pea genotypes grown in three locations in 1974

Source	Yield variance	Protein variance
Genotype	0*	2.59
Genotype x location	97,917	1.10
Error	55,801	2.08

Table 4.12b Variance components for yield and protein content of 25 pea genotypes grown at Nipawin and Saskatoon in 1974

Source	Yield variance	Protein variance
Genotype	64,049	4.60
Genotype x location	2,725	.32
Error	63,631	2.35

Table 4.12c Variance components for yield and protein content of 22 pea genotypes grown for three years at Saskatoon

Source	Yield variance	Protein variance
Genotype	39,719	2.106
Genotype x year	6,309	0 *
Error	43,529	1.539

* Best estimates of negative value.

However, when the Bellevue location was removed from the analysis, the components of variance are altered markedly (Table 4.12b). The most important change was in the proportion of the variance due to genotype x location variance. That component dropped from 64% to 2% for yield and from 19% to 4% for protein content. This decrease in genotype x location variance resulted in a relative increase in the genotypic variance component, from zero to 49% for yield and from 45% to 63% for protein content. These proportions represent broad sense heritability, or the ratio of genotypic to total observed variance. The exclusion of one location (Bellevue) had a considerable effect on the calculation of heritability.

The effect of years on yield and protein content was quite different (Table 4.12c). Genotypic variance for yield decreased slightly from 49% to 44% compared with the two-location estimate, and decreased from 63% to 58% for protein content. These values represent an additional estimate of broad-sense heritability. The genotype x year interaction variance was low for yield and zero for protein content. Thus, in spite of large differences in yield among years, the genotypes did not vary greatly in yield relative to one another over different years. Since year variance for protein content was small, the low genotype x year interaction variance was not unexpected.

4.2 Effect of stage of maturity on protein content

This study was undertaken to provide information on the effect of maturity on protein content of field peas as an integral part of Objective 2 (see Introduction) and also to substantiate the hypothesis that the anomalous results at Bellevue (Section 4.1) in 1974 were explainable on the basis of immaturity. Thus, the aims of this experiment were as follows:

(1) To trace the accumulation of seed components, namely fresh weight, dry weight, protein content and starch content, of 25 pea genotypes through maturation;

(2) To provide information on the yield-protein relationships of those 25 pea genotypes in an adjacent large-plot study by correlation with the results from (1) above;

(3) To explain the results at Bellevue by correlation with the results from (1) above.

4.2.1. Analysis of variance for stage of maturity

The genotypes were harvested by hand as described previously (Materials and Methods) on four dates from pod-filling to maturity, i.e. July 21 and 28, August 7 and 21. Fresh weight, dry weight, protein content, and starch content of the seeds were recorded and all traits except starch content were subject to analysis of variance (Table 4.13). The mean values for each genotype are given in Tables 4.14 and 4.15. There were significant differences ($p = .01$) among harvests and genotypes, and significant ($p = .01$) genotype x harvest interactions for each trait. The genotypes displayed similar developmental patterns, although differing widely in amounts of dry matter accumulated.

Table 4.13 Analysis of variance for fresh weight, dry weight, and protein content of 25 pea genotypes at 4 harvests at Saskatoon, 1975

Source	d.f.	M.S. fresh wt.	M.S. dry weight	M.S. protein content
Genotype	24	49,985**	18,507**	23.2**
Harvest	3	242,114**	601,741**	467.7**
Genotype x harvest	72	12,801**	3,689**	7.4**
Error	100	1,687	963	2.1

** Significant at the .01 level

Table 4.14 Mean values for fresh weight and dry weight (g/plot) of 25 pea genotypes at each harvest at Saskatoon, 1975

Genotype:	Fresh weight				Dry weight			
Harvest #	1	2	3	4	1	2	3	4
W703	516	689	578	402	163	295	356	393
Trojan	220	543	740	367	41	177	371	360
P.I.324705	234	384	430	306	38	143	246	275
W718	372	432	292	278	111	218	230	264
MP783	129	334	500	284	33	118	257	248
MP790	286	430	316	262	77	193	246	246
Triumph	150	443	392	258	22	124	199	236
P.I.356837	232	338	347	261	44	128	234	236
P.I.356846	226	442	277	240	50	182	207	227
MP789	300	424	323	248	93	195	221	226
MP702	188	374	213	230	45	178	193	214
MP39	68	383	385	226	12	106	259	208
P.I.269812	258	328	259	222	72	180	226	206
P.I.357001	168	349	266	215	38	140	193	200
Lincoln*	418	510	252	208	49	141	220	195
Trapper	188	259	186	208	49	141	158	188
P.I.356885	92	376	320	203	14	126	184	184
P.I.356834	298	301	204	188	82	160	177	178
MP761	298	486	219	188	66	212	184	177
Petit Pois	260	261	162	182	70	164	146	172
Century	132	321	218	175	25	139	158	163
P.I.206790*	298	390	208	176	60	129	160	160
Dashaway	168	283	200	172	39	150	178	158
Palouse	356	192	143	152	114	136	134	142
Mean	242	385	305	235	60	164	213	218
S.D.	103	103	139	60	36	41	57	59

* - wrinkle-seeded genotype

Harvest dates
1. July 21
2. July 28
3. August 7
4. August 21

Table 4.15 Days to flower, percent protein and percent starch of 25 pea genotypes at each harvest at Saskatoon, 1975

Genotype	Days to Flower	Percent Protein at Harvest Number 1	2	3	4	Percent Starch at Harvest Number 1	2	3	4
P.I.206790 *	53	30.1	25.5	24.7	27.0	20.7	30.5	32.5	30.5
MP783	47	30.3	27.6	24.6	25.2	35.8	40.6	44.1	42.8
P.I.269812	47	27.3	26.8	25.2	24.7	35.5	42.6	43.8	43.3
P.I.324705	57	33.4	28.8	28.1	24.5	24.9	34.2	35.0	37.9
P.I.357001	55	31.9	26.7	23.7	24.5	19.2	35.7	40.1	39.4
Lincoln*	50	29.1	23.9	23.9	24.2	23.4	35.9	34.0	33.7
W718	46	28.4	24.7	24.1	23.8	34.3	43.1	40.9	43.8
P.I.356846	53	26.4	25.1	24.4	23.7	30.3	40.6	41.9	38.9
W703	46	28.4	24.7	24.1	23.8	34.3	43.1	40.9	43.8
P.I.356885	56	35.5	23.9	22.0	23.3	15.0	39.4	45.6	45.6
Palouse	48	28.2	21.3	23.3	23.1	40.6	43.4	43.3	43.8
Triumph	57	34.1	24.4	23.9	23.1	19.7	40.9	44.6	44.3
Petit Pois	51	27.6	24.3	25.4	22.8	32.3	42.6	42.4	42.6
P.I.356834	50	26.1	23.8	23.9	22.7	35.7	42.6	43.1	43.8
P.I.356837	57	32.0	26.5	26.7	22.4	26.1	42.9	43.1	42.4
MP790	51	31.4	25.7	24.4	22.1	38.6	43.4	43.6	44.1
MP702	55	31.4	22.5	22.4	21.8	29.1	43.8	43.1	41.9
Trapper	51	27.5	23.5	22.9	21.7	32.5	41.9	43.6	43.6
Dashaway	55	25.9	22.8	22.3	21.5	34.7	42.6	45.1	45.3
MP789	48	26.7	23.3	24.2	20.9	32.5	43.8	45.1	45.1
Trojan	51	33.3	27.2	23.4	20.4	22.4	39.4	43.3	41.9
MP712	53	26.7	25.4	21.7	20.3	36.2	43.8	45.8	45.1
Century	51	29.6	22.1	21.7	20.1	29.3	44.3	45.1	45.1
MP39	57	35.2	23.9	18.8	19.8	16.0	36.9	45.1	45.2
MP761	50	22.9	20.2	20.5	18.2	38.2	40.9	45.6	45.8
Mean	51.8	29.5	24.5	23.6	22.6	29.9	40.7	42.4	42.4
S.D.	3.6	3.3	2.1	1.9	1.9	7.6	3.5	3.6	3.7

* wrinkle-seeded genotype

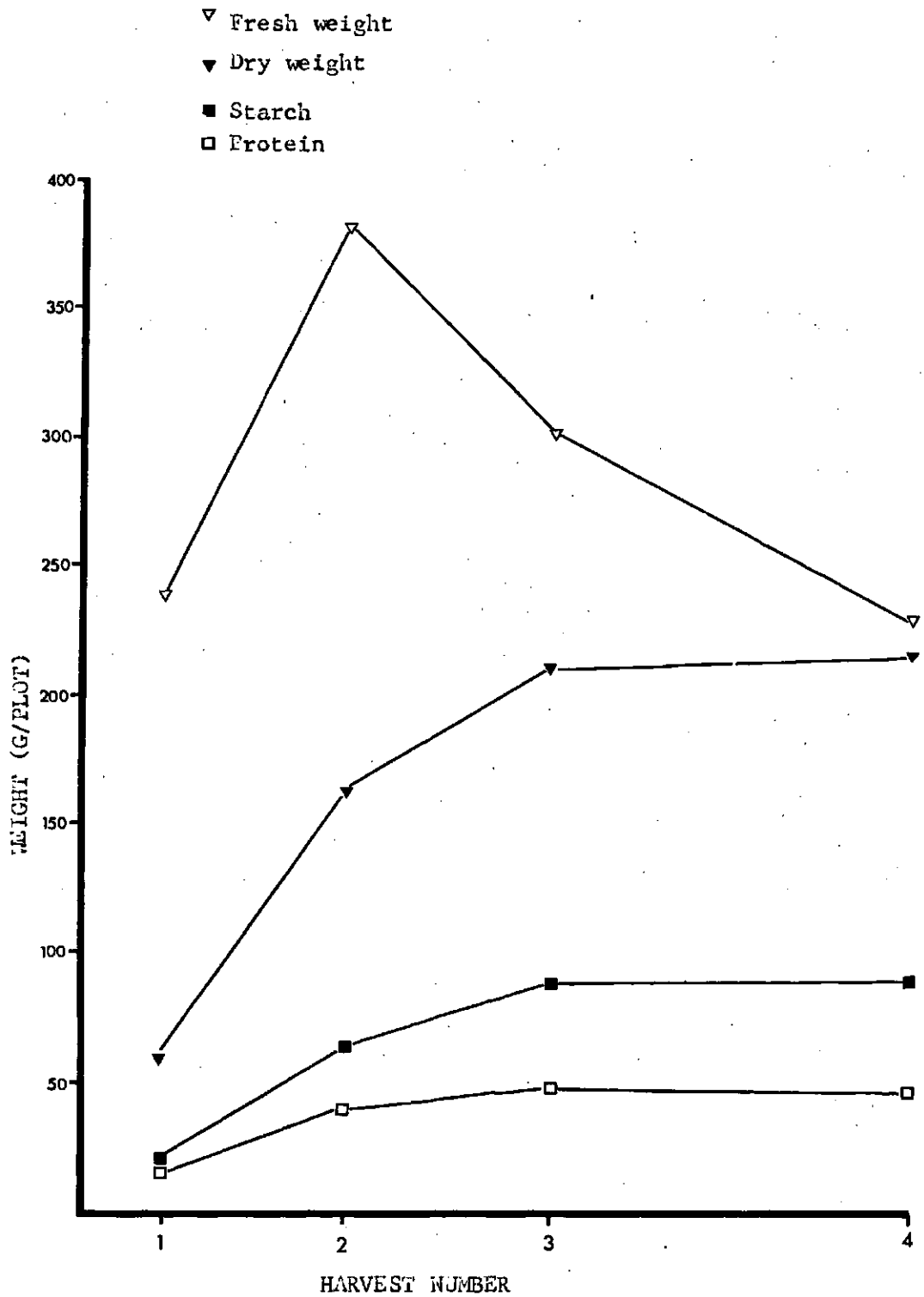
The first harvest (H1) on July 21 was 13-23 days post-flowering, depending upon the genotype, and was chosen when the latest flowering genotype had pods with ovules large enough to permit harvesting.

Fresh weight of most genotypes reached a maximum at harvest 2 (H2) and declined subsequently as the moisture content of the seeds decreased (Figure 4.1). There were some exceptions and these resulted in the significant genotype x harvest interaction. Palouse, an early flowering determinate cultivar, had a maximum fresh weight at H1, whereas MP 783, P.I.324705 and Trojan did not reach a maximum until the third harvest (H3). However, the latter two were mid-late flowering and were situated in a moist hollow in the plot area which allowed them to continue development longer than other genotypes with less available moisture. MP 783 was early flowering, but continued to accumulate fresh weight up to H3. It had considerably less fresh weight at H1 than the other early flowering genotypes, indicating a slower period of development. The range of fresh weight among genotypes was greatest at H3 and smallest at H4, indicating that differences among genotypes increased to a maximum 28-38 days after flowering and then decreased markedly at full maturity, i.e. 42-52 days after flowering.

The pattern of accumulation for dry weight was different from that for fresh weight (Figure 4.1). Dry weight more than doubled between H1 and H2, then subsequently increased slowly. Mean dry weight at the last three harvests was not significantly different. However, maximum mean dry weight was reached at H4 where the range among genotypes was also greatest. All weight lost on drying was assumed to be water and the moisture content of the dried peas, as determined by oven drying, was 6.5%. Thus, percent dry matter was calculated as 100 (dry

Figure 4.1 Weight of seed components accumulated during maturation.

Mean of 25 pea genotypes



weight-(.065xdry weight))/fresh weight). On this basis the mean dry matter contents for H1 to H4 were 23.2%, 39.7%, 65.2% and 86.8%, respectively. After H1 the genotypes displayed a markedly similar pattern of dry weight accumulation and did not differ in dry weight between H3 and H4. Six genotypes decreased in dry weight from H3 to H4 and probably contributed to the significant genotype x harvest interaction.

Mean protein content decreased from H1 to H4, the largest decrease occurring between H1 and H2 (Figure 4.2 and Table 4.15). Mean protein contents of the last three harvests were not significantly different, as with fresh weight and dry weight, the genotypes displayed a similar pattern of change in protein content. There were two exceptions and these resulted in the significant genotype x harvest interaction. MP 761 had a very low protein content (22.9%) at H1 in contrast to all other genotypes which were above 25.9%. MP 761 was also lowest in protein content at maturity. The protein content of P.I.206790, a high-protein wrinkle-seeded genotype, decreased from H1 to H3, but then increased and was the highest at maturity. The reasons for MP 761 being low initially and for P.I. 206790 increasing at a late stage are not apparent. Although percent protein content decreased with maturity, the actual weight of protein increased as shown in Table 4.16 and Figure 4.1.

For starch, both percentage content and weight increased with maturity, the latter more rapidly than the former. From H2 to H4, starch content increased by 4% (1.7 percentage points; Table 4.15)

Figure 4. 2 Change in percentage of seed components with maturation. Mean of 25 pea genotypes.

▼ Dry matter
■ Starch
□ Protein

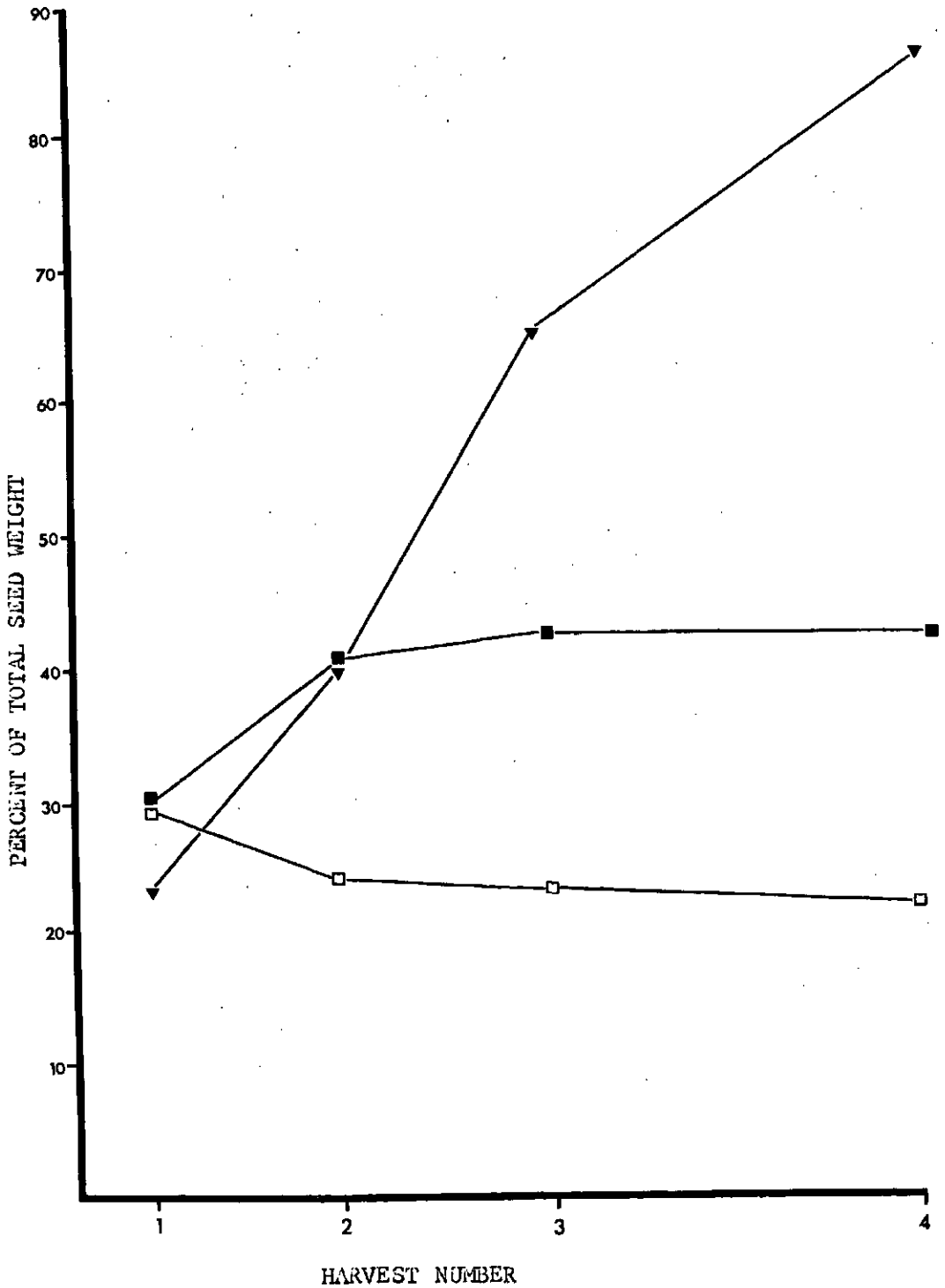


Table 4.16 Weight (g/plot) of protein and starch accumulated by 25 pea genotypes at each harvest at Saskatoon, 1975

Genotype	Weight of protein at harvest number 1	2	3	4	Weight of starch at harvest number 1	2	3	4
W703	42.4	66.0	82.4	92.0	62.6	124.9	148.2	172.3
Trojan	13.7	48.1	86.8	73.5	9.2	69.7	160.8	150.7
P.I.324705	12.7	40.9	69.2	67.2	9.5	48.6	86.0	103.9
W718	31.5	53.8	55.4	62.7	38.1	93.9	94.0	115.3
MP783	10.0	32.3	63.3	62.2	11.8	47.5	113.3	105.8
Triumph	7.5	30.2	47.7	54.4	4.3	50.7	88.7	104.6
MP790	24.2	49.5	60.0	54.2	29.7	83.7	107.3	108.0
P.I.356846	13.2	45.8	50.5	53.9	15.1	73.9	86.7	88.4
P.I.356837	14.1	33.9	62.1	52.7	11.5	54.9	100.4	99.6
P.I.269812	19.6	48.2	56.9	50.9	25.5	76.7	99.1	89.3
P.I.357001	12.1	37.4	45.8	48.7	7.3	49.9	77.5	78.4
MP789	24.8	45.4	53.5	47.4	30.2	85.5	99.6	101.8
Lincoln *	32.0	47.5	52.5	47.2	25.7	71.6	74.8	65.8
MP702	14.1	40.1	43.2	46.8	13.1	78.0	83.2	89.6
P.I.206790 *	18.1	32.9	39.6	43.3	12.4	39.4	52.0	48.9
P.I.356885	5.0	30.2	40.5	42.9	2.1	49.7	83.8	83.8
MP712	12.3	41.1	41.1	42.6	16.7	71.0	86.6	94.6
MP39	4.2	25.5	48.8	41.3	1.9	39.2	116.7	93.7
Trapper	13.5	33.2	36.0	40.5	15.9	59.0	68.5	81.5
P.I.356834	21.4	38.1	42.4	40.4	29.3	68.2	76.3	78.0
Petit Pois	19.3	39.7	36.9	39.2	22.6	69.4	61.4	73.3
Dashaway	10.1	34.2	39.5	33.7	13.5	63.9	79.8	71.1
Century	7.4	30.7	34.2	32.8	7.3	61.6	71.2	73.5
Palouse	32.2	29.0	31.2	32.8	46.3	58.9	58.1	62.2
MP761	15.1	42.7	37.7	32.3	25.2	86.7	83.8	81.1
Mean	17.2	39.8	50.3	49.4	19.4	67.0	90.3	92.6
S.D.	9.5	9.3	14.3	13.9	14.4	19.1	25.1	26.3

* wrinkle-seeded genotype

and weight of starch by 38% (Table 4.16), while the dry weight and protein weight increased by 34% (Table 4.14) and 24% (Table 4.16), respectively, in the same period. Increases in dry weight, weight of protein, and weight of starch were small or negligible between H3 and H4. In other words, by 28 to 38 days after flowering accumulation of the major seed components was virtually complete.

4.2.2 Simple correlations between harvests for various traits

Correlations between harvests for various traits were studied in an effort to characterize development with maturity. Correlations between harvests for fresh weight, dry weight, protein content and starch content are shown in Table 4.17. Dry weight at H1 was positively correlated ($p = .01$) with dry weight at H2. Likewise, fresh weight and protein content were correlated ($p = .05$) between the two harvests, but starch content was not. None of the traits was correlated between H1 and the last two harvests. The values obtained at H2 were all correlated ($p = .05$ and $= .01$)) to corresponding values at H3 and H4, but the coefficients were only moderate. Thus by H2, a characteristic pattern for each genotype was beginning to emerge. Correlations for each trait between H2 and H4 and between H2 and H3 were similar. However, the correlations for both fresh weight and dry weight between H3 and H4 were higher than those for either protein or starch content. Thus, final genotype values for fresh and dry weight (yield) were well established by H3, but protein and starch content values were not. Both these latter traits underwent changes among genotypes between H3 and H4. Thus, the genotypes in this experiment had remarkably similar patterns of deposition of seed

Table 4.17 Simple correlation coefficients between harvests for fresh weight, dry weight, protein content and starch content in the developing seeds of 25 pea genotypes

Harvest number	Trait	Harvest number 1	2	3
2	F. wt.	.450*		
	D. wt.	.788**		
	Protein %	.465*		
	Starch %	.096		
3	F. wt.	-.021	.650**	
	D. wt.	.199	.442*	
	Protein %	.073	.699**	
	Starch %	.021	.555*	
4	F. wt.	.268	.725**	.895**
	D. wt.	.284	.535*	.931**
	Protein %	.178	.509*	.648**
	Starch %	.136	.591*	.710**

* and ** Significant at the .05 and .01 level respectively

components, allowing for initial differences in days to flowering.

4.2.3 Simple correlations between traits within harvests

Simple correlations between traits within harvests were performed to provide information on the strongly negative yield-protein content relationship recorded among these genotypes in a previous experiment (section 4.1) and to note any changes in those correlations with advancing maturity. The correlation coefficients between traits at each harvest are given in Table 4.18. Fresh

Table 4.18 Simple correlation coefficients between traits within each harvest of 25 pea genotypes at Saskatoon, 1975

	Harvest number			
	1	2	3	4
F.wt.:D.wt.	.961**	.612**	.922**	.993**
Days to flower:F.wt.	-.630**	-.118	-.052	-.179
Days to flower:D.wt.	-.734**	-.458*	-.210	-.205
Days to flower:Protein %	.574**	-.273	-.038	-.093
Days to flower:Starch%	-.624**	-.361	-.043	-.123
D.wt:Protein %	-.556**	-.313	-.081	-.020
D.wt:Starch %	.895**	-.204	.015	-.021
Protein %: Starch %	-.777**	-.396*	-.510**	-.666**

* and ** Significant at the .05 and .01 level, respectively

weight and dry weight were positively correlated at all harvests (p= .01). The lower correlation at H2 occurred when fresh weight was at a maximum. Days to flower were negatively correlated with fresh weight, dry weight and starch content at H1 (p= .01) and with dry weight at H2 (p= .05), since these traits increased with maturity in the short term. Protein content was positively correlated with days to flower at H1 (p= .01). Since percent protein decreased over time, the

positive correlation merely reflected the immaturity of the later flowering genotypes. Dry weight was negatively correlated with protein content ($p = .01$) and positively correlated with starch content at H1 ($p = .01$). Protein content and starch content were negatively correlated ($p = .01$) at all harvests (H2, $p = .05$). The correlations of protein content and starch content with days to flower and dry weight were significant ($p = .01$) and of opposite sign at H1. However, these relationships did not extend to later harvests where correlation coefficients between protein content and starch content were lower than at H1, but still significant. Dry weight (yield) and protein content were not correlated after H1 in this study.

At H3 and H4, fresh weight and dry weight were positively correlated ($p = .01$) indicating that the seed of the different genotypes had matured uniformly. Among the other traits, only starch and protein content were correlated (negatively, $p = .01$). The influence of days to flowering on the other traits was no longer evident.

4.2.4 Relationship of the maturity study to the large-plot study in 1975

Plots measuring 4.8 by 1.2m of the same 25 pea genotypes were seeded adjacent to the maturity study and allowed to mature fully before harvest on August 21, concurrent with the final harvest of the maturity study. Seed yield and protein content were measured, and the protein yield/plot was calculated. The analysis of variance is given in Table 4.19 and the mean genotypic values are given in Table 4.20. Genotypes were significantly different ($p = .01$) for all

Table 4.19 Analysis of variance for yield, protein content and protein yield of 25 genotypes at Saskatoon, 1975

Source	d.f.	M.S. yield	M.S. protein	M.S. protein yield
Genotypes	24	160721**	4.66**	6,245**
Replicates	2	22668	1.14	528
Error	48	48061	1.21	2,764
TOTAL	74			

** Significant at the ,01 level

Table 4.20 Mean values for yield (g/plot), protein content (%) and protein yield (g/plot) of 25 pea genotypes at Saskatoon, 1975

Genotype	Yield g/plot	Percent protein	Protein yield g/plot
MP39	2259	22.9	519
MP789	2145	22.5	482
MP712	2098	22.5	471
MP761	2084	23.0	474
W703	2054	23.7	487
Petit Pois	2024	24.3	491
Century	2005	23.7	476
P.I.269812	2003	23.5	473
MP783	1990	23.5	468
MP790	1953	22.8	446
MP702	1889	22.9	434
Trojan	1862	25.4	475
P.I.357001	1862	25.6	477
Triumph	1821	22.3	407
Trapper	1814	23.7	429
Dashaway	1812	23.1	417
W718	1752	23.8	418
P.I.356885	1706	23.4	401
P.I.356837	1612	24.8	399
P.I.356846	1593	25.3	404
P.I.356834	1555	23.7	368
P.I.324705	1526	26.7	406
Palouse	1519	23.0	350
Lincoln	1483	25.0	370
P.I.206790	1429	26.7	381
Mean	1834	23.9	437
S.D.	433	1.2	46
C.V.	11.9%	4.6%	12.0%

three traits and their performance was similar to that of the same genotypes grown at Saskatoon in the two preceding years (Table 4.7). Simple correlations between traits are shown in Table 4.21. Seed

Table 4.21 Simple correlation coefficients between yield, protein content and protein yield of 25 pea genotypes at Saskatoon, 1975.

	Seed yield	Protein content	Protein yield
Seed yield		-.596**	.925**
Protein content			-.253

** Significant at the .01 level

yield and protein content were negatively correlated (p= .01). Protein yield was positively correlated (p= .01) with seed yield, but not with protein content.

Correlations between the maturity study and the large plot study for yield and protein content are given in Table 4.22. There

Table 4.22 Simple correlation coefficients between the maturity study and the large-plot study at Saskatoon for yield and protein content of 25 pea genotypes

	Harvest number			
	1	2	3	4
Yield:dry weight	-.116	.039	.269	.189
Protein %:Protein %	.252	.536**	.540**	.551**

** Significant at the .01 level

was no relationship whatsoever between yield of the large plot study and dry weight at any of the harvests in the maturity study. The correlations between the two experiments for protein content were positive and significant (p= .01) at all harvests except H1.

4.2.5 Relationship of the maturity study to the 1974 Bellevue large-plot study

The third objective of the maturity study was to relate the findings to the yield and protein contents of the same genotypes grown at Bellevue in 1974. Accordingly, yield and protein data from the 1974 Bellevue large plot study were correlated with yield and protein data, respectively, from the 1975 maturity study over the four harvests. Yield at Bellevue in 1974 was correlated (p = .01) with yield of the same genotypes at H1 and H2 at Saskatoon in 1975 (Table 4.23).

Table 4.23 Simple correlation coefficients of yield and protein content at 4 harvest dates, and days to flower at Saskatoon, 1975, with yield and protein content at Bellevue, 1974. (25 genotypes)

	Saskatoon				
	Harvest number				Days to
Bellevue	1	2	3	4	flower
Yield	.626**	.551**	.011	.116	-.758**
Protein %	.435*	.485*	.304	.459*	.481*

* and ** Significant at the .05 and .01 level, respectively

Protein content at Bellevue in 1974 was positively correlated (p= .05) with protein content at each harvest stage at Saskatoon in 1975 except H3. Thus, the 1974 Bellevue data on yield and protein content were closely related to the 1975 Saskatoon data at the first two harvest

stages, suggesting that the 1974 Bellevue experiment was harvested at a stage physiologically comparable to H2 (20-30 days post flowering). The negative correlation (r= -.758**) between days to flower at Saskatoon in 1975 and yield of peas at Bellevue in 1974 further supports this by indicating that the later flowering genotypes were the lowest yielding.

4.3 Heritability of agronomic traits, protein content and methionine content

As outlined in the Introduction, the objectives of this study were to **calculate heritability estimates** for several agronomic traits, protein content and methionine content. This experiment was also designed to provide information on the mode of inheritance of, and relationship between, protein content and methionine content, particularly as they relate to breeding strategies for protein improvement.

4.3.1 Analysis of variance for agronomic traits, protein content and methionine content

Yield, seed weight, days to flower, protein content and methionine content of the 19 parents and 21 F_2 populations in this experiment (see Materials and Methods) were measured. Methionine content was expressed both as weight of the meal (mg met/g meal) and as a percentage of the protein (mg met/g protein expressed as %). The analysis of variance for those traits is given in Table 4.24 and the mean genotype values for each trait of the parents and F_2 populations are given in Tables 4.25 and 4.26, respectively. There were significant differences ($p = .01$ and $= .05$) among parental genotypes for all traits measured. However, among F_2 populations neither protein content nor methionine content differed significantly. There were significant differences between replicates ($p = .01$ and .05) for days to flower, seed weight, and the two methionine content traits.

Most traits were characterized by similar means for both parental and F_2 population classes (Tables 4.25 and 4.26). In addition, range (Tables 4.25 and 4.26) and variance (Table 4.27) of the F_2 populations were generally smaller than for parents.

Table 4.24 Analysis of variance for six traits in parents and F_2 populations in 21 crosses in peas at Saskatoon, 1975

Source	d.f.	Yield M.S.	Day to flower M.S.	Seed weight M.S.	Protein M.S.	mg met/g meal M.S.	mg met/g protein M.S.
Genotypes	39						
Parents	18	39490**	28.9**	9364**	9.46**	0.0711 *	0.0025*
F_2 populations	20	34500**	12.3**	4291**	1.40	0.0100	0.0013
Remainder	1	19034	0.1	42	15.82	0.1380	0.0010
Replicates	1	1891	5.0*	696**	6.16	0.3960**	0.0282**
Error	39	7237	1.1	69	1.05	0.0083	0.0014
TOTAL	79						

* and ** Significant at the .05 and .01 level of F, respectively

Table 4.25 Mean values for six traits of 19 parental lines of peas at Saskatoon, 1975

Genotype	Yield g/plot	Days to flower	Seed weight g/1000 seeds	Protein %	mg met/g meal	mg met/g protein
Triumph	952	55.5	276.5	24.0	1.86	.77
MP706	915	49.0	208.5	25.6	2.00	.78
P.I.164853*	844	49.0	192.5	29.5	2.24	.76
NRC335-338	829	45.5	141.5	27.6	2.10	.76
MP39	810	55.0	130.5	26.4	1.96	.74
NRC 89-304*	770	51.5	214.0	28.9	2.31	.80
Ceser	767	48.5	221.5	25.7	1.86	.72
Century	760	50.0	214.5	24.7	1.83	.74
VW188	752	47.5	289.5	24.3	2.00	.82
P.I.324705	749	55.5	121.5	28.6	2.10	.73
P.I.210768*	749	50.5	235.0	28.9	2.20	.77
Trapper	709	48.5	129.5	24.2	1.87	.77
Vedette	696	40.5	230.5	23.6	1.78	.75
NRC89-297*	688	50.5	215.0	29.4	2.14	.73
P.I.210675*	686	47.0	265.5	29.1	2.41	.83
P.I.179969	571	46.0	94.0	27.8	2.00	.72
P.I.206790*	556	51.5	298.5	28.0	2.31	.83
NRC210-49W	444	45.0	82.5	28.3	2.04	.72
Tiny *	419	46.5	102.0	30.9	2.32	.75
Mean	719	49.1	192.8	27.1	2.07	.76
S.D.	140.4	3.8	68.3	2.2	.19	.04

* wrinkle-seeded genotype

Table 4.26 Mean values for six traits of 21 F_2 populations of peas at Saskatoon, 1975

F_2 Population	Yield g/plot	Days to flower	Seed weight g/1000 seeds	Protein %	mg met/g meal	mg met/g protein
VW188 x MP706	1043	48.5	231.0	26.3	1.90	.72
P.I.210678 x Trapper	894	49.9	183.5	26.9	1.93	.72
P.I.210675 x Trapper	871	49.0	216.0	25.6	2.04	.80
VW188 x Trapper	870	48.5	207.0	25.0	1.86	.74
NRC89-297 x Trapper	859	49.5	169.0	26.2	2.12	.80
VW188 x MP39	817	48.5	210.0	25.9	1.93	.74
NRC89-304 x Trapper	816	50.5	182.5	25.6	2.00	.78
P.I.324705 x MP706	813	49.0	135.5	27.2	2.09	.77
P.I.206790 x MP39	802	49.5	193.5	26.9	2.05	.76
NRC335-338 x Trapper	761	48.5	174.0	24.0	1.94	.81
P.I.206790 x Trapper	752	48.5	202.5	27.3	2.05	.75
P.I.206790 x MP706	738	49.0	226.0	27.2	2.05	.75
P.I.179969 x Ceser	726	45.0	145.5	26.7	1.99	.74
P.I.164853 x Ceser	717	48.0	214.5	27.2	2.01	.74
P.I.206790 x Ceser	713	48.0	293.5	25.8	1.93	.75
VW188 x Ceser	694	49.0	289.0	25.2	1.86	.74
P.I.324705 x Triumph	670	55.5	158.0	26.5	2.01	.76
P.I.324705 x MP39	619	55.5	131.5	26.1	2.00	.76
Tiny x Ceser	594	48.5	167.0	25.9	2.00	.77
NRC210-49W x Trapper	552	45.5	109.5	27.0	2.04	.76
P.I.324705 x Vedette	452	47.0	179.0	26.6	1.96	.74
Mean	751	49.0	191.3	26.2	1.99	.76
Std. deviation	131.4	2.5	46.3	0.86	.07	.03

Table 4.27 Mean and variance of six traits in parental and F_2 populations of peas at Saskatoon, 1975

Trait	Class	Mean	Variance
Yield (g /plot)	Parents	719	19711
	F_2 populations	751	17250
	difference	32.0**	
Days to flower	Parents	49.1	14.48
	F_2 populations	49.0	6.15
	difference	0.1	
Seed weight (g /1000 seeds)	Parents	192.8	4679
	F_2 populations	191.3	2145
	difference	1.5	
Protein content (%)	Parents	27.1	4.93
	F_2 populations	26.2	.736
	difference	.9**	
mg methionine/g meal	Parents	2.07	.036
	F_2 populations	1.99	.005
	difference	.08	
mg methionine/g protein	Parents	.76	.001
	F_2 populations	.76	.001
	difference	.00	

** Significant at the .01 level by the t test

However, mean yield of the F_2 populations was 4.5% greater than for the parental class (Table 4.27), indicating possible dominance. In addition, the range in yield of the F_2 populations (452 to 1043 g/plot; highest 131% greater than lowest) was similar to that of the parental class (419 to 952 g/plot; highest 127% greater than lowest) even though the variance was slightly smaller (Table 4.27). Thus, it was apparent that yield, alone among the traits measured, maintained a large proportion of the observed among-parent variability.

