ANALYSIS OF YIELD IN TWO HIGH YIELDING WHEAT VARIETIES

A Thesis

Submitted to

The Faculty of Graduate Studies and Research

The University of Manitoba

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

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1967

ABSTRACT

Yield in the two varieties Manitou and Pembina was studied in two experiments. In the first study, the yield and the yield components in the parents, the F1, the F2 and the two backcross F1's were analyzed. It was found that Manitou and the backcross F1 to it were higher yielding than Pembina. The two parents differed in the number of heads per plant and the thousand kernel weight. Yield and the yield components were influenced by additive gene action except in the case of thousand kernel weight. All the yield components were significantly correlated to the same extent with yield per plot while they differed in their degree of correlation with single plant yield. There was no heterosis in the cross probably due to the relationship between the two parents.

The object of the second experiment was to study the yield distribution in the F3 and the two backcross F2 populations. It was found that correcting the plot yield as percent of or difference from the adjacent check plots overcame the environmental effect. It was also found that the F3 population mean was between the two parental means, while the backcross F2 means were shifted towards the recurrent parent.

The three populations of percent of or differences from the checks indicated that there was more transgressive segragation in the backcross F2 to Manitou than in the F3. These results suggested that one backcross to the better parent would be of value in adding valuable genes to an already adapted variety.

ACKNOWLEDGEMENT

This study was made possible by a scholarship from the Government of the United Arab Republic for which the author wishes to express his sincere appreciation.

The author wishes to express his gratitude to Dr. L.E. Evans for helpful advice and assistance given him during the course of the research and the preparation of the thesis. Sincere thanks is expressed to Dean L.H. Shebeski, for his guidance and encouragement, Dr. G.I. Paul for his advice on the statistical analysis, Dr. A.K. Storgaard, Dr. S.B. Helgason for their constructive criticism and suggestions, and to Mr. F.S. Chebib for assistance in the computer programming.

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INTRODUCTION

To increase productivity or yield, is the major objective of most plant breeding programs. To aid the breeder in this aim, a knowledge of the distribution of yield genes in the population and an understanding of their behaviour would be invaluable.

In breeding for yield, Frankel (10) has described two distinct methods: "Overcoming limiting factor" and "Assembling productivity genes". The former involves breeding for improved agronomic characters such as disease resistance, lodging resistance, earlier maturity, etc. Breeders have had considerable success in this area due to the ease of selecting for these characters. Breeding for yield per se or "Assembling productivity genes" has proven much more difficult due mainly to the complexity of yield inheritance (i.e. number of genes and influence of environment).

The object of this study was to determine the distribution of yielding ability in a large population of F3 lines and to compare this distribution with that occurring in two equally large backcross F2 populations involving the same parents. Based on this information, the two parental varieties are compared relative to their yield contribution to the hybrid. The expression of yield is further analysed by means of regression analysis of yield and its components in the parents, F1, F2, and backcross populations.

LITERATURE REVIEW

Breeding for greater yield in cereals has become more difficult now that an apparent plateau has been reached. This may be due either to the inefficiency of breeding methods or to the lack of understanding of yield inheritance.

Early Generation Yield Evaluation

A number of independent investigations have been conducted to assess the value of early generation testing for predicting yield potential. In an early study of this nature, Harrington (15) studied a random population of 40,000 F2 plants of the cross *Marquis* X *Marqillo* in order to determine its potential as a source of desired recombinants. Earliness of maturity, plant height, and rust resistance were studied. During a five year period, this cross was handled as an extensive breeding investigation involving nursery, greenhouse and laboratory tests. The number of lines was reduced each year based on rust reaction, earliness, yield, and milling and baking quality. Six lines remained at the time of final testing. From this study, he concluded that the F2 analysis gave a reasonably accurate prediction of the value of the cross. He also stated that an F2 distribution may sometimes be misleading. Furthermore, linkage may be present as a distinct obstacle to the accomplishment of the breeding purpose.

Later (16) he studied six crosses of compatible varieties differing in yielding ability, to determine the usefulness of F2 heterosis as an indicator of yielding capacity. Unselected bulk F2 and F3 generations of each cross were placed in replicated half-rod-row yield trial along the parental varieties. The practical yielding value of the six crosses was ascertained later by replicated rod-row yield tests of selected lines in F6, F7, and F8. The results suggested that replicated bulk F2 tests may be used to indicate the yielding potential of wheat crosses, and that bulk F3 tests had a supplementary value in this regard.

Immer (18) studied barley populations and suggested that the average yield performance of different crosses may be determined by means of replicated yield trials in the F2 and F3 generations. Such trials may be used to discard certain crosses since the proportion of high-yielding genotypes in a low yielding cross is less than in crosses with a high average yield.

Grafius et al (14) found that selection for yield in F2 barley hybrids was not effective due to the large environmental and nonheritable genetic variance.

Fiuzat and Atkins (8) also demonstrated that selection for yield in the F2 generation was ineffective. According to Allard (2) the effect of environment on single plant yields is so great that attempts to select for heritable high yield in the F2 is futile.

Weiss, Weber and Kalton (35) working with soybeans found that early generation tests of bulk populations gave reasonably accurate evaluation of crosses for qualitative characters, but were of little value in predicting yield and maturity.

Atkins and Murphy (3) with hybrid oat populations, Peterson (28) and, Taylor and Atkins (34) using barley populations and Fowler and Heyne (9) working with winter wheat have all concluded that selection for yield in F2 was not effective.

Mahmud and Kramer (23) working with soybean hybrid populations, pointed out that good estimates of yield potential, of late generation segregates, from F3 lines could be obtained if the interaction of generations with seasons and spacing are avoided. They tested F4 populations made up of bulks of equal quantities of seed from individual F3 plants and tested the F3 and F4 lines in the same year to avoid season interaction. From the results they concluded that F3 lines provide good estimates of the yielding potential of late generation segregates.

Lupton (21) studied the predictability of yielding ability in combinations of six winter wheat varieties, based on the analysis of yielding capacity and yield components in the F1 and F2 generations. The validity of these predictions was estimated by comparing them with estimates of mean yield and yield variance of trials in F3 and F4 of randomly selected F2 plant progenies. He found that F1 and F2 trials were of little value in assessing these crosses in later generations, because the sensitivity of the test is reduced as the degree of homozygosity of the crosses is increased. He also pointed out that analysis of F3 and F4 gives estimates of the mean and genetic variance of each cross which provides a direct indication of the degree of transgressive segregation shown by each parental combination and hence of the likelihood of obtaining high yielding segregates.

McKenzie and Lambert (25) studied two barley crosses to determine whether or not testing families in F3 for yield and other characters was a reliable index of their breeding potential. From the correlation coefficients obtained between yield in F3 lines and their related F6 families for the two crosses, they concluded that early generation tests are more likely to be useful in crosses where there is a wide range in yield of the segregates.

Heritability of Yield

The heritability of yield has been studied in many plants.

Worzella (37) stated that yield in wheat is difficult to analyze and that it may be regarded as the ultimate expression of all environmental conditions and inherited factors.

Kronstad et al (20) showed that the breeder of self-pollinated crops can utilize only that segment of the total genetic variability which results from the action of additive genes and epistatic interactions which behave additively, because only these types of gene action can be retained by subsequent inbreeding.

