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# Effect of population structure on protein-yield improvements in spring wheat (*Triticum aestivum* L. em Thell)*

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**Summary.** In a study designed to develop a more efficient breeding method for concurrent protein-yield improvements in wheat (*Triticum aestivum* L. em. Thell), 7 base populations [2 $F_2$'s, 1 intermated $F_2$ ($IF_2$) and 4 partial backcross (PBC) populations] developed from biparental crosses involving 2 Canadian hard red spring (CHRS) and 2 Canadian utility (CU) wheat cultivars were evaluated in Winnipeg, Manitoba, Canada. The $IF_2$ and PBC populations were generated for comparison with conventional $F_2$ populations and to determine which of the 4 methods of population development would provide a more efficient means of producing potentially superior genetic recombinants. Parameters pertaining to means, variances, correlations, heritabilities and frequencies of desirable and undesirable progenies were used to evaluate the limitations to genetic gain that may be expected from selection for GY and GPC in $F_2$, $IF_2$, CHRS-PBC and CU-PBC populations. Analysis of protein and yield data from 105 $S_1$ lines derived from each of the 7 populations showed the CU-PBC's to have the highest grain yield (GY) and the lowest grain protein concentration (GPC) means; and the CHRS-PBC's, the lowest GY and the highest GPC means. The $F_2$ and $IF_2$ populations were intermediate for both characteristics. Populations developed from the same biparental cross did not differ significantly with respect to the majority of genetic parameters. However, desirable progenies combining high GY with high GPC were more frequent in the CU-PBC, and least frequent in the CHRS-PBC populations. The observed superiority of the CU-PBC populations appeared to be related to the advantage the system has in preserving the genetic integrity of a proven cultivar, while adding desirable genetic factors from another cultivar, thus capitalizing on introgression and upgrading simultaneously.

**Key words:** Wheat – Grain yield – Grain protein – Population structure – Intermating – Partial backcrossing

## Introduction

Two major market classes of spring wheat, the Canadian Hard Red Spring (CHRS) wheat and the Canadian Utility (CU) wheat are produced and marketed in Western Canada. Typical CHRS cultivars are characterized by excellent baking and milling qualities, adequate disease resistance and relatively good agronomic characteristics. The doughs made from CHRS cultivars have excellent handling properties, and are not critical in their mixing and fermentation requirements (Waterer and Evans 1985). Unfortunately, however, all current CHRS cultivars have a relatively low yield potential.

Canadian utility wheat cultivars are typified by good milling qualities and adequate disease resistance, but they are generally inferior in baking qualities. Their major attribute is a distinct and significant yield advantage over CHRS cultivars (Waterer and Evans 1985).

Attempts to combine in one genotype the desirable attributes from CHRS and CU wheats has had limited success. There is a general consensus among wheat breeders that this lack of success is mainly due to negative correlations that exist between grain yield (GY) and grain protein concentration (GPC). Attempts to explain further the cause or causes of the negative correlations between GY and GPC have drawn much

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less consensus with the result that there is a proliferation of theories on the subject. Baker et al. (1968) suggested that genetic factors such as linkage or pleiotropy are the basis for negative protein-yield relationships. Pepe and Heiner (1975) postulated that physiological factors such as complex source-sink interactions during a major part of the grain filling period are the primary causes of the negative correlations between GY and GPC.

Similar explanations were provided by McNeal and Davis (1966) whose experiments showed that the supply of nitrogenous products needed for protein production could become limiting before the additional kernels produced by high yielding genotypes mature, thereby causing unfavourable protein-yield relationships.

A biochemical postulate was forwarded by Bhatia and Rabson (1976). They reasoned that since more energy is needed to synthesize proteins than is required to synthesize the same mass of carbohydrates, competition for energy and substrate between these two metabolic end-products (proteins and carbohydrates) could cause negative yield-protein relationships.