Mean protein content of F_2 populations was 0.9 percentage points lower ($p = .01$) than the parental mean and variance underwent a 7-fold reduction (Table 4.27). The parental range of 23.6 to 30.9% protein (highest 31% greater than lowest) was very narrow relative to the range in yield and led to an even narrower range among the F_2 populations (24.0 to 27.2%, or a range of 13%) where there were no significant differences (Table 4.24). In general, low-yielding parents were high in protein content and vice versa.

There was a 15 day range in days to flower among parents (Table 4.25) which was reduced to 10.5 days among F_2 populations (Table 4.26). The decrease in range came from the lower end. In other words, there were no F_2 populations that flowered as early as the earliest parent. Lateness for days to flower (55.5 days) in two F_2 populations was due to the fact that they were derived from late-flowering parents which did not differ in days to flower. The reduced variance among F_2 populations (Table 4.27) is indicative of the intermediacy of the progeny means between parental

values.

Seed weight of parents (Table 4.25) ranged from 82.5 to 298.5 g/1000 seeds (highest 262% greater than lowest). This range is double that for yield among the present genotypes and about eight times greater than the range for protein content. Among F_2 populations (Table 4.26), the range decreased to 109.5 to 293.5 g/1000 seeds (highest 168% greater than lowest). As with days to flower, the reduction came from the lower end of the range, with the upper level being maintained by the population P.I. 206790 x Ceser F_2, which has a mean seed weight equal to that of its larger parent. The variance among F_2 populations was less than half the variance among parents (Table 4.27) and the mean of the two classes was virtually identical.

Among parents, both methionine content traits exhibited a very narrow but significant range (Table 4.25). The range in mg met/g meal was from 1.78 to 2.41 (highest 35% greater than lowest), but the range in mg met/g protein was .72 to .83 (highest 15% greater than lowest). Among F_2 populations the range of methionine as mg met/g meal decreased by half while the range in mg met/g protein decreased only marginally (Table 4.26). There were no significant differences for either methionine trait among F_2 populations.

4.3.2. Analysis of covariance to remove the effect of protein content on methionine content

Since the seven wrinkle-seeded parents were the seven highest in mg met/g meal, it was considered valid to correct for initial differences in protein content before comparing these two groups for

mg met/g protein. Both methionine traits were regressed on protein content and the regression values are shown in Table 4.28. The regression of methionine as mg/g meal on protein content was positive and significant (p= .10 to .05), but the regression of methionine as percent of protein on protein content was negative and highly significant. These regressions show that as protein content increased, methionine content of the meal increased slightly, but methionine content expressed as percent of protein decreased significantly.

Table 4.28 Regression of methionine as mg/g of meal and as percent of protein on protein percent of parents and F_2 populations of 21 pea crosses at Saskatoon, 1975.

	b	$S.E_b$	t
Methionine as mg/g of meal on protein %	.0265	.0138	1.921
Methionine as mg/g of protein on protein %	-.0186	.0051	3.628**

4.3.3 Comparison of smooth-seeded and wrinkle-seeded parents

Mean values of each trait of the seven wrinkle-seeded genotypes were compared with the mean values of the remaining 12 smooth-seeded parental genotypes and the results are shown in Table 4.29. Wrinkle-seeded genotypes were lower yielding, heavier seeded, higher in protein content and methionine content (mg/g meal), and after covariance adjustment for initial differences in protein content, slightly higher in methionine as a percent of protein. Thus, the higher

Table 4.29 Effect of seed shape on agronomic traits, protein content and methionine content of 19 pea genotypes at Saskatoon, 1975

Seed type	Yield g/plot	Days to flower	Seed weight g/1000 seeds	Protein content %	Methionine mg/g meal unadjusted	Methionine mg/g meal adjusted	Methionine mg/g protein unadjusted	Methionine mg/g protein adjusted
Wrinkled n=7	673	49.5	217	29.3	2.28	2.23	.78	.83
Smooth n=12	746	49.3	178	25.9	1.95	1.97	.75	.74
Difference	73**	.2	39**	3.4**	.33**	.26**	.02	.09*

* and ** Significant at the .05 and .01 levels respectively by the "t" test.

methionine content of wrinkle-seeded genotypes is a function of both higher protein content and higher methionine content of that protein. The difference in methionine content between the two seed types is however, of minor importance because the absolute level of methionine found in the genotypes of this experiment was extremely low.

4.3.4 Correlation analysis

Correlations between protein content and the other plant traits provide information on the likely effects of selection for protein content on those traits. In the present study, simple correlations between traits were based on the total number of entries as well as on parental and F_2 population classes and these correlation coefficients are given in Table 4.30. All correlations were of low order and generally non-significant. The exceptions were yield and protein content which were negatively correlated ($p = .05$) for all entries and the parental class but not for the F_2 population class. Yield was correlated ($p = .05$) positively with seed weight for all entries, but not for the parental or F_2 population classes. Protein content was not related to either seed weight or days to flower, indicating that these traits could be altered without undue effect on protein content.

The two methionine content measurements were moderately positively correlated, $r = +.450^{**}$ (Table 4.31). The methionine traits were not correlated with yield or days to flower but mg met/g protein was positively correlated ($p = .05$) with seed weight. Mg met/g meal was positively correlated ($p = .01$) with percent protein. That was to be expected since higher percent protein would mean

Table 4.30 Simple correlation coefficients between yield, days to flower, seed weight and protein content of peas at Saskatoon, 1975

			Yield	Protein content	Days to flower
Protein content	All entries	(n=40)	-.346*		
	Parents	(n=19)	-.455*		
	F_2 populations	(n=21)	-.133		
Days to flower	All entries	(n=40)	.254	-.033	
	Parents	(n=19)	.428	-.055	
	F_2 populations	(n=21)	-.061	.370	
Seed weight	All entries	(n=40)	.342*	-.246	-.058
	Parents	(n=19)	.396	-.296	-.149
	F_2 populations	(n=21)	.286	-.256	-.078

* Significant at the .05 level

Table 4.31 Simple correlation coefficients between two methionine traits and yield, days to flower, seed weight, and protein content of peas at Saskatoon, 1975. 40 genotypes

	Yield	Protein content	Days to flower	Seed weight	mg met/g protein
mg met/g meal	-.271	.733**	.072	-.031	.450**
mg met/g protein	.079	-.112	.090	.335*	

* and ** Significant at the .05 and .01 level, respectively

more methionine on a weight basis. Thus, mg met/g meal is really another indicator of protein content rather than an intrinsic measure of protein quality. However, mg met/g protein could be more correctly considered as an indicator of protein quality. This trait is not related to protein content. Thus, protein content and methionine as a percent of protein could probably be improved simultaneously without negative interaction.

4.3.5 Heritability estimates for agronomic traits, protein content and methionine content

Heritability of protein content in legume seed crops ranges from zero to very high (see Literature Review). The reasons for this range include different methods of estimation and differences in non-genetic and genetic variation.

The value of the regression coefficient of F_2 mean on mid-parent value is numerically equal to heritability in the narrow sense (Falconer, 1960). The data from the present study are given in Table 4.32 and Figures 4.3 to 4.8 .

Table 4.32 Narrow sense heritability of yield, days to flower, seed weight, protein content, mg met/g meal and mg met/g protein among 21 pea crosses

	Yield	Days to flower	Seed weight	Protein content	mg met/g meal	mg met/g protein
Heritability $h^2=b$	.608n.s	.800**	.970**	.449*	.486*	-.055n s

* and ** Significant at the .05 and .01 level, respectively

Figure 4.3 Regression of F_2 on mid-parent yield of 21 pea crosses.

$y = 308.6 + .608x$ n.s.

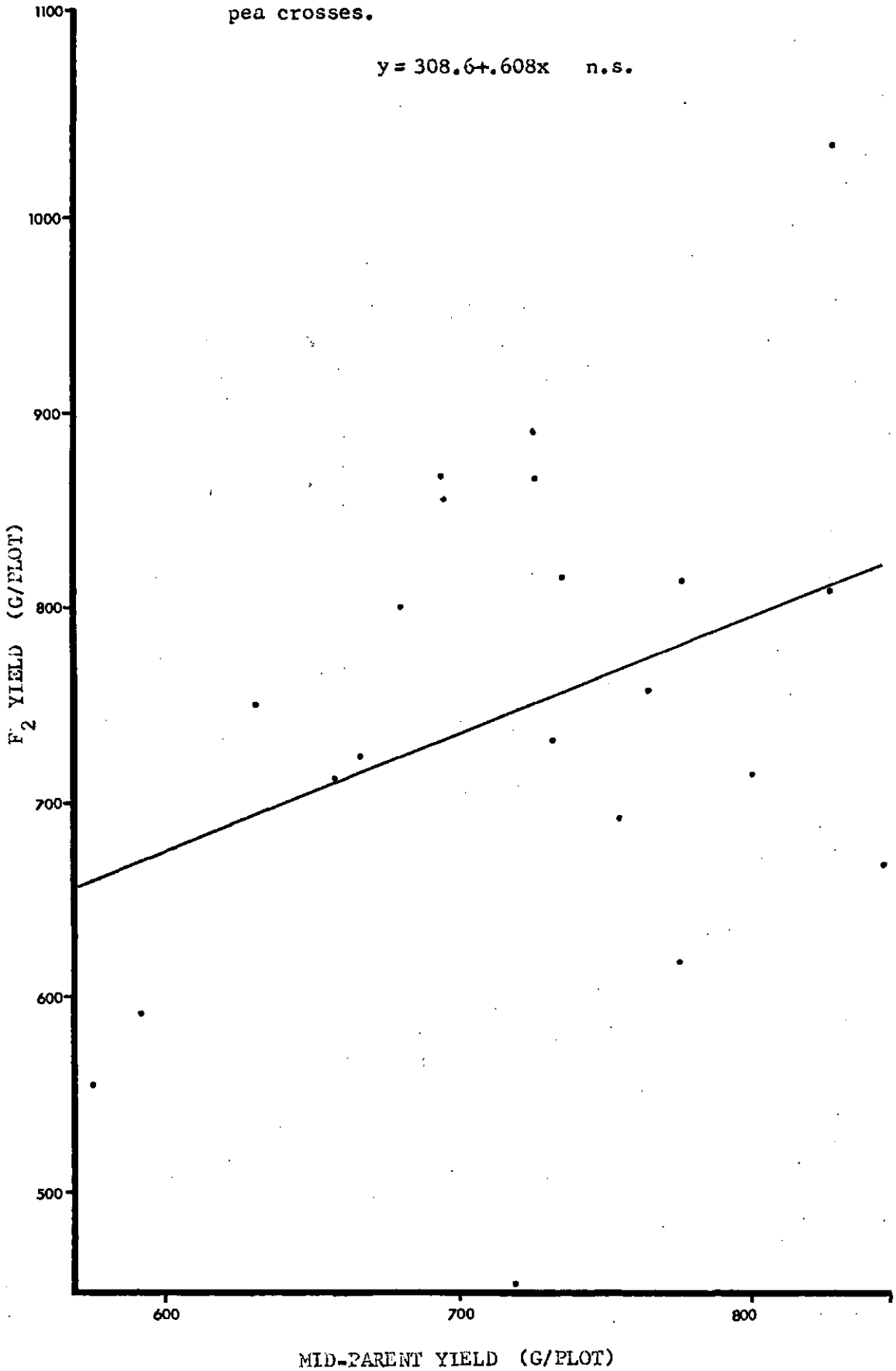


Figure 4.4 Regression of F_2 on mid-parent days to flower of 21 pea crosses.

$y = 9.26 + .800x^{***}$

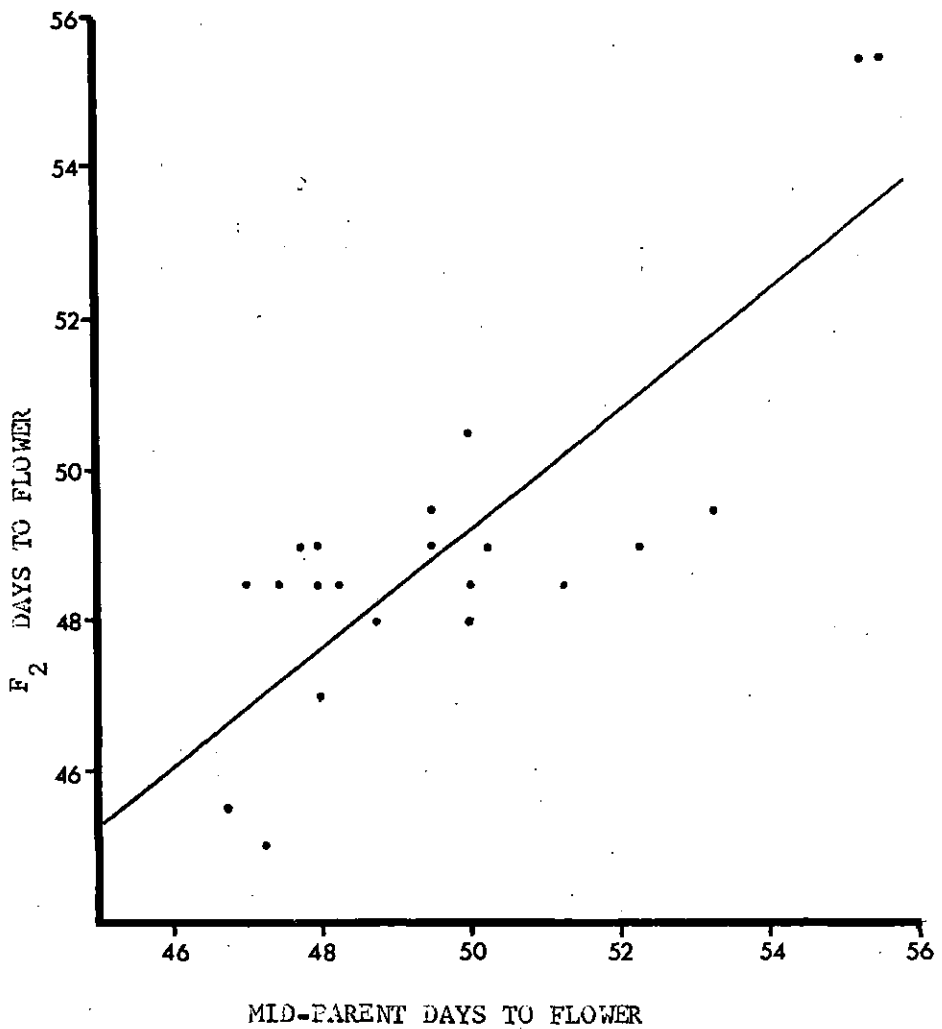


Figure 4.5 Regression of F_2 on mid-parent seed weight of 21 pea crosses.

$y = 4.94 + .970x^{***}$

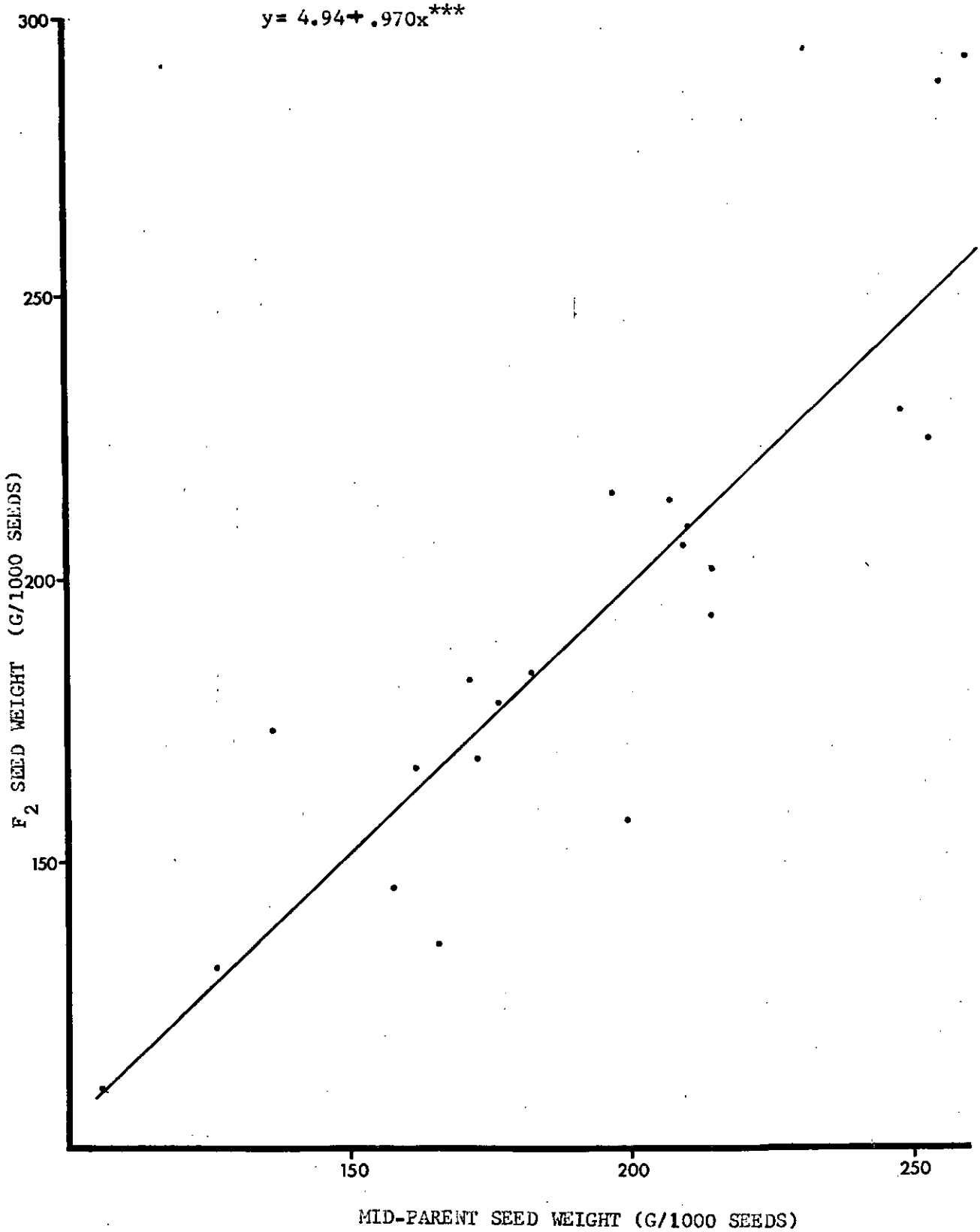


Figure 4.6 Regression of F_2 on mid-parent protein content of 21 pea crosses.

$y = 14.35 + .449x^*$

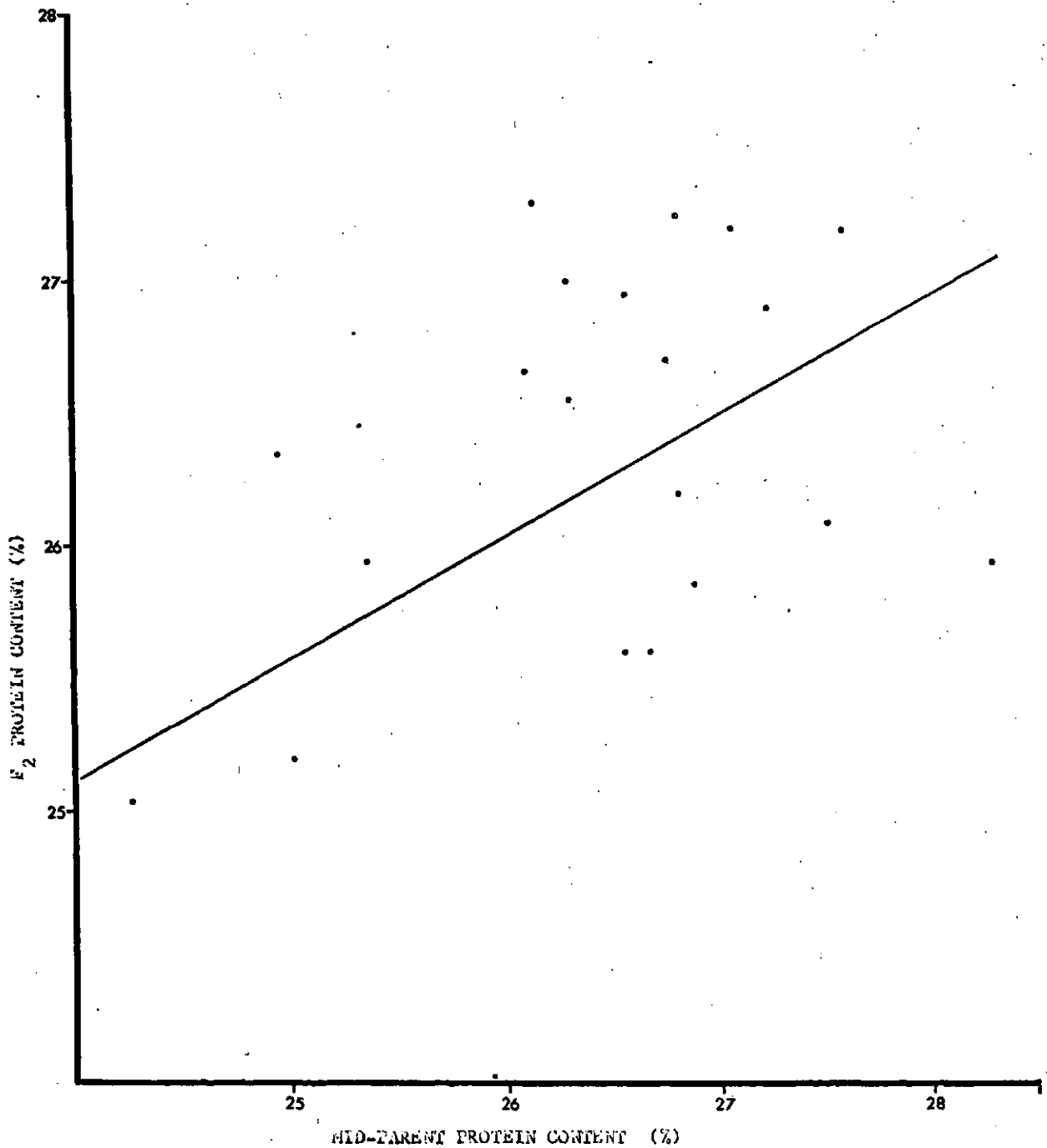


Figure 4.7 Regression of F_2 on mid-parent mg met/g meal of 21 pea crosses.

$y = 1.00 + .486x^*$

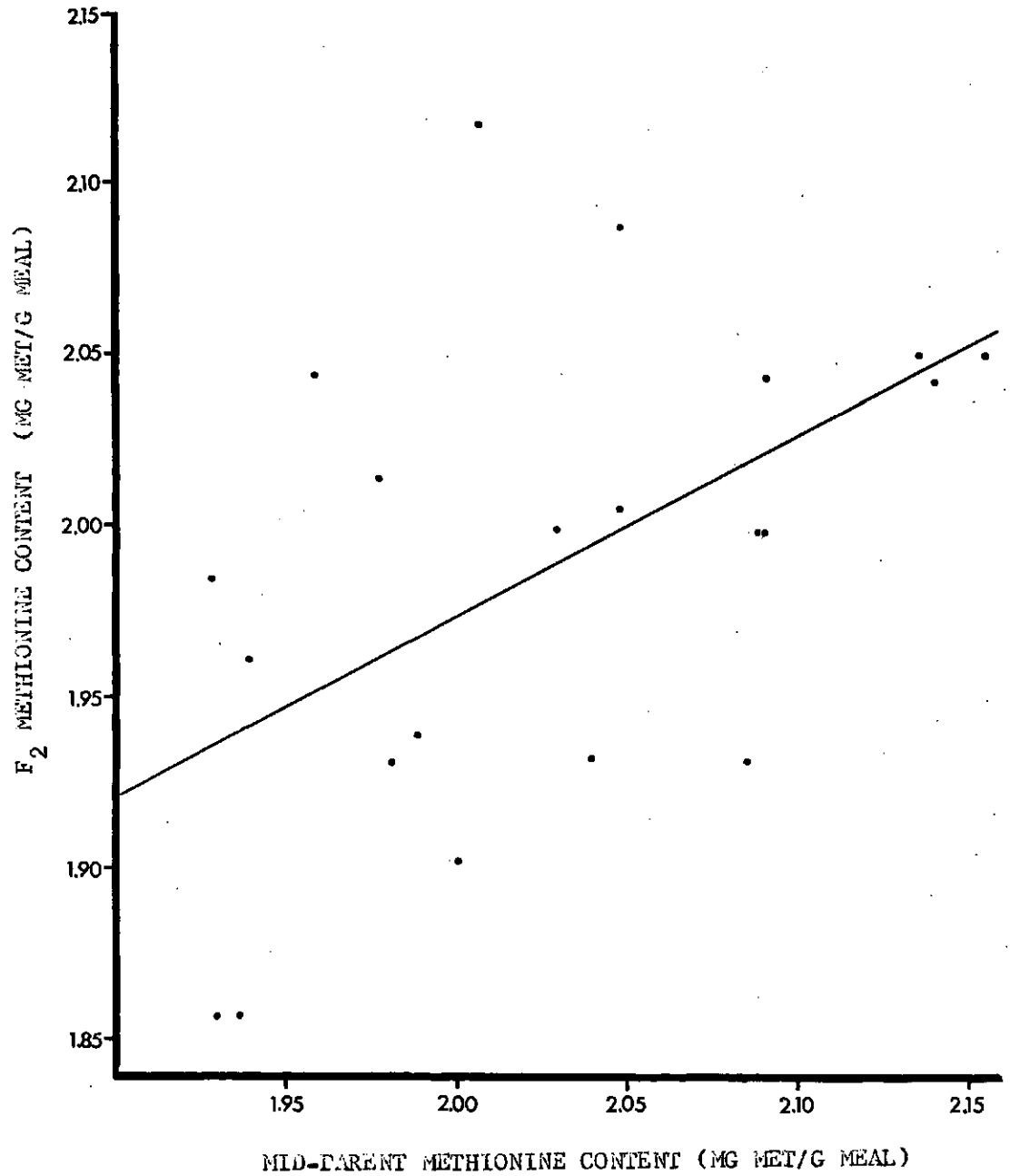
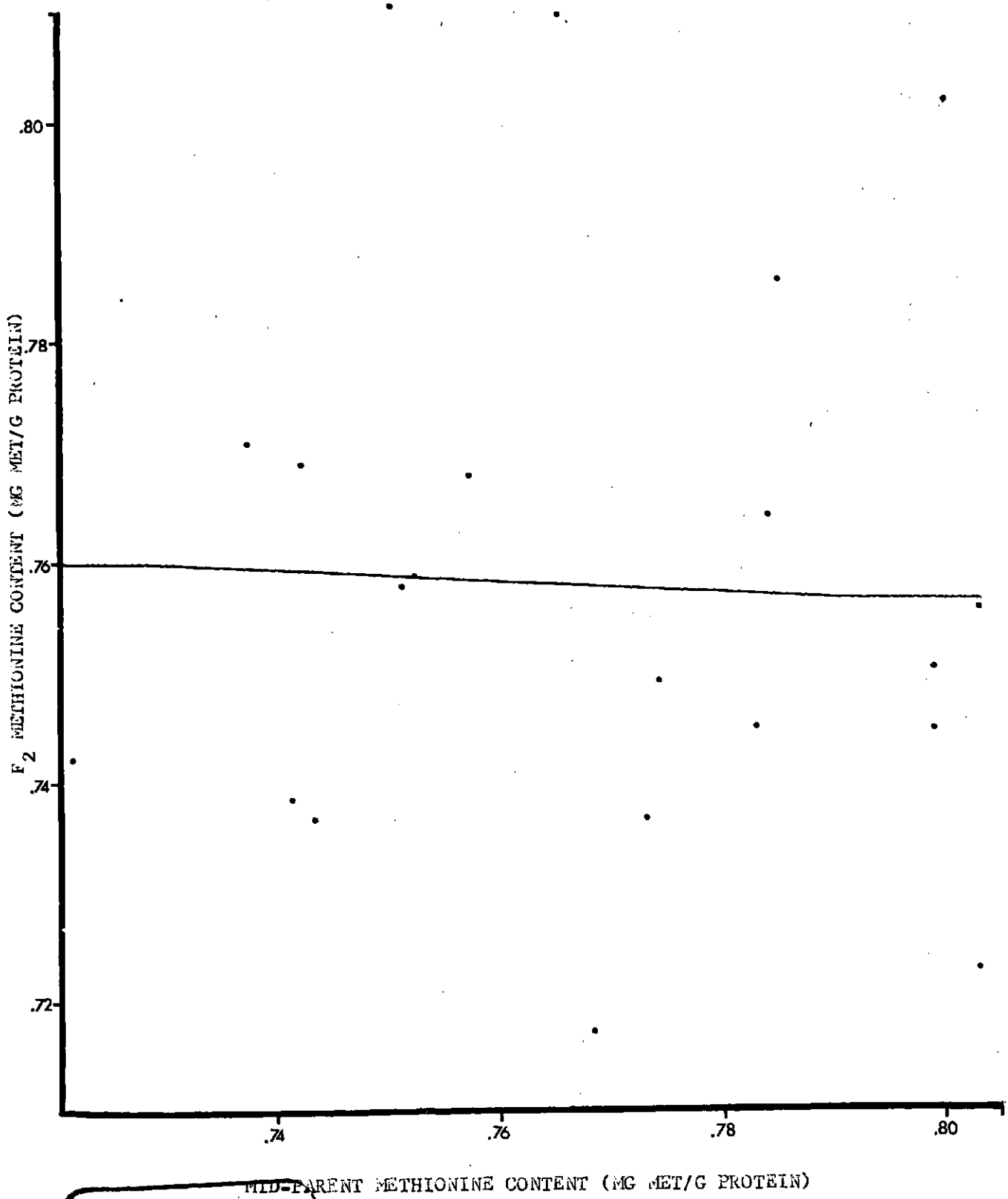


Figure 4.8 Regression of F_2 on mid-parent mg met/g protein of 21 pea crosses.

$y = .80 - .055x$ n.s.



Yield was not heritable. The regression coefficient was moderately high (b= .608), but the points did not conform to the regression line as shown by the large standard error of the coefficient (Fig. 4.3). Days to flower was highly heritable (b= .800**). The F_2 values showed very good agreement with the mid-parent, as evident from the regression line (Fig. 4.4). This indicated that simple additive gene action controlled days to flower. Three F_2 populations flowered approximately two days before their mid-parent value but, since there were no common parents, this could not be taken to indicate non-additive genetic effects for the control of days to flower.

Heritability of seed weight was very high (b= .970**, Table 4.32), indicating excellent agreement with the regression line (Fig. 4.5). Thus, seed weight was additively inherited and intermediate between parents. Although six F_2 populations deviated strongly from the regression line, three in each direction, non-additive gene action could not be inferred as other populations with parents in common did not exhibit the same pattern. For example, in two of the five populations with Ceser as a parent, dominance for high seed weight was indicated but in the other three populations, F_2 values were intermediate. Cesar was the male parent in all crosses. Maternal effects were ruled out as the maternal parents involved did not show similar effects in the other populations where they were the female parent.

Heritability of protein content was moderate (b= .449*), indicating that this trait was generally intermediate between parents

in the F_2 although deviations from the regression line were greater than for days to flower and seed weight. No consistent pattern due to common parents was evident from the regression line (Fig.4.6) so that non-additive gene action could not be inferred.

Heritability of methionine content expressed as mg met/g meal was significantly heritable at a slightly higher level than protein content (b = .486*, Fig. 4.7). However, when methionine content was expressed as a percent of protein, it was no longer heritable (b= -.055, Fig. 4.8). As noted previously, mg met/g meal was highly correlated with protein content (Table 4.31) and it is possible that the heritability value may in fact be another estimate of heritability of protein content rather than of methionine content. Since methionine expressed as a percentage of protein more accurately reflects protein quality, the fact that it is not heritable has important ramifications for breeding strategies.