Frey (13) concluded that yield in oats is due to additive gene action, and that epistatic effects behave additively because of gene linkage.

Whitehouse (36) studied the behaviour of four wheat varieties in terms of the following characters, weight per grain, grain per spikelet, spikelets per ear, ears per plant and yield of grain per plant. From the results of this study, it was emphasized to him by Mather, that since yield is the arithmetic product of several characters, each of which has an additive gene system, then the gene system controlling yield is multiplicative. They stated that if this is so, then there is nothing special about any particular component of yield, and breeding should be directed towards accumulating as many desirable genes as possible. This means that in effect the gene system should be treated as if it were additive.

Lupton (21) studied the yielding capacity in a diallel cross involving six varieties of winter wheat using two methods of planting, space planting and drilled trials. He found that in the drilled trials, high yielding capacity is inherited as a dominant character. In the space planted trial, on the other hand, dominance was not evident. He concluded that the apparent difference in the mode of inheritance must result from the contrasting envirnments in which the two trials were grown.

McNeal (26) demonstrated that heritability values for yield and the various yield components, were so low that selection for these characters in the F2 generation is of doubtful value.

Yield Components

Grain yield has for sometime been considered a complex character and during the last 30 to 40 years, many attempts have been made to analyze it into its components (1,11,12,13,19).

Lupton (22) showed that the study of these components can aid the breeder in selecting suitable parental combinations.

Whitehouse (36) showed that in a hybrid population, yielding ability can be estimated by measuring these components and calculating discriminant functions in which each character is weighted according to the contribution it makes to yield.

Johnson *et al* (19) studied yield components in four winter wheat varieties and found that adverse interactions of yield components exist. They concluded that individual yield components are merely indicators of the complex metabolic and physiologic processes of the wheat plant as is yield itself, and therefore have little value to the breeder that yield alone does not provide. They also concluded that, since yield is the product of yield components, it provides little specific information about the component relationships on which it depends other than the fact that they exist.

Rosenquist (29) found that the number of fertile tillers per plant was closely related to the plant yield, and that it was inherited as a partially dominant character.

Fadrohns (7) studied the productiveness of some varieties of wheat, barley and rye, and in particular the relation between yield, tillering capacity, weight and number of grains per ear, and thousand grain weight. He found that yield per unit area of all the above cereals depended upon a combination of good tillering capacity and productive ears, the latter characteristic being associated with high thousand grain weight.

Stoskopf and Reinbergs (32) conducted an experiment to study the relationship among tillers, grains per head, and grain weight and their influence on yield in oats and barley. They found that grains per head, rather than tillers per plant, was the most reliable component to use in estimating yield. However, both tillering rate and grain per head were variable and found to be influenced by variety, seeding rate, and soil fertility levels. Grain weight was less influenced by these factors, and contributed little to the yield variation. Tillering was negatively correlated with grains per head.

Sprague (31) found a high negative correlation between yield per unit area and grain yield per spike and kernel weight in wheat. There was no relationship between the number of grains per spike and grain weight, which led him to conclude that both of these characters were of about equal importance in influencing yield.

Bridgford and Hayes (4) found that yield in wheat was positively correlated with thousand kernel weight.

Shebeski (30) found that each of the components of yield in wheat was significantly correlated with yield, but that none of the components were transmitted from parent to hybrid in a consistent manner indicating that the component values of the parents were not useful in predicting relative hybrid performance.

Heterosis in Wheat

An excellent review of heterosis in early generations of wheat was made by Briggle (5). In his review, it was reported that the F1 yielded up to 84% more than the higher yielding parent. He found that in virtually all the experiments conducted, plants had been space planted and very small populations were used. Therefore, "caution must be exercised when considering reported instances of hybrid vigor in wheat".

McNeal et al (27) found that the F1 and F2 populations were usually intermediate to the parents, and that in no case did they exceed the high parent significantly. They concluded that closely related parents may give hybrid populations showing little or no heterosis.

Briggle et al (6) showed that the F1 means for yield were usually significantly greater than the mean of the respective parents. They also found that heterosis was expressed for grain per spike, kernels per spike and thousand kernel weight.

MATERIALS AND METHODS

The two parents used in this study were the varieties Manitou and Pembina. Manitou was derived from the complex cross (Thatcher^{7}-Frontana X Thatcher^{6}-Kenya Farmer) X (Thatcher^{6}-P.I. 170925) and Pembina was selected from the cross Thatcher X ((McMurchy X Exchange) X Redman^{3}). Both are resistant to stem rust, and Manitou is only moderately resistant while Pembina is susceptible to leaf rust. Both varieties are recommended for production in Manitoba.

Two thousand F1 seeds and two thousand seeds of each of the BC F1's were produced by hand crossing.

In the first experiment the two parents, the F1, the two backcross F1's and a random F2 population were grown in a six replicate, randomized block design in the field in 1966. Plots consisted of two rows twelve feet long and one foot apart with the plots two feet apart. Eighty-five seeds were sown per row. Border plots of Manitou were sown to overcome border effects.

At maturity, twenty plants were pulled at random from each plot (120 plants per treatment). Spikes per plant, seeds per spike, seeds per plant and thousand kernel weight were determined. From this data, average yield per plant, seeds per spike, and seeds per plant were calculated for each plot. Total plot yield was also determined by adding the yield of the twenty plant sample to the remaining plot yield.

For each of the characters studied, the following analysis of variance was performed:

SOURCE OF VARIATION	DEGREES OF FREEDOM
Replicates	5
Treatments	5
Experimental Error	25
TOTAL:	35

Where the treatments mean square was significant, treatment means were compared using the Least Significant Differences. In addition, comparisons were made of the F1, F2, and the backcross F1's with the mid-parent values for each character studied. The differences between the mid-parent means and the hybrid means were tested for significance by a "t" test using the standard error obtained from the analysis of variance. For example, to test the significance of the difference between the F1 mean and the mid-parent value, a "t" value was calculated as shown below,

$$t = \frac{\overline{F1} - \overline{MP}}{\sqrt{\frac{MSE}{6} + \frac{MSE}{12}}}$$

where $\overline{F1}$ is the mean of the F1 generation, $\overline{MP}$ is the mid-parent value, MSE, the mean square for error.

Scaling for gene action for each character was studied by comparing the mean measurements of F2, and backcross F1's to their theoretical value which Mather (24) expressed as follows:

$$F2 = \tfrac{1}{4}\,(\overline{P1} + \overline{P2} + \overline{2F1})$$

$$\overline{B1} = \tfrac{1}{2}\,(\overline{F1} + \overline{P1})$$

$$\overline{B2} = \tfrac{1}{2}\,(\overline{F1} + \overline{P2})$$

The differences between the observed and theoretical values was tested using the formula:

$$t = \frac{\overline{X}_o - \overline{X}_r}{\sqrt{\frac{MSE}{r_o} + \frac{MSE}{r_t}}}$$

where $\overline{X}_o$ is the mean of the observed value $\overline{X}_r$ the mean of the theoretical value, MSE the mean square for error from the analysis of variance, r_o the number of replications of the observed values and r_t the total number of replications for calculating the theoretical values (24 for the F2 and 12 for the backcrosses).

The calculated t value was compared to the tabulated t value with the error degrees of freedom.

Simple correlation coefficients were calculated for the characters in order to determine the degree of association between them.

