THE EFFECTS OF SELECTION FOR YIELD IN WHEAT

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INTRODUCTION

In the introductory paper to this series, Frankel (1946) has discussed the general problems encountered in selection for total yield. Once the maximum resistance is reached to factors which limit yield and whose effects are observable, further progress can be achieved only by increasing the components of yield.

The principal difficulty at this stage arises from the fact that yield components are so subject to environmental variation that the recognition of favourable genotypes is difficult even in replicated yield trials. Genetic concepts require segregating populations greatly exceeding in number those which can normally be included in such trials. Hence the efficiency of selection of single plants and their immediate progenies constitutes a major problem in selecting for yield itself.

This paper examines the efficiency of selection of single plants and their progenies in a practical plant breeding scheme on wheat. It seeks an answer to the following questions :—

A (1) Are the effects of selection in one generation, on the yield of the next, large enough to overcome the effects of environmental variation ?

(2) Is selection for components of yield likely to make greater advances than selection for yield alone ?

(3) Is selection for an agronomic character, such as straw length, itself not a component of yield, likely to have an effect on yield in the following generation ?

B (1) Is selection by eye-judgment, instead of actual measurement, effective in retaining a large proportion of the material which would have been selected by measurement ?

MATERIAL AND METHODS

The material used was part of an F_2 generation of a compound cross (F_1 Holdfast × Tainui) × Cross 7.

The use of crosses between two F_1s—or in this case an F_1 and a third variety—enables the desirable characters of several varieties to be brought together for simultaneous selection. For gene differences in the first crosses, a compound F_2 is in fact an F_3 ; for those in the second cross it is an F_2. Hence a compound F_2 possesses high intra-plot segregation combined with inter-plot segregation, the measure of both depending on the genetic differences between the parents concerned.

In practice, more often than not selection in self-fertilised plants does not commence until an advanced hybrid generation has been reached. Since in this study mean values per plot are used in the F_3 generation, the effects of selection in F_2 and, say, F_8 would differ only if F_3 plots possessed genetic skewness due to dominance.

Parents

Name	Origin	Agronomic characteristics	Yield and yield components 1944			
			eng	e	n	g
Holdfast	Produced by Plant Breeding Institute, Cambridge	Yield—usually below or close to—Cross 7. Shattering of grain a serious fault	...	3·08	...	36·7
Tainui	Produced by New Zealand Wheat Research Institute. Selection from Portuguese sample	Yield—close to or above Cross 7. Used as a spring wheat	3·43	3·77	17·2	53·8
Cross 7	Produced by New Zealand Wheat Research Institute. Cross : Tuscan × White Fife	Principal standard wheat in New Zealand	4·22	4·51	23·7	40·0

Cf. p. 226

The tendency to shattering, inherited from Holdfast, materially weakened the F_2-F_3 correlations.

History of cross

Year	Generation	Segregation
1940	Cross : Holdfast × Tainui	None
1941	Compound cross : (F_1 : Holdfast × Tainui) × Cross 7	None
1942	Compound F_1	Intra-plot or inter-plant
1943	,, F_2	Intra-plot and inter-plot
1944	,, F_3	Intra-plot, intra-family, inter-family

A block of five compound F_2 plots and their F_3 progeny was studied. In F_3, 200 progenies of both unselected and selected F_2 plants were raised, affording a test for inter-plot selection in F_3 and for selection in F_2. In the test for eye-judgment, the F_2 was selected by two, the F_3 by three observers, working independently.

Throughout the discussion the following terms and symbols are used :—

Plot : Progeny of a single plant—contains about 50 plants.
Family : Group of F_3 plots containing progenies of plants from a common parent plot.
e : number of ears per plant.
n : number of grains per ear.
g : average weight of one grain in mg.
ng : weight of grain per ear in mg.
eng : yield per plant (F_2) or mean yield per plant (F_3).

A. THE EFFECT OF SELECTION IN F_2 ON YIELD IN F_3

The F_2 plants were arrayed plotwise and again " over all plots," in order of their measurements of *eng* and its components. Selection limits were set at 10 and 20 per cent. of each array. The mean yields per plant of the F_3 progenies raised from these top fractions were averaged, and related to the mean yield per plant of the whole corresponding F_3 family (table 1).