Successful pure line breeding requires superior segregating populations from which homozygous lines can be selected. The study reported herein was conducted to identify an operationally simple population structure that will enhance concurrent protein-yield improvements in Canadian spring wheats. The stimulus to conduct the research came from several empirical and computer simulation studies which developed the concept that intermating (Hanson 1959; Miller and Rawlings 1967; Humphrey et al. 1969; Meredith and Bridge 1971) and partial backcrossing (Lawrence and Frey 1975; Reddy and Comstock 1976; Kenworthy and Brim 1979; Ho and Comstock 1980; Dudley 1982) could augment existing genetic variability and thereby improve the efficiency of selection for desirable genetic recombinants. Specific objectives of the study were: (1) to compare the $F_2$, intermated $F_2$ ($IF_2$) and partial backcross (PBC) populations developed from the same set of biparental crosses for genetic parameters affecting the improvement of GY and GPC; and (2) based on these comparisons, to identify a breeding method that would provide increased opportunities for selecting high yielding-high protein cultivars.

## Materials and methods

Four common spring wheat (*Triticum aestivum* L.) genotypes, 'Sinton', 'Coteau', NB-131 and 'Glenlea' were chosen for use as parental lines. Sinton is a CHRS wheat developed from the cross CT-262/'Manitou'. Coteau is also a CHRS cultivar bred in North Dakota, USA, from the cross ND-496 sib//ND-487/'Fletcher'. NB-131 is an experimental high yielding-low protein genotype derived from the cross 'Tobari-66'/'Gaines'. Glenlea is a CU wheat selected from the cross 'Pembina'/2*'Bage'//CB-100. From these 4 genotypes 7 populations [2 $F_2$'s, 1 intermated $F_2$ ($IF_2$), and 4 partial backcross (PBC) populations] were generated. Four of the populations were developed from Glenlea-Sinton parental combination (hereafter designated as 'cross 1') and the remaining 3 populations were produced from NB-131 and Coteau parental combination (hereafter designated as 'cross 2'). The pedigrees and experimental designations (abbreviated names) of the 7 populations are listed in Table 1.

**Table 1.** Pedigrees and experimental designations of 7 populations developed from 2 biparental crosses

| Parental combination | Pedigree | Experimental designation |
|---|---|---|
| | Cross 1 | |
| Glenlea × Sinton | Glenlea/Sinton | F2-1 |
| | Glenlea/Sinton(F2)/Glenlea/Sinton(F2) | IF2 |
| | Glenlea/2*Sinton | PBC-SINT |
| | Glenlea*2/Sinton | PBC-GLEN |
| | Cross 2 | |
| NB-131 × Coteau | NB-131/Coteau | F2-2 |
| | NB-131/2*Coteau | PBC-COTE |
| | NB-131*2/Coteau | PBC-N131 |

Each $F_2$ population was produced by self-pollinating about 20 $F_1$ plants. Each PBC population was developed using more than 50 $F_1$ plants and a single dose of backcrossing. A minimum of 590 kernels were produced for each $F_2$ and PBC population. The $IF_2$ population was generated only in cross 1 using the following procedure. About 240 $F_2$ kernels were planted in each of two greenhouse benches designated as 'bench 1' and 'bench 2', to produce about 120 $F_2$ plants in each bench. To preclude chances of assortive mating, multiple planting dates were used in each greenhouse bench. At anthesis one spike from bench 1 was used to pollinate at random one and only one spike grown in bench 2; and similarly one spike from bench 2 was used to pollinate at random one and only one spike in bench 1. In this manner, about 287 $F_2$ spikes were successfully pollinated, out of which 192 produced 3 or more kernels. Three kernels from each of the 192 spikes were bulked to produce a balanced composite sample of the $IF_2$ population.

Seed of all populations were increased in a spaced plant nursery during the summer of 1978. The field experiments were conducted the following year at the University of Manitoba Research Farm in Winnipeg, Canada, on fertile soils that were planted to faba beans (*Vicia faba* L.) in the previous season. The experiments comprised two tests. Test 1 consisted of multiple (15) entries of each of Glenlea and Sinton, and a random sample of 105 $S_1$ lines derived from each of the 4 populations in cross 1. Similarly, test 2 consisted of 15 entries of each of NB-131 and Coteau along with a random sample consisting of 105 $S_1$ lines derived from each of the three populations in cross 2. Each test was conducted as a modified RCBD with 3 replications. The modifications entailed a block-within sets-within replicate arrangement in which the 105 entries from each population were divided into 15 groups, each group consisting of 7 entries. A block was assigned to each population and included all 7 members in a group plus a

single entry of each of the corresponding parental cultivars for a total of 9 plots/block. A set was composed of 4 blocks in test 1, and 3 blocks in test 2. The entries within blocks and the blocks within sets remained together in all replications, but were randomized to assign populations to blocks first, and then entries within blocks. Plots were 3 rows, 3.0 m long with 15 cm between rows. A seeding rate of 510 kernels $m^{-2}$ was used.