The second experiment was a study of yielding capacity in F3 lines compared to the yield of the BC1F2 to each parent. One thousand seeds were taken at random from F2 and from both BCF1 generations; these three thousand seeds were space planted in beds in the greenhouse with 4.5" between plants in the row and 6" between rows. At maturity, each plant was harvested, threshed and its seeds counted. The number of seeds per plant ranged from 34 seeds to 460 seeds. Plants that produced less than 100 seeds were discarded, and the remainder were classified into seven groups having 100, 150, 200, 250, 300, 350 or 400 seeds.

Three seeding rates were used namely, 50, 75 and 100 seeds per twelve foot row with two row plots. On this basis, plants producing 200 seeds or less were sown in single plots whereas higher yielding plants were replicated (i.e. plant yielding 250 seeds would yield one 75 seed per row plot and one 50 seed per row plot).

Three field nurseries were planted, one for each tested generation. Commercial seed of the variety Manitou was used in the check plots. The nursery was arranged so that each hybrid line was adjacent to a check plot. In other words, every check plot was followed by two hybrid plots. Each nursery was sub-divided into sub-nurseries based on seeding rate. The check plots had the same seeding rate as the adjacent hybrid lines. Replicated lines were sown at random among the unreplicated lines.

There were 892 hybrid plots in the F3 nursery, 485 in the backcross F2 to Manitou nursery, and 519 in the backcross F2 to Pembina nursery.

Pembina plots were planted randomly in each nursery at the level of ten percent of the number of hybrid plots in each sub-nursery. At maturity, plots were harvested and yields determined. The yield of each hybrid and of Pembina was corrected by each of the following methods:

(1) Percent of the adjacent check plot yield,

(2) Difference from the adjacent check plot yield,

(3) Corrected additively for the sub-populations differences based on their means using the formula:

$$Aij = Yij + (\bar{Y}j - \bar{Y})$$

where Aij is the corrected yield of plot i in the $j^{th.}$ sub-population, Yij the actual yield of the same plot, $\bar{Y}ij$ the mean yield in the sub-population j, and $\bar{Y}$ the overall weighted mean yield in the population. This correction was computed for all plots.

The means and standard errors for the actual yields of the plots in each sub-population were computed. The means and standard errors for the corrected plot yields were also calculated. Frequency distribution tables were constructed for each population in order to study the distribution of yield in the three large populations and the two parental varieties.

RESULTS AND DISCUSSION

Experiment I

The data from the characters studied in the two parents, the F1, the F2, the two backcross F1's and the mid-parent values are presented in Table I. The analysis of variance for each character studied is presented in Table II.

Heads per Plant:

Pembina possessed significantly fewer heads per plant than Manitou, the F1 or the backcross to Manitou. Comparisons of the F1, the F2, and the backcrosses to the mid-parent value showed no significant differences. The scaling test for gene action showed no significant differences between the theoretical and observed values, (Table III), indicating a degree of dominance, little heterosis and additive gene action for this character.

Seeds per Plant:

Pembina had the lowest number of seeds per plant, but was not significantly different from Manitou. The F1 and the backcross to Manitou were significantly higher than Pembina and the mid-parent value. The scaling test for gene action indicated that a degree of dominance and additive gene action were operative, (Table III).

Seeds per Head:

There were no significant differences for this character. Scaling tests suggest additive gene action, (Table III).

Thousand Kernel Weight:

Manitou kernel weight was higher than Pembina, the F1 or the backcrosses. The F1 kernel weight was higher than that of the F2 and the backcrosses to Pembina. Both the F1 and the backcross to Manitou had a lower thousand kernel weight than the mid-parent. The F2 and the backcross to Pembina were significantly lower than the mid-parent indicating a degree of dominance for the genes affecting this character. Similarly because the backcross to Manitou was significantly lower than the mid-parent value and lower than Manitou, non-allelic interaction must be involved. This is further suggested by the scaling test for additive gene action, (Table III).

Plant Yield:

Manitou and the backcross to Manitou were significantly higher yielding than Pembina. The F1 and the backcrosses did not differ significantly from the mid-parent value. Scaling tests of the F2 and backcross data suggest additive gene action.

Yielding Capacity:

Manitou was significantly higher yielding than Pembina or the backcross to Pembina as were the F1 and the F2. However, deviations from the mid-parent value were not significant. The scaling test for gene action showed no significant differences between the theoretical and observed values, (Table III).

This indicates that yielding capacity results from additive gene action with some degree of dominance and very little or no heterosis. It also indicates that Manitou carries more desirable genes for high yielding capacity than Pembina.

TABLE I

MEANS OF CHARACTERS STUDIED IN MANITOU, PEMBINA, THE F1, THE F2, AND THE BACKCROSSES AND THE MID-PARENT VALUES

CHARACTER	MANITOU	PEMBINA	MID-PARENT VALUE	F1	F2	BACKCROSS F1 TO MANITOU	BACKCROSS F1 TO PEMBINA
Heads per plant	7.43	6.07	6.75	7.59	7.20	7.57	7.02
Seeds per plant	223.3	196.0	209.6	247.5	231.9	240.9	226.3
Seeds per head	30.04	32.4	31.2	32.4	32.8	31.9	31.6
1000 k.wt. (in grams)	28.25	25.96	27.10	26.82	24.83	25.81	24.74
Plant yield (in grams)	6.754	5.434	6.094	6.522	6.123	6.745	5.735
Plot yield (in grams)	858.4	677.5	768.5	796.3	786.2	757.8	713.8

TABLE II

ANALYSIS OF VARIANCE FOR CHARACTERS STUDIED

Source of Variation	Degrees of Freedom	MEANS SQUARES					
		Heads per Plant	Seeds per Plant	Seeds per Head	1000 k.wt.	Yield per Plant	Yielding Capacity
Replicates	5	1.040	5832.60	70.51	2.02	5.261	55212.79
Treatments	5	1.958*	1938.20*	5.77	10.45**	1.817**	24576.00**
Error	25	.716	620.87	6.85	.78	.556	4892.81
Coefficient of Variability		11.8%	10.9%	8.3%	3.4%	11.9%	9.2%

* Significant at the 5% level.

** Significant at the 1% level.

TABLE III

THE SCALING TEST FOR GENE ACTION FOR EACH CHARACTER

CHARACTER	F2			Backcross to Manitou			Backcross to Pembina		
	Observed	Theoretical	Difference	Observed	Theoretical	Difference	Observed	Theoretical	Difference
Heads per plant	7.20	7.17	0.03	7.57	7.51	0.06	7.02	6.84	0.18
Seeds per plant	231.9	228.6	3.3	240.9	285.4	-44.5**	226.3	221.9	4.4
Seeds per head	32.8	31.8	1.0	31.9	31.2	0.7	31.6	32.4	-0.8
1000 k.wt.	24.83	26.71	-1.88**	25.81	27.53	-1.72**	24.74	26.39	-1.65*
Yield per plant	6.123	6.308	-0.185	6.745	6.639	-0.104	5.735	5.978	-0.243
Yield per plot	787.2	784.6	2.6	757.8	827.3	-69.5*	713.8	736.9	-23.1

* Significant at 5% level.

** Significant at 1% level.

Relationships between Characters Studied:

Simple correlation coefficients between the characters studied are presented in Table IV. All correlation coefficients are positive except for that between heads per plant and seeds per head. Significant correlations were found between all yield components and plot yield. Individual plant yield was also significantly correlated with all other characters studied. The thousand kernel weight was significantly correlated only with yield per plant.