4.4 Effect of seed shape on seed weight

The differences between smooth- and wrinkle-seeded peas have been well documented recently by Kooistra (1962). They include differences in starch content, amylose content of the starch, sugar content, water uptake capacity, and starch granule size and shape. Shia (1976) added protein content to that list, reporting that wrinkle-seeded peas were approximately three percentage points higher in protein content than smooth-seeded sibs in progenies from three crosses. He also found that the wrinkle-seeded types were lower in yield, seed weight, and starch content and attributed the increase in protein content partly to the diminution of these other traits.

This present study was undertaken as an integral part of Objective Two (see Introduction) to examine the effect of seed shape on seed weight and its consequent influence on protein content, especially following the apparent anomaly between the results of the previous study (section 4.3.3) and those of Shia (1976) with regard to seed weight. Both studies showed that wrinkle-seeded peas were about three percentage points higher in protein content than smooth-seeded peas. However, the wrinkle-seeded parents were higher in seed weight (section 4.3.3), where Shia (1976) reported that the wrinkle-seeded progenies were lower in seed weight than the smooth-seeded peas with which they were compared.

4.4.1 Seed weight of parents and progeny of segregating populations

Seven of the parents in the previous heritability study were wrinkle-seeded and 10 of the F_2 populations were segregating for seed shape. These parents and F_2 populations were used to examine the effects of seed shape on seed weight and, indirectly, protein

Mean seed weight for parents and progeny of the 10 F_2 populations segregating for seed shape is given in Table 4.33. As noted in the heritability study, mean seed weight of the F_2 populations was intermediate between the parents and in fact was no different from the mid-parent value. However, when the populations were subdivided into smooth and wrinkled seeds, the mean seed weights of those groups differed by 30.3 g/1000 seeds ($p = .2$ to $.1$). Within each F_2 population, wrinkled seeds were lower in weight than their smooth counterparts and lower than the population mean. The weight differential was 14%. However, wrinkle-seeded parents in 8 of the 10 crosses were heavier seeded than the smooth-seeded parents by an average of 76.5 g/1000 seeds, or 46% ($p = .025$). Thus, in two generations there has been a complete switch of the association between wrinkled seeds and high seed weight to wrinkled seeds and lower seed weight.

4.4.2 Number and size distribution of smooth and wrinkled seeds from segregating populations

In order to test the possibility that the wrinkled seeds had a lower 1000-seed weight by virtue of a different size distribution from smooth seeds, all seeds harvested from the plots in one replicate were sorted into smooth and wrinkled, counted, and then size graded (see Materials and Methods). Each population was tested by Chi-square for goodness of fit to the 5:3 ratio expected for a single gene dominant trait in the F_3 generation (Table 4.34). The weight and number of seeds in each size category are given in Table 4.35. The Chi-square test (Table 4.34) showed that the observed frequency matched the expected in only one population,

Table 4.33 Mean seed weight of smooth-seeded and wrinkle-seeded parents and 10 F_2 populations segregating for seed shape

F_2 populations	Mean seed weight g/1000 seeds					
	F_2	Wr. F_2	S. F_2	mid-parent	Wr.parent	S.parent
P.I.206790 x MP706	226	210	250	254	299	209
P.I.206790 x Trapper	202	195	228	215	299	130
P.I.206790 x Ceser	293	270	315	261	299	222
P.I.206790 x MP39	193	185	217	215	299	131
NRC89-304 x Trapper	182	163	177	172	214	130
NRC89-297 x Trapper	169	165	195	173	215	130
P.I.210678 x Trapper	183	155	180	183	235	130
P.I.210675 x Trapper	216	183	222	198	266	130
P.I.164853 x Ceser	214	210	240	208	193	222
Tiny x Ceser	167	155	170	162	102	222
Mean	204.5	189.1	219.4	204.1	242.10	165.6
S.D.	36.95	35.11	43.43	33.72	64.23	45.9
Difference		-30.3			76.5	
t		1.73 ns			3.06 *	

* Significant at the .05 level

Table 4.34 Number of smooth and wrinkled seeds in 10 F_2 populations from crosses between smooth- and wrinkle-seeded parents

Population	Wrinkled seed no. observed	Wrinkled seed no. expected	Smooth seed no. observed	Smooth seed no. expected	Total number	Chi-squared 5:3
P.I.206790 x MP706	848	1083	2040	1805	2888	81.8(.005)
P.I.206790 x Trapper	990	1073	1872	1789	2862	10.32(.005)
P.I.206790 x Ceser	889	859	1403	1432	2292	1.6 (.25-.1)
P.I.206790 x MP39	1773	1605	2508	2676	4281	27.9(.005)
NRC89-304 x Trapper	1035	1713	3523	2854	4567	429.6(.005)
NRC89-297 x Trapper	2121	1722	2472	2870	4593	147.6(.005)
P.I.210678 x Trapper	1589	1878	3428	3129	5008	75.5(.005)
P.I.210675 x Trapper	1375	1308	2112	2179	3487	5.5(.01)
P.I.164853 x Ceser	1100	971	1491	1619	2591	27.3(.005)
Tiny x Ceser	1058	1222	2200	2036	3258	35.2(.005)
TOTAL	12778	13434	23049	22389	35827	51.5(.005)

P.I. 206790 x Ceser. Over all populations, the number of wrinkled seeds was less than expected.

The Chi-square test for independence is presented in Table 4.35. The null hypothesis was that seed size distribution was independent of seed shape. The null hypothesis was rejected in all populations but one. Thus, seed size was dependent on seed shape in all F_2 populations except P.I. 206790 x Ceser (Table 4.35). Although the mean seed weight of smooth seeds was higher than for wrinkled seeds (Table 4.33), this relationship is not evident in Table 4.35 where seed size is compared instead of seed weight. Further, Table 4.35 shows that there were not more smooth seeds than expected in the larger size categories, nor more wrinkled seeds than expected in the smaller size categories, which could have contributed to the mean weight differential.

When seed weight determinations were made for each size category, the heavier seed weight of the smooth seeds was again evident (Table 4.36). Thus, in each size category, where smooth and wrinkled seeds have the same external diameter, wrinkled seeds are lighter than their smooth counterparts. Seed size and seed weight are not synonymous, especially when comparing smooth- and wrinkle-seeded peas.

Table 4.36 100-seed weight (in grams) in each size category of smooth and wrinkled seeds from 10 segregating F_2 populations

F_2 population	=18/64"			=16/64"			=14/64"		
	Smooth	Wrinkled	Difference	Smooth	Wrinkled	Difference	Smooth	Wrinkled	Difference
P.I.206790 x MP706	29	23	6	22	17	5	16	-	-
P.I.206790 x Trapper	28	23	5	21	16	5	15	12	3
P.I.206790 x Ceser	33	30	3	23	18	5	-	-	-
P.I.206790 x MP39	27	24	3	21	17	4	16	13	3
NRC89-304 x Trapper	26	23	3	21	17	4	16	12	4
NRC89-297 x Trapper	24	21	3	20	17	3	15	13	2
P.I.210678 x Trapper	25	22	3	20	16	4	15	-	-
P.I.210675 x Trapper	28	23	5	22	17	5	16	13	3
P.I.164853 x Ceser	29	25	4	22	16	6	17	-	-
Tiny x Ceser	23	20	3	20	15.5	4.5	17	12.5	4.5
Mean	27.2	23.4	3.8*	21.2	16.6	4.6**	15.9	12.6	3.3**
S. D.	2.9	2.72		1.03	.75		.78	.49	

* and ** denotes significance at the level of .05 and .01, respectively by the 't' test

4.5 Variation in protein content and other traits among 1071 genotypes from the U.S.D.A. World Pea Collection

In 1975, 1071 genotypes were grown in 17, 2-replicate 8x8 partially-balanced lattices along with the check variety Trapper in each lattice. Bartlett's test for homogeneity of error variance showed that the separate lattices could not be combined for a complete analysis of variance. Thus, an analysis of variance was performed on each lattice separately. To obtain distribution curves, genotype values were converted to a percentage of the lattice mean and then analyzed for skewness and kurtosis. Correlation coefficients between the traits were calculated on a single lattice basis.

4.5.1 Analysis of variance for yield, protein content, protein yield and seed weight

Analysis of variance and covariance was performed for each trait in each lattice. Where relative efficiency was greater than 100 relative to RCBD, the genotype means were adjusted. They were then tested for significance by the approximate-F test. The L.S.D. value was Bayesian (Duncan, 1965) which tends to avoid type II errors when the F ratio is large and tends to avoid type I errors when the F ratio is small.

4.5.1.1 Yield

The analysis of variance for yield showed that there were significant differences among genotypes in all but two of the lattices (lattices 2 and 4, Table 4.37). The efficiency of the partially balanced lattice design ranged from 91.5 to 160.1% relative to RCBD. However, in most of the lattices the value was just slightly greater than 100. Two lattices were exceptions with efficiencies of 125.9 and 160.1. Only three were noticeably less efficient than RCBD. Lattice mean yield ranged from 593.6 to 1148.4 g/plot. Three of the

4.37 Data from analysis of variance for yield in 17 partially balanced 8x8 lattices at Saskatoon in 1975

Lattice #	Yield M.S.	Relative efficiency vs. RCBD	Mean g/plot	L.S.D.	C.V.%
1	49384**	102.1	756.7	185.5	12.2
2	26637	100.0	760.0	274.8	17.9
3	27091*	100.3	687.8	247.4	17.9
4	37880	91.5	651.2	336.5	25.8
5	46904**	102.3	686.0	276.6	20.2
6	39212**	104.4	698.8	200.9	14.4
7	39025**	98.0	814.5	204.6	12.6
8	50905**	103.6	915.3	258.2	14.1
9	67526**	125.9	1148.4	274.5	11.9
10	124486**	100.2	1040.1	273.8	13.2
11	14882**	160.1	595.7	140.5	11.7
12	20483**	99.9	696.8	160.5	11.5
13	22094**	108.4	617.6	199.7	16.0
14	19710**	106.6	724.6	164.4	11.3
15	28725**	94.5	631.6	158.4	12.5
16	13045**	100.5	694.5	152.3	10.9
17	12450**	108.7	593.6	138.3	11.6
Mean			747.0		

* and ** significant at the .05 and .01 level of F, respectively

lattices, nos. 8, 9 and 10, were situated in a moist hollow and they had more available water than the other lattices. Consequently, the genotypes grew taller, matured approximately two weeks later, and yielded higher than genotypes in the other lattices. Coefficients of variation (C.V's) ranged from 10.9% to 25.8% and averaged 14.5%. Eleven of the values were 16% or below, which may be considered acceptable for two-replicate tests involving a considerable number of genotypes. Genotype mean yields are shown in Appendix 2.

4.5.1.2 Protein content

There were highly significant differences among genotypes in each of the lattices for protein content (Table 4.38). Relative efficiency of the partially balanced lattice design was in the range of 84.5 to 126.4% relative to RCBD. As noted earlier for yield, most of the lattices gave efficiency values close to 100, indicating that variability for protein within plots was not greatly reduced by the lattice design. It also indicates that local variability over the area of the lattice was not very great except in one case (lattice no. 6) where the efficiency was 126.4%.

Mean protein content of each lattice ranged from 24.5 to 27.6% with an overall mean of 26.1%. Thus, protein content was much less variable among the lattices than yield. C.V's for protein content were low, ranging from 2.8 to 4.9%. Genotype mean protein contents are shown in Appendix 2.

4.5.1.3 Protein yield

Protein yield was calculated from yield x protein percentage and expressed in grams/plot. Analysis of variance (Table 4.39) showed that results were very similar to the results of yield on a lattice

Table 4.38 Data from analysis of variance for protein content in 17, 8x8 partially balanced lattices at Saskatoon in 1975

Lattice #	Protein M.S.	Relative efficiency vs. RCBD	Mean protein %	L.S.D.	C.V.
1	3.25**	84.5	26.4	2.24	4.2
2	2.16**	113.1	26.0	1.79	3.4
3	5.55**	102.3	25.9	1.78	3.4
4	3.41**	100.0	26.1	2.08	4.0
5	7.09**	102.3	26.7	2.07	3.9
6	6.57**	126.4	26.8	1.81	3.4
7	5.00**	108.7	26.4	1.47	2.8
8	4.19**	100.1	25.7	2.17	4.2
9	4.28**	103.9	24.5	2.42	4.9
10	5.84**	100.5	26.1	1.78	3.4
11	2.89**	93.6	25.6	1.79	3.5
12	3.36**	87.4	26.2	2.10	4.0
13	4.88**	89.1	27.4	2.05	3.7
14	5.45**	99.8	25.9	2.12	4.1
15	3.24**	91.0	25.5	2.54	4.9
16	1.80**	100.1	25.3	1.74	3.4
17	4.75**	100.0	27.6	1.88	3.4
Mean			26.1		

* and ** Significant at the .05 and .01 level of F, respectively

Table 4.39 Data from analysis of variance for protein yield in 17 partially balance 8x8 lattices at Saskatoon in 1975

Lattice #	Yield of protein M.S.	Relative efficiency vs. RCBD	Mean yield of protein g/plot	L.S.D.	C.V.
1	2841**	100.1	198	54.0	13.5
2	1491	99.9	196	68.4	17.3
3	1545*	100.0	177	60.7	17.0
4	2253	92.7	169	82.3	24.3
5	3683**	101.0	183	75.4	20.6
6	2592**	103.8	186	55.4	14.9
7	2339**	100.1	214	55.0	12.8
8	2804**	103.2	234	64.8	13.8
9	3583**	107.0	280	77.9	13.9
10	6572**	107.5	269	67.3	12.5
11	835**	154.6	152	37.3	12.2
12	1375**	100.0	182	46.3	12.6
13	1552**	106.9	108	54.3	16.0
14	945**	112.3	187	42.7	11.3
15	1545**	93.0	160	44.1	13.7
16	911**	103.7	175	40.5	11.5
17	837**	111.0	163	36.1	11.0
Mean			194		

* and ** Significant at the .05 and .01 level of F, respectively

basis. Again, in lattices 2 and 4, genotypes were not significantly different for protein yield and the level of significance in lattice 3 was .05 compared to .01 for all other lattices where significant differences existed. Lattice mean protein yield ranged from 160.1 to 280.1 g/plot. C.V's for protein yield in each lattice also followed C.V's for yield very closely. The close relationship between these two traits will be described later (section 4.5.6). Mean genotypic values for protein yield for each of the lattices is given in Appendix 2.

4.5.1.4 Seed weight

There were significant differences (p= .005) in 200-seed weight among genotypes in all lattices (Table 4.40). Although the range in seed weight of individual genotypes was considerable (see Appendix 2), the range of lattice means was not, indicating that the genotypes were randomly distributed among the lattices with regard to seed weight. For this trait there was no marked or consistent increase in the efficiency of the partially balanced lattice design, which is similar to the findings for the other traits. Mean C.V. was relatively low (6 to 7%), but the range among lattice mean C.V. was greater than that for the other traits. This was due in part to the use of an electronic seed counter for the genotypes in lattice no. 7. When the machine was subsequently found to be inaccurate, its use was discontinued. Seed counts of genotypes in all other lattices were made by hand.

4.5.2 Distribution of each trait among the genotypes

The objective of this study of a large number of genotypes under replicated conditions was to evaluate the distribution of yield, protein content, and seed weight over a wide genetic base.

Table 4.40 Data from analysis of variance for seed weight in 17 partially balanced 8x8 lattices at Saskatoon in 1975

Lattice #	Seed weight M.S.	Relative efficiency vs. RCBD	Mean 200-seed weight	L.S.D.	C.V.
1	288.9**	91.3	33.5	3.7	5.5
2	289.5**	88.4	33.2	5.9	8.9
3	202.8**	104.5	36.9	2.7	3.6
4	131.0**	100.2	31.5	2.4	3.7
5	122.5**	100.1	37.7	4.2	5.6
6	143.4**	100.3	41.0	3.5	4.3
7	218.1**	100.0	43.1	10.6	12.3
8	414.6**	105.3	44.8	6.5	7.2
9	293.8**	106.1	37.4	4.8	6.5
10	365.5**	87.7	33.7	4.5	6.6
11	251.1**	95.8	34.2	7.7	11.2
12	281.5**	96.0	34.8	4.9	7.0
13	136.5**	100.4	36.2	5.3	7.2
14	174.7**	99.0	35.0	4.9	7.0
15	688.6**	91.1	43.7	3.9	4.4
16	206.6**	97.2	44.2	5.5	6.2
17	151.3**	106.9	40.5	5.0	6.1
Mean			37.7		

*** Significant at the .01 level of F

However, Bartlett's test for homogeneity of error variance showed that the data from each of the lattices could not be combined for analysis of variance. Further, since the value for mean yield of each lattice varied from 593.6 to 1148.4 g/plot it was considered that individual genotype means from all lattices could not be combined to produce a valid distribution curve for that trait. Since yield was associated with yield of protein and protein content, non-genetic variation in yield would lead to spurious distribution curves in those traits too.

The licensed cultivar Trapper had been included in each lattice for use as a conversion factor for the other genotypes. Mean yield and protein content of Trapper were compared with the lattice mean values to ascertain the response to changes in environment (Table 4.41). The regression of Trapper yield and protein content on the lattice means showed that this variety had a virtual unit response to the environment (b= 1.03*** and 0.96*, respectively for these traits). However, correlation coefficients showed that, while Trapper yield and mean yield of all genotypes in each lattice were closely related (r= +.878**), the relationship for protein content was only moderate (r= +.577*). Thus, Trapper protein content was not strongly indicative of the mean levels of protein content in a given lattice. The range exhibited by Trapper over these 17 lattices, 24%, was relatively high, compared to the variation in protein content shown by this variety in Cooperative Tests across Canada, i.e.1971 - 22% (11 locations), 1972 - 30% (10 locations), 1974 - 12.4% (8 locations), 1975 - 16% (5 locations). For this reason, the Trapper check was not used as a conversion factor.

Table 4.41 Relationship between Trapper mean and lattice mean for yield and protein content

Lattice #	Mean yield g/plot		Mean protein %	
	Trapper	Lattice	Trapper	Lattice
1	858	757	25.9	26.4
2	887	760	25.4	26.0
3	849	688	25.0	25.9
4	643	651	24.9	26.1
5	889	686	26.1	26.7
6	592	698	27.9	26.8
7	983	814	25.6	26.4
8	1032	915	24.6	25.7
9	1258	1148	22.5	24.5
10	1173	1040	24.3	26.1
11	711	596	23.1	25.6
12	689	697	23.9	26.2
13	727	618	25.6	27.4
14	903	725	24.0	25.9
15	888	632	25.4	25.5
16	866	692	26.1	25.3
17	691	594	25.6	27.6
$\bar{x}$	861	747	25.1	26.1
b	1.03** $\pm$.14		.96* $\pm$.35	
r	.878**		.577*	

* and ** Significant at the .05 and .01 level, respectively

Hence, genotype mean values for each trait were converted to a percentage of the lattice mean for those traits and then all genotypes were combined to provide distribution curves. Presumably, the lattice mean provided a reasonable estimate of the environment (or non-genetic variation) over the area of that lattice, since it contained 64 randomly assigned genotypes and, thus, would not be strongly biased by genotype x environment interactions.

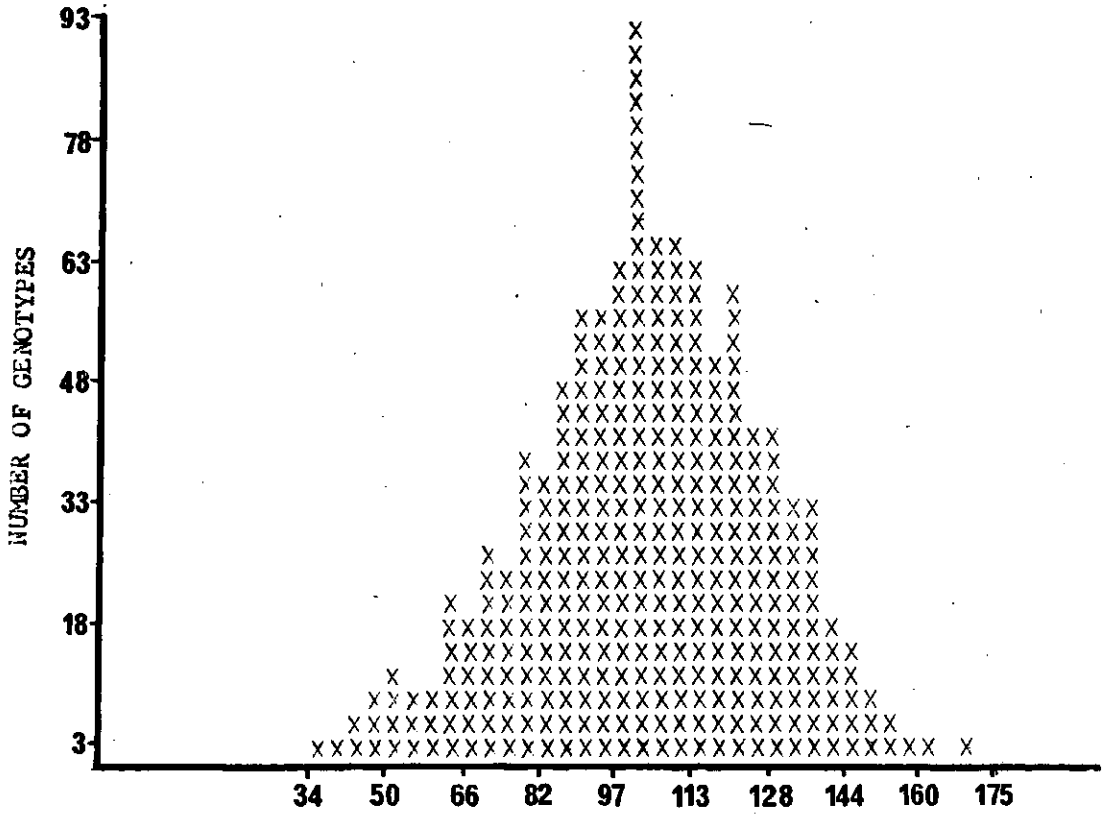
4.5.2.1 Distribution of yield

The distribution curve for yield of 1071 genotypes closely resembled a normal distribution (Figure 4.9). Mean, median, and mode were essentially identical. Yield of genotypes ranged from 34.6 to 172.4% of the mean, i.e. a 4-fold difference from lowest to highest. The curve was negatively skewed (p= .02), i.e..to the lower end, but the skewness was not particularly evident by eye. The test for kurtosis was negative (p= .01), indicating that there were fewer values close to the mean and far from it than expected. In other words,the central portion of the curve was broader than normal.

4.5.2.2 Distribution of protein content

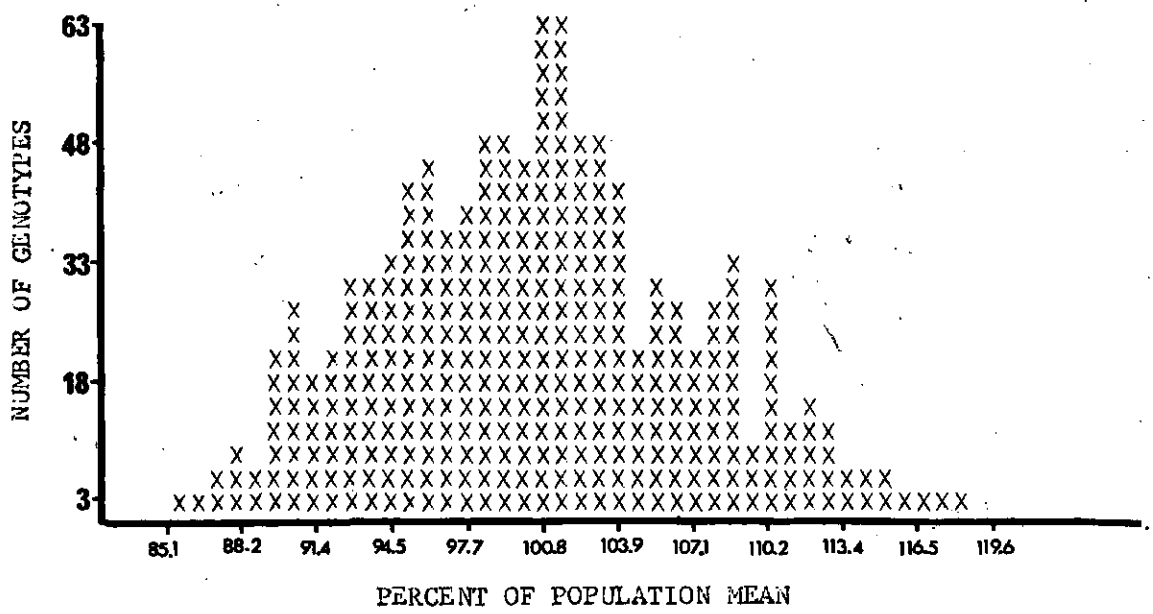
The distribution curve for protein content also closely resembled a normal distribution (Figure 4.10) Mean, median and mode were similar. There appeared to be a slight surfeit of genotypes on the lower shoulder of the curve and a slight deficit on the upper shoulder. There was very slight tailing to the upper end of the curve as indicated by the skewness (p= .1). The range in protein content among the 1071 genotypes was narrow, i.e. 85.1 to 118.7% of the mean. Thus, there was only a 0.4 - fold difference between lowest and highest. This is only one-tenth of the range in yield of these same

Figure 4.9 Distribution of yield among 1071 genotypes from the U.S.D.A. World Pea Collection.



Minimum	34.69
Maximum	172.39
Range	137.69
Class width	2.75
Mean	99.98
Median	100.47
Mode	99.41
Variance	321.20
Std.dev.	17.92
Skewness	- .26
Kurtosis	.41
Coeff. of var.	17.92
S.E. of mean	.54

Figure 4.10 Distribution of protein content among 1071 genotypes from the U.S.D.A. World Pea Collection.



(100% = 26.1% protein)

Minimum	**85.10**
Maximum	**118.69**
Range	**33.59**
Class width	**.67**
Mean	**99.98**
Median	**100.00**
Mode	**100.22**
Variance	**32.12**
Std.dev.	**5.66**
Skewness	**.17**
Kurtosis	**-.28**
Coeff. of var.	**5.66**
S.E. of mean	**.17**

genotypes. There was negative kurtosis (p= .01) indicating that, as for yield, the distribution was broader and flatter across the top than would be expected in a theoretical normal distribution.

4.5.2.3 Distribution of protein yield

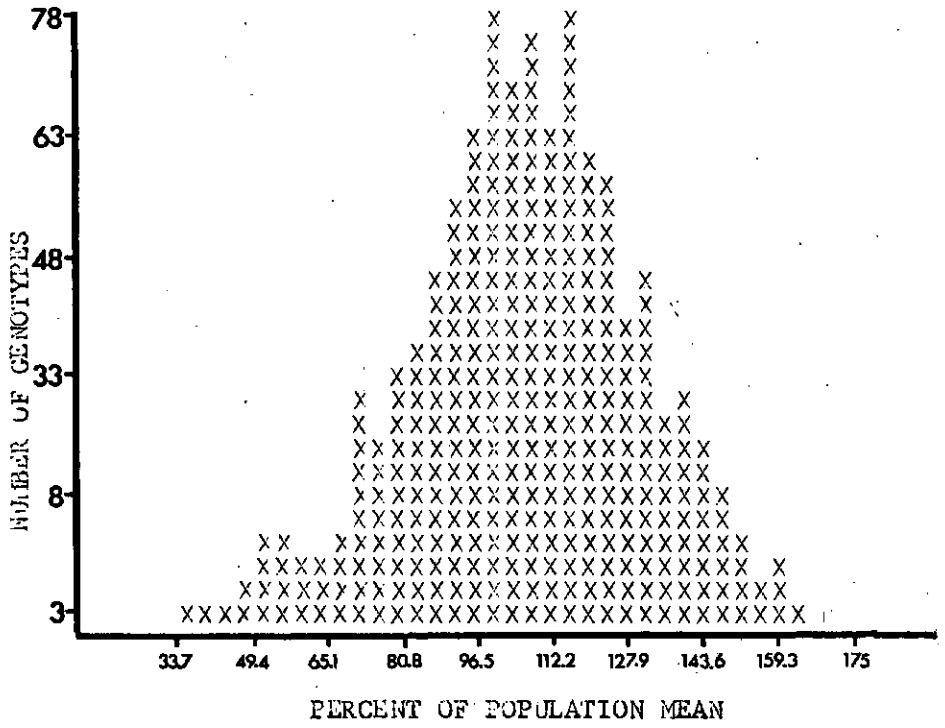
The distribution of protein yield closely resembled a normal distribution (Figure 4.11) and was similar in most respects to the curve for yield. Mean and median were identical (100.0), but the mode was slightly higher (106.2). Protein yield among genotypes ranged from 33.6 to 165.5% of the mean, giving a 4-fold range from lowest to highest. There was negative skewness (p=.2) and negative kurtosis (p= .01). The curve was slightly more noticeably skewed to the lower end than the yield curve.

4.5.2.4 Distribution of seed weight

The distribution curve of seed weight was similar to a normal distribution (Figure 4.12). Mean, median and mode were virtually identical. There was slight but positive skewness (p= .02) to the upper end of the curve. There was no kurtosis, indicating that this curve most strongly resembled a normal distribution in proportion of values close to and distant from the mean. Range was considerable. There was an 8-fold increase from smallest to the largest value.

On the assumption that seed weight was negligibly affected by environmental variation (as evidenced by its high heritability), a distribution curve of actual seed weight was drawn from unconverted genotypic values (Figure 4.13). This curve varied little from the curve of converted values. Mean, median and mode were virtually identical. The range in seed weight among genotypes was from 10.4

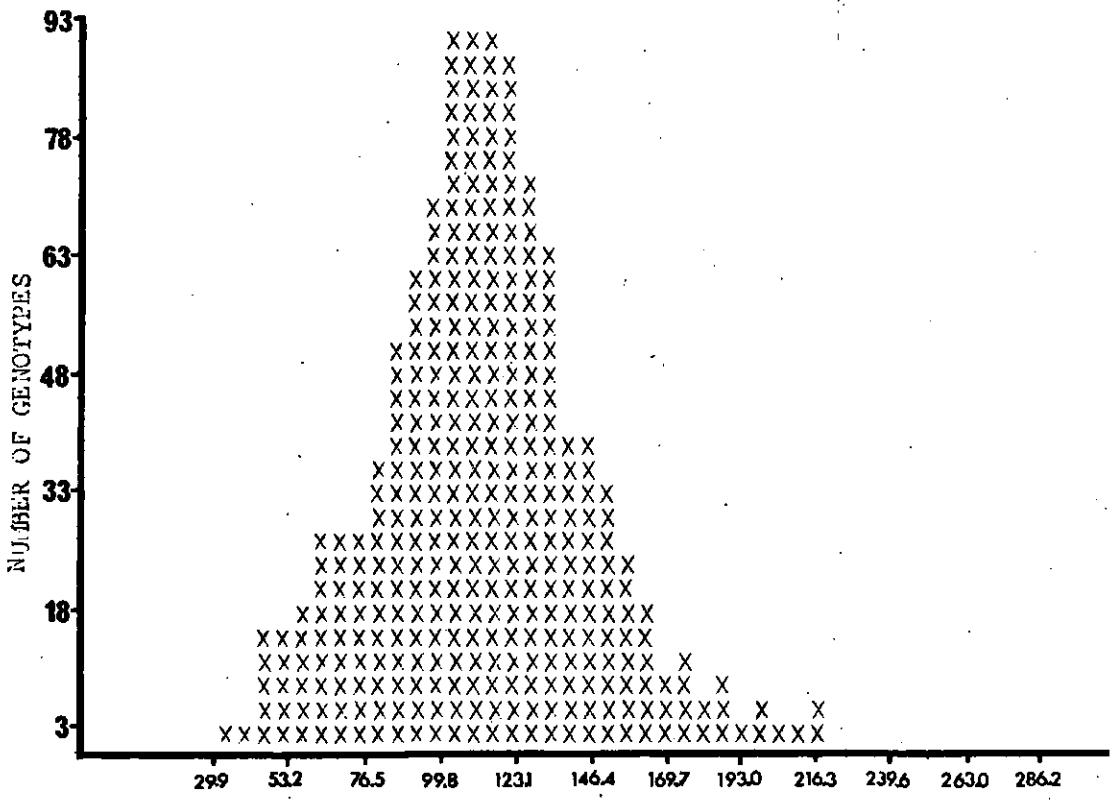
Figure 4.11 Distribution of protein yield among 1071 genotypes from the U.S.D.A. World Pea Collection.



(100% = 194 g/plot)

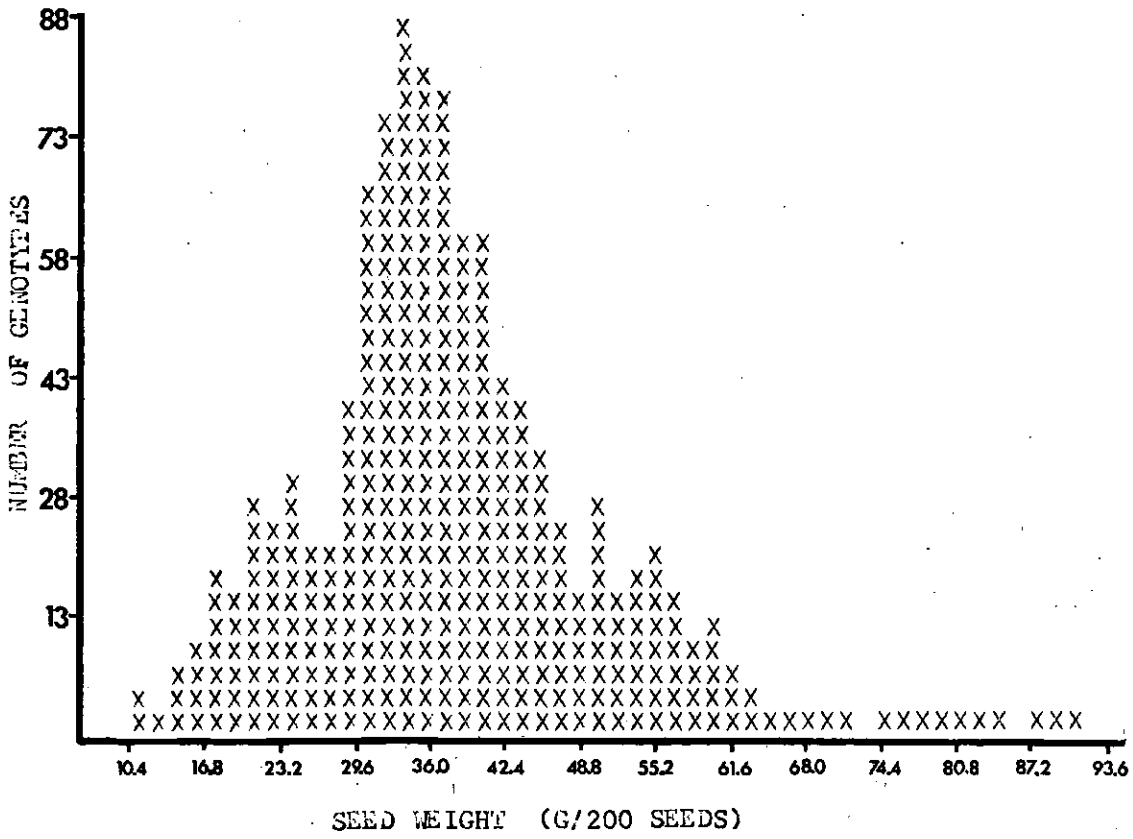
Minimum	**33.69**
Maximum	**165.50**
Range	**131.80**
Class width	**2.64**
Mean	**100.00**
Median	**100.46**
Mode	**106.18**
Variance	**286.74**
Std.dev.	**16.93**
Skewness	**-.20**
Kurtosis	**.47**
Coeff. of var.	**16.93**
S.E. of mean	**.51**

Figure 4.12 Distribution of seed weight among 1071 genotypes from the U.S.D.A. World Pea Collection.