Grain yield and GPC were recorded on a plot basis. Grain yield was measured as the total weight of grain harvested from each plot. Grain protein concentration was determined on a 0% moisture basis using the standard Kjeldahl (boric acid modification) method. Environmental conditions in the nursery were conducive to uniform stand establishment and vigorous plant growth, but because of errors during planting and combine harvesting, GY or GPC data from 13 plots were missing. The missing values were estimated using the procedure outlined by Steel and Torrie (1960).

Analyses of variance (ANOVA) were conducted in two ways. First, ANOVA for blocks-within sets-within replications design were conducted to compare population means within each of the two tests. Thereafter, ANOVA and ANCOVA (analysis of covariance) were calculated for each population separately to obtain estimates of phenotypic and genetic variances and covariances. Inclusion of blocks and sets as sources of variation and covariation in the latter analyses caused two problems: (1) genetic variance estimates for some of the population became negative when sets and blocks were included in the analyses; and (2) the phenotypic variance estimates for some of the population became smaller than the phenotypic variance estimates calculated for the corresponding parental genotypes. To avoid these problems, blocks and sets were ignored. The pertinent portions of the ANOVA and ANCOVA from which variances and heritabilities of GY and GPC, and covariances and correlations between GY and GPC were estimated were as follows:

| Source | Mean square | Variance expectation | Mean cross product | Covariance expectation |
|---|---|---|---|---|
| Replications | MS 3 | $\sigma_e^2 + g\sigma_r^2$ | CP 3 | $\sigma_{exy} + g\sigma_{rxy}$ |
| Genotypes | MS 2 | $\sigma_e^2 + r\sigma_g^2$ | CP 2 | $\sigma_{exy} + r\sigma_{gxy}$ |
| Error | MS 1 | $\sigma_e^2$ | CP 1 | $\sigma_{exy}$ |

Genetic variances ($\sigma_g^2$) were estimated as:

$$\sigma_g^2 = (MS\,2 - MS\,1)/r\,.$$

Standard errors of the genetic variances were calculated using the method of Anderson and Bancroft (1952).

Phenotypic variances ($\sigma_p^2$) were estimated as:

$$\sigma_p^2 = \sigma_g^2 + \sigma_e^2/r\,.$$

Genetic covariance ($\sigma_{gxy}$) was estimated as:

$$\sigma_{gxy} = (CP\,2 - CP\,1)/r\,.$$

Phenotypic correlations ($r_p$) were calculated as Pearson's product moment correlations (Steel and Torrie 1960). Entry means over replicates were used in the analyses.

Genetic correlation ($r_g$) was estimated as follows:

$$r_g = [\sigma_{gxy}/(\sigma_{g1}^2 + \sigma_{g2}^2)]^{-0.5}\,,$$

where $\sigma_{gxy}$ is the genetic covariance of GY with GPC; and $\sigma_{g1}^2$ and $\sigma_{g2}^2$ are the genetic variances of GY and GPC, respectively. The standard error for the $r_g$'s were estimated using the method outlined by Mode and Robinson (1959); $r_g$'s were considered significant if their absolute values exceeded twice the S.E.

Broad-sense heritability was estimated on a plot basis by using the formula

$$h_b = [(\sigma_g^2)/(\sigma_g^2 + \sigma_e^2/r)]^{-0.5}\,.$$

## Results

### *Comparison of means*

Although the parental cultivars were included in the same experiments as the populations, the parental data were analyzed separately. A paired *t*-test (Steel and Torrie 1960) was used to compare the parental lines within each cross (i.e. Glenlea with Sinton, and NB-131 with Coteau). The results (Table 2) indicated that Glenlea was clearly superior to Sinton in GY, but its GPC was relatively inferior. Similarly, NB-131 outyielded Coteau by more than 25%, but its GPC compared to the same cultivar was about 2.0% points lower.