Pairs of correlation coefficients which were correlated with plot yield were compared using the "Z" transformation method (33). Inasmuch, as no significant differences were obtained between pairs of correlation coefficients, it would appear that in this material yield components were equal in their effect on plant yield.

Seeds per plant and heads per plant were more highly correlated with single plant yield than were seeds per head and thousand kernel weight. However, there was no significant difference between the correlation of single plant yield with each of seeds per head and thousand kernel weight.

TABLE IV

SIMPLE CORRELATION COEFFICIENTS BETWEEN CHARACTERS STUDIED

	Heads per plant	Seeds per plant	Seeds per head	1000 k.wt.	Yield per plant
Seeds per plant	0.7118**				
Seeds per head	-0.1341	0.5846**			
1000 k.wt.	0.2450	0.2175	0.470		
Yield per plant	0.7380**	0.9229**	0.4710**	0.4055*	
Yield per plot	0.3584*	0.4940**	0.3327*	0.5080**	0.5080**

* Significant at 1% level.

** Significant at 5% level.

Experiment II

The Analysis of Replicated F3 Plots:

The replicated plots were compared using the "t" test for paired variables , (33) to test the hypothesis that the means of differences between pairs of plots presented as actual yields, and percentages of, or differences from, adjacent checks were zero.

The results are presented in Table V. No significant differences existed between replicates with the same seeding rate. There was however, a highly significant difference between replicates having differences in seeding rate at the 50 versus 75 seeds per row rate but not at the 75 versus 100 seeds per row level. In no cases were their significant differences when the means of percent of the adjacent checks, or means of differences from the adjacent checks were tested. This indicates that the use of the percentages of or the differences from the adjacent checks overcome differences due to environmental factors including differences in seeding rates.

TABLE V

MEAN DIFFERENCES AND STANDARD ERROR BETWEEN PLOTS

OF THE SAME GENOTYPE

COMPARISON	Actual Yield	Percent of Check	Difference from Check
Plots of 50 seeds vs. 75 seeds per row (50 pairs)	-83.30±15.88**	2.70±2.51	-72.09±48.81
Plots of 75 seeds vs. 75 seeds per row (17 pairs)	32.47±35.47	-0.855+4.30	27.30±18.64
Plots of 75 seeds vs. 100 seeds per row (11 pairs)	-46.73±37.56	-9.08±6.67	-7.50±48.32

** Significant at 1% level.

Study of Hybrid Populations:

The means for each of the sub-populations and the two parents are presented in Table VI. Because of the small number of plots in each sub-population, and because of the differences in seeding rates, the means of the plot yields were corrected by the additive method, (Table VII). The means of the Manitou populations in the three nurseries were tested using the "Student's t" test (33) and found to be significantly different as were the means of the Pembina plots yields. These results showed that each nursery should be studied as a unit composed of three different populations.

The yield distribution in the F3 nursery presented in Figure 1 indicates that the F3 population falls between the two parents and is significantly different from them, (Table VIII).

The yield distribution in the backcross to Manitou nursery, is presented in Figure 2. The mean plot yield for this population was significantly higher than the mean of Pembina, but not significantly different from the mean of Manitou, (Table VIII).

The yield distribution of the backcross to Pembina nursery is presented in Figure 3. The mean plot yield for the backcross to Pembina differed significantly from that of Manitou, but not from that of Pembina, (Table VIII).

TABLE VI

THE MEANS OF THE PLOT YIELDS IN THE SUB-POPULATIONS

IN THE THREE NURSERIES

	F3 NURSERY			BACKCROSS TO MANITOU NURSERY			BACKCROSS TO PEMBINA NURSERY		
Sub-Population	Manitou	Hybrid	Pembina	Manitou	Hybrid	Pembina	Manitou	Hybrid	Pembina
50 seeds/row Plots	680.528 ±6.0105	631.502 ±5.1523	564.891 ±13.6155	526.899 ±8.4436	603.817 ±6.9786	509.947 ±17.7895	813.440 ±11.0184	668.132 ±8.0998	694.947 ±34.0892
75 seeds/row Plots	779.134 ±7.1998	714.771 ±6.2874	608.470 ±14.3264	672.551 ±6.9871	662.824 ±7.4987	581.727 ±20.5986	854.696 ±10.3576	749.839 ±7.6957	709.665 ±19.987
100 seeds/row Plots	695.545 ±10.0656	638.646 ±8.827	544.636 ±19.7475	622.327 ±16.7291	622.1511 ±12.755	577.760 ±32.3540	509.238 ±25.1370	489.080 ±17.3752	508.636 ±21.8984

TABLE VII

THE MEANS OF THE CORRECTED PLOT YIELDS USING

THE ADDITIVE MODEL FOR THE THREE NURSERIES

NURSERY	MANITOU	HYBRID	PEMBINA
F3	621.40 ± 4.3856	566.59 ± 3.7876	479.73 ± 9.0563
Backcross to Manitou	503.903 ± 4.2934	524.54 ± 6.5745	452.22 ± 11.6783
Backcross to Pembina	657.32 ± 6.4056	548.65 ± 9.1332	550.00 ± 19.3755

TABLE VIII

THE CALCULATED "t" VALUES FOR TESTING THE DIFFERENCES

BETWEEN THE PLOT MEANS IN THE THREE NURSERIES

POPULATION	MANITOU	PEMBINA
F3	9.417**	8.837**
Backcross F2 to Manitou	1.248	3.213**
Backcross F2 to Pembina	3.142**	0.466

** Significantly different at the 1% level.

Fig. 1. Yield distribution of the populations in the F_3 nursery.