Minimum	29.89
Maximum	273.39
Range	243.49
Class width	4.87
Mean	100.01
Median	98.34
Mode	100.51
Variance	905.60
Std.dev.	30.09
Skewness	.95
Kurtosis	3.25
Coeff. of var.	30.09
S.E. of mean	.91

Figure 4.13 Distribution of actual seed weight among 1071 genotypes from the U.S.D.A. World Pea Collection.



Minimum	**10.39**
Maximum	**91.89**
Range	**81.50**
Class width	**1.63**
Mean	**37.73**
Median	**36.34**
Mode	**34.03**
Variance	**146.19**
Std.dev.	**12.09**
Skewness	**.86**
Kurtosis	**1.86**
Coeff. of var.	**32.04**
S.E. of mean	**.37**

to 81.5 g/200 seeds, i.e. an 8-fold increase. The skewness to the upper end of the curve was more evident, and negative kurtosis (p= .01) was present. Thus, conversion to a percentage of the lattice mean affected seed weight distribution by slightly decreasing tailing to the upper end of the curve, and by grouping genotypes closer to the mean.

4.5.3 Distribution of the traits among smooth-seeded and wrinkle-seeded genotypes

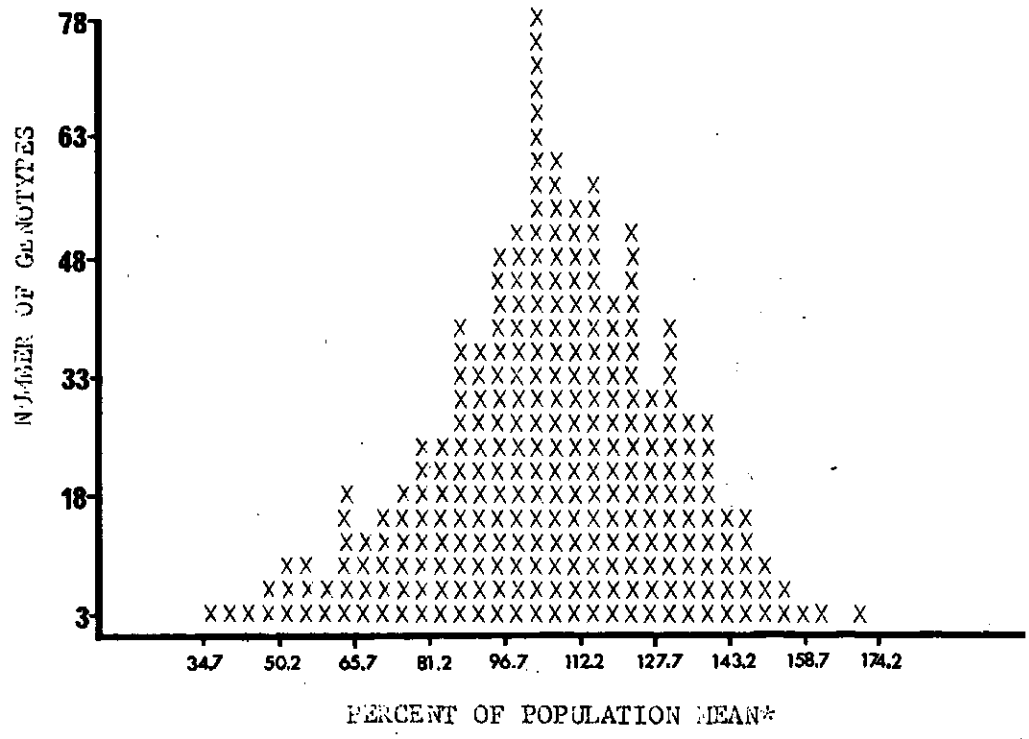
To test for differences between smooth-seeded and wrinkle-seeded pea genotypes in the measured traits the whole population was subdivided into the two seed shape categories and a distribution was formed from each for the 4 traits. The percentages expressed were those obtained by converting individual genotype means to a percentage of the lattice mean. There were 864 smooth-seeded(plus 17 Trapper values) and 207 wrinkle-seeded genotypes.

4.5.3.1 Distribution of yield

The distribution curve for yield of the smooth-seeded genotypes **(Figure 4.14) was not noticeably different from that of the whole population.** Maximum and minimum values were unchanged and, thus, the 4-fold difference between smallest and largest still applied. Both skewness and kurtosis were negative as before. There was a 1% increase in the mean and median, but no change in the modal value.

The distribution curve for yield among the wrinkle-seeded genotypes was basically normal-shaped **(Figure 4.15),but considerably more uneven than the curve for all genotypes.** The range in yield was narrower than for smooth-seeded genotypes, i.e. 48.1% to 144.9% of the whole population mean. Thus, there was only a 2-fold difference between lowest and highest yielding genotypes. Wrinkle-seeded genotypes did not reach the low or high yield values of smooth-

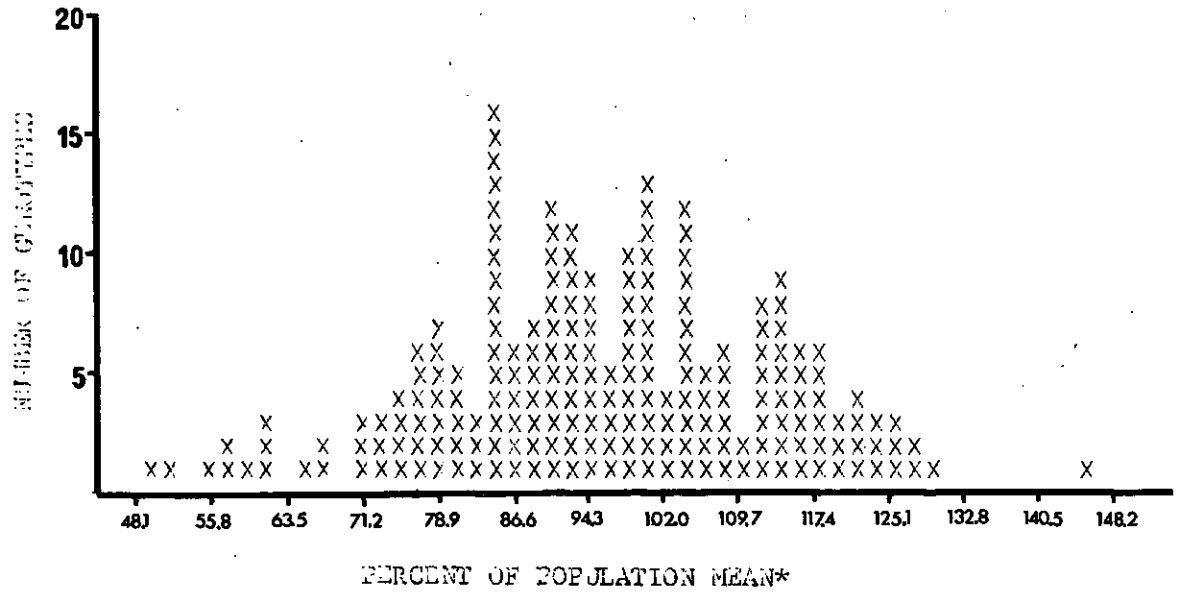
Figure 4.14 Distribution of yield among 864 smooth-seeded genotypes from the U.S.D.A. World Pea Collection.



* denotes mean of 1071 genotypes. **100% = 747 g/plot.**

Minimum	**34.69**
Maximum	**172.39**
Range	**137.69**
Class width	**2.75**
Mean	**101.15**
Median	**101.64**
Mode	**99.42**
Variance	**323.36**
Std.dev.	**17.98**
Skewness	**-.31**
Kurtosis	**.56**
Coeff. of var.	**17.78**
S.E. of mean	**.61**

Figure 4.15 Distribution of yield among 207 wrinkle-seeded genotypes from the U.S.D.A. World Pea Collection.



* denotes mean of 1071 genotypes. **100% = 747 g/plot.**

Minimum	**48.10**
Maximum	**144.89**
Range	**96.79**
Class width	**1.94**
Mean	**95.02**
Median	**94.46**
Mode	**83.91**
Variance	**282.90**
Std.dev.	**16.82**
Skewness	**-.15**
Kurtosis	**-.46**
Coeff. of var.	**17.70**
S.E. of mean	**1.17**

seeded genotypes. The distribution was not skewed, but negative kurtosis (p= .01) indicated that the distribution was broader and flatter than expected. The major difference between the distributions was in mean value. Both mean and median of the wrinkled seeded genotype distribution were 95% of the whole population mean, but the mode was considerably lower at 83.9%.

4.5.3.2 Distribution of protein content

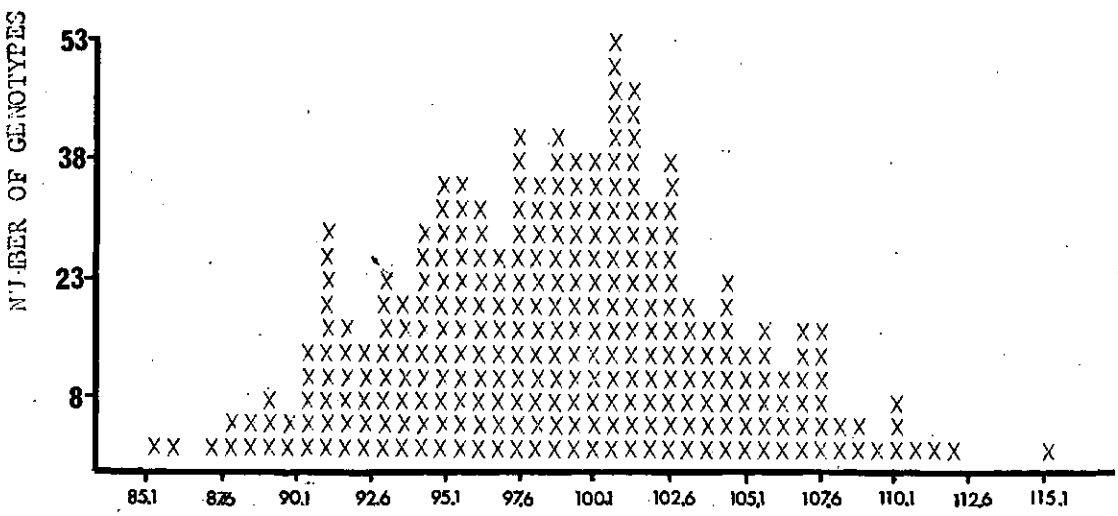
The distribution curve of protein content among smooth-seeded genotypes was very similar to that for the whole population, and approximated a normal curve, (Figure 4.16). The minimum value was unchanged, but the maximum decreased by 3% and, thus, range was slightly decreased. The curve was not skewed, but exhibited negative kurtosis (p= .01). Mean and median dropped slightly to 98.8% whereas the mode remained at 100% of the whole population value.

The curve for protein content among wrinkle-seeded genotypes was basically dome shaped and somewhat uneven (Figure 4.17). It was skewed (p= .02) to the lower end and exhibited negative kurtosis (p= .01). Range was marginally smaller than that for smooth-seeded genotypes and the decrease was from the lower end of the range. The difference between extremes was 0.3-fold. However, there was an increase of 5% in both mean and median. The modal value increased further to 108.2% of the whole population value. Thus, average protein content of the wrinkle-seeded group exceeded that of the smooth-seeded group by approximately 6% of the mean.

4.5.3.3 Distribution of protein yield

Distribution of protein yield of the smooth-seeded geno-

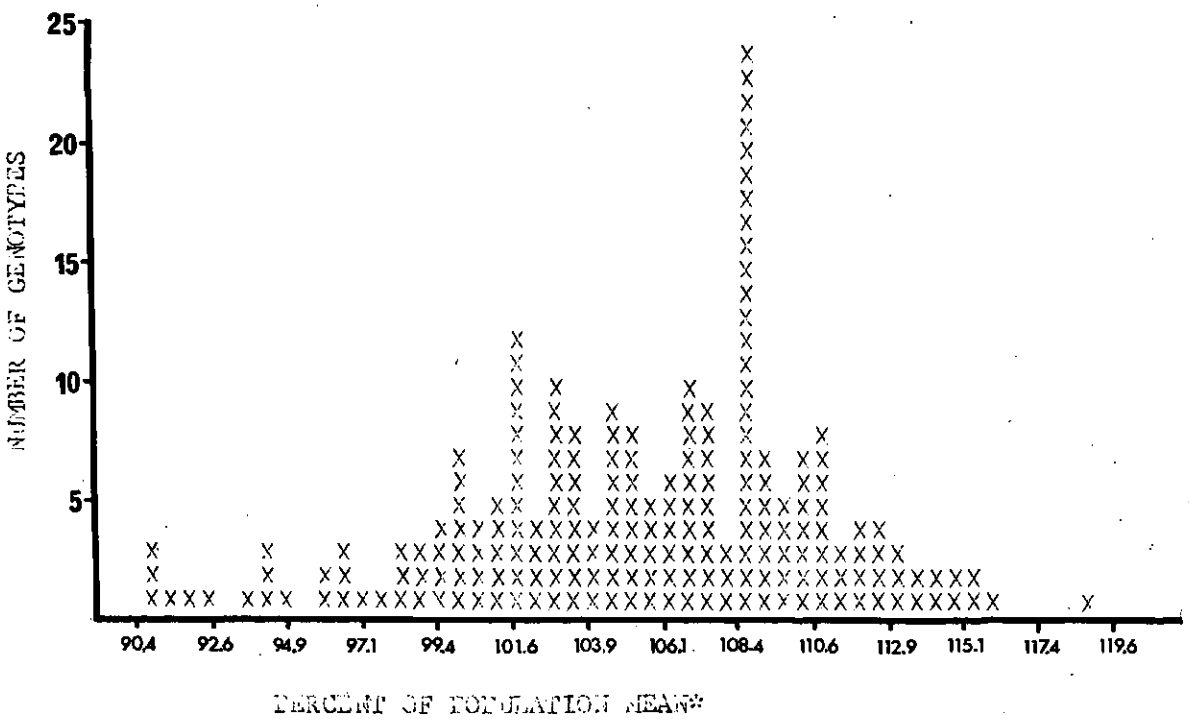
Figure 4.16 Distribution of protein content among 864 smooth-seeded genotypes from the U.S.D.A. World Pea Collection.



* denotes mean of 1071 genotypes. **100% = 26.1% protein.**

Minimum	**85.10**
Maximum	**115.10**
Range	**30.00**
Class width	**.60**
Mean	**98.81**
Median	**98.89**
Mode	**100.39**
Variance	**25.66**
Std.dev.	**5.06**
Skewness	**.12**
Kurtosis	**-.13**
Coeff. of var.	**5.13**
S.E. of mean	**.17**

Figure 4.17 Distribution of protein content among 207 wrinkle-seeded genotypes from the U.S.D.A. World Pea Collection.



* denotes mean of 1071 genotypes. **100% = 26.1% protein**

Minimum	**90.39**
Maximum	**118.69**
Range	**28.30**
Class width	**.57**
Mean	**105.01**
Median	**105.62**
Mode	**108.22**
Variance	**28.59**
Std.dev.	**5.35**
Skewness	**-.44**
Kurtosis	**.11**
Coeff. of var.	**5.09**
S.E. of mean	**.37**

types was very similar to the distribution of protein yield for the whole population as well as the yield distribution of the smooth-seeded group (Figure 4.18). The curve resembled the normal, although there was slight negative skewness and kurtosis (p= .02 and .01 respectively). Range, mean, median, and mode were identical with the distribution of the whole population.

The distribution curve for protein yield among wrinkle-seeded genotypes resembled that of yield, being basically normal shaped, but rather uneven (Figure 4.19). Mean and median were virtually identical with the whole population values, whereas the mode was 6% lower than for the whole population. As with yield, range of protein yield of the wrinkle-seeded group was decreased compared with the range of the smooth-seeded group.

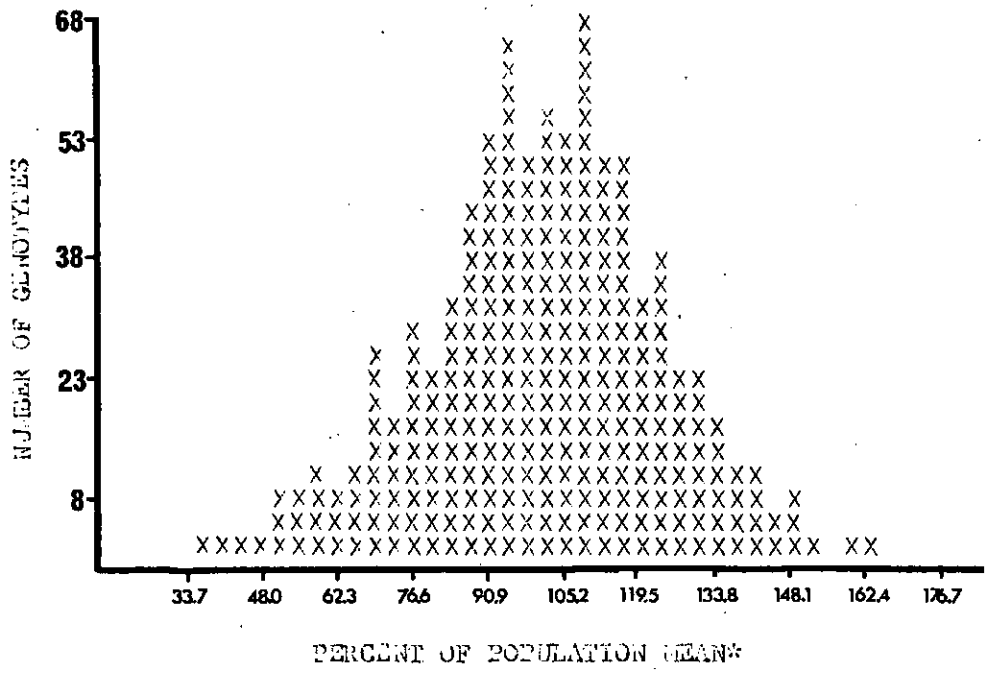
Thus, mean protein yield did not differ between smooth-seeded and wrinkle-seeded groups, but range was smaller in the latter. Both curves closely resembled their corresponding curves for yield.

4.5.3.4 Distribution of seed weight

The distribution curve for seed weight among smooth-seeded genotypes appeared normal (Figure 4.20), but was positively skewed (p= .02) to the upper end of the range like that of the whole population. Kurtosis was absent. Mean, median and mode were all slightly lower than the whole population values, but range was identical. Thus, smooth-seeded genotypes represented the extremes.

On the other hand, range of seed weight among the wrinkle-seeded genotypes was considerably reduced, especially from the lower end (Figure 4.21). The difference between largest and smallest

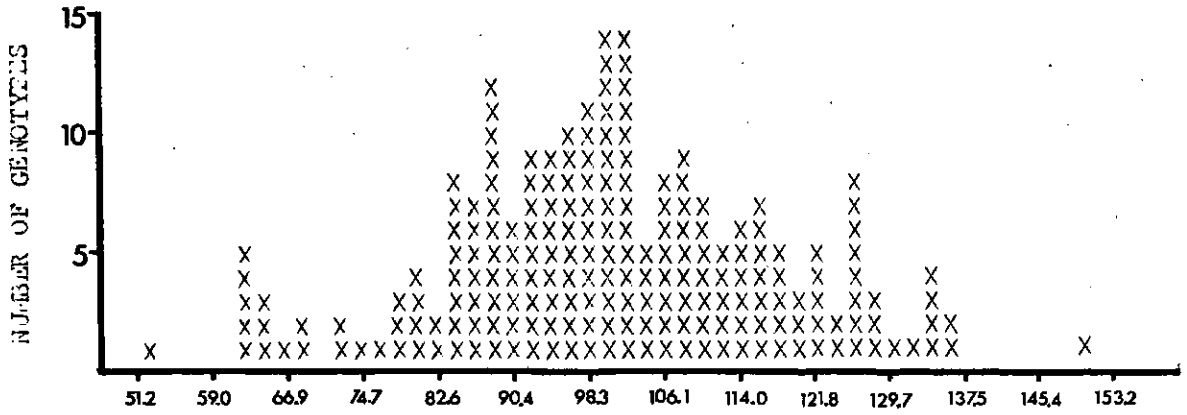
Figure 4.18 Distribution of protein yield among 364 smooth-seeded genotypes from the U.S.D.A. World Pea Collection.



* denotes mean of 1071 genotypes. **100% = 194 g/plot.**

Minimum	**33.69**
Maximum	**165.50**
Range	**131.80**
Class width	**2.64**
Mean	**100.00**
Median	**100.75**
Mode	**106.18**
Variance	**285.64**
Std.dev.	**16.90**
Skewness	**-.23**
Kurtosis	**.57**
Coeff. of var.	**16.89**
S.E. of mean	**.57**

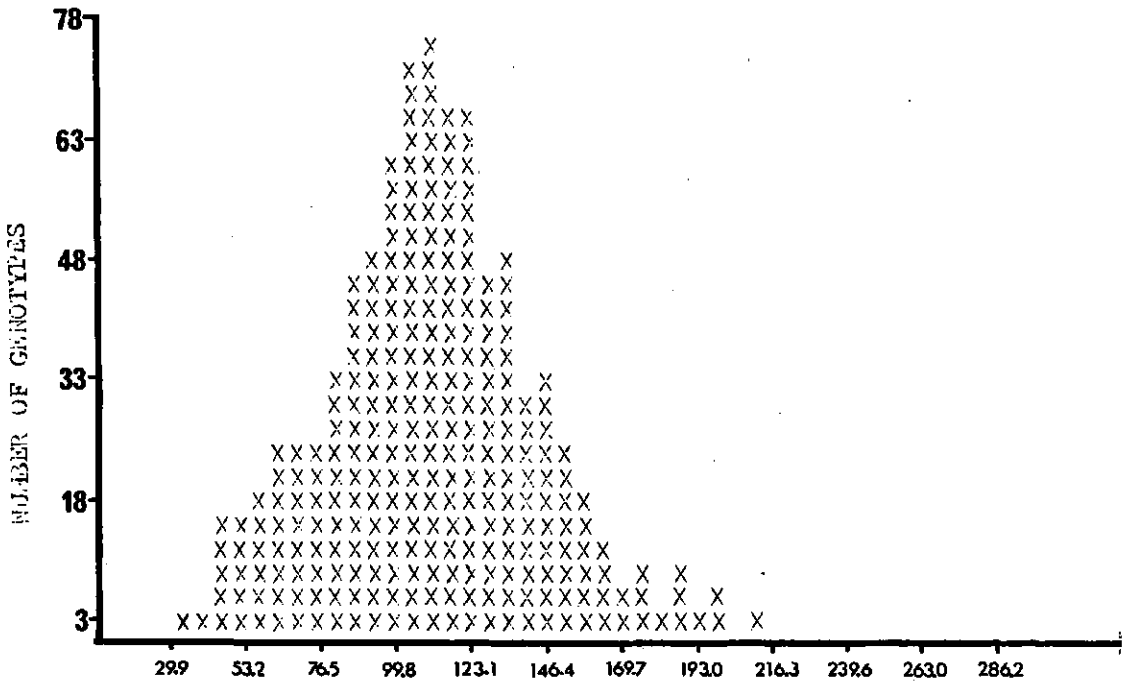
Figure 4.19 Distribution of protein yield among 207 wrinkle-seeded genotypes from the U.S.D.A. World Pea Collection.



* denotes mean of 1071 genotypes. **100% = 194 g/plot.**

Minimum	**51.19**
Maximum	**150.10**
Range	**98.90**
Class width	**1.98**
Mean	**100.00**
Median	**99.59**
Mode	**99.66**
Variance	**292.87**
Std.dev.	**17.11**
Skewness	**-.79**
Kurtosis	**.11**
Coeff. of var.	**17.11**
S.E. of mean	**1.19**

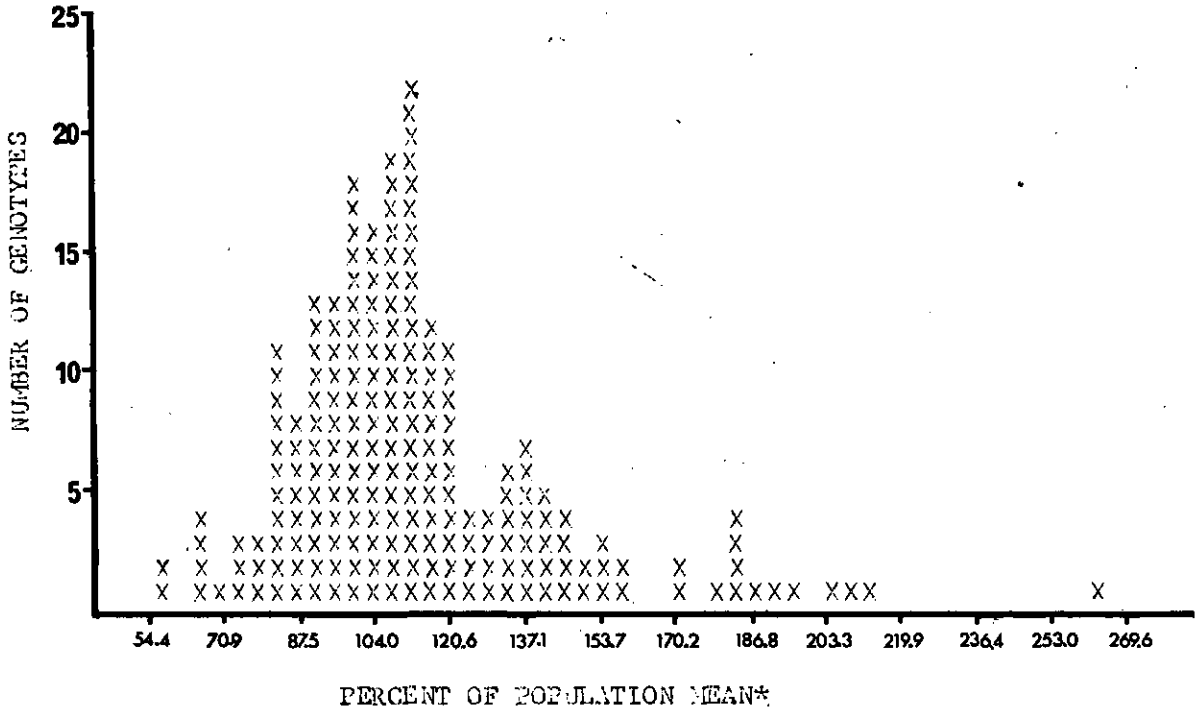
Figure 4.20 Distribution of seed weight among 864 smooth-seeded genotypes from the U.S.D.A. World Pea Collection.



* denotes mean of 1071 genotypes. **100% = 37.7 g/200 seeds.**

Minimum	**29.89**
Maximum	**273.39**
Range	**243.49**
Class width	**4.87**
Mean	**97.18**
Median	**95.83**
Mode	**95.64**
Variance	**869.41**
Std.dev.	**29.48**
Skewness	**.86**
Kurtosis	**3.13**
Coeff. of var.	**30.34**
S.E. of mean	**.99**

Figure 4.21 Distribution of seed weight among 207 wrinkle-seeded genotypes from the U.S.D.A. World Pea Collection.



* denotes mean of 1071 genotypes. **100% = 37.7 g/200 seeds.**

Minimum	**54.39**
Maximum	**262.89**
Range	**208.49**
Class width	**4.17**
Mean	**112.09**
Median	**106.96**
Mode	**110.69**
Variance	**883.78**
Std.dev.	**29.73**
Skewness	**1.54**
Kurtosis	**4.01**
Coeff. of var.	**26.51**
S.E. of mean	**2.07**

values was less than 4-fold compared to the 8-fold difference between extremes in the smooth-seeded group. The distribution curve for the wrinkle-seeded group was distinctly skewed (p= .02) to the upper end of the scale, and, while there was only one distinct modal class, there were indications of lesser modal groupings toward the upper end of the scale. There was one extreme value at the maximum which was several classes above the nearest genotype. Mean, median, and mode had shifted upward 12, 6 and 10% respectively, from the corresponding whole population values. Thus, mean seed weight between the seed shape groups differed by 15% in favor of the wrinkle-seeded genotypes. Although the mean of this group was higher, and the distribution was strongly skewed upward (p= .02), the highest genotypic value was less than that of the highest smooth-seeded genotype.

4.5.4 Comparison of smooth-seeded and wrinkle-seeded populations

The smooth-seeded and wrinkle-seeded genotypes differed by one major gene (R_b and r_b, respectively) and comparison of the means of those groups indicates the effect of that gene. Mean values for yield, protein content, protein yield, and seed weight were compared and tested by the paired 't' test for unequal class numbers (Table 4.42).

Wrinkle-seeded genotypes were lower yielding, higher in protein content, and heavier seeded than smooth-seeded genotypes. When converted back to actual unit values, these differences represented 46 g/plot, 1.6% protein, and 5.6 g/200 seeds, respectively. Both

Table 4.42 Comparison of smooth-seeded and wrinkle-seeded populations for mean yield, protein content, protein yield and seed weight expressed as a percentage of the whole population mean.

Population	Yield	Protein content	Protein yield	Seed weight
Smooth-seeded n=881	101.15	98.81	100.01	97.18
Wrinkle-seeded n=207	95.01	105.02	100.00	112.09
Difference	6.14**	6.21**	.01	14.91**

** Significantly different by the 't' test (.01)

groups had identical mean protein yield, reflecting the balancing effects of the decreased yield and increased protein content.

4.5.5 Effect of error control on range

The range of protein content in this study of 1071 genotypes from the U.S.D.A. World Pea Collection was quite narrow, and much less than that found for 1500 genotypes grown at Saskatoon in 1971 (Slinkard, mimeo report of the University of Saskatchewan). Range in yield and protein content was undoubtedly narrowed to some extent by the exclusion of genotypes (approximately 10%) which failed to produce more than 350 seeds when grown in 1971. Those genotypes either were unadapted to the Saskatoon environment, or germinated very poorly in 1971.

This experiment was designed to show how the range of a trait could be reduced by replication or by expressing the data as percent of the lattice mean, both of which effectively reduced environmental effects. Comparisons of range for each trait with and without replication and percentage conversion are shown in Table 4.43.

Data from Table 4.43 show that replication reduced range for all traits, having least effect on the range of seed weight (8% reduction) and largest effect on the range of protein content (33% reduction). Thus, at least one third of the range of protein content observed among single plots was due to environmental effects both within and among lattices. The ranges in yield and protein yield were considerably reduced (by 30%) by conversion to a percent of the lattice mean. The reduction occurred at the upper end of the range, i.e. the high-yielding genotypes in the high yielding lattices became comparable with the high yielding genotypes in other lattices when converted to lattice mean. The range in protein was virtually the same as

Table 4.43 Range and percent of range of yield, protein content, protein yield and seed weight from unreplicated, unconverted, and converted genotypic values among 1071 genotypes

	Yield		Protein content		Protein yield		Seed weight	
	Range g/plot	% range	Range % protein	% range	Range g/plot	% range	Range g/200 seeds	% range
Single plot values	225-1715	100	19.7-32.2	100	64-432	100	11.4-96	100
Mean of duplicates (unconverted)	233-1586	91	22.6-31.0	67	68-388	87	11.7-91.9	92
Mean of duplicates (% of lattice mean)	259-1287	69	22.2-31.0	70	65-321	70	11.3-103	108

that for unconverted duplicate values. Seed weight range after conversion was greater than that among unreplicated plot values. This was probably due to the chance occurrence of a large-seeded genotype in a lattice which had a low mean seed weight.

4.5.6 Simple correlations between traits

Simple correlation coefficients between yield, protein content, protein yield, and seed weight among the genotypes in each lattice are presented in Table 4.44. Only two of the relationships were consistent over the lattices. Yield and protein content were negatively correlated **in all but 2** lattices ($p = .01$ in 11, $p = .05$ in 4). Coefficients of determination of the significant correlations ranged from 6% to 35% indicating the extent to which variation in protein content was associated with variation in yield. In each lattice the correlation between yield and protein yield was very high and positive ($p = .01$). Coefficients of determination ranged from 78 to 96%. Thus, variation in protein yield was almost completely associated with variation in yield.

Yield was correlated with seed weight in only eight of the 17 lattices. However, these correlations were small and ranged from low positive to low negative. Coefficients of determination ranged from 6.5 to 14% indicating that where the relationships existed, only a small amount of variation in yield could be explained on the basis of seed weight.

The correlations between protein content and protein yield were not consistent. Only four were significant (3 negative, 1 positive). Protein content was not correlated with seed weight [illegible] where the correlation coefficients were [illegible] .01). Although the other correlation

Table 4.44 Simple correlation coefficients between yield, protein content, protein yield, and seed weight in 17 lattices of the 1071 genotypes randomly selected from the U.S.D.A. World Pea Collection

Lattice number	Yield-protein content	Yield-protein yield	Yield-seed weight	Protein content-protein yield	Protein content-seed weight	Protein yield-seed weight
1	-.593**	.979**	.288*	-.434**	-.487**	.233
2.	-.470**	.966**	-.256*	-.237	.117	-.270*
3	-.426**	.931**	-.053	-.075	-.011	-.058
4	-.358**	.974**	.365**	-.147	-.199	.346**
5	-.086	.952**	-.030	.211	-.192	-.085
6	-.279*	.944**	-.052	-.041	-.201	-.117
7	-.310*	.924**	-.330**	-.067	-.096	-.301*
8	-.387**	.953**	.286*	-.101	-.077	-.296*
9	-.502**	.929**	.272*	.167	-.182	.247*
10	-.527**	.957**	.373**	-.280*	-.224	.350**
11	-.418**	.956**	-.095	-.144	-.331**	-.195
12	-.244*	.941**	-.151	-.092	-.118	-.117
13	-.292*	.944**	.232	-.032	-.018	.266*
14	-.532**	.885**	.200	-.089	-.209	.115
15	-.519**	.966**	-.024	-.286*	-.072	-.015
16	-.041	.951**	-.328**	.258*	-.423**	-.432**
17	-.393**	.914**	-.200	-.002	-.003	.234

* and ** Significant at the 5% and 1% level, respectively.

coefficients were non-significant, they were generally negative. The correlation between protein yield and seed weight among the lattices merely reflected the correlation between yield and seed weight, modified by the correlation between yield and protein yield.