TABLE 1

Effect of selecting for eng *and its components in F_2 on* eng *in F_3*

F_2 plots or F_3 families	Number of F_2 plants and F_3 plots	Level of selection	Percentage increase over unselected F_3 family means by selection for *eng* and its components in F_2					Per cent. increase by selecting in F_2 for short straw
			eng	e	n	g	ng	
		Per cent.						
1659	42	10	16·5	5·8	12·0	−11·0	17·1	−10·5
		20	13·1	8·8	12·0	−15·3	10·1	0·2
1660	45	10	−2·7	−12·1	−13·0	−13·0	−15·7	−8·0
		20	−7·7	−9·5	−8·0	−13·9	−8·0	−5·4
1661	34	10	34·5	26·8	5·6	−12·7	4·4	−16·3
		20	13·8	6·4	11·7	−5·1	19·4	3·8
1663	35	10	34·5	2·0	12·2	11·4	18·1	−11·9
		20	−1·9	...	5·5	19·6	14·0	−14·1
1664	44	10	−2·5	−3·2	−5·9	1·4	−4·2	10·4
		20	−3·1	2·6	−3·6	−5·4	3·6	9·0
Over all plots	200	5	9·4	11·7	−5·2	14·6	−11·5	−22·0
		10	13·1	8·5	−4·4	−14·6	3·1	−11·8
		20	10·8	2·5	−6·7	...	6·8	−5·8

(1) *Efficiency of selection for yield* (eng)

(*a*) *Selection within plots* (plantwise). Selection for *eng* in F_2 was successful in raising the mean yield per plant in only two of the five

F_3 families. Owing to the small number of F_2 plots tested this result is inconclusive (table 1, column 4).

(*b*) *Selection between plots* (plotwise). The correlation between the mean yields per plant of the F_2 plots and the resulting F_3 families ($r = \cdot 79 \pm \cdot 17$) indicates that selection between plots was justified.

(*c*) *Selection over all plots* (plantwise). The selection in F_2 over all plots was successful in raising the mean yield of the progenies of selected plants above the mean yield of the unselected F_3 population (table 1, column 4, bottom line). This was achieved, in part, by the differential selection between plots, since those with the highest means had greater than random representation in the over-all sample. This fact, however, fails to account for the whole of the increase of 10·8 per cent. at the 20 per cent. selection level ; for a random sample taken within plots in the same proportions raises the mean of the F_3 by only 3·4 per cent. This indicates some success of plantwise selection.

(2) *Efficiency of selection for yield components* (e, n, g)

Using Fisher's (1936) concept of discriminant functions, H. F. Smith (1936) suggested a method for selection based on the inequality of environmental variances of the individual components of yield. He found that between wheat varieties, selection based almost entirely on grain weight was most effective. Whether this principle could be used to discriminate between individuals of an early hybrid generation has yet to be established.

In this material (table 1, columns 5-8) the only yield component which consistently varies with yield is *n*. The range of variation of *n*, however, is in general below that of *eng*. Since *n*, which requires a count, is a good deal more cumbersome to establish than *eng* which is based on weight, no advantage would accrue from the use of *n* in preference to that of *eng*.

(3) *The effect of selection in F_2 for a character, not itself a component of yield, on yield in F_3*

Table 1, column 9, shows that straw length and yield are not wholly unconnected ; yet the direction of the correlation, as well as its strength, varies from plot to plot. The effect on yield of selection for short straw is therefore unpredictable. In this material the conclusion is justified that should straw length be of relevance, selection for yield is not likely to be affected seriously by a consideration of this character in addition to yield.

B. THE EFFICIENCY OF SELECTION BY EYE-JUDGMENT

From the foregoing sections it is evident that in this material *eng* is the only reliable measure in selecting for yield. However, the weighing of each plant is cumbersome and limits the size of the material which can normally be handled. Selection by eye-judgment on the other hand is comparatively rapid and facilitates selection from a large population. Its efficiency in selecting for yield is examined in this section.