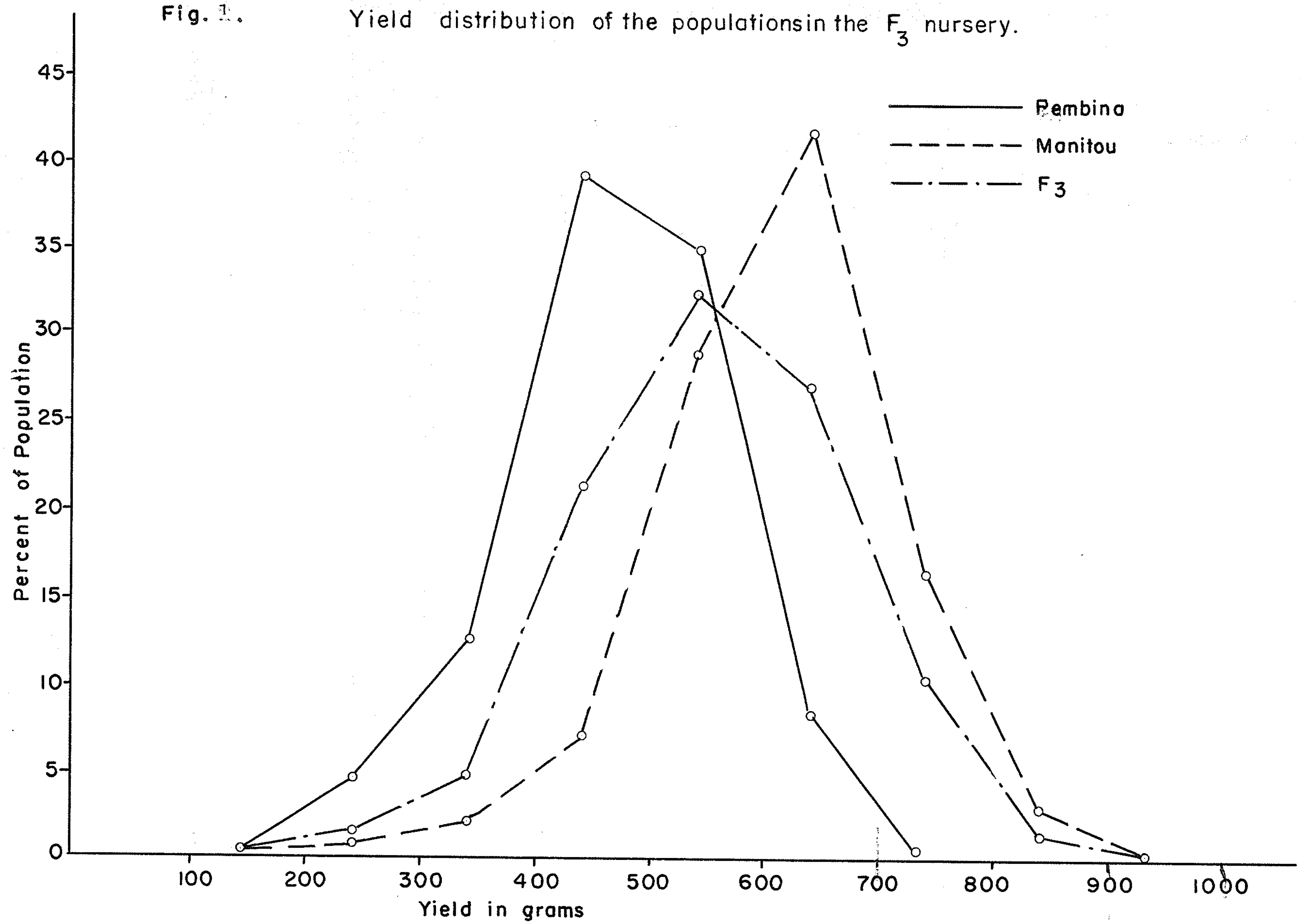


Fig. 2. Yield distribution of the populations in the backross to Manitou nursery.

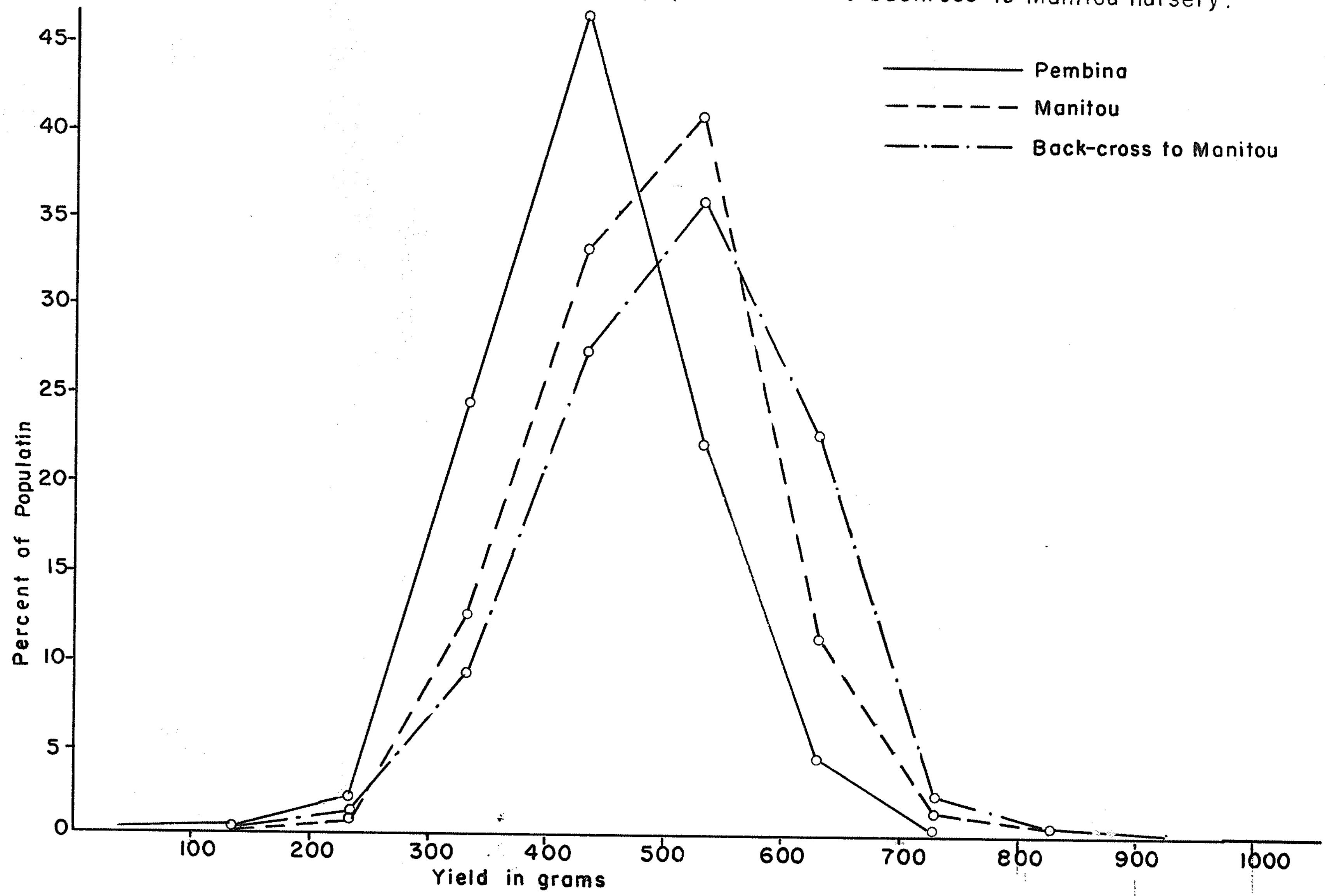
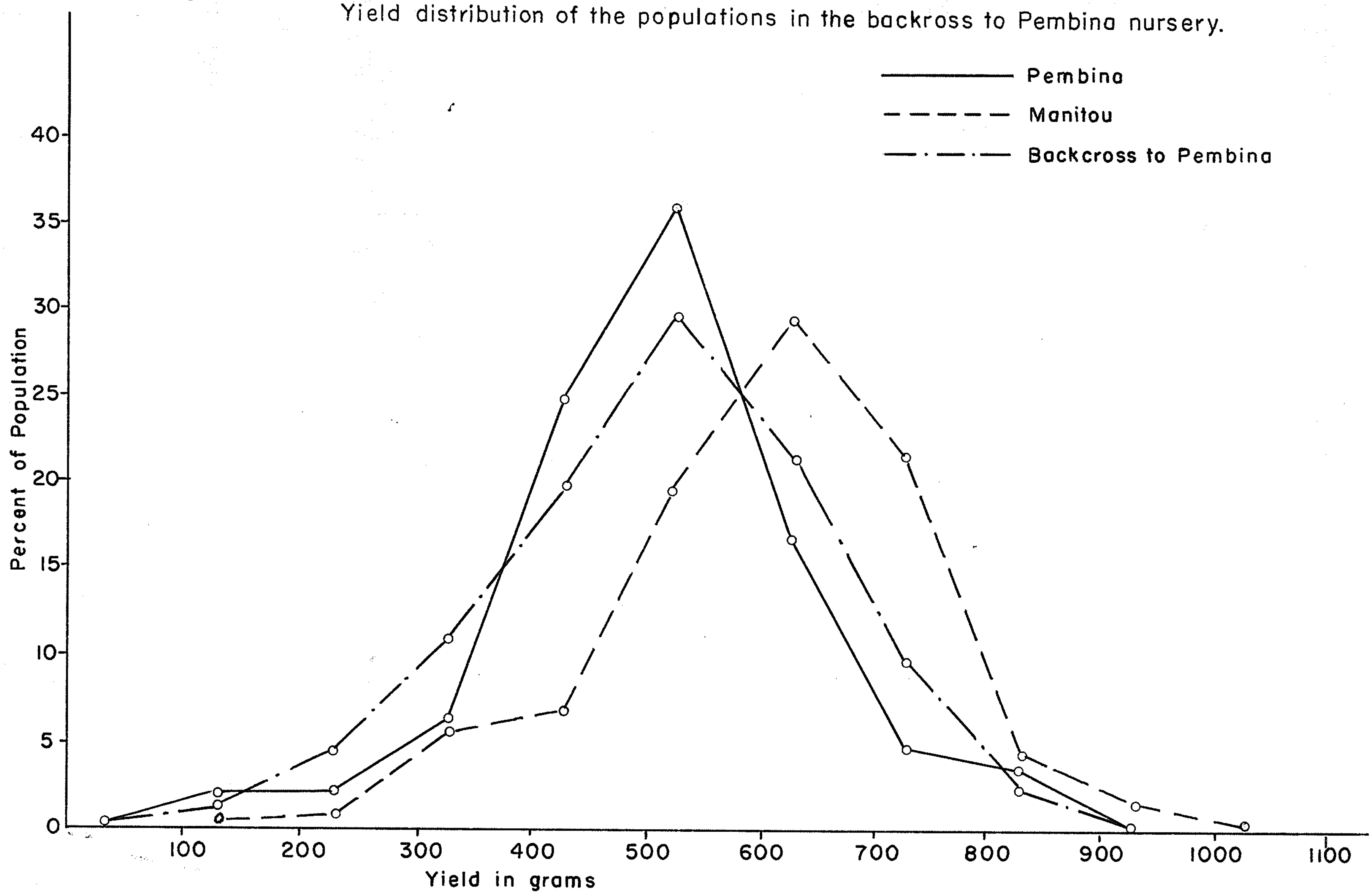