5. DISCUSSION

5.1 Genotype by environment study

Since crop varieties in commercial production are usually grown over a range of environments and years where variation is unpredictable, evaluation of new varieties or new breeding material should cover a representative range of these environments and years in order to estimate the true potential of the new material as accurately as possible. Breadth of adaptability may also be determined as part of the evaluation.

5.1.1 Analysis of variance for 1974 data from Saskatoon, Nipawin and Bellevue

Results of the analysis of variance at three locations showed that the genotypes differed over locations for both yield and protein content. Genotypes also showed a considerable range of expression for both traits. Evaluating the genotypes over a number of locations resulted in establishment of genotypic values considerably different from what would have been recorded at any one location. Further, the effect of location relative to genotype could be assessed, and in fact variation over locations was almost as great as that among genotypes for both traits. This variability over locations as well as the existence of genotype x location interactions emphasizes the need for multiple-location testing of genotypes to estimate genotypic value, especially if absolute values are to be used as selection criteria. For example, if a level of 26.0% protein was accepted as a lower cut-off point for selecting high-protein genotypes, then out of 25 tested, 2, 6, and 17 would be selected if tested in

1974 at Nipawin, Saskatoon or Bellevue, respectively. Over the three locations, five genotypes would have been selected on this basis. If selection for yield was practised at single locations, MP 39 would have been selected among the top five at both Saskatoon and Nipawin, but at Bellevue this genotype was lowest yielding by a considerable margin. MP 761, which ranked 4, 7, and 7 at Saskatoon, Nipawin and Bellevue, respectively, would have been selected among the top five only at Saskatoon, whereas over the three locations it was the highest yielder.

Thus, from the analysis of variance for yield and protein content of 25 genotypes over three locations, the extent of variation with environment was considerable for both traits, although more variable for yield than for protein content. The C.V's. for yield in these tests were higher than those commonly reported for yield of field peas in Saskatchewan (Slinkard, unpublished data), but those for protein content were of the same order. The limitations of testing at only one location were shown. Protein content was almost as variable over three locations as among the 25 diverse genotypes.

At Bellevue, seeding was delayed, and the growing season was moister and cooler than at the other locations. There was a heavy frost on September 1, which severely affected those genotypes which were later flowering and relatively indeterminate, i.e. MP 39, W 703, Dashaway, and P.I. 356885. None of those genotypes had completed flowering when harvested.

5.1.2 Analysis of variance for 1974 data from Saskatoon and Nipawin

When data from the Bellevue location was removed from the analysis, genotype x location interactions were no longer significant. Inclusion of height in the analysis showed that the genotype x location interaction was not significant for this trait either. Since height was not measured at Bellevue, it is not known if this trait is subject to environmental interaction, as were yield and protein content when subjected to a somewhat different environment. However, plant height in other species is a highly heritable trait and thus less likely to exhibit significant genotype x environment interactions. The Saskatoon and Nipawin sites were similar, although differing in productive capacity as indicated by their mean yield. Saskatoon was the more productive location in 1974. The data indicate that yield was more responsive to a change in fertility than either protein content or height.

A certain pattern of expression of protein content emerges from the comparison of the three-location and two-location analyses. Genotype x location interaction for protein content was present and significant from the three- but not the two-location analysis. Thus, there was interaction with the Bellevue location only. However, because the climatic conditions prevailing at Bellevue throughout the growing season and maturation period were considerably different from those at the other two locations, it is suggested that the interaction was with climatic conditions rather than location per se. It is arguable that weather forms an integral part of the 'location' which might be more properly referred to as an environment. There is no apparent interaction of genotype with soil fertility

which was the basic difference between the Saskatoon and Nipawin locations.

There was little positive response of protein content to increased fertility (8.7%) in contrast to the response of yield (22.7%), when comparing the Saskatoon and Nipawin results. This lack of response may be a barrier to increasing protein productivity with fertilizers and in fact reports (see Literature Review) indicate that protein content of legumes is not consistently responsive to fertilizer application. Conversely, the advantage of this lack of response is seen when lower fertility does not substantially depress protein content. In view of the negative correlation between yield and protein content, the considerable response of yield to increased fertility may have moderated the response of protein content.

The implications for plant breeding of these results are that environments rather than mere locations differing in fertility must be tested in any evaluation program, because it has been shown that protein content responds to and interacts with changes in environmental conditions, but to a lesser extent than does yield. Differences in yield between locations confound the location effect on protein content per se and should be accounted for before estimating the actual location effect on protein content. The Saskatoon location gave the highest yields and tallest plants, but did not produce the high protein contents recorded at Bellevue. Superficially, it appears that Bellevue is a high-protein location. However, low yields were recorded at that location because a heavy frost during the pod-filling period prevented the genotypes from completing their normal maturation phase. Thus, it is considered

likely that the high protein content at Bellevue was a function of the lower yields and interrupted maturity. A later experiment will attempt to verify this hypothesis.

5.1.3 Analysis of variance for single plant traits

Analysis of variance for single plant traits at Saskatoon and Nipawin revealed that these traits were more variable than those measured on a whole plot basis. The five-plant sample was inadequate for reasonable determinations of seed yield/plant, total protein weight/plant, and haulm protein weight/plant as indicated by the very high C.V's for those traits, especially at Saskatoon. All traits, except harvest index, were lower at Nipawin than Saskatoon, and the difference between location means was greater for single-plant than for whole-plot values of both yield and protein content. Since single plants were taken from the inner two rows of each plot, the difference could perhaps be accounted for by edge effect, the plants in the outer rows yielding more and accumulating more protein due to the reduced competition for light, water, and nutrients. The relationship between single plant and whole plot yield and protein content is described in a later section. Haulm protein content was more responsive to a change in fertility than seed protein content. This indicates that seed protein content assumes priority of accumulation under lowered N availability. Thus, the plant compensates for low N by either reducing accumulation of protein in the haulm, or else transferring protein from the haulm to the seed prior to maturity. Since protein was measured only at maturity it was not possible to discern between these two possibilities. This compensatory phenomenon was general among the genotypes and not restricted

to higher protein genotypes as in winter wheat where Haunold et al. (1962) reported that Atlas 66 and Atlas-derived lines were consistently two to four percentage points higher in protein content than normal cultivars . Haunold et al. (1962) reported that the increase in protein content was due to two genes, one of which was associated with a gene for rust resistance. Further, the higher protein genotypes were consistently lower in leaf protein content than normal varieties, and the authors concluded that the Atlas types had a more efficient system of transfer of nitrogenous compounds from leaves to the seeds. That system does not appear to operate among the 25 field pea genotypes in the present test.

The term harvest index was coined by Donald (1962) to describe the proportion of harvested dry matter (usually the seed) to total above-ground dry matter, expressed as a percentage. The quest for high yielding cereals has led to an interest in harvest index as a possible selection criterion, since the semi-dwarf rice and wheat cultivars released by the IRRI and CIMMYT programs have shown considerable productivity increases particularly when coupled with increased inputs of water and fertilizer. These new semi-dwarf cultivars have higher harvest indices than their taller predecessors (Chandler, 1969). For example, the newer cultivars of rice have H.I.'s in the range 47 to 57% compared to 23 to 38% previously. The response of these newer cultivars to applied nitrogen is seen in seed dry matter, rather than whole plant dry matter. In other words, H.I. increases with applied nitrogen. Harvest index was negatively correlated with height and positively associated

with yield. Harvest index was considered to be a cultivar characteristic. Donald (1962) referred to unpublished work of Silsbury who measured the harvest index in two cultivars of field pea. White Brunswick had a harvest index of .35, but was higher yielding than No. 14315 which had a harvest index of .45. Donald considered that, if the yield of White Brunswick could be combined with the greater harvest index of No. 14315, then a much more productive genotype would be obtained. The ranges in H.I. (see Appendix 1.4) of 38 to 60% at Saskatoon and 44.5 to 58% at Nipawin indicated that there was considerable variation among the genotypes for this trait. The range was less than that reported for some tropical legumes (Jain, 1975) but greater than that in barley (Rosielle and Frey, 1975). The genotypes Lincoln, Palouse, and Petit Pois were consistently high in harvest index and thus might be considered potential parents in a crossing program to improve the economic portion of total dry matter production. However, these genotypes were all short, determinate, early maturing and low yielding. In addition, Palouse was low in protein content. Although high in harvest index, these genotypes were almost without redeeming features on a productivity basis. The mean H.I. value of approximately 50% did not alter noticeably over locations. Reduced fertility had the effect of raising the lower end of the range. In other words, there was slightly less vegetative dry matter produced by genotypes which have a lower harvest index under conditions of reduced fertility. This is perhaps a further mechanism to compensate for decreased fertility, but unlike haulm protein content/plant, compensation occurs only among genotypes originally lower in harvest

index. Thus, a change in fertility affected accumulation of haulm dry weight and seed dry weight similarly.

Single plant protein content was lower than whole plot protein content, especially so at Nipawin. Part of the difference was due to a difference in methods of determination of protein content. The correlation between the dye-binding method (Udy, 1971) and the infra-red reflectance spectroscopy method (Neotec Instruments Co.) is in the vicinity of r= +.9 (Wu, pers.comm.). In addition, individual plants were harvested from the centre rows where competition for water, light and nutrients was more severe, resulting in lower protein content.

Seed yield/plant was extremely variable at both locations but more so at Saskatoon than at Nipawin. The range among genotypes for this trait was 3.9 to 16.7 g/plant at Saskatoon and 4.4 to 7.8 g/plant at Nipawin (Appendix 1.5). The lower fertility at the latter location resulted in reduced yield/plant and also decreased range among genotypes. In particular, the effect was on those genotypes with high yield/plant at Saskatoon and minimal on those at the lower end of the range. Thus, Palouse, Triumph, Lincoln, P.I. 206790, MP 712, and MP 783, which were highest in yield/plant at Saskatoon, decreased by an average of 47%, compared to the average decrease (31%) of all genotypes.

From the results of analysis of variance for total protein weight/plant, the average at Nipawin was 47% below that at Saskatoon. This reflects decreased protein content of both seed and haulm, and also decreased weight of both. The importance of protein content

to productivity can be seen when this 47% is compared to a difference of 23% in yield and 9% in protein content between locations. Thus, nitrogen availability or total uptake may severely limit yield, but it certainly does not seem to limit protein content expression. Although the hypothesis could not be tested in the present study, it seemed likely that seeds were favoured at the expense of haulm in an environment limiting nitrogen accumulation.

5.1.4 Analysis of variance for data from three years at Saskatoon

Evaluation trials are usually conducted in more than one season in order to remove the bias of a single season which may favour some genotypes over others. Furedi (1970) commented that some high-protein pea cultivars may only express their higher protein content under optimal seasonal conditions. The significant differences among genotypes for protein content was as expected from the earlier genotype x location study. However, the genotype x year interaction was not significant. This is in contrast to the findings of Furedi (1970) and Ali-Khan and Youngs (1973). Not only was the interaction not significant, but there were very small differences in mean percent protein over the three seasons. C.V's in each year indicated by their similarity that local variability due to soil conditions and moisture supply was constant from year to year. Although three consecutive years may be considered a valid sampling of all possible seasons, the present data suggest that either the seasons were similar, or that the genotypes in this test were very stable to seasonal fluctuations. While none of the seasons was extreme, they could be considered representative of the likely range at Saskatoon. The 1973 summer was marked by a severe drought

in late July and August, causing premature ripening and reduced yield, whereas the 1974 summer was cooler and moister than usual. The summer of 1975 was characterized by adequate moisture, about average temperatures, and about average season length. The implications of these results are that an evaluation program at several locations in a single year would be adequate to provide a reliable estimate of protein performance of pea genotypes, both on a relative and an absolute basis. The only proviso would be that if the season was clearly abnormal, such as experiencing severe drought or frost, and rainfall preventing full maturity (as happened at Bellevue in 1974), then evaluation should be repeated another year. This conclusion is supported by the findings of Shutz and Bernard (1967) who studied genotype x environment interactions from seven regional Uniform Soybean Tests from 1954 to 1956. Genotype x year interactions were generally smaller than genotype x location interactions. These authors showed that locations could be substituted for years to permit rapid turnover of breeding material in the Uniform Tests, and suggested that 10 to 15 locations/year were sufficient to remove low-yielding genotypes. Fewer locations would be required for adequate testing of other traits such as oil or protein content.

5.1.5 Analysis of covariance for within-location variability

The principle benefit of the covariance analysis was the improvement of experimental precision. It had little effect on either ranking or range of the genotypes; and thus confirmed that four replicates gave an adequate estimate of genotypic performance.

However, if selection was to be practised among the genotypes, then covariance analysis was advantageous in allowing the recognition of smaller real differences than without covariance. In terms of the time, labour, and space requirements, the value of covariate plots as used in the present study is certainly open to question, when judged against the benefits.

5.1.6 Simple correlations among traits

In any breeding or improvement program it is necessary to know if selection has an effect on non-selected traits which may be of economic or agronomic importance. Further, it is also useful to know if traits may be improved concurrently.

5.1.6.1 Yield and single plant traits

Locations were analyzed separately and corresponding correlation coefficients tended to be of the same sign and magnitude. Plot yield and seed yield/plant were moderately negatively correlated, but significantly so only at Saskatoon. The reasons for this negative relationship were not indicated from other correlations. However, this may have been because insufficient plants (5) were used for individual plant data or due to competition effects. While it is difficult to believe that inter-plant competition among individual plants in the centre rows could account for this negative relationship in the absence of differing plant populations, it is the most plausible explanation. Some of the genotypes were of branching habit which would have allowed them considerable scope for response to the less competitive conditions in the outer rows.

Some of the genotypes highest in yield/plant were single-stemmed, short, determinate, and early maturing. These genotypes were not able to take full advantage of the growing season and would not have been able to respond with extra branching in the outer rows under more favourable conditions of light, moisture and nutrients.

Since yield was not related to harvest index, this latter trait may be considered valueless as a selection criterion in peas. It is possible that in previous selection and improvement of pea genotypes, there has been unconscious selection for high harvest index, since the mean value of the genotypes in the present study is at a level (50%) considered desirable in cereals. Further, the correlation in cereals between yield and harvest index may be due partly to the confounding influence of height, wherein the semi-dwarf and dwarf cultivars of rice and wheat have high harvest index, but it has not been shown that high yield is a direct result of the latter. The absence of a relationship in field peas indicates that among the present genotypes, yield is not limited by the source - sink relationship.

The strong negative correlation between plot yield and single plant protein content reflects the close relationship between the latter and plot protein content combined with the strong negative correlation between yield and plot protein content. The negative association between plot yield and total protein weight/plant at both locations is most probably related to the negative correlation between plot seed yield and seed yield/plant since seed yield/plant is a major component of protein weight/plant. The same explanation

would apply for haulm protein weight/plant. Thus, yield did not seem to be affected by the level of protein accumulated in the vegetative tissue, which is not surprising in view of the fact that mere protein content does not indicate 'source' capacity from which yield may be derived.

5.1.6.2 Protein content and single plant traits

Plot protein content and single plant protein content were highly positively correlated. Thus, in contrast to yield, determination of protein content on a single plant basis would be a reasonable estimation of the genotypic value relative to other genotypes. A single plant is not necessarily representative of the population, but the mean of at least five single plants, and preferably more, gives a reasonable estimate of relative protein content. The correlation between plot protein content and haulm protein content was positive and non-significant. This, coupled with the positive correlation ($p = .05$) between protein content and protein weight/plant at Nipawin indicates that higher protein genotypes may accumulate more nitrogen in the whole plant than lower protein genotypes. If true, then peas differ from winter wheat, where Haunold *et al.* (1962) showed that higher protein genotypes translocated more protein from the leaves to the seeds than lower protein genotypes. Since this evidence is tentative, it cannot be concluded that higher protein genotypes accumulate more nitrogen, but the suggestion warrants further investigation.

5.1.6.3 Single plant traits

Harvest index and height were strongly negatively related. This finding is in line with other crops. Thus, the weight of haulm was more important as a determinant of harvest index than seed weight. The idea that harvest index should be related to yield has a strong appeal to logic, but has not been supported in fact. However, the important determinants of yield are not yet well defined for any major crop. As expected from analogy to the findings of Shia (1976) that seed yield and protein yield were very highly correlated, seed yield/plant and total protein weight/plant were highly correlated.

5.1.6.4 Yield and protein content

Yield and protein content were strongly negatively correlated over locations and seasons. Although negative associations between these two traits have been reported for cereals and other legumes (see Literature Review), the few reports pertaining to field peas are variable and conflicting. Ali-Khan and Youngs (1973) found a moderate positive correlation (r= +.57) but it was not significant. Furedi (1970) reported a negative association of low order and considered it of little obstruction to protein improvement. Pandey and Gritton (1975) found values ranging from moderate negative (-.38**) to moderate positive (+.34**) among F_3 populations. None of the reports had values approaching those found in the present study. The sign and magnitude of the relationship was sufficiently stable over locations and seasons to rule out the possibility of unknown bias. The slight difference in correlation coefficients among the 25 pea genotypes and 22 common genotypes at Saskatoon in

1974 can be attributed largely to the removal of three genotypes and the use of three replicates for the 22 genotypes as compared to four replicates for the 25 genotypes, which would lead to a less precise estimate of the genotype mean for both yield and protein content.

Coefficients of determination show that between one third and two thirds of the variation in protein content was associated with variation in yield. This correlation has far-reaching implications for programs aimed at improvement of field peas. Firstly, no protein content value should be considered in isolation from the yield value of that genotype. Secondly, a decision has to be made as to the extent to which protein is to be improved at the expense of yield. There is a trade-off between the two. This is evident in other crops too, as exemplified by the newly licensed Canadian oat cultivar Hinoat, which has a protein content approximately 3% higher, but yields only about 75% as high as standard cultivars (Anonymous, 1973) in Western Canada.

Reference to **Tables 4.2 and 4.3** shows that there are no outstanding 'correlation breakers' among the genotypes as tested at Saskatoon, although three, P.I. 356834, P.I. 269822, and MP 783 were just slightly above average for both yield and protein content. However, at Nipawin, P.I. 324705 was substantially higher than average in both traits. On the basis of the Nipawin results, this genotype might be seen as a potential parent for increasing protein productivity, but over all locations it was third lowest yielding of the 25 genotypes in the test (Table 4.2). It seems possible that high yield or high protein content may be combined with average levels of the other trait, but there is no evidence to suggest that a

combination of high levels of both traits would be easily obtainable. Zoschke (1970) rejected the idea of a linkage between yield and protein content which could be broken by crossing over and put forward the theory that the relationship is inherently physiological and that to be overcome, research was first needed to establish the physiological determinants of both traits. One of the possible physiological explanations for the relationship is the existence of a finite capacity to provide nitrogen for seed incorporation, which is independent of yield. Differences in yield are not matched by differences in protein content, as seen by the lack of response of protein content to a change in fertility between the Saskatoon and Nipawin locations.

Peas obtain approximately 30% (Holl and LaRue, 1975) of their nitrogen requirements through symbiotic nitrogen fixation by Rhizobium leguminosarum in the root nodules. This process, and absorption and nitrate reduction of mineral nitrates are equally energy expensive (Hardy and Havelka, 1975). Roots, supplying nitrogen for the plant by either or both processes, compete with the developing seeds for recently produced photosynthate and it is possible that the negative yield-protein relationship is a reflection of this internal competition. It is plausible that some genotypes tend to favour the developing seeds (high yield, low protein), while others divert relatively more photosynthate into energy for nitrogen accumulation than into developing seeds (lower yield, high protein).

Adams (1973) reported that as protein content of Phaseolus

vulgaris L. increased from 21 to 27% protein, cystine in the protein dropped from .70 to .54%. More important, Adams remarked that the increased protein, which was of lower biological value, acted as a depressant to yield since it costs the plant more energy to produce protein than carbohydrate. Sinclair and DeWit (1975) calculated that from one unit of glucose, plants can produce about .83 units of carbohydrate, .40 units of protein, or .33 units of lipid. If a finite amount of photosynthate is assumed, then indeed yield (largely carbohydrate) will compete with protein for glucose in the developing seed.

Is an energy restriction responsible for the negative yield-protein relationship? The legume plant has competition at two points: will roots or the developing seed be favoured for photosynthate; and in the developing seed, will carbohydrate (yield) or protein be favoured for the photosynthate supplied to that sink?

It is highly likely that genotypes will differ in response to the competition at those points, and therefore plausible that a group of such genotypes will exhibit a negative yield-protein content relationship.

5.1.7 Variance component analysis

Variance component analysis confirmed the conclusions drawn from analysis of variance. Both locations and seasons were major sources of variation for yield, and less important sources for variation in protein content. Genotype x location and genotype x season interaction variances were relatively small except when Bellevue data were included in the analysis. Shutz and Bernard (1967), using data from Uniform Soybean Tests, reported that geno-

type x location interaction variances were generally greater than genotype x year interaction variances, but both were substantially less than genotype variances. Further, interaction variances for oil and protein content were considerably less than those for yield.

The three estimates of broad-sense heritability were 0, 27 and 24% for yield and 21, 41 and 53% for protein content from variance component analysis of the three-location, two-location and three-year data. Broad sense heritability, based on variance component analysis, is limited by the extent to which it is independent of non-genetic variation. Thus, heritability values will increase with decreasing variability of those non-genetic components. It would be safe to conclude only that yield had low heritability and protein content had low to moderate heritability in the broad sense. These broad-sense values however, give no indication of purely additive genetic variance, upon which improvement by selection is largely dependent.

5.2 Effect of stage of maturity on protein content

Previous studies of developing legume seeds (see Literature Review) have utilized very small numbers of seeds of one genotype at progressive stages of maturity to trace the development of seed components. Harvests were usually more frequent and closer together than in the present study. However, the present study had multiple objectives and was designed to include a large number of genotypes subjected to simulated interruptions in development at different stages of maturity from pod-filling to ripeness.

5.2.1 Analysis of variance for stage of maturity

Differences existed among genotypes for each of the traits at each of the harvests, but the results clearly indicated closely parallel patterns of development. The patterns also verified previous findings that, as maturity progressed, percent protein decreased, while protein weight continued to increase. Only two genotypes departed from established patterns. MP 761 had a low protein content at H1 and continued to decline with maturity. Further, it declined in both dry weight and protein weight from H2 to H4. From the data recorded, there was no explanation for this decrease. P.I. 206790 also departed from the usual pattern in that protein content increased by 2.2 percentage points from H3 to H4 and was the highest in protein content at H4. This genotype has been consistently high in protein content in previous trials in Western Canada (section 4.1 and Slinkard, unpublished data). The increase was 9% over the value at H3 and was entirely due to a 9% increase in the weight of protein accumulated while the total dry weight did not increase. Other genotypes accumulated protein weight between H3 nd H4, but

this was usually accompanied by an increase in dry weight. Thus, P.I. 206790 may be higher than average in protein content due to a slower accumulation in non-protein dry matter at a late stage of maturity rather than an inherent superiority in accumulation of protein. P.I. 206790 is a wrinkle-seeded genotype, as is Lincoln, and this may partly account for the higher protein content of these genotypes (see Shia, 1976 and section 4.3.3).

In agreement with a previous maturity study (Smith 1973), it was found that starch accumulation began later than protein accumulation, but it increased more rapidly than protein after H1. Thus, protein tended to be 'diluted' by a greater deposition of starch and other non-protein, non-starch dry matter as maturity progressed. One of the reasons for the rapid development of all components and the similarity of the genotypes may have been the weather conditions prevailing during the period under study. During the latter part of July, mean daily temperatures were higher than average, and for the month the total number of growing degree days (GDD) was 461 compared to the long-term average of 438. August was cooler, cloudier, had 100 hours less bright sunshine than July and had 301 GDD's compared to the long-term average of 395. In a year in which GDD's were closer to the monthly averages, the patterns of fresh and dry weight accumulations would tend to be slightly less rapid in July and probably greater in August than those recorded in this study for 1975. Snoad and Arthur (1974) showed that accumulated heat units were correlated with development in peas to a greater extent than was time (days to flower).

5.2.2 Simple correlations between harvests for various traits

None of the traits measured at H1 were correlated with their counterparts beyond H2 and starch content was not even correlated between H1 and H2. Thus, H1 was considerably different from the other harvests, except in dry weight where there was a close relationship with H2. At H1, 13 to 23 days after flowering, the later flowering genotypes were just beginning to accumulate dry matter, and the genotypic values for each trait more likely indicated physiological age rather than inherent genotypic differences at the actual time of the harvest. Harvests 2, 3 and 4 were moderately correlated for all traits, but coefficients of determination were generally less than 50%, i.e. variability between harvests was due more to non-genetic than genetic differences among genotypes. More important for predictive purposes, if a series of genotypes was harvested at any time prior to 30 to 40 days after flowering, the yield and protein content data obtained would bear very little relationship to the data obtained at full maturity. Further, if harvest occurred within approximately two weeks of full maturity, then the fresh and dry weights obtained would be reasonable indicators of final values, whereas protein content and starch content would not be as reliable.

5.2.3 Simple correlations between traits within harvests

The correlations between traits at H1 indicate the influence of date of flowering on all traits measured at that harvest. The high correlation between fresh weight and dry weight ($r = .961^{**}$) indicated that the moisture content of the seeds of these 25 genotypes was relatively uniform. The negative correlation between protein content and starch content was high ($r = -.777^{**}$) at H1. This relationship

is due to their opposite correlation with a third trait (dry weight). However, this explanation is not applicable to later harvests. The negative relationship between protein content and starch content declined at H2 but was still significant, and then increased at H3 and H4. This negative relationship has been reported in Vicia faba L. (Bhatty, 1974; Cerning et al., 1975). The correlation calculated from Bhatty's data was r= -.575* among 12 cultivars, and Cerning et al. reported that starch content ranged from 30.0 to 42.3% and was negatively correlated with protein content but the coefficient was not given. Shia (1976) considered that the lower starch content of wrinkle-seeded peas may have contributed to the observed higher protein content of these peas over their smooth-seeded counterparts. Wrinkle-seeded peas were 13% lower in starch, about 3 percentage points higher in protein content, smaller seeded, and lower yielding than their smooth-seeded sibs from the same cross. The present study shows that after H1 starch content increases much more rapidly than protein content. It is axiomatic that as the proportion of one major seed component increases, the proportion of the remainder must decrease. Protein content decreases with maturity, indicating an increasing proportion of non-protein dry weight. Starch, as a proportion of that non-protein dry weight, increases with maturity. Thus, non-protein, non-starch dry weight stays relatively constant as a proportion of the seed as maturation takes place. The negative correlation between protein content and starch content also indicates that there are genotypic differences in the starch: protein ratio.

One of the objectives of this study (see Introduction) was to throw light on the negative yield-protein content relationship

which seems to be prevalent in the peas. The starch-protein content relationship shown in this experiment is possibly a contributing factor, but that could not be verified in the present study because yield (dry weight) and protein content were not negatively related at maturity. All that can be said with certainty is that protein content and starch content are negatively correlated ($p = .01$) throughout the span of maturity from 13 to 23 days after flowering to full ripeness. However, it was not conclusively shown that this relationship contributed to a negative yield-protein relationship.

For the other between-trait correlations at harvests 2, 3 and 4, only that between fresh weight and dry weight was significant. Days to flower did not influence any of the traits at these harvests except dry weight at H2 where the correlation was negative and moderate ($r = -.458^*$).

5.2.4 Relationship of the maturity study to the large-plot study in 1975

As seen in Table 4.22, yield of the two studies was not related and protein content of the large-plot study was only moderately related to protein content at the last three harvests of the maturity study. Thus, it was not possible to infer that the yield and protein content values for any genotype in the large-plot study were related to the pattern of seed development of that genotype. The only possible exception was P.I. 206790 which accumulated protein at a late stage of maturity without a concomitant increase in dry matter.

It was surprising that the yield at full maturity of both studies was totally unrelated ($r = .189$). Although the maturity

study means were based on two samples and the large-plot means based on three replicates, coefficients of variation were not greatly different, i.e. 15.4 and 11.9% respectively. Plot sizes were about 10-fold in difference and, while it seems logical that this difference should not be responsible for the poor relationship, it is the most plausible explanation. It is possible the small plots were too small to provide a reliable yield estimate. The lack of correlation between yield of these two studies, coupled with the negative correlation between plot yield and single plant yield of these same genotypes in the previous large-plot studies (section 4.1), suggests that edge effect might be considerable in the large-plot studies.

5.2.5 Relationship of the maturity study to the 1974 Bellevue large-plot study

Reasonable evidence was obtained to fulfill the third objective of this study, namely, the verification that the anomalous results at Bellevue in 1974 could be explained on the basis of maturity.

Many of the genotypes failed to mature at Bellevue due to a damaging frost on September 1 during their flowering period which effectively forestalled further development. The correlation of protein content in the maturity study with protein content in the 1974 Bellevue large-plot study was nearly the same as with protein content in the 1975 Saskatoon large-plot study. However, yield at Bellevue was positively correlated ($p = .01$) with dry weight (yield) in the maturity study at H1 and H2 ($r = .626^{**}$ and $.551^{**}$, ~~respectively~~). Further, yield at Bellevue was negatively correlated ($p = .01$) with days to flower at Saskatoon despite a

difference in location and season. In fact the correlation was almost identical (r= -.758**) with the correlation between dry weight at H1 and days to flower (r= -.734**). This evidence strongly suggests that at Bellevue in 1974, the damaging frost on September 1 interrupted maturity at between 2 and 3 weeks after flowering and the genotypes remained at that physiological age until harvested on October 12. It was this event which contributed to the genotype x location interaction ascribed to the Bellevue location in the previous experiment (section 4.1). Such results could be expected to recur with damaging frosts or other maturity-inhibiting phenomena at any given location.

5.3 Heritability of agronomic traits, protein content and methionine content

5.3.1 Analysis of variance for agronomic traits, protein content and methionine content

The significant differences among parents for all traits indicated that they were diverse and rich in genetic variability for all except protein and methionine contents. However, the intermediacy of the F_2 population values and the lack of significant differences among them for the protein and methionine content traits showed that a breeding program for improvement of these traits would have to be based on either a wider range of parents or selection would have to be made on a within-cross basis among F_2-derived F_3 or F_4 lines. A breeding program to improve the agronomic traits such as seed weight or days to flower could be based on a moderate number of crosses utilizing selection both among and within crosses, whereas a breeding program for improving protein content and quality might be successful if based on judicious crosses between widely divergent parents followed by selection among lines within a cross.

There was no evidence of dominance for late flowering as has been reported by Rassmusson (1935) and Watts et al. (1970). However, the value recorded in the present experiment was days to first flower, which does not necessarily reflect the mean flowering date of a bulk F_2 population while being accurate for a non-segregating population. Figure 4.4 indicates that there were no early flowering segregates within F_2 populations and that days to flower was intermediate between parents. The conclusions drawn from the days to flower data are certainly valid for the material

under study, but since the range of days to flower was relatively narrow (15 days) caution should be used before extending conclusions to cover genotypes with a greater range. Saskatchewan has essentially a one-sowing-date season for field peas (the frost-free period at Saskatoon is 114 days) in contrast to more temperate regions in lower latitudes where field peas may be seeded over a greater time span and where the range of days to flower between early and late genotypes is greater (Aitken, 1974).

There was a wide range in seed weight among parental genotypes which would allow considerable scope for selection of parents initially and for families of the desired seed weight among the progeny. In contrast, the range in protein content was very narrow, 7.3 percentage points, and even narrower among the F_2 population means, 3.4 percentage points. In terms of implications for breeding increased protein content, this range would be totally inadequate to provide the scope for selection of high protein genotypes from among the F_2 populations. In other words, hybridization did not provide increased variability for protein content. On the contrary, hybrid material is unlikely to approach the range of parents. In the present study the reduced range in protein content was largely from the upper end of the hybrid distribution. The lowest parent and lowest F_2 population had the same protein content. Thus, the scope for selection of high protein genotypes from among F_2 populations appears slight. However, the within-population variability and range were not determined in this study and it is possible that utilizable variability occurred within populations. The narrow range in protein content among parental lines and the even narrower range among F_2 populations in this experiment

emphasized the need to screen a very large number of genotypes to obtain the widest possible range in protein content before attempting to breed for improved protein content. The likelihood of improving protein content by breeding in the material of the present study is put into perspective when it is realized that protein content exhibits about 1/8th of the range and 1/2 of the heritability of seed weight. In other words, genetic improvement would be minimal, with increases achieved very slowly and, probably, at the expense of yield.

The range among parents for methionine content as either mg met/g meal or mg met/g protein was narrow and indicates that the genotypes in this test do not vary greatly and thus would not be a suitable base on which to establish a breeding program for the improvement of methionine content. Herrick et al. (1972) reported a range of 0.9 to 1.3% methionine as mg met/g protein in nine pea cultivars. From the present study and that of Herrick et al., the range in methionine content of peas appears very narrow, but it is not known if the narrow range is a function of the few genotypes surveyed in each study or a function of the actual variability of the trait. However, Kelly (1971) reported a 2.4-fold range in methionine content of 3600 single plant determinations of 480 P.I.'s and cultivars of common beans, Phaseolus vulgaris L. Thus, perhaps a larger population of peas would also contain a much wider range of methionine content.

The range in methionine as mg met/g meal of the F_2 populations was half that of the parents. Again, most of the decrease came from the upper end of the range. It is probable that the

similarity between behaviour of methionine content and protein content was largely due to the close positive correlation between those traits (Table 4.31).

The situation is also similar with regard to methionine as a percent of protein, except that for this trait, the range among parents and among crosses was virtually identical. Thus, although range does not decrease upon hybridization, it is too small to be of value in breeding for protein quality improvement. It should be emphasized that it is not known whether this is a function of the genotypes tested or the actual variability of the trait.

5.3.2 Analysis of covariance to remove the effect of protein content on methionine content

Analysis of covariance showed that as protein content increased, methionine as mg met/g meal increased and methionine as a percent of protein decreased. Those findings are supported by the correlation analysis among these traits (Table 4.31). In comparing wrinkle-seeded with smooth-seeded genotypes, methionine as a percent of protein did not differ between the groups until they had been adjusted for initial differences in protein content. Although the difference was small after adjustment, it was statistically significant. However, the difference has no biological importance. The levels of methionine as a percent of protein in the present genotypes are so low and the range so small that even the difference between wrinkle-seeded and smooth-seeded genotypes is of no consequence, since methionine content of the protein would have to be at least trebled before substantially improving the protein quality of the present pea genotypes to acceptable levels for human nutrition.