(I) *Efficiency of selection by eye in F_2* (plantwise)

(*a*) *Selection within plots.* Fig. 1*a* shows that both workers tended to select plants with yields well above the mean yield of each plot.

(*b*) *Selection between plots.* The proportion of plants selected within each plot varied with the mean yield per plot (fig. 1*a*). This difference in intensity of selection, between plots, resulted in an over-all increase in mean yield per plant regardless of the efficiency of single plant selection (*cf.* p. 226 (*c*)).

(*c*) *Over all plots.* The relative efficiency of selection was measured by the proportions of the highest yielding twentieth, tenth and fifth (by measurement) of the whole population, which were detected by the selectors ; that of rejection, by the proportions rejected in the remainders. There was no attempt made to group the selected plants by eye-judgment (table 2). The distributions of the unselected population, and the plants selected by either A or B are shown in fig. 2.

TABLE 2

Efficiency of eye-selection and rejection in F_2

Level of top fraction	5 per cent.		10 per cent.		20 per cent.		100 per cent.
	Selected	Rejected	Selected	Rejected	Selected	Rejected	Selected
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
Selector A	67	86	61	88	45	90	17
„ B	92	90	78	93	47	94	14
A+B	67	93	57	95	34	96	10
A or B	92	82	83	85	58	88	21

Selected $= \left(\dfrac{\text{selection by eye}}{\text{selection by weight}} \times 100\right)$ Rejected $= \left(\dfrac{\text{rejection by eye}}{\text{rejection by weight}} \times 100\right)$

The success of selection at the 5 per cent. level and the partial failure at 10 and 20 per cent. is due to the wide difference between the yields of a few top plants and the mean yield of the population, as illustrated in fig. 1. With a decreasing intensity of selection, this difference also decreases, and selection becomes more difficult. At the 20 per cent. level, the yields of the majority of the plants differ only slightly from the population mean and selection is more or less random. At this stage personal bias would seriously modify selection.

Selector A, while retaining a larger proportion of the whole population, was less efficient than B in detecting the top fraction,