According to Dyke and Baker (1975), if selection is equally effective in populations with unequal means, highest performing progenies will be found more frequently in the population with the highest mean. Consistent with this theory, we assumed that concurrent protein-yield improvement could be achieved if the breeding strategy involved a method of increasing the mean GY of the population without reducing its mean GPC, or conversely, if the mean GPC was increased without causing a significant reduction in mean GY. Since the majority of the wheat breeders in Canada are using the $F_2$ and subsequent generations in the selfing series, we decided to compare the GY and GPC means of the $S_1$ lines in the intermated and partial backcrossed populations with the means calculated in the corresponding $F_2$ population as represented by $F_3$ lines. The results (Table 3) indicated that partial backcrossing to the CU parent increased the mean GY (relative to the $F_2$) by 12.5% and 5.0% in crosses 1 and 2, respectively. In both crosses, the associated reductions in mean GPC were relatively small (0.2 and 0.7% points in crosses 1 and 2, respectively) leading us to speculate that partial backcrossing to the CU parent could provide a larger number of desirable progenies than one would hope to find in conventional $F_2$ populations. In contrast, partial backcrossing to the CHRS parent increased the mean GPC by only 0.2 and 0.4% points in crosses 1 and 2, respectively; but these GPC increments were accompanied by large and significant yield reductions (approximately 6% in cross 1 and 7% in cross 2). These results indicate that it could be more difficult to select for superior genetic recombinants in the CHRS-

**Table 2.** Means and standard errors of GY and GPC of 4 parental genotypes used in the study

| Parental genotype | GY (g/m²) | GPC (%) |
|---|---|---|
| Glenlea | 231.4±4.3 | 18.2±0.1 |
| Sinton | 129.2±3.8 | 19.6±0.1 |
| Difference | 102.2** | 1.4** |
| NB-131 | 225.7±6.9 | 18.1±0.1 |
| Coteau | 180.4±2.9 | 20.1±0.1 |
| Difference | 45.3** | 2.0** |

** Significantly different at the 1% level of significance using student *t*-test

PBC populations than it would be in conventional $F_2$ populations.

Intermating was performed in cross 1 only. The results (Table 3) showed that a single dose of intermating did very little to improve the mean GY, and caused only slight improvement in mean GPC.

*Comparison of variances*

Estimates of phenotypic and genetic variance components are presented in Table 4. Application of the F-ratio (Steel and Torrie 1960) as a test criterion for determining the equality of the phenotypic variances revealed that populations within each cross were essentially similar in phenotypic variations for GY and GPC.

The genetic variances were compared after adding or subtracting the associated standard errors to establish the 95% confidence limits. Compared to the corresponding $F_2$'s, the PCB-SINT and the PBC-COTE populations had lower ($P < 0.05$) genetic variances for GPC and GY, respectively. It would appear that the reduced genetic variation in these populations could be a major constraint in maximizing GY and GPC.

The PBC-GLEN and the PBC-N131 populations did not differ significantly from the corresponding $F_2$'s in terms of genetic variation for GY and GPC, indicating that these two populations could have provided as much opportunity as the $F_2$'s for selecting in either trait. The $F_2$ and $IF_2$ populations in cross 1 had similar genetic variances for both traits. These results indicated that there was very little to be gained, in terms of increased genetic variability, from a single cycle of intermating an $F_2$ population.

*Comparison of correlation coefficients*

Estimates of phenotypic, genetic and environmental correlations between GY and GPC are presented in Table 5. The phenotypic correlations ranged from −0.309 to −0.411 and from −0.410 to −0.550 in crosses 1 and 2, respectively, and were highly significant ($P < 0.01$).

**Table 3.** Mean GY and mean GPC in 7 populations developed from 2 biparental crosses

| Population | GY (g/m²) | GPC (%) |
|---|---|---|
| | Cross 1 | |
| F2-1 | 167.7 b | 19.2 b |
| IF2 | 172.0 b | 19.4 a |
| PBC-GLEN | 188.7 a | 19.1 b |
| PBC-SINT | 158.3 c | 19.4 a |
| | Cross 2 | |
| F2-2 | 209.8 b | 19.5 b |
| PBC-N131 | 220.3 a | 18.8 c |
| PBC-COTE | 194.1 c | 19.9 a |

* Means within a cross followed by the same letter were not significantly different at the 5% level of significance on Duncan's multiple range test