(F.A.O., 1970).

5.3.3 Comparison of smooth-seeded and wrinkle-seeded parents

Apart from the difference in methionine as percent of protein mentioned above, wrinkle-seeded parents were lower yielding, higher in protein content and methionine content of the protein, and heavier seeded than the smooth-seeded parents. This agrees with the report of Shia (1976) who found that wrinkle-seeded progenies from a cross between smooth- and wrinkle-seeded parents were lower yielding, lighter in seed weight, lower in starch content, and higher in protein content than their smooth-seeded sibs. The only difference between these two studies was the reversal in the relationship to seed weight, but Shia's study compared sib progenies while the present experiment compared parents.

These differences associated with seed shape introduce a bias of unknown dimensions into the calculations of heritability of all traits except days to flower which did not differ between seed shape types. The present experiment included 10 F_2 populations which were segregating for seed weight. Shia (1976) showed that heritability of protein content decreased or became non-significant when populations segregating for seed shape were sub-divided into smooth- and wrinkle-seeded lines. However, heritability of seed weight remained about the same when these populations were sub-divided.

In the present experiment the populations were not sub-divided into crosses segregating and non-segregating for seed shape since 10 and 11 crosses, respectively, were considered

too few to permit reliable estimation of heritability by regression. However, in the light of Shia's (1976) results, it is most probable that heritability estimates of protein content and both methionine content traits were biased.

5.3.4 Correlation analysis

Yield and protein content were significantly negatively correlated. However, among this group of genotypes the coefficient was lower than that found in the earlier study (section 4.1). When the genotypes were subdivided into parental and F_2 population classes, the correlation increased when only parents were considered, but for the F_2 population group it decreased to almost zero order. Thus, there appears to be a difference in this negative yield-protein content relationship between homogeneous and heterogeneous populations. Homogeneous populations behave in a relatively predictable negative pattern, whereas the F_2 populations do not show that pattern when only population means were considered. The narrow range among F_2 population means for protein content contributed to the lower correlation between yield and protein content. In addition, each F_2 population is a mixture of genotypes, each of which may exhibit a negative yield-protein relationship, but when the population mean is taken, that negative relationship is probably masked. The lack of homogeneity among early generation populations may be one of the reasons for the generally low correlations, both positive and negative, reported by Pandey and Gritton (1975) among F_3 populations of peas, and the low negative correlations among early generations of soybean populations by several authors (see Caldwell et al., 1973, p.160).

The means of early generation populations, which are segregating for yield and protein content, are therefore unsuitable for detecting correlations between these traits. The same would apply to correlations between any traits for which a series of populations are segregating. The present study shows quite clearly that if a given group of genotypes which demonstrate a negative yield-protein content relationship are intercrossed, the relationship is reduced among the F_2 populations, and it is most reasonable to conclude that the relationship has been diluted by the intermediate nature of the population means and heterogeneity. The previous experiment (section 4.1) showed that the negative yield-protein content relationship among a group of pea genotypes was quite stable over years and locations.

The only other significant correlation was that between yield and seed weight of the combined group. It was positive and of low order. Thus, it indicated that protein content, seed weight, and days to flower could be subjected to selection without undue influence on the other traits.

Protein quality traits were generally unrelated to the agronomic traits except that methionine as a percent of protein was positively correlated with seed weight at a low level. This relationship has no immediate simple explanation, since neither protein content and seed weight, nor protein content and mg met/g protein are correlated. It would be very convenient for breeding purposes if protein quality was associated with an easily identifiable trait such as seed weight, however in this instance the relationship is not strong enough (r^2= 11.2%) to indicate that seed weight could

be used as a 'marker'.

Mg met/g meal was positively correlated (p= .01) with protein content and is therefore more an indicator of protein content than protein quality. Thus, it should not be used as a selection criterion unless the absolute amount of methionine in whole pea meal became nutritionally important, e.g. if whole pea meal was used as a protein supplement rather than the more frequently used protein concentrate. It is not the concern of this study to recommend which of the two methionine measurements should be used, but only to show the merits and possibilities of each to contribute to the breeding of improved protein quality. In this light then, methionine as a percent of protein is the more valid criterion, but as is shown in section 4.3.5, it is not heritable and, therefore, not genetically manipulatable.

There was no significant correlation between protein content and mg met/g protein (r= -.112).

Likewise, Bajaj (1973) found no relationship between crude protein content and protein quality of peas as measured by rat growth test. However, Holt (1976) reported that methionine as a percent of protein was negatively correlated with protein content among 16 samples of Century peas (r= -.64**), and among 17 cultivars of field peas (r= -.21). Reports in other legume crops, i.e. Vicia faba L. (Munck et al. 1973), Phaseolus vulgaris L. (Adams, 1973), Cajanus cajan (Royes, 1973), and Cicer sp. (Sandhu et al., 1974), also indicate that the two traits were negatively related to varying degrees. Adams (1973) concluded that in dry beans, Phaseolus vul-

garis L., attempts should be made to fix the protein content at about 22% and then breed for improved protein quality. Above that level, quality was sacrificed for higher protein content.

5.3.5 Heritability estimates for agronomic traits, protein content and methionine content

Heritability of yield is low. In this experiment narrow sense heritability was zero and in a previous study (section 4.1.4) broad sense heritability ranged from 0 to 27%. Thus, in the short term, response to selection for yield would probably be negligible. Selection among F_2 populations would offer little possibility of advance. It was not determined in the present study if heritability within populations was greater, but Shia (1976) found that narrow sense heritability of yield determined by F_3/F_2 regressions in three crosses ranged from 0 to 4%, although he added that one of the reasons for the low values may have been the use of single plant determinations for F_2 values.

Thus, attempts to improve yield by breeding would have to concentrate on genetic manipulation of components of yield which are generally more heritable than yield alone. For example, Crampton (1970) selected for pods per node and seeds per pod at the first three flowering nodes to improve the yield of processing peas.

Days to flower was highly heritable ($h^2 = 80\%$) and showed good agreement with mid-parent values. This trait can be easily manipulated and the outcome of selection readily predicted.

The same is true for seed weight. This trait is highly

heritable (h^2 = 97%). It is, thus, almost completely genetically controlled and exhibits little or no response to the environment. In between these extremes of yield and seed weight, protein content and methionine content exhibit low to moderate heritability (h^2 = 44.9 and 48.6%, respectively). These traits are subject to considerable nongenetic variation.

Methionine content as a percent of protein, perhaps the true indicator of protein quality, is not heritable in the pea genotypes of this study. This finding is in marked contrast to the results of Kelly and Bliss (1975) who reported very high broad sense heritabilities for methionine as a percent of protein in Phaseolus vulgaris L. The lack of heritability in the present study may be due in part to the very narrow range exhibited by the parents for this trait. It indicates that mg met/g protein would not respond to selection and thus, may be a valueless selection criterion. However, the situation may be analogous to that of yield. Both traits are the end products of complex and dynamic plant processes and both are of low heritability. Yield increases have been achieved by breeding for yield components which are generally higher in heritability than yield. Breeding for increased methionine as a percent of protein by increasing methionine-rich components of the seed protein may be feasible since the chemical composition of individual proteins is genetically determined and independent of environmental influences, i.e. methionine-rich protein components may be more heritable than total methionine in the protein.

For example, the Opaque-2 gene in corn (Zea mays L.) increases lysine content by suppressing synthesis of zein, the lysine-poor fraction of corn protein (Mertz et al., 1964). Smartt et al. (1975) reported that genetically manipulatable variation occurred in the major storage proteins (globulins) of Phaseolus sp. and Arachis hypogea L. Romero et al. (1975) electrophoretically analyzed the major seed protein, G1 globulin, from four bean (Phaseolus vulgaris L.) cultivars. Two cultivars high in methionine had a three-banded sub-unit pattern in the globulin whereas the two cultivars low in methionine had a two-banded sub-unit pattern. The difference in banding was due to a single gene.

However, the molecular-genetic approach to protein improvement is presently limited by inadequate methodology which does not permit rapid, precise isolation and separation of seed protein components.

5.4 Effect of seed shape on seed weight

5.4.1 Seed weight of parents and progeny of segregating populations

This study confirmed the findings of Shia (1976) that progeny from crosses between smooth-seeded and wrinkle-seeded parents bear wrinkled seeds which are lighter than their smooth sibs, in this case by an average of 14%. This result is surprising since in eight of the 10 crosses seed of the wrinkle-seeded parent was heavier by an average of 46%. Thus, while there is no strict association between seed shape and seed weight, there is a definite effect of the gene for wrinkling (r_b) which causes a reduction in seed weight of wrinkle-seeded segregates. The effect is independent of parental seed weight since even in the two crosses where the wrinkle-seeded parent had lighter seed, the same phenomenon occurred.

5.4.2 Number and size distribution of smooth and wrinkled seeds from segregating populations

Only one of the populations, P.I. 206790 x Cesen, conformed to the expected 5:3 ratio of smooth:wrinkled seeds. Among the others, five populations had fewer wrinkled seeds than expected and four had an excess of wrinkled seeds. No consistent genotypic pattern was apparent. One possible explanation for the paucity of wrinkled seeds in some populations could be the lower germination of wrinkled seeds in an earlier generation.

When the seeds from each population were size graded, results indicated that seed size was dependent on seed shape except

in one cross. In each size category, wrinkled seeds were significantly lighter than their smooth counterparts. These results indicate that although smooth and wrinkled seeds may reach the same external diameter, the greater water loss on maturation of the wrinkled seed (Kooistra, 1962) leads to the convoluted shape and decreased weight. The weight loss was between 16 and 28% greater than that experienced by smooth seeds of the same diameter. Ottoson (1958) suggested that wrinkled seeds lagged in development of dry matter compared with smooth peas.

For some reason, wrinkled seed borne on F_2 plants accumulate less dry matter than comparable smooth seeds. Since approximately 1/5th of the smooth seeds and 1/3rd of the wrinkled seeds in the F_3 generation are borne on segregating plants, it is unlikely that a competitive advantage to the smooth seeds (when both types are borne on the same plant) could be responsible for the differences observed. Consideration of the chemical components of each seed type suggests that differences in efficiency of conversion of energy supplied as carbohydrate during seed development would be too small to account for the seed weight differential. The 3 percentage point difference in protein content would account for only a 2% weight differential, since protein is more energy-expensive to synthesize than storage carbohydrate (Sinclair and DeWit, 1975). The heavier seed weight of wrinkled parents compared with their smooth counterparts indicates that neither the wrinkled seed itself nor the plant on which it is borne are inherently more limiting to seed weight than smooth seeds or the plants bearing them.

Thus, the effect of the r_b gene for wrinkle-seededness in reducing seed weight in the F_3 generation of crosses between smooth (R_b) and wrinkled (r_b) parents is documented. Although Kooistra (1962) observed that wrinkle-seeded peas underwent a greater water loss on maturation than smooth-seeded peas, this does not fully explain the phenomenon.

5.5 Variation in protein content and other traits among 1071 genotypes from the U.S.D.A. World Pea Collection

A narrow range of genotypic variability in protein content was found in previous experiments (sections 4.1 and 4.3). This suggested a survey of a large number of genotypes to gauge the possible limits of genetic variability for protein content. The experiment involved 1071 pea genotypes and was designed so that the effects of environment and genotype could be separated.

5.5.1 Analysis of variance for yield, protein content, protein yield and seed weight

When efficiency of the lattice was compared with that of RCBD there was, overall, no great increase, but considerable increases in efficiency in some of the lattices, notably lattice numbers 9 and 11 for yield and protein yield, and lattice number 6 for protein content. Where the efficiency was less than 100, no adjustment was made, since Campbell and Goodchild (1973) have shown that the adjusted error mean square is greater than the unadjusted if there is a poor regression between the error in the variable and error in the covariate. The range of C.V's from 10.9 to 25.8% for yield indicates that, although only two replicates were used, reasonable error control was obtained. At Saskatoon C.V's of 10 to 15% for yield of field peas in 4-replicate, 4 row plots are common (Slinkard, unpublished data).

There were significant differences for yield among genotypes in all but two of the lattices. Although the F-test was not significant in these two cases, the Bayesian L.S.D. showed

that there were in fact real differences among genotypes. The Bayesian L.S.D. requires only that the F ratio be greater than 1.0, and not necessarily significant. Thus, a considerable diversity of yield was found among the genotypes. However, since the range of lattice means was considerable, and error variances were heterogeneous the genotypes could not be grouped together either to form a distribution or for multiple comparisons.

The range in protein content was smaller than for yield within and among lattices. There were significant differences ($p = .01$) among genotypes in all lattices. The generally low C.V's (2.8-4.9%) indicated that there was good error control with replication for this trait. Covariance adjustment had relatively little effect on efficiency, further indicating that within replicates, variability for this trait was low except in one or two lattices. The range in protein content among lattice means was very small (24.5-26.7%), but since error variances were heterogeneous, the genotypes were not grouped together for analysis.

The data for protein yield were similar to yield in terms of significance, efficiency, range among the lattice means, and C.V's. This indicated that protein yield was more closely linked to yield than to protein content, which was borne out by correlation analysis (section 4.5.6).

There were significant differences ($p = .001$) among genotypes for seed weight in all lattices. The lattice design was less efficient than RCBD (98.2%) overall for this trait. This trait was, thus, very stable within replicates and the small range in

lattice means indicated that it was also quite stable over a range of environments. C.V's were low, indicating good error control.

5.5.2 Distribution of each trait among the genotypes

The data from the lattices could not be combined for analysis due to heterogeneity of error variance for all traits. There were two possible conversions. The genotypic values in each lattice could either be expressed as a percent of the check variety Trapper or as a percent of the lattice mean. As outlined in section 4.5.2, use of the Trapper values for conversion may have been acceptable for yield, but it would not have been a reliable conversion factor for protein content when the correlation coefficient between Trapper and lattice mean values was r= +.577**. The mean of an experiment comprising several genotypes at a given location has been used as a measure of the environment at that location, particularly for recording the response of genotypes over a range of environments (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966). However, in those instances, the experiments over the locations contained common genotypes. Although the use of experiment mean is not precise due to the possibility of genotype x environment interaction and bias in the choice of genotypes, it serves as an indicator of the environment in the absence of a reliable mathematical model. In the present study, the use of lattice mean is subject to uncontrollable bias in that the genotypes are not common in each lattice. However, since (1) the genotypes were randomly assigned to the lattices; (2) each lattice contained a large sample (5.9%) of the total, and (3) the lattices were all adjacent, the use of the lattice

mean as a conversion factor was considered more reliable than the use of Trapper. Thus, a distribution based on the converted genotype values would be a reasonable approximation of the true distribution of each trait.

5.5.2.1 Distribution of yield

There was a wide range in yield among the genotypes (34.6 to 172.4% of the mean yield), i.e. a 4-fold difference between extremes. This large range shows that the genotypes tested constitute a rich source of variability, providing wide scope for selection of high yielding parents. It is noteworthy, however, that the licensed variety Trapper was usually in the upper third of the genotypes in yield and averaged 123% of the population mean. It was exceeded in yield by 183 of the 1071 genotypes if lattice #6 is disregarded. The yield of Trapper in that lattice was very low due to an unaccountable low yield in one replicate. The difference between replicates was greater than for any other genotype by a wide margin, indicating a possible accident or human error.

5.5.2.2 Distribution of protein content

The distribution curve for protein content was normal-shaped, but showed a slight surfeit of values on the lower shoulder of the curve and a tailing-off to the upper end of the curve. In this respect it was similar to the distribution of protein content among 1452 genotypes (Slinkard, unpublished data) at Saskatoon in 1971 and also among 506 genotypes grown at Morden (Ali-Khan and Youngs, 1973). The range among 1071 genotypes was extremely narrow, from 22.6 to 30.9% protein. The highest protein genotype

was only 0.4 times greater than the lowest protein genotype. This range is only 1/10th that of yield. Thus, protein content is less subject to environmental influence, and also less variable over genotypes than yield. Among the genotypes in this present study, which represent a very large sample of the U.S.D.A. World Pea Collection, protein content is not very variable. It is probable that the range among these genotypes was narrower than previously reported for other large groups of pea genotypes for the following reasons: (1) the fact that each genotype was replicated led to a considerable reduction in range (33%) due to the removal of environmental variability (see section 4.5.5); (2) the plots were relatively large, i.e. 3 m x 2 rows 30 cm apart and germination was uniform which reduced variation of the population as occurred in the study of 1452 genotypes at Saskatoon in 1971 (Slinkard, unpublished data); and (3) in the initial selection of genotypes for this study only those genotypes that produced sufficient seed in 1971 for seeding in 1975 were available. This eliminated some of the very low yielding genotypes, which were frequently high in protein content. Thus, 1071 genotypes were chosen randomly from among approximately 1300 which were available. Further, yield and protein content were negatively correlated (section 4.5.6) and, thus, variation in yield would affect variation in protein content. The actual effect of yield on range in protein content cannot be calculated, but its existence cannot be discounted. The narrow range of protein content has important repercussions for breeding strategies. It means in effect that the U.S.D.A. World Pea Collection does not represent a rich

source of variability for protein content. The range is not much greater than that found previously among 25 and 19 genotypes (sections 4.1 and 4.3).

Given a heritability value of less than 50%, additive inheritance, and a genetic range of approximately 8% protein, the limit to improvement of genotypes with average protein content (26%) by breeding would be in the vicinity of two percentage points. However, the collection does offer scope for selection of genotypes with protein contents of approximately 30% should it appear desirable to produce a high-protein pea without regard to productivity. Correlation analyses show that agronomic traits such as seed weight, days to flower (section 4.2), and height (section 4.1) can be manipulated without affecting protein content.

5.5.2.3 Distribution of protein yield

The distribution curve for protein yield was virtually identical to that of yield, strengthening the finding in correlation analysis (section 4.5.6) that yield and protein yield were very highly positively related, on an almost one-to-one basis. The closeness of this relationship reflects the large range in yield compared with the very narrow range in protein content.

5.5.2.4 Distribution of seed weight

The range among genotypes for this trait was very large, i.e. 8-fold from lowest to highest, which is double the range for yield and 20 times the range for protein content. This range in

seed weight, indicates that the genotypes tested are extremely diverse and provide a valid sample of available pea genotypes. In retrospect, it seems more likely that the narrow range in protein content is a function of the trait rather than the genotypes tested.

The distribution curves indicate that there is extensive genetic variability for yield and seed weight among the 1071 genotypes tested, and selection of potential parents in an improvement program for either of these traits would not be difficult.

5.5.3 Distribution of the traits among smooth-seeded and wrinkle-seeded genotypes

Kooistra (1962) reviewed the differences between smooth- and wrinkle-seeded peas and proposed a two gene (r_a and r_b) mechanism to account for the differences. The differences between smooth-seeded peas (R_aR_b) and the most common wrinkle-seeded type (R_ar_b) are determined by the segregation of only one of these genes. Shia (1976) showed that from three crosses between R_b and r_b genotypes, wrinkle-seeded (r_b) progeny were **higher** in protein content, **lower** in starch content, **lighter** in seed weight, and lower yielding than their smooth-seeded (R_b) sibs.

The comparison between these two seed types was made in the present study to verify that Shia's (1976) findings applied over a wide range of genotypes. Since the groups had unequal numbers, it was expected that the smaller group distribution would deviate further from the normal by chance and standard error of the mean would be greater than for the larger group of genotypes. Further, since the smooth-seeded genotypes comprised 4/5 of the whole population, it was not likely that their distribution curves would deviate greatly from those of the whole population.

5.5.3.1 Distribution of yield

The distribution of yield of the smooth-seeded genotypes was virtually identical with that for the whole population. Mean and median increased by 1%. However, the distribution of yield among wrinkle-seeded genotypes was somewhat different. The curve

was more uneven than that for the whole population, but that may have been due to fewer genotypes spread over the same number of classes. The range in yield was reduced from 4-fold in the smooth-seeded genotypes to 2-fold, with a considerable reduction in range from both ends of the curve. Thus, the range of yield for wrinkle-seeded genotypes was intermediate, although the mean was 5% lower than for the whole population. This confirms Shia's (1976) finding that wrinkle-seeded genotypes are lower yielding than their smooth-seeded counterparts.

Thus, there were two reasons for the reduced range; (a) the reduced number of genotypes in the group, which probably affected range at both ends of the curve, and (b) wrinkle-seeded genotypes do not attain the high yields found among smooth-seeded genotypes.

5.5.3.2 Distribution of protein content

There was a marginal decrease in the range of protein content among smooth-seeded genotypes, the reduction coming from the upper end of the distribution. The curve closely resembled that of the whole population and was normal in shape. The other major difference was that mean and median dropped by 1.2% from the whole population values.

The distribution curve for protein content among wrinkle-seeded genotypes was more dome-shaped than normal, and was more uneven than the yield curve for this same group of genotypes. The mean was 5% greater than the whole population mean. This is in agreement with Shia's (1976) finding that wrinkle-seeded peas have

higher protein content than genetically similar smooth-seeded peas. Range is partly a function of sample size, but mean is largely a function of the trait under measurement. Thus, range in the smaller population would tend to be narrower than that in the larger population, as was the case for yield. For protein content, however, range was only very slightly reduced in the wrinkle-seeded group compared with the smooth-seeded group. Thus, it seems that variability in protein content is different in the two seed types.

5.5.3.3 Distribution of protein yield

Protein yield curves for both smooth-seeded and wrinkle-seeded groups very closely resembled their corresponding yield curves. However, in contrast to yield and protein content, mean and median for protein yield of the two groups were virtually identical. This lack of difference reflected a balance between the 6% yield difference in favour of the smooth-seeded genotypes and the 6% protein content difference in favour of the wrinkle-seeded genotypes. This finding supports the conclusion of Shia (1976) that increased protein content of wrinkle-seeded peas was at least partly due to their decreased yield in comparison with smooth-seeded sibs.

5.5.3.4 Distribution of seed weight

The distribution for seed weight among smooth-seeded genotypes very closely resembled that of the whole population. There was a slight decrease in the mean of the group but the range was

unchanged.

The distribution of the wrinkle-seeded group, however, was markedly altered. Range was reduced considerably, from an 8-fold difference to a 4-fold difference between lightest and heaviest. This reduction was particularly evident at the lower end of the scale. The curve was noticeably skewed to the upper end, and was not normal-shaped. Although there was only one large modal class, the distribution indicated possibly two lesser groupings between the mode and the upper end of the range. These lesser groupings were too distinct to be dismissed as accidents of sampling due to the relatively smaller number of wrinkle-seeded genotypes as compared to the smooth-seeded genotypes. Although the number of genotypes in these lesser groupings was very small, the data may be suggestive of one or a few major genes for high seed weight. Thus, the genetic control of seed weight may differ between the smooth- and wrinkle-seeded types .

More importantly however, the mean seed weight of the wrinkle-seeded group is 12% higher than that of the whole population. This corresponds with the finding that seed weight of wrinkle-seeded parents was greater than smooth-seeded parents in an earlier section of this study (4.4). However, this contrasts with the results of comparing progeny of crosses between those parents in this study (section 4.4) and also the results of Shia (1976) who found that wrinkle-seeded progeny were 6, 8 and 10% lighter than their smooth-seeded sibs in three crosses. In this present study, wrinkle-seeded genotypes were both higher in protein content and seed weight than smooth-seeded genotypes.

5.5.4 Comparison of smooth-seeded and wrinkle-seeded populations

The populations were compared by the "t" test for unequal sample size (Snedecor and Cochran,1967). The mean of the wrinkle-seeded population was higher ($p = .01$) in protein content and seed weight, and lower in yield than the mean of the smooth-seeded population. The yield difference has frequently been alluded to in literature on pea production, usually unsourced, but was confirmed by Shia (1976). Similarly, the protein difference was evident from the data of Furedi (1970) and Shia (1976). However, the difference in seed weight has not been previously reported. Since the difference is on a population basis, it cannot be categorically stated that all wrinkled seeds are **heavier** in seed weight than smooth seeds. The data indicate that yield may influence protein content, but seed weight does not seem to adversely affect protein content. The actual difference of 1.6% protein content between the two seed-shape groups is less than that found by Shia (1976) and in an earlier section of the present study (section 4.5), but in both those cases the sample size was considerably smaller.

5.5.5 Effect of error control on range

As noted earlier in the discussion on distribution of protein content (section 5.5.2.2) replication led to a considerable reduction in observed range of that trait. This experiment was performed to show the extent to which error control by replication and by covariance adjustment affected the range of the traits measured. When the actual unconverted data was used, replication resulted in a considerable reduction in range of protein content (33%) and a lesser reduction in yield and seed weight (8%). Thus, replication increased precision by controlling environmental influences among replicates.

When converted duplicate means were used, removing the effect of differences between lattices, the range in protein content was similar to the range in unconverted duplicate means. Replication was as effective in reducing environmental variability as conversion to percentage of lattice mean. In other words, for protein content, replication would give control over environmental variability as good as conversion, so that it may have been possible to draw a distribution curve for protein content without first converting each genotype value.

It is noteworthy that, even allowing for a 33% reduction in range due to replication, the range in protein content among the genotypes was still very narrow.

5.5.6 **Simple correlations between traits**

5.5.6.1 Correlation between yield and protein content

Yield and protein content were negatively related (p= .05 and .01) in 15 of the 17 lattices. The r values were low to moderate and gave coefficients of determination ranging from 6% to 35.2%. That this correlation exists and is consistent over a wide range of genetic material cannot be ignored. The r values are lower than those found in a genotype x environment study reported earlier (section 4.1). Because the number of genotypes in each lattice is considerably greater and the genotypes were randomly assigned to lattices, it is considered that the r values from this experiment are more indicative of the true relationship than those from the genotype x environment study.

The data beg the question, "Is this relationship important in plant breeding?"

Where it has been encountered in other legume crops, authors have usually been compelled to conclude that this relationship poses no substantial threat to the improvement of yield and protein content, although those conclusions are often not supported by the data (see Literature Review). Zoschke (1970) considered that the relationship was physiologically based and that "correlation-breakers" would not be found without investigation of the physiological basis for this relationship. When the data from the present study are considered, coefficients of determination from 6 to 35.2% do not appear too large to be circumvented with an extensive breeding program. However, when this is coupled with the fact that the range in protein content is very small, that the higher protein genotypes are likely to be wrinkle-seeded, and that the heritability

of protein content is only moderate, the possibility of improving both yield and protein content appears slight. Furthermore, since pea yields are not all that high in relation to other crops with which they would compete for production area, any yield decrease for the sake of protein content would probably not be acceptable. Lastly, and perhaps most important, protein content was not related to protein quality (section 4.3). Thus, it is erroneous to breed for increased protein content as a means of improving protein productivity.

5.5.6.2 Correlation between yield and protein yield

Yield and protein yield were positively correlated ($r = +.885^{***}$ to $+.979^{***}$). The relationship is virtually on a one-to-one basis. Similar findings have been reported in *Phaseolus vulgaris* L. (Leleji *et al.*, 1972) and peas (Shia, 1976). It has very important implications for protein breeding strategy. Given that a desirable aim is the increase of protein productivity per unit area, this correlation shows that greatest protein production will come from genotypes with the greatest yield. In other words, yield should become a major breeding objective for improvement of protein productivity.

5.5.6.3 Correlations between other traits

Protein content and protein yield were uncorrelated except in four lattices where the coefficients ranged from $r = -.487^{**}$ to $+.286^{*}$. Thus, in general there was no consistent relationship between these two traits. Protein content does not contribute to

protein productivity. This finding reinforces the discussion above (section 5.5.6.2) that yield rather than protein content is the important determinant of protein yield.

Correlation coefficients between yield and seed weight were generally of low to moderate order, variable in sign, significant in four and highly significant in four more lattices. In other words, the relationship was inconsistent. Both traits could be manipulated without adversely affecting the other. Given the close relationship between yield and protein yield, it was not surprising that yield of protein and seed weight were correlated to the same degree as yield and seed weight.

All but two of the correlation coefficients between yield and seed weight were negative, and all except three were virtually of zero order and non-significant. The relationship between these traits is in one direction, but rather significant. There is no apparent reason for the three lattices showing significant correlations, and their occurrence may be due to chance.

6. SUMMARY

The contributions of genotype, location, and year to variability in yield and protein content were estimated from a study of 25 pea genotypes grown at three locations in one year and 22 genotypes grown at one location for three years. Both traits varied over locations and years, although yield was more variable than protein content. The genotype x location interaction was attributed to one location which was characterized by an abnormal growing season, but there was no interaction between genotypes and years. Protein content was almost as variable over locations as among genotypes. Variance component analysis showed that locations, genotypes, and unaccountable variation were the major sources of variance for protein content. Covariance analysis, to correct for within-location differences in soil fertility, resulted in improved precision, but the improvement did not warrant the expense of including covariate plots.

Protein content was correlated with several plant traits, and the relationships had important ramifications for protein improvement strategies. Yield and protein content were strongly negatively correlated among 25 genotypes over years and locations. Coefficients of determination showed that between 34 and 66% of the variation in protein content was associated with variation in yield. The negative relationship was lower but still significant among 19 genotypes in a heritability study, and low to moderate among 1071 genotypes from the U.S.D.A. World Pea Collection. Among the latter genotypes, coefficients of determination showed that between

6 and 35% of the variation in protein content was associated with variation in yield. The relationship was absent among 21 F_2 populations, indicating that heterogeneity has a masking effect on correlations between traits. The consistent negative relationship between yield and protein content shows that (a) protein content data should not be considered in isolation from yield data, and (b) the environment has an indirect effect on protein content through yield, in addition to the direct effect. Further, the relationship indicates that increased protein content may not be a desirable objective in the quest for improved protein productivity.

Protein content was not correlated with height, seed weight, days to flower, or harvest index. Thus, these traits could be manipulated independently of protein content. Since harvest index was not related to yield, it was without merit as a selection criterion for protein productivity improvement in field peas.

In a maturity study, 25 genotypes were harvested at four stages of maturity between pod-filling and ripeness. Fresh weight, dry weight, protein content, and starch content were measured. Protein content decreased throughout maturity. The genotypes displayed considerable parallelism in development, preventing inferences on final yield and protein content values from being drawn from development patterns. Unseasonal weather during the harvest period contributed to these similar development patterns. Accumulation of seed components was similar to that previously reported, but two genotypes were noticeably different from the rest. The maturity study data were moderately correlated with data from a large-plot study with the same genotypes at another location in the previous

year, indicating that the genotype x environment interaction attributable to that location could be explained on the basis of interrupted maturity. Starch content and protein content were consistently negatively correlated throughout maturation. However, the data did not show that this relationship contributed to the negative yield-protein content correlation. There was some indication that high protein genotypes accumulated more nitrogen than low protein genotypes, but no indication that they transferred more nitrogen from the haulm to the seed.

Among the 19 parents of the heritability study, protein content was positively correlated with mg met/g meal, but not significantly correlated with mg met/g protein, indicating no relationship between protein content and protein quality. However, the regression between protein content and mg met/g protein was significantly negative, but small and without biological importance. The absolute level of mg met/g protein of the pea genotypes studied was very low, and the range was narrow, in common with previous findings in field peas and other legumes.

Broad-sense heritability estimates were low for yield (0 to 41%) and low to moderate for protein content (21 to 53%) but the values were probably more indicative of non-genetic than genetic variability. Narrow-sense heritability was estimated by F_2/mid-parent regression in 21 field pea crosses. Yield and mg met/g protein were not heritable, while protein content and mg met/g meal were moderately, and days to flower and seed weight were very highly heritable. These results indicated that protein improvement by breeding would be slow, and improvement of methionine as a percent of protein would not be [illegible] for that trait. It was suggested that

methionine as a percent of protein, like yield, could possibly be improved by selecting for components.

Smooth and wrinkled seeds borne on F_2 plants in crosses segregating for seed shape were compared for weight. Wrinkled seeds were lighter in seed weight than their smooth-seeded counterparts of comparable size in all crosses, although the wrinkle-seeded parent was the heavier in 8 of the 10 crosses. Wrinkled seeds lose more water on maturation than smooth seeds, but this does not account for the lower accumulation of dry weight initially. This phenomenon has not been reported previously.

1071 genotypes from the U.S.D.A. World Pea Collection were grown in replicated lattices at Saskatoon in 1975. Yield, protein content, protein yield, and seed weight were recorded. The genotypes spanned a wide range in yield and a very wide range in seed weight. The range in protein content was very narrow (22 to 30% protein), due to the trait rather than to the sample of genotypes.

Yield and protein yield were highly positively correlated and the relationship was consistent over all lattices, indicating that yield is the major determinant of protein yield. 33% of the observed variability in protein content was environmentally determined.

Comparison of 207 wrinkle-seeded genotypes with 864 smooth-seeded genotypes showed that the former were significantly lower yielding, higher in protein content, and had higher seed weight than the latter. Data were suggestive of one or a few major genes for high seed weight in wrinkle-seeded, but not smooth-seeded genotypes. Seed weight was not correlated with yield.

Thus, a breeding strategy for increased protein productivity should concentrate on yield alone. Increased protein quality, in the form of increased levels of the first-limiting amino-acid, methionine, will not be obtained by breeding for mg met/g protein. Protein content has little value as a selection criterion in field peas by virtue of its narrow range, negative relationship with yield, and possibly negative relationship with protein quality. Its use in breeding programs for legume protein improvement should be reassessed in the light of these findings.

7. CONCLUSIONS

(1) Protein content was variable over locations and years, but did not interact strongly with either.

(2) Harvest index of field peas was high, but not related to productivity.

(3) Yield and protein content were consistently negatively correlated over locations, years, and a wide range of genotypes. The relationship diminished among heterogeneous populations. This negative correlation is a major barrier to breeding for increased protein content, since between 6% and 66% of protein content variation is related to yield variation. Physiological explanations for the relationship were offered.

(4) Protein content decreased with maturity, and was negatively correlated with starch content throughout maturation. Immaturity at harvest contributed largely to a genotype x environment interaction for protein content.

(5) Broad-sense and narrow-sense heritability estimates of protein content were low to moderate.

(6) Methionine content of protein was low, displayed a narrow range, and was not heritable. A strategy for improvement was suggested.

(7) Reported differences between wrinkle-seeded and smooth-seeded genotypes were verified and a new one added. The gene for wrinkling causes a seed weight reduction in wrinkle-seeded compared with smooth-seeded progeny of crosses between parents of different seed shape.

(8) Yield and protein yield were very highly related. Protein content and protein yield were unrelated.