Fig. 3.

Yield distribution of the populations in the backross to Pembina nursery.



Populations Expressed as Percentage of or Difference from Check

From the results obtained by testing the replicated F3 plots, the three populations of percent of as well as the three populations of differences from the check could be compared together. Table IX presents the means and the standard deviations for the three hybrid populations as percent of and differences from the check.

TABLE IX

MEANS AND STANDARD DEVIATIONS OF THE POPULATIONS OF PERCENT AND DIFFERENCES

	PERCENT OF CHECK		DIFFERENCE FROM CHECK	
	MEAN	STANDARD DEVIATION	MEAN	STANDARD DEVIATION
F3	92.188±0.4013	19.82	-67.27±5.788	172.984
Backcross F2 to Manitou	106.385±1.205	24.13	32.64±8.567	188.245
Backcross F2 to Pembina	88.889±0.5667	17.15	-101.85±5.978	136.200

Figure 4 presents the three populations of percent. The mean percent of the backcross to Manitou is the highest followed by the mean of the F3 and the backcross to Pembina. "t" values for the comparisons are, 11.64, 3.464, and 13.058 for the percent F3 vs. the backcross to Manitou, the percent F3 vs. the backcross to Pembina, and the backcross to Manitou vs. the backcross to Pembina respectively.

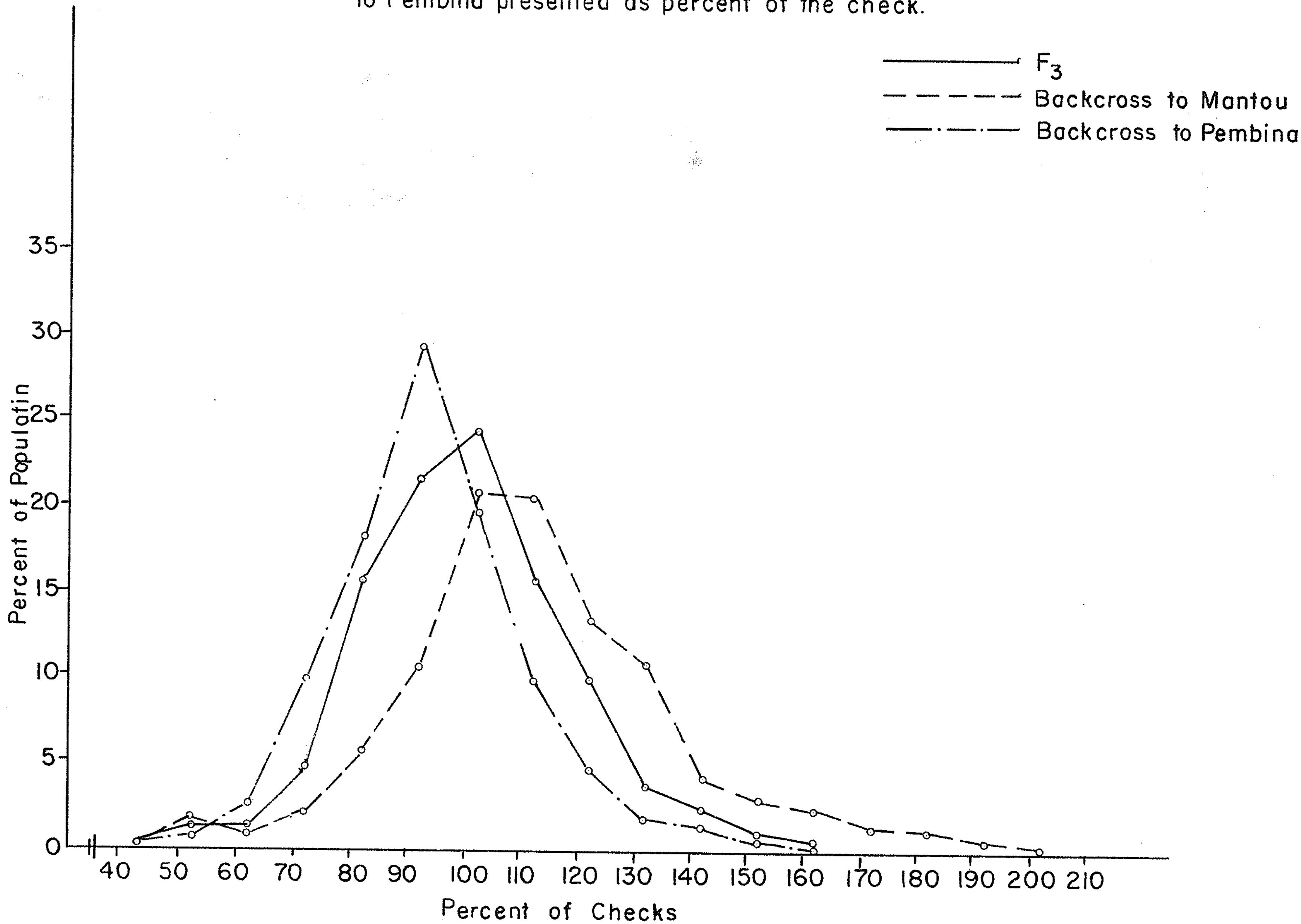
The highest ten plots percentage-wise in the three populations are presented in Table X. The means of these ten in the three populations were found to be 178.63 percent, 153.513 percent and 143.46 percent for the backcross to Manitou, the F3 and the backcross to Pembina, respectively.