**Table 4.** Estimates of phenotypic ($\sigma_p^2$) and genetic ($\sigma_g^2$) variance components and standard errors for GY and GPC in 7 populations developed from 2 biparental crosses

| Population | $\sigma_p^2$ | | $\sigma_g^2$ | |
|---|---|---|---|---|
| | GY | CPC | GY | GPC |
| | Cross 1 | | | |
| F2-1 | 6,778 | 0.320 | 2,610±555 | 0.180±0.030 |
| IF2 | 6,344 | 0.305 | 2,014±477 | 0.150±0.030 |
| PBC-GLEN | 6,445 | 0.294 | 1,780±378 | 0.130±0.028 |
| PBC-SINT | 5,606 | 0.236 | 1,930±433 | 0.090±0.020 |
| | Cross 2 | | | |
| F2-2 | 4,310 | 0.602 | 1,650±332 | 0.203±0.018 |
| PBC-N131 | 3,470 | 0.441 | 1,503±341 | 0.190±0.011 |
| PBC-COTE | 4,736 | 0.456 | 630±243 | 0.220±0.014 |

Fisher's z transformation (Steel and Torrie 1960) was applied to test the homogeneity of the phenotypic correlation coefficients within each cross. The results indicated that the method of population development had no effect on the degree of phenotypic association between the two traits.

The genetic correlation between GY and GPC was significant in only 1 of the 7 populations, suggesting that the negative phenotypic correlations were not caused by genetic factors such as linkage or pleiotropy.

Environmental correlations between GY and GPC were highly significant ($P < 0.01$), but the coefficients (within a cross) were not significantly different from each other when compared by means of Fisher's z transformation.

**Table 5.** Estimates of phenotypic ($r_p$), genetic ($r_g$) and environmental ($r_e$) correlations between GY and GPC in 7 populations developed from 2 biparental crosses

| Population | Correlation coefficients | | |
|---|---|---|---|
| | $r_p$ | $r_g$[a] | $r_e$ |
| | Cross 1 | | |
| F2-1 | −0.33** | −0.57 | −0.85** |
| IF2 | −0.35** | −0.60 | −0.88** |
| PBC-GLEN | −0.41** | −0.70 | −0.84** |
| PBC-SINT | −0.31** | −0.64 | −0.88** |
| | Cross 2 | | |
| F2-2 | −0.44** | −0.55 | −0.79** |
| PBC-N131 | −0.41** | −0.78 | −0.87** |
| PBC-COTE | −0.55** | −0.71 | −0.30** |

** Correlation coefficients significant at the 1% level of significance

[a] Underlined genetic correlation coefficient exceeded twice its standard error

**Table 6.** Broad-sense heritability estimates for GY and GPC in 7 populations developed from 2 biparental crosses

| Population | Heritability | |
|---|---|---|
| | GY | GPC |
| | Cross 1 | |
| F2-1 | 0.39 | 0.46 |
| IF2 | 0.27 | 0.42 |
| PBC-GLEN | 0.37 | 0.38 |
| PBC-SINT | 0.34 | 0.32 |
| | Cross 2 | |
| F2-2 | 0.34 | 0.51 |
| PBC-N131 | 0.33 | 0.42 |
| PBC-COTE | 0.50 | 0.46 |

*Comparison of heritability estimates*

Broad-sense heritability estimates were calculated according to component of variance method (Mather and Jinks 1971) and the results are presented in Table 6. In cross 1, both traits appeared to be moderately heritable, based on the estimates that ranged from 0.27 to 0.39 for GY, and from 0.32 to 0.46 for GPC. In cross 2, broad-sense heritability estimates ranged from 0.33 to 0.50 for GY, and from 0.42 to 0.51 for GPC, and were high enough to indicate that genetic improvement of both traits could be made through selection.

A comparison of the heritability estimates using the exact 90% ($1-\infty=0.90$) confidence limits (Knapp et al. 1985) indicated that populations within a cross did not differ significantly with respect to heritabilities for either trait.

*Frequencies of desirable and undesirable progenies*

Linear regression analyses were used to compare the relative potential of each population to produce desirable genetic recombinants. These analyses were conducted with the assumption that a population in which higher GPC values are predicted (at a series of GY levels) would yield a larger number of desirable progenies, compared to one that does not show this attribute. In cross 1, the regression coefficients (b values) were highly significant and ranged from a low of −0.089 in the PBC-SINT population to a high of −0.151 in the PBC-GLEN population (Fig. 1). For the majority of the GY values, predicted GPC was higher in the PBC-GLEN population than in any of the other 3 populations generated from the same cross.