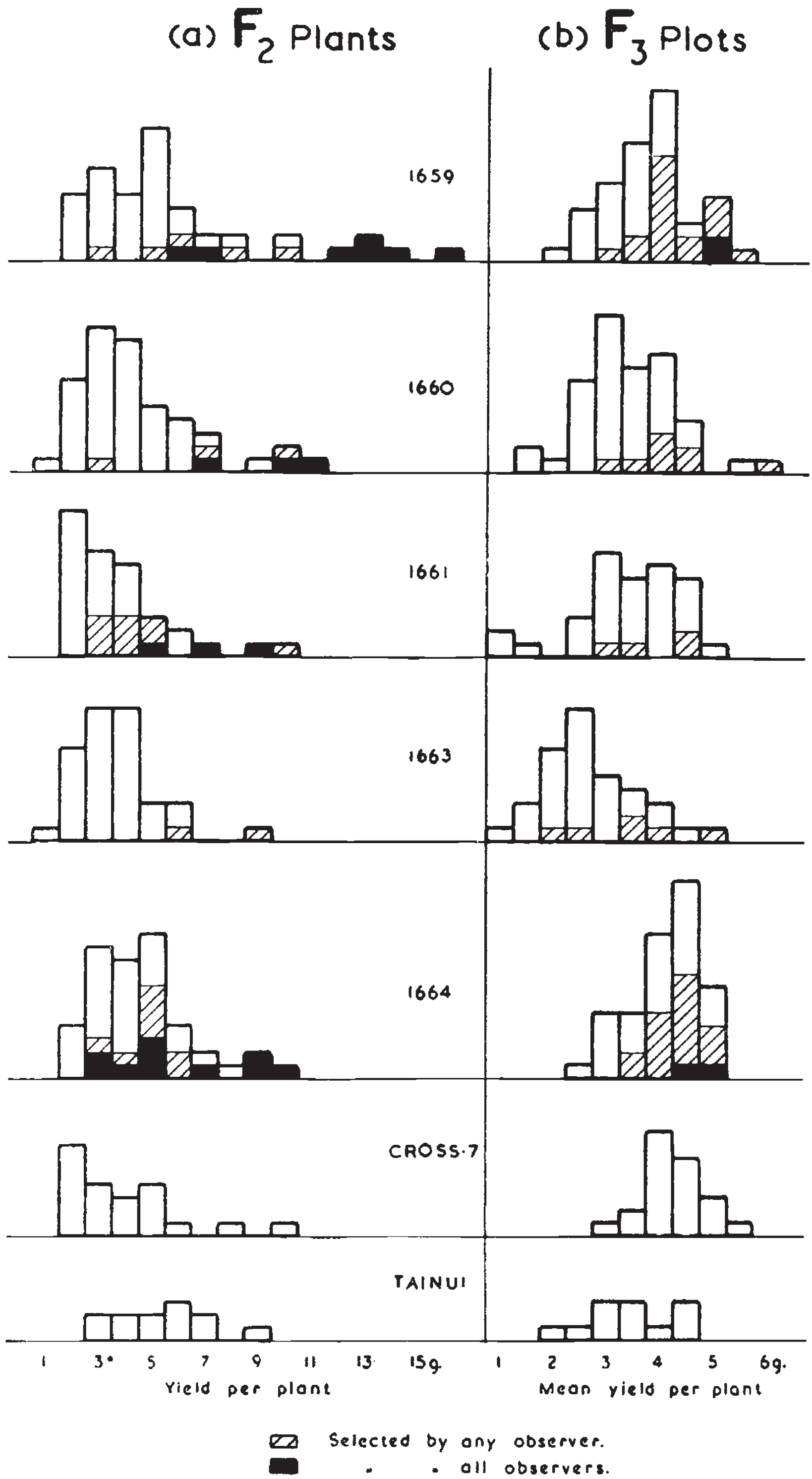

FIG. 1.—Frequency histograms showing distribution of selections by eye. Plantwise in F_2 and plotwise in F_3.

and in rejecting unwanted material. This may have been due to a bias in selecting for plant type. A comparison of the means of yield components and mean straw length of selected and rejected plants

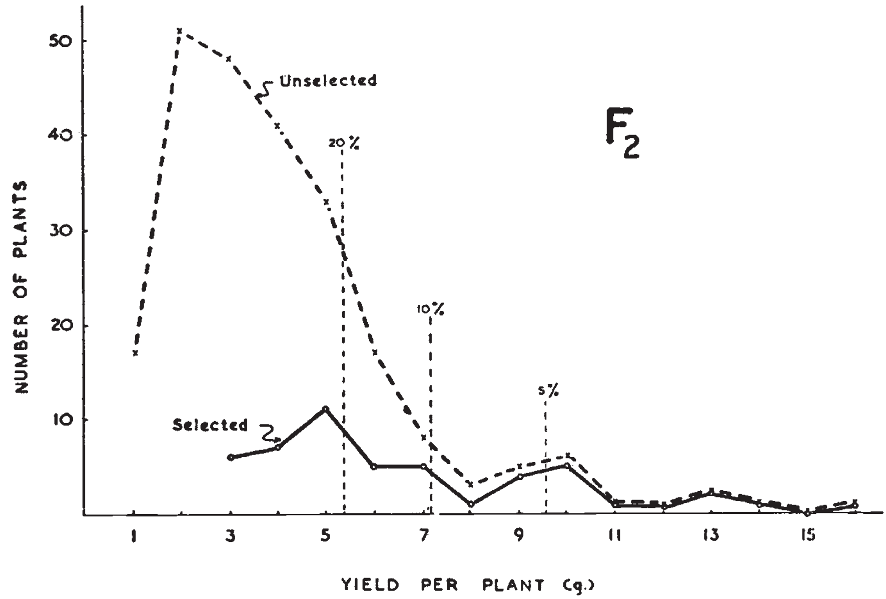

FIG. 2.—Distributions of the unselected F_2 population and the plants selected by eye.

shows that selector A tended to give greater weight to short straw than selector B. In this generation short straw was negatively correlated with yield, which may explain in part the lower efficiency of A. Both selectors rejected a few high yielding plants with signs of shattering.