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9. APPENDIX

Appendix 1 Mean values for single plant protein content, height, haulm protein content, harvest index, seed yield/plant, total protein weight/plant, and haulm protein weight/plant of 25 genotypes grown at Saskatoon and Nipawin, 1974.

Appendix 1.1 Single plant protein content of 25 genotypes at Saskatoon and Nipawin, 1974

Genotype	% Protein Saskatoon	Nipawin
Palouse	24.9	18.4
P.I.356846	26.1	20.6
MP783	24.7	17.8
Triumph	23.0	17.4
MP761	21.4	18.7
MP702	23.2	18.7
Century	23.5	19.5
MP790	23.4	18.5
Trojan	24.4	18.2
P.I.356885	23.8	20.0
P.I.206790	27.4	23.4
P.I.357001	25.7	22.6
Trapper	24.9	18.7
Lincoln	26.9	22.0
Dashaway	24.9	18.3
MP789	23.3	18.5
W718	24.0	20.1
P.I.356837	24.1	18.0
W703	24.5	20.5
P.I.324705	25.9	20.8
Petit Pois	26.0	17.8
MP712	23.0	18.4
P.I.356834	23.6	19.9
P.I.269812	23.0	19.4
MP39	22.9	17.6
Mean	24.2	19.4

Appendix 1.2 Height of 25 genotypes at Saskatoon and Nipawin, 1974

Genotype	Height (cm) Saskatoon	Nipawin
Palouse	65	47
P.I.356846	95	100
MP783	116	107
Triumph	65	67
MP761	108	95
MP702	110	110
Century	105	115
MP790	98	85
Trojan	87	81
P.I.356885	107	108
P.I.206790	98	111
P.I.357001	118	118
Trapper	90	85
Lincoln	51	43
Dashaway	122	107
MP789	83	73
W718	101	100
P.I.356837	102	97
W703	125	88
P.I.324705	131	115
Petit Pois	61	58
MP712	111	100
P.I.356834	110	101
P.I.269812	112	105
MP39	101	75
Mean	99	92

Appendix 1.3 Haulm protein content of 25 genotypes at Saskatoon and Nipawin, 1974

Genotype	Haulm protein content % Saskatoon	Nipawin
Palouse	8.85	5.34
P.I.356846	10.04	7.08
MP783	8.56	4.25
Triumph	8.07	5.11
MP761	9.47	6.04
MP702	8.69	5.65
Century	8.04	5.84
MP790	6.67	5.97
Trojan	7.50	5.16
P.I.356885	7.03	7.63
P.I.206790	8.87	5.39
P.I.357001	9.42	7.05
Trapper	8.02	5.24
Lincoln	7.93	5.89
Dashaway	7.52	5.92
MP789	7.96	5.57
W718	6.88	6.22
P.I.356837	8.74	5.34
W703	8.26	5.34
P.I.324705	10.02	6.98
Petit Pois	9.52	5.96
MP712	9.24	5.24
P.I.356834	7.94	6.77
P.I.269812	7.47	6.07
MP39	8.56	6.15
Mean	8.37	5.89

Appendix 1.4 Harvest index of 25 genotypes at Saskatoon and Nipawin in 1974

Genotype	Harvest index (%) Saskatoon	Nipawin
Palouse	59.5	58.2
P.I.356846	49.5	48.7
MP783	50.7	47.2
Triumph	57.2	54.0
MP761	53.2	54.2
MP702	43.7	48.0
Century	49.0	48.2
MP790	54.2	57.2
Trojan	47.7	51.7
P.I.356885	48.0	44.5
P.I.206790	45.7	47.0
P.I.357001	47.2	49.2
Trapper	48.5	49.5
Lincoln	60.0	56.5
Dashaway	47.2	48.2
MP789	53.0	53.0
W718	54.2	52.7
P.I.356837	48.0	50.2
W703	52.5	53.5
P.I.324705	38.2	51.2
Petit Pois	55.2	56.7
MP712	50.5	50.7
P.I.356834	51.0	51.2
P.I.269812	51.2	49.2
MP39	49.7	49.7
Mean	50.6	51.1

Appendix 1.5 Seed yield/plant of 25 genotypes at Saskatoon and Nipawin, 1974

Genotype	Seed yield/plant (g) Saskatoon	Nipawin
Palouse	16.7	7.6
P.I.356846	3.9	5.5
MP783	10.9	6.3
Triumph	12.9	6.5
MP761	6.7	5.9
MP702	6.7	6.2
Century	9.2	7.6
MP790	9.9	5.4
Trojan	6.1	6.4
P.I.356885	8.3	4.8
P.I.206790	16.7	7.8
P.I.357001	5.5	5.7
Trapper	9.3	5.1
Lincoln	13.9	6.8
Dashaway	8.2	5.6
MP789	7.6	6.3
W718	5.3	4.7
P.I.356837	5.2	4.7
W703	7.9	5.3
P.I.324705	4.3	4.5
Petit Pois	7.8	6.8
MP712	10.9	7.5
P.I.356834	6.2	4.9
P.I.269812	4.7	4.5
MP39	6.1	4.4
Mean	8.5	5.9

Appendix 1.6 Total protein weight/plant of 25 genotypes at Saskatoon and Nipawin, 1974

Genotype	Total protein weight/plant (g) Saskatoon	Nipawin
Palouse	5.12	1.70
P.I.356846	1.45	1.48
MP783	3.57	1.40
Triumph	3.81	1.43
MP761	2.02	1.41
MP702	2.42	1.52
Century	3.15	2.01
MP790	2.92	1.28
Trojan	1.99	1.46
P.I.356885	2.56	1.44
P.I.206790	6.57	2.34
P.I.357001	2.01	1.71
Trapper	3.01	1.20
Lincoln	4.57	1.82
Dashaway	2.63	1.35
MP789	2.38	1.37
W718	1.57	1.20
P.I.356837	1.75	1.10
W703	2.50	1.29
P.I.324705	1.92	1.17
Petit Pois	2.66	1.51
MP712	3.64	1.79
P.I.356834	1.97	1.24
P.I.269812	1.41	1.15
MP39	1.90	1.05
Mean	2.78	1.45

Appendix 1.7 Haulm protein weight/plant of 25 genotypes at Saskatoon and Nipawin, 1974

Genotype	Haulm protein weight/plant (g) Saskatoon	Nipawin
Palouse	1.00	.28
P.I.356846	.41	.37
MP783	.85	.29
Triumph	.81	.28
MP761	.59	.30
MP702	.85	.37
Century	.95	.50
MP790	.58	.28
Trojan	.50	.30
P.I.356885	.62	.47
P.I.206790	1.92	.51
P.I.357001	.58	.42
Trapper	.76	.27
Lincoln	.80	.30
Dashaway	.70	.34
MP789	.56	.27
W718	.29	.26
P.I.356837	.49	.24
W703	.57	.21
P.I.324705	.81	.28
Petit Pois	.63	.31
MP712	1.08	.38
P.I.356834	.47	.28
P.I.269812	.33	.28
MP39	.57	.28
Mean	.71	.32

Appendix 2 Mean values for yield, protein content,,protein yield and seed weight of 1071 genotypes from the U.S.D.A. World Pea Collection grown in 2-replicate partially-balanced lattices at Saskatoon, 1975.

Lattice #1

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 174925	1025.52	25.65	265.81	32.3
PI 172340	990.55	23.80	234.57	36.1
PI 179461 STR	970.28	26.30	256.43	22.9
PI 177521 WR	944.49	26.55	249.94	22.3
PI 174322	943.77	23.95	225.10	50.8
PI 171816	939.20	25.10	236.58	22.4
PI 175227A	931.77	24.70	230.15	41.7
PI 173779	923.30	26.10	241.80	21.6
PI 179449	904.40	26.40	240.39	21.4
PI 177054	903.11	28.30	253.98	20.4
PI 167250	893.28	26.20	237.00	35.1
PI 167205	890.31	26.50	236.98	52.9
PI 167204	882.77	24.70	217.79	41.3
PI 175232	877.77	25.00	217.71	28.3
PI 169604	870.06	24.25	211.82	55.9
TRAPPER	858.19	25.90	223.93	25.3
PI 174320 WH	857.77	26.55	226.60	36.7
PI 167253	855.61	27.00	225.93	23.7
PI 179972	853.14	25.15	216.48	31.8
PI 169609	849.98	26.95	227.63	38.5
PI 179722	849.80	27.00	230.67	33.9
PI 179454	849.67	24.70	209.11	41.1
PI 171814	849.31	25.10	209.68	24.6
PI 173930	848.31	25.10	212.37	41.4
PI 171812	848.22	24.65	211.42	43.9
PI 175227B	840.75	24.05	201.10	40.8
PI 179019	833.74	26.20	220.43	30.4
PI 179448 STR	824.27	27.10	222.26	44.4
PI 173052	822.69	26.90	218.77	25.1
PI 169601	821.02	26.75	221.54	39.7
PI 177056	817.38	26.85	219.19	43.1
PI 173040 WR	812.19	28.50	230.51	45.4
PI 179453	797.59	25.90	210.22	32.3
PI 173059	788.90	26.20	205.75	29.4
PI 175233	786.84	25.90	205.85	33.3
PI 169602	782.30	25.80	202.29	45.5
PI 176721	765.33	25.90	198.25	36.8
PI 177053 STR	763.33	26.00	197.92	52.8
PI 170669	752.49	25.65	193.50	54.1
PI 179450	747.98	27.80	207.94	33.6
PI 169608	744.02	26.80	198.02	32.4
PI 172338	740.88	25.10	185.37	33.4
PI 174923	734.77	26.85	192.90	21.0
PI 180470	720.63	26.50	193.18	22.6
PI166187	715.72	25.10	178.64	44.8
PI 179451	687.42	26.70	184.11	52.4
PI 167273	681.23	27.05	187.59	36.4
PI 172341	675.69	25.80	175.96	41.8
PI 174320	660.56	26.60	172.85	54.3
PI 169606	628.91	26.75	169.60	40.5
PI 172339	596.52	24.35	151.59	53.8
PI 175228	584.67	26.35	155.47	30.1
PI166188	579.58	27.25	158.29	25.1
PI 174921	553.91	27.85	153.56	16.3
PI 175229	544.77	28.45	149.20	18.5
PI 175231	543.64	28.10	154.01	14.3
PI 174920	538.05	27.50	152.55	52.9
PI 173929	519.53	28.15	146.26	14.6
PI 174918	512.05	28.20	139.36	18.1
PI 174922	478.95	28.30	134.89	19.1
PI 175230	453.11	28.55	129.56	16.6
PI 175226	417.55	27.15	113.52	25.3
PI 174919	376.06	28.15	107.99	16.8
PI166159	373.33	28.85	108.19	13.1
MEAN	756.70	26.37	198.40	33.5
LSD (P=0.05)	185.52	2.24	54.04	3.7
CV	12.20			

Lattice #2

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 193581	989.32	24.38	240.09	32.3
PI 193837	945.79	25.34	240.53	33.9
PI 193583	942.63	25.90	244.92	34.3
PI 193586 PSBM	942.16	25.94	245.73	30.8
PI 183946	928.40	25.01	226.19	28.5
PI 197451	914.34	25.89	235.98	33.9
TRAPPER	887.45	25.37	223.78	23.5
PI 193838	882.06	25.03	218.22	35.1
PI 196031	870.32	27.10	235.45	29.1
PI 193584	869.50	24.97	217.10	29.8
PI 196025	866.87	26.11	224.24	30.3
PI 193585	851.82	26.05	220.28	29.2
PI 181801	848.48	25.31	215.79	42.9
PI 183466	837.59	24.67	208.69	37.5
PI 180867	833.25	26.16	220.91	24.3
PI 196015	833.17	27.06	223.11	30.0
PI 193587 SP	830.37	25.20	208.39	36.6
PI 193835	827.33	25.88	214.19	30.3
PI 196024	825.28	27.85	225.81	30.6
PI 183413	824.94	23.87	197.50	31.5
PI 197450	820.28	25.13	207.74	29.3
PI 193578	816.52	24.63	201.89	28.8
PI 184131 STR	816.44	23.22	192.96	41.1
PI 196023	815.65	27.57	221.99	28.8
PI 193591	810.84	25.29	204.20	33.1
PI 193588	801.36	25.60	205.34	27.4
PI 183910	798.39	24.74	198.30	22.2
PI 189168 WRR	798.10	25.10	197.08	61.5
PI 196020	790.40	25.75	202.78	30.8
PI 184128 WR	787.54	26.30	209.02	38.6
PI 181800	783.82	24.63	194.18	23.9
PI 183910B	783.64	24.42	191.91	40.1
PI 193580	782.31	26.59	209.03	34.9
PI 183910A	782.01	25.95	202.47	24.7
PI 180471	772.17	27.10	210.42	28.7
PI 180868	769.23	25.67	199.16	24.9
PI 193840	765.56	26.29	203.50	33.9
PI 196017	755.75	26.25	199.96	34.0
PI 193836	754.61	24.64	187.24	25.8
PI 193579	740.76	25.66	191.46	30.4
PI 193589	734.67	24.93	183.18	31.9
PI 196012	722.71	26.22	189.89	29.8
PI 193582	720.85	25.59	182.95	29.2
PI 184129	714.73	27.07	189.84	23.4
PI 196033	703.54	26.96	189.10	26.0
PI 196026	699.86	26.17	179.80	30.3
PI 183714	698.59	25.25	177.49	22.2
PI 193841	688.48	26.56	181.85	30.8
PI 184130 STR	684.81	25.27	175.36	33.9
PI 183467	678.70	26.38	176.31	24.8
PI 196022	677.79	27.24	185.42	32.4
PI 193590	662.35	27.47	181.05	30.9
PI 196030	649.08	26.39	172.33	35.6
PI 181799 WR	643.10	28.53	184.59	48.9
PI 189171 WRR	639.42	27.22	170.14	87.3
PI 181984	631.79	25.80	163.35	42.6
PI 180693	621.57	26.74	163.43	30.5
PI 180702	608.72	26.33	160.41	31.1
PI 196027	579.53	26.69	154.03	29.6
PI 196029	569.62	27.00	155.42	25.9
PI 196032	563.58	28.94	162 76	25.4
PI 180694	558.36	27.35	154.12	22.4
PI 193587 W	479.80	25.15	119.58	29.7
PI 197987	416.39	27.44	114.58	90.8
MEAN	760.02	25.97	196.63	33.2
LSD (P=0.05)	274.78	1.79	68.37	5.9
CV	17.99			

Lattice #3

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 209068	943.20	24.10	228.82	35.7
PI 201497	857.06	24.28	208.67	34.8
PI 197452	854.67	26.26	223.81	28.8
PI 193042	851.73	25.41	214.61	35.5
TRAPPER	848.53	24.97	212.72	24.8
PI 210309	847.73	25.82	218.77	30.2
PI 197454	839.90	25.02	210.52	38.1
PI 203064	829.02	25.07	215.65	31.4
PI 210604	820.54	26.20	213.73	29.1
PI 193845	807.17	25.16	201.63	35.6
PI 206844	788.94	24.06	188.13	46.0
PI 194007	785.71	25.98	204.28	30.5
PI 193843	785.68	26.14	205.21	34.8
PI 209335	779.91	26.24	205.94	40.0
PI 197442	775.40	26.23	203.42	27.8
PI 193840	774.98	26.10	201.92	35.7
PI 209300W	772.17	24.58	189.12	37.4
PI 193847	769.16	25.62	196.21	35.4
PI 210308	767.19	25.79	196.35	27.0
PI 157990 NR	766.82	25.45	195.60	77.9
PI 178872	766.34	26.49	202.63	49.8
PI 204307	764.26	25.52	194.40	35.1
PI 210574 NR	762.98	29.23	223.58	51.5
PI 196011	762.06	25.96	197.75	32.1
PI 233067	757.62	25.30	190.56	35.8
PI 196309	734.23	24.18	175.95	31.6
PI 206861	731.87	22.36	163.64	36.4
PI 210593	727.85	22.91	167.04	45.7
PI 195627	720.07	26.24	189.02	30.4
PI 210613	711.91	25.13	177.93	37.6
PI 210587 NR	709.80	25.76	182.03	61.9
PI 196735	702.34	24.97	175.36	19.5
PI 206938	702.03	27.47	192.63	31.2
PI 209536	701.55	22.77	160.84	37.6
PI 196314	686.20	25.12	171.05	36.5
PI 196313	666.13	25.59	174.62	31.3
PI 196373	679.85	29.05	196.78	42.9
PI 193849	664.71	25.67	170.75	34.4
PI 196310	664.24	27.20	180.17	30.9
PI 206945	658.36	25.97	172.12	39.5
PI 209507W	653.09	22.64	147.76	33.8
PI 203065	651.50	24.57	160.37	38.8
PI 210617	650.80	25.56	165.63	35.1
PI 196536	637.04	23.75	151.83	43.7
PI 196631	616.31	26.71	164.18	34.1
PI 210563	614.24	27.26	169.66	30.4
PI 206843	613.25	23.59	144.01	39.6
PI 204308	606.38	25.44	155.24	39.6
PI 206989	605.02	26.56	158.65	36.4
PI 206835 NR	594.43	27.25	161.42	22.1
PI 210575 NR	587.01	28.58	166.35	43.8
PI 197939	564.56	27.54	154.67	41.9
PI 210577 NR	559.63	23.36	124.31	40.1
PI 207536	532.27	28.50	151.85	29.8
PI 206736 NR	531.17	26.60	142.50	16.2
PI 210573 NR	529.91	28.01	150.04	38.7
PI 195403	529.25	28.11	149.23	40.0
PI 210570	522.38	25.99	136.34	63.6
PI 210572 NR	520.44	25.33	136.86	27.0
PI 179969	520.85	30.84	160.72	50.6
PI 206833	487.77	27.85	136.28	18.2
PI 210560 NR	473.70	26.81	127.17	30.5
PI 202044	457.58	29.97	137.95	33.9
	436.30	26.36	113.48	55.4
MEAN	687.87	25.96	177.51	36.9
LSD (P=0.05)	247.18	1.78	60.75	24.7
CV	17.69			

Lattice #4

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 194345	951.50	26.04	247.94	33.2
PI 194340	929.00	26.06	242.88	35.2
PI 210666	916.00	25.85	234.47	33.6
PI 222071	870.50	26.31	228.34	17.7
PI 206819	866.00	24.18	209.37	34.6
PI 206823	863.00	24.45	207.67	33.8
PI 214344	860.00	25.68	219.36	52.5
PI 210669	843.00	24.75	208.25	44.6
PI 212023	830.00	25.60	212.50	33.9
PI 194338	803.00	26.17	209.91	35.0
PI 224677	790.00	26.17	206.81	32.4
PI 210638	788.50	25.59	195.59	38.5
PI 194342	759.50	25.97	196.75	34.0
PI 195021	757.00	27.24	204.97	30.3
PI 194341	755.00	25.03	188.74	32.4
PI 194348	743.00	25.59	190.69	33.5
PI 212030	726.00	25.22	183.81	41.3
PI 195019	725.00	25.67	184.18	34.5
PI 219735	721.50	24.35	175.72	30.6
PI 194347	710.50	27.82	198.44	29.9
PI 194350	705.00	25.85	182.27	35.7
PI 206821	705.00	24.78	174.84	38.3
PI 194343	698.50	26.09	183.10	35.5
PI 221697	687.00	26.78	182.04	30.0
PI 194345	685.00	23.75	164.09	36.7
PI 210665 MR	678.50	28.30	191.30	36.5
PI 194338	677.50	24.90	169.31	33.7
PI 195016	669.50	26.35	176.24	28.9
PI 210044	648.50	24.51	159.10	23.7
PI 215766	647.50	24.26	157.32	33.0
PI 210652	646.00	26.91	173.92	20.8
PI 210664	643.50	25.51	163.72	36.0
TRAPPER	642.50	24.66	159.74	24.9
PI 194349	642.00	26.36	170.11	35.2
PI 210632	634.00	26.30	166.73	32.2
PI 195026	630.50	24.48	154.60	32.6
PI 220174	627.00	26.40	165.54	17.8
PI 223284	620.00	26.15	161.98	20.2
PI 194339	618.00	26.15	161.53	39.8
PI 212031	607.50	25.40	154.60	37.8
PI 195027	600.00	23.44	141.24	33.7
PI 222069	596.00	26.58	158.71	16.0
PI 212916	586.50	25.75	150.93	40.9
PI 195022	583.00	26.80	155.98	32.0
PI 195020	577.00	25.81	147.38	31.0
PI 194344	575.50	26.10	150.25	34.1
PI 210624 MR	571.50	28.79	164.09	46.6
PI 195025	564.50	27.90	157.13	28.5
PI 222117	551.00	27.26	146.48	16.9
PI 212112	546.00	26.19	142.30	20.2
PI 212029 MR	545.50	28.22	154.85	40.7
PI 210665Bmr	544.00	29.66	161.40	34.8
PI 216045	528.00	26.19	139.35	32.3
PI 222534	523.00	24.84	129.92	37.4
PI 222077	510.00	28.72	146.37	17.2
PI 220189	501.00	27.11	135.50	17.0
PI 210654 MR	493.00	29.00	142.90	37.2
PI 220675	468.00	25.55	119.50	20.4
PI 195023	464.00	27.34	126.90	32.2
PI 195024	460.00	27.85	128.40	29.4
PI 212918	459.00	25.00	114.75	43.1
PI 223926	387.00	27.64	106.49	15.0
PI 220175	373.50	26.83	100.17	17.0
PI 213014	348.00	25.85	89.98	21.5
MEAN	654.63	26.13	169.20	31.5
LSD (P=0.05)	336.41	2.08	82.33	2.4
CV	25.83			

Lattice #5

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 244104	1304.13	26.91	268.59	36.7
PI 244109 WR	993.69	27.49	274.81	44.6
PI 226562	939.93	27.28	252.80	31.6
PI 226561	932.01	26.68	249.03	33.8
PI 236489	919.74	26.85	248.91	38.8
TRAPPER	889.32	26.11	231.55	22.2
PI 244103	888.15	27.01	239.62	37.6
PI 244118 WR	883.03	28.15	249.01	27.6
PI 244101 WR	867.13	24.16	208.11	45.5
PI 226564	862.47	26.34	227.72	33.9
PI 244130	843.99	23.90	201.52	40.3
PI 240514 WR	832.82	28.36	234.54	41.1
PI 244091 W	832.46	25.26	211.45	42.6
PI 240515	831.12	24.67	199.47	44.4
PI 244096 WR	829.95	29.46	245.15	38.6
PI 244092	828.99	24.55	204.03	36.5
PI 244129W	818.56	24.18	197.38	45.0
PI 236503	803.01	27.71	221.97	32.8
PI 240517 WR	802.69	29.86	240.44	31.4
PI 244125 WR	778.01	27.47	214.73	34.6
PI 244106 WR	771.09	30.40	234.36	36.1
PI 244124	758.07	24.66	186.31	36.6
PI 240516	746.76	26.47	198.96	41.1
PI 244141	745.78	26.09	196.72	34.0
PI 244119	739.33	26.69	194.12	31.7
PI 244105	736.14	24.96	182.19	40.6
PI 240513 WR	727.24	24.69	180.38	42.2
PI 244126	720.20	28.63	210.15	37.1
PI 244128W	699.21	30.54	213.25	35.0
PI 244127 WR	686.26	30.19	210.74	35.4
PI 244111	684.35	28.29	193.17	34.1
PI 244130W	680.58	24.40	167.06	42.4
PI 244117	678.07	26.53	179.34	38.7
PI 229538	678.27	25.96	175.30	31.4
PI 244120 STR	669.69	25.37	168.00	46.6
PI 241593	663.79	27.55	182.68	39.4
PI 244112	657.29	26.06	171.99	32.9
PI 244113	651.98	24.56	162.16	37.1
PI 244108 WR	636.75	29.98	190.66	43.1
PI 242022	636.23	26.75	170.94	48.4
PI 244100	634.02	25.72	162.56	42.3
PI 244129	619.29	24.21	150.09	45.9
PI 240519	615.46	24.65	152.36	52.4
PI 244131	615.06	24.90	153.92	30.3
PI 244110W	607.42	24.59	147.98	38.2
PI 236494	605.72	27.61	167.99	32.3
PI 244095 WR	591.38	30.18	176.96	39.4
PI 244089 WR	578.50	28.98	167.89	46.4
PI 244114	568.19	25.79	148.77	53.3
PI 244124W	557.22	25.57	139.27	41.5
PI 244124W	552.06	24.40	133.85	35.6
PI 244123WR	530.83	28.96	154.04	43.7
PI 227256	519.88	26.82	137.86	17.1
PI 236493 WR	514.47	26.50	135.35	57.2
PI 244115	511.11	25.30	129.75	38.6
PI 244116	498.84	25.29	127.22	52.9
PI 236493	486.98	25.09	122.01	29.8
PI 244121 WR	481.04	25.67	123.94	40.4
PI 244122	464.59	24.39	112.21	39.1
PI 227457	435.92	27.10	117.16	11.9
PI 244095	430.96	29.98	124.28	25.0
PI 244098	412.44	29.72	124.31	27.6
PI 244090 WR	394.62	29.92	114.49	47.1
PI 244107 WR	330.67	29.01	93.77	49.2
MEAN	686.02	26.73	183.04	37.8
LSD (P=0.05)	276.63	2.07	75.45	4.7
CV	20.16			

Lattice #6

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 244161W	1204.85	26.05	308.41	53.4
PI 244186	1048.68	26.31	276.81	30.0
PI 244215	913.10	23.99	216.03	50.0
PI 244220	904.39	28.63	257.63	37.1
PI 244144	880.14	23.24	203.97	50.8
PI 244188 HR	878.84	28.71	249.42	39.5
PI 244155	874.91	26.54	232.75	41.9
PI 244213	864.47	26.19	227.89	47.5
PI 244157 HR	856.94	29.25	250.45	38.5
PI 244227 HR	837.35	28.11	235.47	31.7
PI 244150 HR	830.64	27.52	227.13	37.7
PI 244225	830.22	25.59	212.94	41.8
PI 244150W	825.69	25.77	213.37	34.3
PI 244198	804.37	25.99	207.37	23.6
PI 244173W	801.14	25.23	201.73	39.3
PI 244152 HR	799.48	28.60	228.57	31.5
PI 244137	794.51	24.43	194.31	41.6
PI 244138	795.24	24.68	195.33	36.9
PI 244195 HR	774.58	28.75	222.59	39.8
PI 244158	760.72	24.47	184.97	33.1
PI 244226	749.03	25.38	191.25	37.1
PI 244199 HR	742.78	27.67	206.77	40.3
PI 244107	733.26	25.72	188.36	50.7
PI 244148 HR	724.86	28.51	205.33	35.2
PI 244181	719.86	24.72	177.14	38.6
PI 244204	719.36	27.50	198.85	49.5
PI 244145 STR	702.29	26.86	187.74	33.3
PI 244200 HR	697.80	28.14	195.47	39.3
PI 244166 HR	694.56	28.72	199.77	36.0
PI 244149	692.58	24.53	170.19	48.1
PI 244191	691.29	24.55	170.07	42.0
PI 244136	687.95	26.38	179.37	33.0
PI 244154W	682.98	26.41	180.31	44.2
PI 244182 HR	682.95	27.05	183.85	37.4
PI 244143	681.12	24.58	167.05	37.0
PI 244184	680.53	26.24	176.20	49.3
PI 244205	661.77	25.00	165.22	38.9
PI 244135	647.24	25.99	168.33	40.3
PI 244220 HR	643.80	29.09	186.14	46.2
PI 244170W	641.72	26.30	169.13	66.0
PI 244174 HR	639.69	25.27	161.93	43.1
PI 244172 HR	639.16	29.04	183.92	37.5
PI 244164W	635.29	29.86	190.23	52.6
PI 244214	632.62	25.04	157.49	53.4
PI 244159 HR	627.73	30.16	186.90	29.9
PI 244168 HR	619.39	28.50	176.35	39.2
PI 244203	618.91	25.25	156.45	42.4
PI 244165	608.39	24.66	149.56	37.8
PI 244156	603.12	25.00	150.37	44.0
TRAPPER	592.32	27.32	162.70	22.7
PI 244150S HR	590.53	25.38	150.99	57.6
PI 244177 HR	587.41	28.76	169.29	40.2
PI 244139 HR	582.01	29.06	170.81	34.2
PI 244150	581.33	26.69	155.40	60.3
PI 244229	581.23	28.03	162.93	38.5
PI 244183	580.02	24.45	142.30	47.4
PI 244222	567.47	24.49	138.26	31.3
PI 244132 HR	557.66	29.72	165.26	57.1
PI 244142 HR	546.58	29.14	159.27	34.1
PI 244206 HR	506.91	28.75	146.10	43.4
PI 244176 HR	486.89	26.67	129.61	46.3
PI 244175	423.87	26.59	113.00	49.1
PI 244200 HR	397.70	30.97	121.63	22.3
PI 244196 HR	384.96	30.84	117.82	46.0
MEAN	696.85	26.93	186.36	41.0
LSD (P=0.05)	200.97	1.81	55.38	3.5
CV	14.38			

Lattice #7

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 250442	1102.50	23.36	257.17	29.7
PI 261665	1096.00	25.84	286.21	50.5
PI 257492	1048.00	25.78	270.32	28.6
PI 254025	1026.00	24.86	255.15	44.4
PI 244262	1025.50	25.33	260.77	40.8
PI 244237 NR	1022.00	27.01	275.74	38.1
PI 244247	1010.50	25.21	253.99	49.9
PI 261635	1000.00	26.95	269.43	42.1
PI 249644	985.50	24.21	237.91	37.6
TRAPPER	983.00	25.65	252.39	22.8
PI 250446 NR	979.50	29.13	284.20	42.6
PI 257593	979.00	26.19	256.14	36.6
PI 261660	976.50	24.17	233.99	47.3
PI 244251	971.00	25.35	246.88	49.5
PI 257244	965.50	25.11	241.48	42.7
PI 244253	950.00	24.84	235.28	40.1
PI 250447 NR	902.00	26.55	257.78	45.1
PI 244232	891.00	26.65	238.57	26.5
PI 249542	865.50	24.61	216.97	33.5
PI 251031	879.50	26.21	230.40	22.1
PI 244271	879.50	27.46	242.17	60.2
PI 261630 NR	862.50	28.37	242.04	35.5
PI 244240	862.00	26.16	226.26	47.8
PI 250448	857.00	24.30	207.61	36.6
PI 261636 NR	842.00	29.09	246.15	40.4
PI 261632	834.50	27.10	227.41	36.6
PI 249646	826.00	24.92	204.78	64.5
PI 250441	824.50	24.95	207.26	44.6
PI 244250	814.50	26.69	218.03	36.9
PI 254626	811.50	26.34	214.06	35.3
PI 249647	808.00	27.84	225.69	50.8
PI 244245	803.00	25.25	204.48	48.9
PI 250438	801.00	24.83	197.04	35.4
PI 244270	789.00	25.71	201.78	58.7
PI 244238 NR	780.00	26.27	203.89	39.6
PI 248181	776.50	26.37	204.05	32.2
PI 261631	772.00	24.85	191.56	52.3
PI 244242 NR	770.50	28.96	223.20	61.4
PI 244234	756.00	24.89	190.46	56.1
PI 261652	755.50	26.77	200.75	37.3
PI 249645	753.00	27.75	208.20	22.7
PI 261624	749.00	23.13	173.57	41.1
PI 244241	747.50	23.99	178.83	43.5
PI 244236	745.00	24.45	180.77	42.3
PI 253970	743.50	27.90	206.54	17.8
PI 244248 NR	736.00	28.74	213.29	43.5
PI 244233	732.50	26.27	192.40	34.2
PI 244239 NR	727.00	28.55	209.45	35.7
PI 244272	719.00	27.04	194.00	55.3
PI 244267 NR	718.50	27.80	198.91	40.5
PI 244235 NR	704.50	28.62	202.46	47.9
PI 261625 NR	693.50	27.80	193.82	47.6
PI 253958	692.50	26.19	176.71	35.0
PI 244257	670.50	24.94	167.60	61.0
PI 261662	667.50	26.41	174.78	44.5
PI 261653	647.00	27.63	179.05	55.5
PI 250443 NR	641.00	30.19	193.25	58.1
PI 261623	609.00	26.70	163.27	56.5
PI 244263 NR	604.50	28.19	170.78	50.5
PI 261663 NR	598.00	27.18	161.83	43.6
PI 250444 NR	596.00	28.59	171.40	49.4
PI 244264	590.00	26.29	156.36	39.1
PI 244231	570.50	29.27	168.41	56.7
PI 244269 NR	569.00	23.97	136.31	56.2
MEAN	814.51	26.40	214.80	43.1
LSD (P=0.05)	204.63	1.47	55.01	10.6
CV	12.56			

Lattice #8

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 189865	1277.77	23.42	299.93	38.3
PI 268670	1236.77	24.75	303.30	34.8
PI 273279	1186.27	25.90	307.46	38.0
PI 269768	1176.69	25.27	298.10	33.2
PI 263028	1147.55	25.40	292.41	32.4
PI 269779	1142.76	23.95	271.49	40.9
PI 269763	1113.90	25.08	277.53	42.8
PI 263003	1108.57	22.85	253.62	46.2
PI 269751	1106.83	24.39	263.65	49.0
PI 269733 NR	1091.39	26.82	293.21	60.5
PI 263011	1088.70	25.50	276.14	41.6
PI 269803	1086.44	24.27	261.99	15.5
PI 269782	1083.41	24.67	266.61	54.8
PI 269751	1062.25	26.39	286.74	19.6
PI 261670	1064.28	24.32	257.96	42.9
TRAPPER	1032.89	24.56	254.05	25.2
PI 269777	1027.11	27.48	281.14	36.5
PI 269776	1017.28	25.52	258.61	36.9
PI 269771	1009.87	26.41	265.51	26.5
PI 269800	1009.06	27.35	274.30	46.7
PI 269733	997.88	25.89	256.68	60.6
PI 103866	988.90	25.80	255.36	30.9
PI 269752	979.34	25.56	250.97	34.5
PI 103858	975.25	26.07	254.83	31.9
PI 269804	973.01	25.03	242.30	34.5
PI 102887	959.75	25.29	242.71	34.3
PI 269797	952.26	25.41	241.49	75.5
PI 242027	941.92	26.20	246.01	34.3
PI 261675	941.11	24.35	229.31	50.5
PI 269774	931.08	26.56	247.59	18.9
PI 261678	929.59	26.60	246.82	53.4
PI 263030	921.19	24.32	225.25	36.7
PI 273239	920.03	27.03	247.74	36.1
PI 261671	916.38	22.96	209.60	43.7
PI 269735	912.06	24.93	228.74	57.7
PI 263010	909.97	24.82	226.38	50.0
PI 269791	909.36	24.70	223.76	55.9
PI 269750	886.13	22.58	202.36	74.6
PI 269770	864.95	26.34	227.08	63.2
PI 261672	864.41	26.83	233.45	43.0
PI 261664	840.92	24.30	204.88	50.4
PI 263013 NR	829.14	24.84	206.49	36.9
PI 269801 NR	826.20	26.98	222.49	61.3
PI 269735 NR	817.55	26.79	217.44	91.3
PI 261677	814.03	25.95	213.31	22.7
PI 269739	808.37	25.15	202.97	46.0
PI 269773	806.17	28.17	226.04	18.0
PI 269767	801.81	24.99	201.54	49.7
PI 269778 NR	800.90	29.46	232.72	48.3
PI 269802	797.45	27.88	220.67	59.6
PI 269793 NR	785.39	28.46	222.84	50.7
PI 263027	770.89	26.76	209.11	63.7
PI 269794 NR	760.17	26.11	198.60	75.8
PI 269775	731.06	27.64	201.47	28.9
PI 269787	724.32	26.59	189.36	59.5
PI 263012	705.05	25.96	182.91	59.5
PI 269769	691.32	25.12	172.27	58.1
PI 263023	683.44	25.52	175.05	40.2
PI 269764 NR	677.58	29.26	196.45	59.0
PI 263009	664.22	23.81	158.40	37.4
PI 261667 NR	650.76	28.14	183.99	41.5
PI 263014	616.19	25.43	155.80	46.3
PI 269765	607.03	24.88	149.13	26.5
PI 261673	605.74	27.53	165.47	60.6
MEAN	915.30	25.74	234.16	44.8
LSD (P=0.05)	258.19	2.17	64.74	8.5
CV	14.10			