In cross 2, the b values ranged from −0.197 to −0.247 (Fig. 2) and were highly significant ($P<0.01$). For the majority of the GY values, predicted GPC's were higher in the PBC-N131 population than in the other 2 populations developed from the same cross.

Populations were also compared for the actual number of 'desirable' and 'undesirable' progenies they contained. 'Desirable' progenies were arbitrarily defined as those lines which, in comparison to the respective parental cultivars, showed either an increase in GPC without a reduction in GY or showed an increase in GY without a significant reduction in GPC. 'Undesirable' progenies were defined as those lines which were inferior in either GY or GPC compared to the parents from which they were generated. A one-tailed LSD test was used to discriminate the statistical difference of each progeny line from its parental cultivars. Since the parents of each cross were on the extreme high and low ends of the GY and GPC distribution curves, we chose to use the 5% probability level for making a type 1 error (Steel and Torrie 1960). In cross 1, a relatively large number of desirable, and a small number of undesirable progenies were identified in the PBC-GLEN population (Table 7). In contrast, the PBC-SINT population was composed of few desirable and a relatively large number of undesirable progenies.

In cross 2, numerous desirable and relatively few undesirable progenies were identified in the PBC-N131; whereas the PBC-COTE population was found to be composed of predominantly undesirable genotypes. These findings are in agreement with the results from linear regression analyses (Figs. 1 and 2) and suggest that partial backcrossing to CU cultivars could

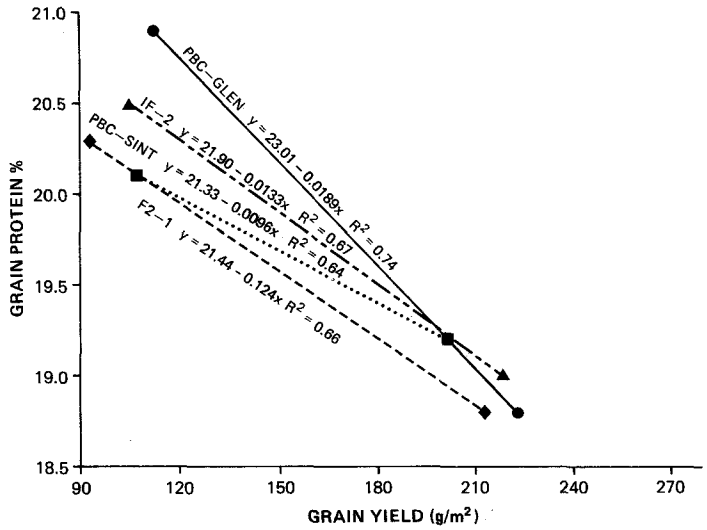


**Fig. 1.** Yield-protein relationships in 4 populations developed from cross 1

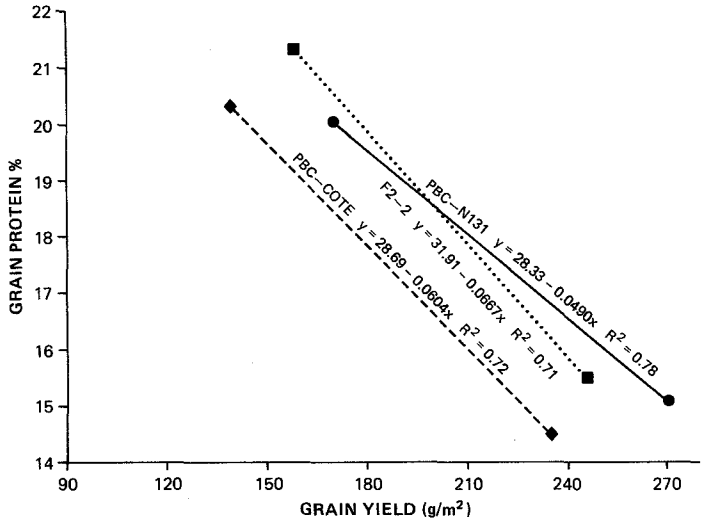


**Fig. 2.** Yield-protein relationships in 3 populations developed from cross 2

**Table 7.** Percent of desirable and undesirable progenies in each of 7 populations developed from 2 biparental crosses

| Population | Percent of progeny lines | |
|---|---|---|
| | Desirable | Undesirable |
| | Cross 1 | |
| F2-1 | 2.9 | 26.7 |
| IF2 | 9.5 | 33.3 |
| PBC-GLEN | 11.4 | 17.1 |
| PBC-SINT | 1.9 | 48.6 |
| | Cross 2 | |
| F2-2 | 33.3 | 16.2 |
| PBC-N131 | 43.8 | 1.9 |
| PBC-COTE | 32.3 | 19.0 |

provide a more efficient means of generating high yielding-high protein populations.