TABLE X

THE HIGHEST TOP TEN PLOTS PRESENTED AS PERCENT OF THE CHECK IN THE THREE POPULATIONS

Backcross to Manitou	209.38	197.73	189.41	189.29	177.93
	170.66	168.40	161.63	161.63	160.73
F3	175.50	169.57	157.00	152.83	151.78
	147.24	145.97	145.28	145.19	144.83
Backcross to Pembina	167.23	167.05	159.64	144.67	140.74
	133.59	131.82	131.48	130.44	127.29

Fig. 4. The three populations of F_3, backross to Manitou and backross to Pembina presented as percent of the check.



The means and standard deviations for differences from check plots in grams are presented in Table IX. The "t" values for testing the differences between the three means were, 9.660, 4.129, and 12.793 for the F3 population vs. the backcross to Manitou, the F3 population vs. the backcross to Pembina and the backcross to Manitou vs. the backcross to Pembina, respectively. Figure 5 shows graphically the three populations together.

The highest top ten plots in their differences from the check in the three populations are presented in Table XI. The means for these top tens are, 328.7, 275.2 and 191.5 grams for the backcross to Manitou, the F3 and the backcross to Pembina respectively.

TABLE XI

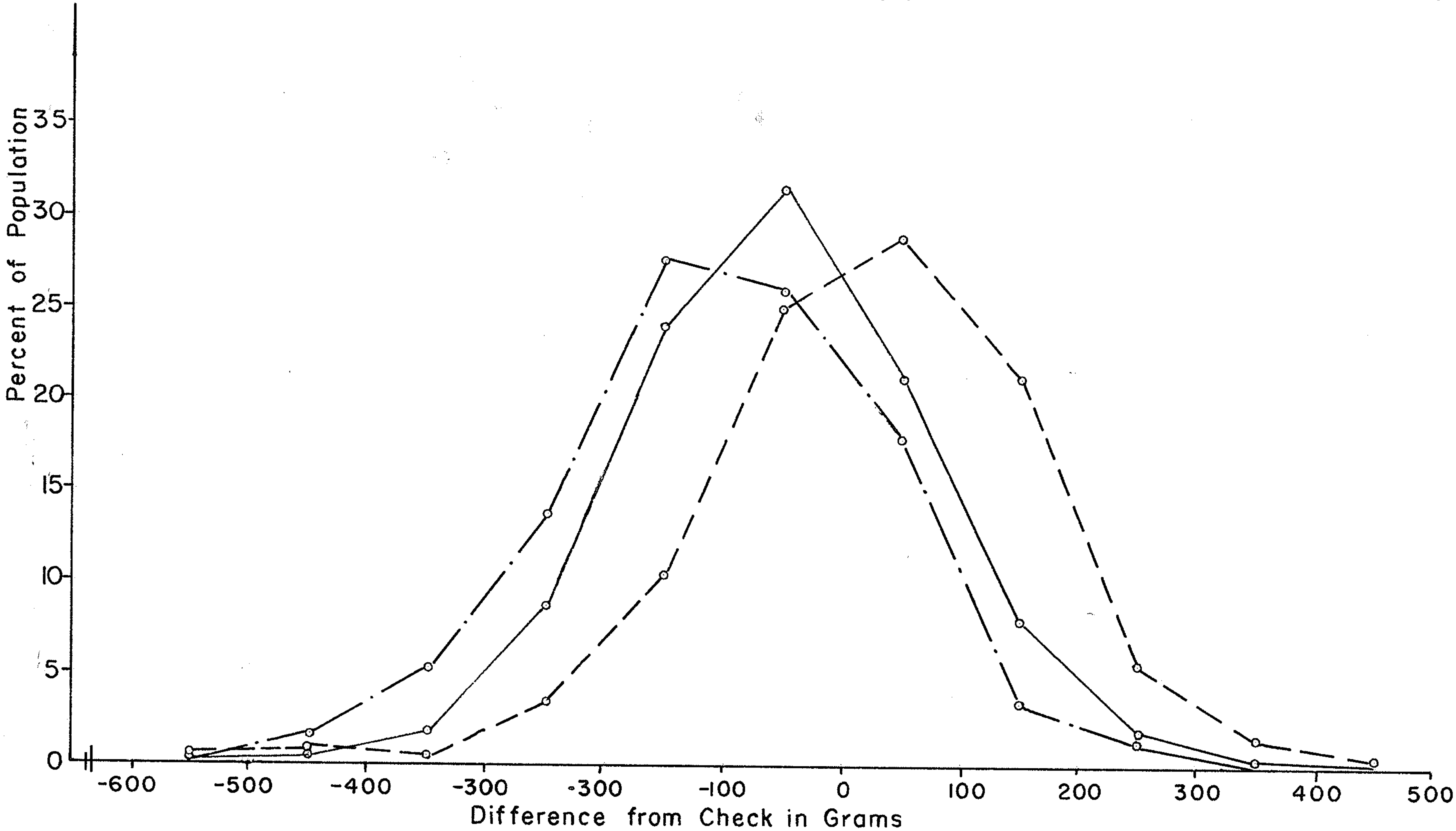
THE HIGHEST TOP TEN PLOTS PRESENTED AS DIFFERENCES FROM THE CHECK PLOTS IN THE THREE POPULATIONS

Backcross to Manitou	430	380	350	339	318	310	305	295	280	280
F3	370	305	300	285	280	277	270	240	235	200
Backcross to Pembina	295	240	238	215	205	200	140	132	130	120

In the F3, 7 of the 10 lines chosen when the material was expressed as a percentage of the check were also chosen when the top 10 lines were picked from the material expressed as a difference from the check. Although the same line was not chosen as the top line in both instances, there was little difference in their ranking of material.

In the two backcrosses, 8 of the 10 lines chosen in each behaved the same as those of the F3.

Fig. 5. The three populations of F_3, backross to Manitou and bӑckross to Pembina presented as differences from the check.



GENERAL DISCUSSION AND CONCLUSIONS

Yield in this study has been regarded as a complex character depending on several yield components, and controlled by a large number of interacting genes. By growing a number of generations simultaneously in the same field, tests could be made to determine additive, dominance, and interacting genic effects.

In the first experiment, the object was to determine the differences between the two varieties in yield and yield components and the relationship between them. In the second experiment, the object was to study the distribution of yield in the large populations of F3 and the two backcross F2 generations.