(2) *Efficiency of selection by eye in F_3* (plotwise)

Each F_3 family contained five standard plots of Cross 7, two of Tainui and two of Holdfast. It was assumed that variations between the yields of consecutive Cross 7 plots might indicate fertility trends and provide the observer with a standard of comparison. It was found that the mean yield per plant of the F_3 families was correlated with the mean yield of the corresponding Cross 7 standard plots ($r = \cdot 85$). Adjustment of the F_3 mean yields according to the variation between the sets of standards removes most of the variation between families.

The number of plots selected from each family show that no observer used the Cross 7 plots as an aid to selection between families (table 3).

(*a*) *Within families.* Environmental variations within plots and between plots render small differences between plots difficult to detect ; especially when they are not adjacent. Yet, as in F_2, all observers tended to select plots with yields above the mean yield of each family (fig. 1*b*).

TABLE 3

Differential selection between families, related to family mean

Family no.	Mean yield per plant		No plots selected			
	F_3 families	Cross 7 standards within families	A	B	C	ANY
1659	3·74	4·39	13	8	13	20
1660	3·39	4·09	1	3	4	8
1661	3·39	3·84	3	1	2	4
1663	2·70	3·94	4	1	3	6
1664	4·11	4·80	14	4	8	19
Over all plots	3·50	4·22	35	17	30	57

(*b*) *Between families.* There are differential intensities of selection in the five families, but their effects on yield are less pronounced than in F_2.

(*c*) *Over all families.* Distributions of the unselected population and the plots selected by each and any of the observers are shown in fig. 3. Selection has increased the proportion of high yielding

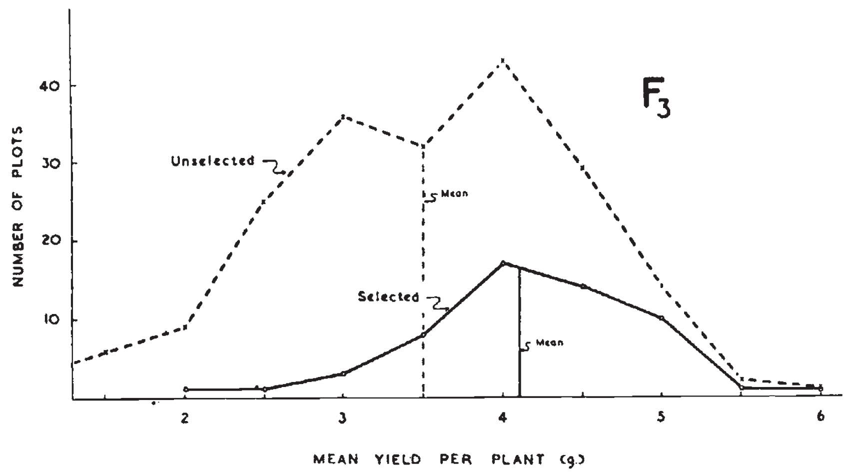

FIG. 3.—Distributions of the unselected F_3 population and the plots selected by eye by each and any of the three observers.

plots. However, here selection covers the full range, for estimating plot yields is more complex than estimating plant yields.

The primary aim of selection at this stage is to retain as much as possible of the top fraction ; a secondary aim is to reject as much as possible of the remainder. Table 4 shows how the judgment of the three selectors was influenced by the two considerations. A and C retained, roughly, twice as many plots as B. The latter selector, however, secured only half the proportion of high yielding plots, whilst his efficiency of rejection was not much better than that of A and C. This argues for a relatively low intensity of selection when using eye-judgment.

TABLE 4

Efficiency of eye-selection and rejection in F_3

Level of top fraction	5 per cent.		10 per cent.		20 per cent.		100 per cent.
	Selected	Rejected	Selected	Rejected	Selected	Rejected	Selected
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
Selector A	40	84	50	86	45	89	18
,, B	10	92	25	93	20	94	9
,, C	50	87	50	89	35	90	15
A+B+C	10	98	15	99	10	100	2
A or B or C	60	73	70	76	60	79	29

$$\text{Selected} = \left(\frac{\text{Selection by eye}}{\text{Selection by weight}} \times 100\right) \qquad \text{Rejected} = \left(\frac{\text{Rejected by eye}}{\text{Rejected by weight}} \times 100\right)$$