## Discussion

The four genotypes, Coteau, Sinton, Glenlea and NB131 were chosen partly because of their diverse (unrelated) parentage, and partly because of their suitability to represent much of the elite germplasm used in crossing programs in Western Canada. All four genotypes are well adapted to Manitoba, Canada, and have agronomic and quality characteristics that are typical of their respective market classes. The $IF_2$ and PBC populations were generated for comparison with

conventional $F_2$ populations and to determine which of the 4 methods of population development would provide a more efficient means of producing potentially superior genetic recombinants.

Since the seven populations were evaluated in one environment only, the estimates for some of the genetic parameters may have been biased due to genotype-by-environment interaction variances. Despite these limitations, however, the study has generated valuable information indicating that intermating did very little to alter the GY and GPC means, or to reduce the strength of the phenotypic and genetic correlations between the two traits. These results are at variance with the findings of other researchers (Miller and Rawlings 1967; Loffler et al. 1983) who showed that intermating would break undesirable linkage blocks, and thereby, would increase the frequency of desirable genetic recombinants in the resultant population. The reasons for the $IF_2$ population not meeting these expectations is not readily discernible from the information on hand. Pederson (1974) and Bos (1977) have discussed the idea that intermating would weaken negative genetic correlations only if it is enforced over several cycles and only when each cycle of intermating is preceeded by selection for superior progenies. In the present study, intermating was restricted to only one cycle and was not preceeded by selection. These factors may have contributed to the discrepancies between the results reported herein and those published elsewhere (e.g. Loffler et al. 1983). Nonetheless, our results are in agreement with other reports (Altman and Busch 1984; Frederickson and Kronstad 1985) showing lack of beneficial results from intermating.

The lack of sufficient differences between the $F_2$ and $IF_2$ populations for the majority of the genetic and statistical parameters considered in this study suggest that the feasibility of improving GY and GPC should be equally difficult in the $F_2$ and $IF_2$ populations. However, since intermating would add an extra generation to the time-scale, the additional labour and time requirements would make it unsuitable for use in most wheat breeding programs.

Briggs and Allard (1953), and more recently Dudley (1982) have suggested that partial backcrossing is more effective than selfing for recombination between linked genes because it allows for a smaller number of substitutions to occur without breaking existing combinations of desirable genes. Our results indicate that partial backcrossing does not always provide superior base populations. In each of the two crosses that we examined, partial backcrossing to the CHRS parent reduced mean GY, increased mean GPC, and produced only minor effects on variances, correlations and heritabilities of GY and GPC. It also reduced the frequency of desirable progenies to very low levels so as to make use of the resultant populations impractical.

Partial backcrossing to CU genotypes, on the other hand, significantly increased the mean GY, slightly depressed the mean GPC, and had only minor effects on the variances, correlations and heritabilities of either trait. Desirable progenies were more numerous and undesirable progenies less numerous in CU backcrossed populations than in other populations (conventional $F_2$, intermated $F_2$, and CHRS partial backcrosses) developed from the same biparental cross.

Some plant breeders have succeeded in obtaining favourable results from the use of partial backcrossing in their breeding programs. The Canadian spring wheat cultivar, 'Selkirk' was selected from a program in which restricted backcrossing was followed by selection for disease resistance, yield and bread-making qualities (Peterson 1958). Grafius et al. (1976) and Meredith (1977) have reported beneficial results from partial backcrossing in barley and cotton, respectively. These authors attribute their success to the method which tended to preserve the genetic integrity of an already proven cultivar while adding genetic factors from another cultivar, thus capitalizing on introgression and upgrading simultaneously. Based on the results from the present study, and the reports cited above, it is postulated that partial backcrossing to CU genotypes could provide a more efficient means of developing superior (high yielding-high protein) base populations.

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