The Yield Components

The results indicated that the two parents differ significantly only in the number of heads per plant, and the thousand kernel weight. Manitou was the higher parent in both characters. The number of heads per plant was found to be controlled by some form of dominance and additive gene action which is in agreement with results of other investigators (1,29). The thousand kernel weight was inherited in a dominant manner but non-allelic interaction exists which does not agree with Aastveit's report (1).

The correlation coefficients of all the components studied were significantly correlated with plot yield which is in agreement with other reports (30,4). The correlation coefficients for the yield components and single plant yield were significantly correlated, but they differ significantly in the degree of correlation.

The only yield components showing variability in this cross are the number of heads per plant and the thousand kernel weight. The correlation coefficient between these two characters is positive but not significant, meaning that selection for both characters is possible. However, the small amount of variability present, would probably allow little progress in selecting directly for plant yield.

Heterosis

Hybrid wheat became an objective of many wheat breeders in recent years. For this reason, heterosis in this cross has been studied since the two varieties are high yielders.

Hayes (17) defined heterosis as the increase of the F1 over the mean of the parents or over the better parent. Briggle (6) judged the occurrence of heterosis if the mean of the F1's was significantly above the mean of the respective parents.

Regardless of what definition is used, if commercial production of hybrid wheat to become a reality, increased yield over "inbred" varieties should be more than sufficient to offset the cost of seed production (30). In this cross, the F1 generation did not exceed the mid-parent value. Although Pembina has been considered a variety of good general combining ability in a previous report (30), it is not of good specific combining ability with the variety Manitou due probably to the relationship of the two varieties.

The Use of Adjacent Check Plots in the Nursery

The replicated plots of different seeding levels were tested for the differences in their yield. The actual yields for 50 pairs of replicated plots of two levels of seeding (50 and 75 seeds per row), showed significant differences in the actual yield. These differences are either due to the differences in seeding levels or to environmental effects or both. When the percent of or the difference from the adjacent check plot of the same level of seeding were tested, there was no significant differences.

Since yield is a quantitative character, its phenotypic expression is a result of genotype environmental interaction and therefore it could be represented as follows:

$$Y = M + a + e + (ae)$$

where Y is a phenotype, M the general population mean, a the genotype, e the environmental factors and (ae) the genotype environmental interaction (2).

In a wheat nursery where a large number of lines are growing, the yield expression could be largely influenced by location. By growing a check plot adjacent to each line, the environmental differences such as soil fertility will be minimized if the yield of the line is evaluated as a percent of or difference from the check. In this case, the formula becomes:

$$Y = M + a + (ae)$$

The interaction may still exist but it should be small.

When selection was done for the highest yielding plots using the actual yield or as corrected by the methods mentioned, no one plot was found to have the highest value in all cases. Percent of and the difference from the check was very similar but not identical. To reach a final conclusion as to which method is the best in evaluating the plot yield, the subsequent generation would have to be studied.

Yielding Capacity

Yield as stated before is a heritable character, influenced by a large number of genes. The mean of yield per plot in the first experiment indicated that the variety Manitou is significantly higher yielding than Pembina or the backcross F1 to Pembina. The F1, and the F2 plot yield were also significantly higher than Pembina.

When the F1 plants were backcrossed to the two parents, the F1's did not differ significantly from each other, or from the F1 itself but Manitou did differ significantly from the backcross to Pembina.

Since the backcross increases the frequency of the recurrent parent genes, and since yield is affected by a large number of genes, the proportion of individuals which would be reconstituted exactly to the recurrent parent would be very small. Nevertheless, the backcross should shift the mean of the character towards the recurrent parent. From the results obtained, it could be concluded that Manitou carries more desirable genes for yield than does Pembina.

The mean of the F3 lines was intermediate between the two parents as would be expected due to the reduction of the heterotic effect. The backcross to Manitou was close to Manitou and significantly higher than Pembina. The backcross to Pembina was close to Pembina and significantly lower than Manitou.

When the populations of percent of and differences from the checks were compared to each other, it was clear that the mean of the backcross to Manitou showed an increase over the mean of the F3 population, while the backcross to Pembina was lower than the F3. This increase or decrease was small but significant due probably to the small number of gene differences separating the parents.

Since the same amount of homozygosity exists in the F3 and the backcross F2 generation ($(3/4)^n$) where n is the number of gene pairs, then the return of the means of the backcrosses to the means of the parents is due largely to the increase in the frequency of the parental genes which behave additively.

Such results would lead to the conclusion that if the goal is to increase the yielding capacity of the variety Manitou, by adding desirable genes for yield the variety Pembina may not be of value in such improvement.

Also it could be concluded that in any breeding program for higher yield, the choice of the parents is of great value. If the F1 of the parents does not show heterosis which could be a measure for specific combining ability, there may be no use in carrying such a cross into subsequent generations.

In breeding for high yielding capacity, there has not been much progress in cererals, due to the methods and procedures used by most plant breeders, altough it is believed that the possibility exists.

It has been demonstrated by several investigators (2,3,8,9,14, 28,34,35), that selection for yield in the F2 generation is not effective.

However, others (21,23,25) concluded that F3 lines provide good estimates of the yielding potential of later generations. Since there is a large number of genes affecting yield in wheat, it is impossible on the basis of probability, to capture all of the desirable ones in one line in the F3 generation. If the F1 generation is backcrossed to the better parent, then some of the desirable genes in the parent will be fixed in the homozygous condition while the rest of the desirable genes will be segregating in the selfed generation of the backcross F2. Such backcrosses will recover the recurrent parent with some transgressive segregation which will push the whole variation towards the good parent. With such a procedure, if the breeder grows one thousand backcross F2 lines, then it should be possible to increase the desirable genes in one line and research higher productivity, particularly with well-adapted varieties available.

Proof of the efficiency of this system can however, only be obtained from a long term breeding programme in comparison to the lines selected from the F3 generation grown together in the same season.

POSSIBLE SHORTCOMINGS OF THIS STUDY

(1) The parents might give better results if the difference between them were greater.

(2) The F2 and the backcrosses F1 generations that were grown in the greenhouse could give large amount of seeds if there were grown in the field and the problem of the different levels of seeding could be avoided.

(3) Competition in the field between the lines could not be avoided since the spacing was one foot apart between plots. This distance is not enough particularly if the higher yielding parent is more competitive than the other.

SUMMARY

Two field experiments were carried out to study yield in two high yielding wheat varieties Manitou and Pembina. The first experiment was a randomized block design of six replicates to study the yield and yield components in the two parents, the F1, the F2, and the two backcross F1's. A scaling test for gene action was used to test for additivity.

The object of the second experiment was to study the distribution of yield in large populations of the F3, and the two backcross F2's Each population was planted in a nursery arranged so that a check plot was planted adjacent to each hybrid plot. Manitou was the check parent, while Pembina was randomly distributed in each nursery at the rate of 10% of the number of hybrid plots.

The main findings were as follows:

(1) Manitou is higher yielding variety than Pembina and carries more desirable genes for yield than Pembina but does not differ greatly from Pembina.

(2) They differ significantly only in number of heads per plant and thousand kernel weight.

(3) All the yield components are significantly and equally correlated with plot yield.

(4) There is no heterosis in the cross probably due to the relationship between the two varieties.

(5) The use of percent of or difference from the adjacent check plot

overcame the environmental factors, particularly those due to location effects.

(6) One backcross to the better parent shifts the variability toward it and offers a better chance to capture some transgressive segregation.

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