Lattice #9

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 142775	1623.67	23.38	377.27	45.9
PI 164436	1449.80	23.13	339.46	32.7
PI 142442	1442.51	24.52	347.43	36.4
PI 164669	1441.58	26.04	380.74	35.4
PI 162692	1435.63	23.64	338.03	46.2
PI 163128	1413.84	23.28	329.49	36.2
PI 164787	1404.09	21.10	292.79	38.5
PI 116056	1394.62	25.06	353.06	35.9
PI 162691	1342.70	20.86	279.78	43.6
PI 143483	1321.29	23.59	311.14	59.7
PI 125675	1319.17	26.05	346.21	26.8
PI 119795	1297.63	25.04	325.27	54.4
PI 121978	1290.05	25.26	324.18	35.2
PI 140295	1286.49	23.34	295.06	31.2
PI 163125	1268.19	23.23	295.20	34.0
TRAPPER	1258.90	22.53	281.02	26.5
PI 164426	1258.69	23.01	288.52	40.9
PI 123556	1257.36	23.56	290.10	42.3
PI 116d44	1251.65	25.76	325.57	49.9
PI 164136	1235.85	23.48	292.54	42.1
PI 164295	1231.58	23.35	286.75	40.0
PI 125033	1223.83	25.48	315.38	20.3
PI 164346	1210.46	24.67	299.83	42.4
PI 123247	1210.10	22.46	280.17	32.6
PI 121352	1203.42	24.77	299.72	30.9
PI 124479	1201.50	24.46	299.56	33.0
PI 113368	1200.17	24.62	297.41	29.2
PI 142441	1192.30	24.47	287.65	31.1
PI 163126	1190.89	23.33	278.72	24.8
PI 163127	1184.49	23.29	275.80	37.0
PI 126033	1181.12	25.49	301.27	68.1
PI 142777 MS	1180.45	24.87	290.46	32.8
PI 163134	1180.03	23.11	270.86	34.5
PI 124238	1167.44	24.75	283.65	37.3
PI 120623	1154.74	24.93	284.09	51.9
PI 140290	1139.05	23.63	268.79	32.9
PI 137120	1137.38	24.79	276.21	30.1
PI 164417	1134.21	25.07	286.64	35.4
PI 137113	1122.07	25.95	284.74	31.3
PI 163129	1113.21	23.37	256.13	35.4
PI 117993	1109.77	26.69	294.22	61.2
PI 164396	1097.16	23.65	259.73	34.3
PI 123246	1096.82	26.24	292.12	32.1
PI 140297	1089.97	23.60	257.84	29.4
PI 140290A	1081.23	24.89	270.05	30.7
PI 125672	1078.21	25.75	287.98	42.4
PI 119794	1077.15	21.24	228.17	55.3
PI 164590	1062.46	21.76	230.98	44.6
PI 162994	1049.26	24.35	256.16	63.2
PI 155109 MR	1036.35	25.72	269.85	65.7
PI 134271	1031.89	26.12	268.10	17.7
PI 116944	972.10	26.80	261.73	17.8
PI 117906	971.46	25.07	238.46	67.3
PI 140290 MR	966.92	27.55	278.63	40.2
PI 121977	962.62	24.27	242.07	23.4
PI 164614	952.54	25.96	235.80	32.0
PI 137119	931.25	25.59	237.57	26.3
PI 142774	915.03	24.28	218.29	32.6
PI 163131	904.17	26.04	232.07	19.2
PI 164612	882.37	25.62	225.31	36.7
PI 120627	871.64	24.61	224.65	43.0
PI 166032	726.71	26.80	195.02	17.1
PI 121976	626.75	25.76	159.37	20.2
PI 125643	449.48	27.99	125.36	17.4
MEAN	1148.44	24.52	280.10	37.4
LSD (P=0.05)	274.53	2.42	77.90	4.8
CV	11.95			

Lattice #10

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 269815	1509.39	24.64	366.44	27.1
PI 269816 STR	1504.72	23.71	344.82	30.2
PI 165564	1372.69	24.48	344.51	34.9
PI 271121	1368.05	24.63	341.81	38.7
PI 269809	1359.71	25.70	352.04	28.3
PI 272148	1351.55	25.01	335.71	30.1
PI 271116	1325.14	26.01	344.27	48.6
PI 269808	1314.06	23.63	304.17	42.4
PI 269805	1311.19	25.75	339.89	49.2
PI 164838	1274.24	26.43	332.05	34.6
PI 269812	1262.44	23.73	302.63	33.2
PI 272144	1245.80	26.64	327.89	38.7
PI 269811	1241.04	23.97	298.17	34.9
PI 164972	1233.78	23.39	280.59	43.9
PI 272152	1225.10	25.55	311.38	23.6
PI 269810	1216.18	27.36	329.87	14.4
PI 272150	1196.31	26.28	320.01	24.9
PI 271507	1195.48	23.45	277.73	58.7
PI 270536	1190.32	24.95	293.31	47.2
PI 164971	1185.69	25.12	301.03	59.3
PI 272151	1184.46	25.91	297.63	39.5
PI 271035	1183.31	23.70	281.68	69.3
PI 164837	1182.87	26.61	313.25	35.1
PI 280064 NR	1182.40	28.82	344.90	31.1
PI 271510 NR	1177.84	28.13	327.60	53.3
TRAPPER	1173.44	24.33	287.44	25.0
PI 271508 NR	1170.13	28.54	335.32	52.3
PI 271511	1140.51	23.22	267.31	57.2
PI 165129	1116.57	24.94	278.43	37.7
PI 272145	1080.05	27.41	287.83	43.6
PI 272140	1079.03	26.91	285.31	27.3
PI 271120	1058.96	26.99	290.80	34.8
PI 272143	1058.66	27.30	288.65	44.9
PI 269825	1036.99	23.78	252.97	45.2
PI 166142	1035.54	24.29	249.16	29.6
PI 272153	1034.46	25.94	273.11	23.0
PI 271036	1026.75	26.38	279.22	34.3
PI 271033 NR	1023.68	28.34	289.79	69.6
PI 271507	1022.35	23.66	236.91	42.5
PI 165577	1021.94	24.86	241.08	32.3
PI 272149	976.84	27.71	286.99	24.1
PI 271114	996.55	23.89	239.70	38.8
PI 165337	985.72	24.13	240.11	31.2
PI 269813	980.22	26.46	260.14	18.9
PI 269814	969.08	26.30	253.17	21.1
PI 269819 NR	957.39	26.91	260.06	37.3
PI 272154	939.20	25.91	238.57	21.9
PI 271034	937.22	28.57	268.24	11.8
PI 271113	898.21	27.83	257.75	20.3
PI 269817	883.79	28.11	251.95	21.0
PI 271037	822.27	26.51	222.44	20.6
PI 165565	798.31	26.90	212.72	19.4
PI 271119	797.17	26.44	210.37	23.8
PI 271117	781.13	27.80	213.87	15.2
PI 272147	730.14	24.54	190.70	15.7
PI 269822	705.10	24.75	177.28	18.8
PI 269820 NR	671.62	30.05	203.39	35.2
PI 269813	664.46	28.91	191.84	45.5
PI 271033	649.30	27.80	178.51	21.1
PI 166031	553.13	28.72	160.70	32.4
PI 165943	551.97	27.20	148.42	19.1
PI 269821 NR	549.11	27.48	155.17	16.6
PI 166038	534.04	28.56	165.14	44.5
	360.40	27.95	90.75	14.5
MEAN	1040.11	26.11	269.13	33.7
LSD (P=0.05)	273.76	1.78	67.50	4.5
CV	13.16			

Lattice #11

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 272218	768.64	25.70	198.18	22.4
PI 272172	749.05	27.10	202.55	34.6
PI 272161	733.12	23.90	176.63	36.0
PI 272202	721.23	24.85	179.62	30.2
PI 272200	717.75	24.65	177.49	39.8
PI 272166	717.48	24.80	179.19	31.9
TRAPPER	711.54	23.10	163.30	25.3
PI 272208	710.87	24.85	174.81	34.8
PI 272191	710.31	23.65	169.26	35.4
PI 272186	707.72	23.95	170.34	31.1
PI 272180	706.99	26.05	182.39	38.8
PI 273675	703.94	25.35	177.04	30.4
PI 272190	694.70	24.45	170.90	29.7
PI 272207	680.02	26.35	178.27	21.4
PI 272201	675.02	26.20	178.41	30.3
PI 272211 STR	674.57	24.50	164.92	60.6
PI 272184	668.03	25.25	168.13	17.4
PI 272168	652.29	25.00	163.33	33.7
PI 272169	651.07	26.10	169.65	19.6
PI 272162	637.67	24.60	157.38	38.9
PI 272179	632.15	26.30	166.59	23.0
PI 272175	625.27	25.65	157.95	29.3
PI 273605	625.15	23.45	150.18	53.1
PI 273674	623.42	25.15	158.72	28.4
PI 272167	623.20	24.10	150.06	53.8
PI 272159	621.73	25.85	164.06	39.9
PI 272215	616.20	25.80	162.02	22.3
PI 272158	615.94	24.95	153.19	50.5
PI 272157	613.19	26.05	158.95	21.8
PI 272171	607.63	24.60	148.83	39.1
PI 272203	607.17	23.40	141.22	32.6
PI 272183	602.16	26.00	156.20	26.6
PI 272164	600.15	25.75	153.22	49.6
PI 272160	595.17	24.95	150.53	40.9
PI 272199	589.48	24.90	145.51	32.4
PI 272178	586.72	24.75	145.07	38.1
PI 272206	585.99	28.35	161.92	18.3
PI 272195	578.67	26.75	154.12	31.6
PI 272194	573.00	27.65	156.33	38.8
PI 272187	571.89	24.00	138.98	56.0
PI 272212 STR	564.06	26.00	143.65	40.2
PI 272181	561.82	25.50	144.18	34.2
PI 272193	561.38	28.05	155.10	34.2
PI 272205	558.68	26.45	147.24	37.5
PI 272204	557.41	26.20	146.96	27.6
PI 272173	554.42	26.60	145.83	32.0
PI 272170	551.88	26.80	150.32	33.9
PI 272198 STR	534.35	24.90	133.65	28.6
PI 272155	534.00	26.95	143.34	20.3
PI 272216	523.16	27.45	145.76	19.3
PI 272214	521.26	25.90	135.56	61.5
PI 272177	517.07	26.10	134.79	39.3
PI 272217	507.73	26.20	134.28	25.6
PI 272189	506.93	27.80	141.99	23.9
PI 272176	504.09	24.85	124.76	37.4
PI 272192	491.17	27.05	129.58	40.5
PI 272156	488.52	27.80	135.80	19.1
PI 272209	488.04	24.75	120.17	45.6
PI 272213	463.96	26.05	123.04	62.9
PI 272165	441.65	26.05	111.21	30.7
PI 272197	432.90	24.80	105.63	26.9
PI 272196	407.16	26.05	106.04	27.4
PI 272185	400.83	27.20	107.41	19.1
PI 272182	365.42	26.40	95.69	55.3
MEAN	595.09	25.64	152.15	34.3
LSD (P=0.05)	140.47	1.79	37.34	7.7
CV	11.73			

Lattice #12

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 280244	920.50	25.50	234.86	37.6
PI 280248	860.00	25.80	222.05	29.0
PI 280237	859.00	26.20	225.26	37.5
PI 273676	846.50	26.35	223.07	30.4
PI 280619	841.50	28.30	238.52	41.4
PI 280249	835.00	25.85	215.80	43.0
PI 273679	824.90	24.55	203.03	36.9
PI 280254	822.50	24.80	204.98	37.5
PI 273680	799.00	25.10	200.70	35.2
PI 275639	797.00	25.90	206.82	33.3
PI 280247	796.00	24.50	194.99	34.3
PI 274584	789.00	25.40	201.56	34.0
PI 280250	784.00	26.10	204.65	33.3
PI 280240	771.50	26.40	203.30	32.8
PI 280241	764.50	26.10	200.23	35.4
PI 280620	758.50	25.10	190.64	38.3
PI 280243	750.00	25.70	192.89	35.9
PI 275638	749.50	25.20	189.58	30.4
PI 280605	748.50	28.45	212.76	16.0
PI 280253	747.50	24.45	182.97	30.2
PI 280618 WR	746.00	28.50	212.38	38.9
PI 279825 WR	738.00	27.35	201.90	34.8
PI 280246	735.50	25.05	184.67	33.0
PI 280616	734.50	27.25	199.86	33.6
PI 273677	726.00	24.45	177.38	31.3
PI 280617	720.00	26.95	194.26	47.2
PI 280252	720.00	26.70	191.08	31.3
PI 275640	718.00	25.30	181.84	36.0
PI 275820	709.50	25.95	184.05	31.9
PI 280234	699.50	25.90	181.73	37.6
PI 280251	698.00	27.60	192.79	32.1
PI 277851	694.00	24.20	168.03	28.8
PI 280245	692.00	26.80	185.31	35.1
PI 280613 WR	692.00	29.60	205.34	39.0
PI 279823 WR	690.00	29.30	202.04	37.6
TRAPPER	689.50	23.95	164.06	26.4
PI 280614 WR	688.50	27.00	185.89	42.8
PI 280603	687.50	25.85	177.76	31.2
PI 280242	686.50	25.40	174.74	34.0
PI 277852	684.50	25.05	171.34	32.8
PI 280608	677.50	25.75	174.36	21.7
PI 279827	677.00	24.10	163.51	49.2
PI 280604	673.50	27.95	188.35	13.3
PI 280621	669.50	26.00	174.40	31.5
PI 273678	666.50	25.35	168.78	35.5
PI 280236	666.00	25.35	168.64	31.8
PI 280235	663.50	26.40	174.88	31.2
PI 280606	658.50	26.50	174.71	21.6
PI 273681	646.50	25.10	161.85	33.5
PI 279826	643.00	26.25	169.04	38.5
PI 280612 WR	639.00	26.85	171.72	38.8
PI 280376	627.50	26.65	167.20	91.9
PI 280607	623.00	25.25	156.79	24.3
PI 275826	605.50	25.35	153.11	31.0
PI 279824 WR	587.00	26.20	153.50	32.7
PI 280615 WR	586.50	28.25	165.60	35.5
PI 280239	585.00	24.45	142.95	36.3
PI 280238	585.00	25.70	150.34	37.3
PI 280609	559.00	26.80	150.36	10.4
PI 275822 WR	499.50	26.60	132.62	36.3
PI 275821	496.00	28.20	140.07	82.4
PI 274308	491.00	27.30	133.94	13.9
PI 280610	432.50	28.50	123.59	29.6
PI 275825 WR	427.00	26.35	113.48	38.1
MEAN	696.86	26.17	182.17	34.8
LSD (P=0.05)	160.50	2.10	46.26	4.9
CV	11.46			

Lattice #13

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 285746	846.47	24.65	209.19	35.4
PI 299024	836.94	26.80	224.01	32.7
PI 285718	776.17	26.95	209.69	33.5
PI 288021	770.85	24.95	192.21	32.4
PI 285740 WR	767.86	29.20	223.45	33.2
PI 314796	737.94	27.35	202.14	46.4
PI 285744 WR	736.03	28.75	212.74	40.0
PI 288031	736.02	25.10	184.64	34.8
PI 288025	729.12	24.15	174.94	41.6
TRAPPER	727.26	25.65	186.89	25.0
PI 288030	726.85	25.00	181.13	36.2
PI 288028	726.17	26.70	193.86	35.4
PI 280626 WR	720.57	29.55	210.52	39.8
PI 285724 WR	715.35	28.50	204.55	40.4
PI 285727	713.13	24.95	178.19	36.3
PI 285721 WR	706.01	28.55	201.53	36.4
PI 285717	682.45	27.45	186.82	37.5
PI 288022	679.32	26.15	176.90	38.4
PI 285730 WR	670.18	27.00	179.35	38.8
PI 285728 WR	665.18	29.15	194.00	37.4
PI 286607	664.74	24.55	162.63	40.3
PI 285725	653.16	29.25	189.14	37.6
PI 293426	649.68	28.40	183.10	21.7
PI 288026	645.91	26.05	169.37	56.1
PI 280625	645.62	27.10	174.44	32.2
PI 285722 WR	643.11	28.20	181.97	39.8
PI 288023	638.71	26.60	169.41	36.4
PI 285734 WR	636.26	29.25	186.39	38.4
PI 285719 STR	634.11	28.00	178.10	28.3
PI 299023	631.59	26.95	170.37	22.6
PI 285720	623.52	27.70	172.28	43.9
PI 280623 STR	621.01	25.95	160.23	39.1
PI 304533	619.56	27.20	167.91	23.1
PI 285715	618.12	26.60	164.25	54.7
PI 285737 WR	614.91	29.05	178.19	33.4
PI 285704	614.58	27.55	171.13	36.3
PI 280622 WR	613.77	28.20	172.91	43.5
PI 285729	612.98	26.20	160.68	40.4
PI 306592	611.88	25.35	153.79	38.2
PI 285712	607.82	26.05	156.66	28.4
PI 285745 WR	603.53	28.05	169.34	38.9
PI 285736 WR	599.73	28.45	170.92	36.0
PI 288027	589.57	27.10	158.70	34.2
PI 285743 WR	565.61	29.75	169.20	52.4
PI 285732 WR	561.52	29.55	168.39	35.7
PI 285742 WR	559.86	29.55	165.88	55.1
PI 285739 WR	558.97	29.20	164.22	47.8
PI 285736 WR	557.00	26.95	150.32	39.2
PI 285733 WR	554.62	29.70	164.43	36.8
PI 306590	549.17	27.75	151.99	19.7
PI 285723 WR	546.58	27.50	148.90	38.2
PI 285709	542.70	25.75	140.24	29.8
PI 285741 WR	527.26	27.75	146.72	37.0
PI 285731 WR	519.06	28.20	148.20	45.9
PI 285714	518.61	27.95	145.41	33.1
PI 285713	509.23	27.40	138.09	37.5
PI 285726	500.42	26.20	130.12	40.1
PI 285749	481.29	25.45	123.12	35.5
PI 288024	474.17	26.80	127.19	35.4
PI 285733 WR	472.19	30.50	144.81	36.2
PI 288036 WR	471.56	28.40	133.25	20.5
PI 297082	395.17	24.85	98.31	38.5
N.R.C.	365.44	29.10	107.07	16.3
PI 285430	233.35	29.25	68.69	11.7
MEAN	617.61	27.37	168.47	36.2
LSD (P=0.05)	199.07	2.05	54.32	5.3
CV	16.04			

Lattice #14

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 312200	928.17	24.35	225.64	36.6
PI 331412	912.84	24.65	226.13	36.1
TRAPPER	903.92	24.05	217.90	24.4
PI 319375	896.29	22.75	203.71	36.8
PI 314793	892.39	26.70	241.78	48.8
PI 343266	877.98	25.40	221.90	40.9
PI 319373	869.71	23.95	205.60	44.6
PI 312199	849.84	23.20	193.10	33.6
PI 314802	845.86	24.10	207.34	26.5
PI 307666	827.32	26.10	219.38	39.6
PI 343264	819.27	25.95	209.45	40.5
PI 343271	817.53	25.45	209.99	40.3
PI 343267	816.21	26.75	219.45	21.4
PI 331413	801.76	25.05	202.67	38.4
PI 343265	790.30	23.20	177.97	32.5
PI 314800	784.07	26.75	209.09	32.1
PI 316586	781.22	24.00	188.05	36.2
PI 312136	775.94	23.70	182.45	70.8
PI 326196	773.56	24.70	189.01	35.3
PI 314801	769.11	26.15	200.33	31.0
PI 314794 STR	768.04	24.80	191.56	32.5
PI 343262 WR	765.41	26.45	202.74	37.8
PI 343272	757.38	26.25	200.68	32.6
PI 324696 WR	752.40	23.55	178.86	47.4
PI 314799	752.16	24.95	187.30	50.3
PI 320973	748.99	23.10	175.14	37.5
PI 340126	747.51	25.55	190.41	24.4
PI 340130	735.05	24.05	179.27	28.4
PI 343270	733.13	24.40	179.46	30.4
PI 324697	730.22	26.25	194.34	33.3
PI 343269	726.76	25.55	186.37	35.6
PI 324702	725.08	27.75	202.52	25.3
PI 311112	722.65	23.05	165.65	54.9
PI 326194	720.97	24.75	178.29	31.7
PI 343250 WR	719.24	28.75	203.64	37.3
PI 343260 WR	717.81	28.30	205.00	37.1
PI 306591 STR	712.22	26.30	185.63	28.1
PI 324699 STR	704.33	25.95	182.33	24.8
PI 343252 WR	698.88	26.55	185.44	44.4
PI 340124	698.16	25.50	175.63	28.1
PI 324706	692.31	27.60	190.88	18.8
PI 324703	689.89	26.80	186.29	25.0
PI 320972	689.69	25.10	173.63	43.3
PI 343273	689.14	24.15	169.50	34.1
PI 324694	684.92	29.40	200.06	21.6
PI 343268	683.85	26.80	185.05	33.1
PI 343255 WR	683.51	27.95	189.82	38.2
PI 343261 WR	679.30	28.00	190.00	39.1
PI 324704	677.67	26.15	177.46	34.1
PI 343259 WR	673.98	28.15	190.58	37.9
PI 343253 WR	668.61	28.70	189.51	41.3
PI 343256	653.40	28.40	182.65	36.0
PI 343274	648.46	26.50	168.49	30.0
PI 331414	617.10	27.10	165.25	27.0
PI 343251 WR	598.45	27.70	166.45	42.0
PI 324695	594.12	25.85	154.69	51.9
PI 343263	593.37	26.15	153.10	22.6
PI 343258 WR	579.61	27.00	156.10	43.0
PI 343254 WR	567.07	28.60	162.72	41.5
PI 341889 WR	560.34	28.00	155.56	32.3
PI 324701	555.59	27.35	154.86	20.6
PI 324693	531.11	27.15	143.54	31.6
PI 314803	529.47	26.50	144.07	32.7
PI 343257	463.26	25.95	119.50	14.9
MEAN	724.59	25.93	187.04	35.0
LSD (P=0.05)	164.42	2.12	42.66	4.9
CV	11.29			

Lattice #15

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
TRAPPER	888.00	25.45	227.33	24.3
PI 343319	837.00	24.90	208.26	52.7
PI 343287	830.50	23.35	194.15	30.8
PI 343296	829.50	25.45	211.07	25.2
PI 343324	822.00	26.45	217.42	34.4
PI 343313	813.00	24.35	197.99	35.7
PI 343966	813.00	23.25	188.98	50.6
PI 343281	801.50	23.75	191.09	40.0
PI 343330	764.50	23.30	177.63	52.9
PI 343314	761.00	24.70	188.06	54.6
PI 343297	742.50	24.95	185.04	46.5
PI 343289 WR	728.50	25.40	185.20	21.4
PI 343298	725.50	27.55	199.78	36.0
PI 343291	713.00	27.25	193.97	34.8
PI 343936	710.00	23.95	170.41	37.0
PI 343312	707.50	25.45	178.98	31.0
PI 343285	707.00	24.55	173.69	36.9
PI 343280	703.00	25.70	180.97	28.9
PI 343279 STP	700.00	23.70	165.22	40.7
PI 343961	691.50	26.00	179.65	47.4
PI 343959	677.00	24.70	167.01	52.0
PI 343310	674.00	25.20	169.46	45.5
PI 343337	671.50	25.35	170.30	34.2
PI 343295	663.00	24.05	159.36	51.5
PI 343935	661.00	24.70	163.27	33.0
PI 343315	657.50	25.80	169.63	32.6
PI 343322	655.00	23.20	151.98	51.2
PI 343325	652.00	26.70	174.27	61.7
PI 343301	649.00	23.50	152.51	44.7
PI 343323	640.00	24.90	159.19	45.5
PI 343304 WR	639.00	24.40	156.29	50.4
PI 343299	638.50	25.45	162.96	44.8
PI 343321 WR	636.50	23.70	151.54	47.2
PI 343335 WR	636.00	25.05	159.77	78.9
PI 343960	633.50	25.70	162.81	79.5
PI 343329	633.50	26.80	169.81	35.1
PI 343334 WR	626.00	25.65	160.12	84.7
PI 343317	615.00	25.50	156.48	79.3
PI 343311	613.00	27.55	169.14	60.6
PI 343327	613.00	25.15	154.18	36.5
PI 343290	608.00	23.65	143.72	50.9
PI 343336 WR	590.00	25.85	152.56	49.9
PI 343316 WR	582.50	28.15	164.01	84.3
PI 343292	581.00	25.45	148.28	82.8
PI 343331	571.50	26.10	149.20	22.5
PI 343965	568.00	26.10	149.01	63.8
PI 343277	567.00	24.55	138.91	32.5
PI 343306	556.50	25.15	140.11	23.4
PI 343293	554.00	24.60	137.[illegible]	24.3
PI 343328	549.50	25.15	138.[illegible]	47.0
PI 343308	543.00	26.45	144.29	59.6
PI 343338	539.00	25.80	139.09	50.7
PI 343300	537.00	25.25	134.84	49.2
PI 343302	531.50	27.00	143.99	17.4
PI 343282	510.00	26.40	133.83	20.6
PI 343294	509.00	26.10	132.85	48.5
PI 343958	457.50	25.20	114.91	50.3
PI 343284	455.00	27.95	127.11	30.4
PI 343303	446.00	27.80	123.99	19.3
PI 343286	426.50	27.40	116.79	18.2
PI 343278	426.00	26.75	113.96	15.9
PI 343283	404.50	26.65	107.82	15.2
PI 343333 WR	367.50	27.20	99.91	18.2
	367.00	27.25	99.81	89.1
MEAN	631.56	25.48	160.14	43.7
LSD (P=0.05)	158.42	2.54	44.13	3.9
CV	12.48			

Lattice #16

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 343969	919.24	26.07	239.67	42.0
TRAPPER	866.97	26.07	225.48	23.6
PI 347278	821.44	24.26	200.71	37.8
PI 343967	821.16	25.30	207.86	41.3
PI 347311	821.13	25.55	210.25	34.1
PI 347294	812.90	25.10	205.32	30.7
PI 347314	808.46	24.89	201.68	33.3
PI 347284	790.40	24.73	193.19	36.2
PI 347300	775.73	25.88	203.13	31.2
PI 347280	767.94	25.25	196.75	41.8
PI 347279	751.11	25.23	190.66	67.6
PI 347288	748.82	24.08	180.79	39.9
PI 347303	747.58	25.41	188.31	34.9
PI 347306	746.78	25.14	186.98	33.1
PI 347296	745.21	25.50	191.95	49.7
PI 347293	744.19	25.35	189.88	33.4
PI 347301	743.34	25.66	192.26	58.5
PI 347320 STR	740.45	25.30	185.00	57.1
PI 347290	739.79	25.07	187.96	33.7
PI 347317	735.55	23.35	171.51	55.6
PI 347329	735.19	25.97	191.94	35.3
PI 347318	731.96	27.45	202.96	27.3
PI 347330	725.42	23.95	173.52	55.6
PI 347271	720.61	25.36	182.83	38.1
PI 347325	717.99	26.02	188.72	33.6
PI 347315	717.69	23.66	170.46	54.8
PI 347285	712.78	25.24	179.10	56.8
PI 347316	712.18	25.88	187.57	44.3
PI 347273	710.12	25.08	174.92	38.1
PI 347275	699.49	26.64	188.00	53.8
PI 347326	699.16	24.53	170.67	56.5
PI 347295	697.42	24.18	167.50	45.1
PI 347322	697.40	25.35	177.75	38.4
PI 347274	697.12	24.79	173.54	34.3
PI 347328	682.66	26.76	182.32	27.2
PI 347282	679.18	24.90	166.03	41.8
PI 347281	678.47	24.19	163.56	45.6
PI 347292	675.95	24.03	161.18	45.2
PI 347324	673.93	25.68	176.05	51.1
PI 347313 STR	673.92	24.19	165.08	54.6
PI 347323	670.48	25.83	173.27	52.6
PI 347297	669.34	25.30	169.50	38.6
PI 347302	669.20	24.13	161.94	55.8
PI 347283	666.57	25.28	169.76	39.9
PI 347298	661.98	25.26	167.46	42.8
PI 347277 WR	661.74	28.25	185.21	49.1
PI 347299	657.42	26.02	170.47	34.0
PI 347309	651.85	24.39	159.05	52.3
PI 347305	633.82	24.56	152.25	55.1
PI 347304	629.92	25.65	160.99	57.7
PI 347321	626.07	24.40	150.33	54.3
PI 347308	617.14	24.17	152.99	56.8
PI 347289	617.12	25.17	151.78	42.4
PI 347276	615.14	25.80	159.20	35.3
PI 347319	607.69	27.64	166.80	31.6
PI 347310	603.89	24.98	148.39	56.1
PI 347331	603.22	24.31	147.44	54.5
PI 347286	601.89	26.27	155 82	29.1
PI 347311	586.87	25.13	144.07	40.0
PI 347307 STR	582.19	23.83	135.77	52.8
PI 347327	575.92	24.57	139.92	55.3
PI 347287	570.72	25.47	145.78	55.0
PI 347312	563.19	25.56	146.79	45.9
PI 343968	420.18	27.02	113.85	47.4
MEAN	694.54	25.25	175.34	44.2
LSD (P=0.05)	152.30	1.74	40.51	5.5
CV	10.91			

Lattice #17

Genotype	Yield g/plot	Protein content %	Protein yield g/plot	Seed weight g/200 seeds
PI 347377 STR	733.26	27.55	202.04	40.6
PI 347360	725.25	27.45	199.71	45.7
PI 347390	709.18	25.25	178.97	34.8
PI 347355	693.46	28.62	199.75	41.7
TRAPPER	691.30	25.65	176.44	23.5
PI 347374	690.35	27.69	190.55	34.2
PI 347394	689.27	25.35	173.34	31.6
PI 347365	689.14	25.84	176.62	46.5
PI 347339	688.81	27.64	190.37	40.4
PI 347351	687.03	27.64	188.61	40.4
PI 347398	682.29	24.60	167.92	39.9
PI 347399	680.47	25.18	169.26	34.3
PI 347342	675.25	28.74	193.28	34.8
PI 347358	669.90	27.89	185.74	47.5
PI 347333	667.16	28.76	193.06	35.8
PI 347369	667.01	28.41	190.24	35.0
PI 347386	664.89	26.85	177.11	41.9
PI 347361	660.15	27.21	181.79	45.2
PI 347349	659.14	28.48	186.35	26.5
PI 347382	657.33	26.00	172.10	43.5
PI 347388	654.98	26.77	176.18	44.6
PI 347356	652.60	26.95	174.87	33.7
PI 347396	649.93	24.94	162.35	44.0
PI 347387	644.82	25.14	161.30	38.9
PI 347367	638.90	28.25	180.49	58.9
PI 347375	638.41	27.09	173.01	37.1
PI 347332	618.67	28.01	174.03	46.7
PI 347371 STR	617.05	26.66	165.47	33.9
PI 347372	616.66	28.66	177.02	40.1
PI 347393	605.51	25.44	153.37	54.4
PI 347335	603.58	29.54	177.89	51.9
PI 347353	600.88	29.20	175.80	35.7
PI 347363	594.65	30.15	178.58	30.0
PI 347397	592.06	25.06	147.97	57.3
PI 347354	585.31	27.85	162.73	41.6
PI 347359	583.87	27.96	165.24	43.3
PI 347337	580.60	27.99	160.90	41.1
PI 347383	576.78	29.22	171.01	32.5
PI 347378	573.07	27.61	159.60	36.4
PI 347381	565.96	28.05	158.69	45.6
PI 347338	563.82	29.45	165.68	53.9
PI 347392	559.49	27.66	156.57	27.4
PI 347357	555.05	26.05	142.86	40.3
PI 347373	552.76	26.44	144.26	40.5
PI 347379	551.43	28.05	154.57	32.4
PI 347368	551.19	28.25	155.26	28.2
PI 347370	550.59	29.36	161.63	34.8
PI 347352	540.15	29.05	156.88	33.4
PI 347385	537.64	28.30	152.30	44.3
PI 347380	526.81	28.06	148.56	37.3
PI 347389	526.20	26.70	141.15	24.1
PI 347364	520.52	29.39	152.48	38.2
PI 347400	515.11	24.35	124.34	46.1
PI 347366	514.11	28.26	145.94	34.0
PI 347334	500.33	29.57	149.76	52.6
PI 347336	496.91	28.74	142.03	48.8
PI 347344	483.20	29.01	141.34	25.9
PI 347376	472.77	30.14	141.45	46.5
PI 347343 STR	470.72	30.85	144.69	25.5
PI 347362	469.97	28.34	132.69	58.2
PI 347395	468.34	25.09	115.45	50.6
PI 347346	467.48	29.14	135.32	56.6
PI 347350	364.98	29.10	103.07	39.2
PI 347347	358.53	29.45	105.38	61.6
MEAN	593.64	27.64	163.49	40.5
LSD (P=0.05)	138.32	1.88	36.13	5.0
CV	11.59			