(3) *Effect of selection by eye in F_2 on yield in F_3*

In four of the five families, the mean yield per plant of the progenies of plants selected in F_2 was above the mean yield per plant of the unselected family. The varying intensity of selection between F_2 plots

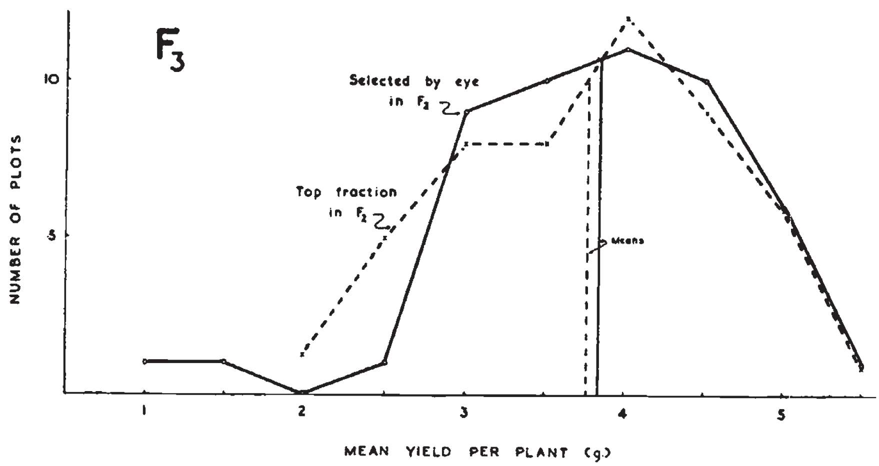

FIG. 4.—Distributions of the F_3 plots selected by eye in F_2 and an equal number selected by measurement in F_2.

is effective in raising the mean yield of the selected progenies above the over-all mean (*cf.* p. 226 (*c*)). The distribution of the progenies of F_2 plants selected by eye and by measurement are shown in fig. 4.

(4) *Effect of selecting in F_3 the progenies of selected F_2 plants*

In the previous section all plots were examined, including those whose parent plants had been rejected in F_2, and a number of such "rejected" plots have been selected in F_3. We now must determine whether selection between plots grown from selected F_2 plants resulted in real progress. Such selection was handicapped by the fact that all plots were grown in consecutive order, "F_2 selected" being mixed at random among "F_2 rejected," thus making comparisons within "F_2 selected" more difficult. Nevertheless, the mean yield of reselected F_3 plots is higher than that of F_3 plots grown from all selected F_2 plants.

	Mean yield per plant of F_3 plots	Number of plots
Unselected F_3 population	3·50	200
All plots selected in F_3	4·11	57
All plants selected in F_2	3·84	49
Plants selected in F_2, plots rejected in F_3 .	3·47	28
Plants selected in F_2, plots selected in F_3 .	4·29	21

CONCLUSION AND SUMMARY

1. In an F_2 from a compound cross, plotwise selection was successful, but plantwise selection within plots was successful only in those plots which had previously been selected plotwise. This may have been due to differential segregation or to environmental variation between plots. Plantwise selection over all plots was successful since it took advantage of segregation both within and between plots.

Whilst these conclusions provide some evidence of positive selection for yield in plants and in non-replicated plots of a self-fertilising crop, they emphasise the complexities and uncertainties of the process. Further studies have been commenced with a view to improving the efficiency of selection.

2. Efficiency of selection was not improved by using yield components in place of yield itself.

3. Selection for an agronomic character, viz. length of straw, did not seriously affect the efficiency of selection for yield.

4. Eye-judgment of single plants, when compared with selection based on weight, was more successful the higher the intensity of selection (table 2). Eye selection of plots was not as successful as that of plants (table 4).

Such comparisons are apt to reveal personal bias. The results show that eye selection by more than one observer raises considerably the efficiency of selection.

5. Selection by eye-judgment was as successful as selection by weight in raising the mean yields of the progenies.

6. The progenies of selected F_2 plants which were selected in F_3, gave higher mean yields than the progenies selected in F_2 but rejected in F_3.

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