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# Effect of selection intensity and population size on percent oil in maize, *Zea mays* L

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**Summary.** The effect of selection intensity and population size on the response to selection for percent oil in the grain of maize (*Zea mays* L.) was evaluated in a replicated experiment over ten cycles of selection. An open-pollinated variety, Armel's Reid Yellow Dent, was divided into subpopulations of 6, 10 and 50 plants. Selection proportions of 17% and 5% were imposed upon each subpopulation. Selection was based on the percentage of oil in individual kernels as determined by wide-line nuclear magnetic resonance spectroscopy. As expected, total response to selection increased with larger population sizes and selection intensities. The concave shape of the response curves suggested that an appreciable part of the genetic variance can be attributed to additive genes at high initial frequencies, dominance genes at low initial frequencies, or to the generation of negative linkage disequilibrium due to selection. The consistently greater loss of vigor experienced by the more intensely selected populations reflects the enhancement of inbreeding due to artificial selection, an effect that increases with the intensity of selection. The results indicate that combined selection, based on kernels and using within- and among-family information, will be more efficient than other conventional selection procedures, including the normal combined scheme where selection is based on plants.

**Key words:** *Zea mays* L. – Population size – Intensity of selection – Inbreeding – Linkage disequilibrium

## Introduction

Continued response to selection over several generations, as well as response to reverse selection in advanced generations, suggests that a large number of segregating loci are involved in the inheritance of oil content in maize (Sprague et al. 1952; Alexander 1963; Dudley 1977). Since most of the oil in the kernel is in the embryo (Leng 1961), variation in oil content is essentially controlled by embryo genotypes. Given the fact that no appreciable dominance or heterosis is found when two inbreds are crossed and, further, that no inbreeding depression is encountered, it can be assumed that oil in maize is under additive genetic control.

With oil content as with other characters in many living organisms, the maternal genotype, independently of the zygote genotype, may be expected to contribute significantly to the phenotypic expression of the character in the zygote. The percentage of oil in the kernel could be controlled by genes in the sporophytic tissue being expressed through maternal processes and by genes in the kernel acting through embryo processes. Although oil is probably synthesized in the kernel itself, many precursors and metabolites involved in the synthesis will be translocated from the maternal tissue. Certain genes will act only through maternal processes, certain ones only through kernel processes, and others through both. The three types of genes will be the source of additive genetic variance of oil content in the kernel and the last type will also be the source of additive genetic covariance. Reciprocal crosses between high and low oil selections from the same segregating population and reciprocal crosses between the population and inbred lines (L. Silvela, D. E. Alexander and R. E. Comstock, unpublished results) show that the maternal genotype does not contribute to variances or covariances.

Theoretical models including selection, either with infinite or finite population size, have been extensively studied (Kempthorne 1957; Falconer 1964; Crow and Kimura 1970). The most thoroughly investigated model is that of mass selection, in which individuals are selected

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[†] Deceased

on their own phenotypic value. Other models use additional information provided by the phenotypic values of relatives, particularly those of half sibs. The phenotype of an individual, measured as a deviation from the overall mean of the population, is partitioned into the deviation of its half-sib family mean from the overall mean, and the deviation of the individual performance from the family mean. The individual is scored giving weights to these two parts. In maize breeding, the most common schemes of this type of selection are "ear to row", where whole families are selected and, more recently, "modified ear to row" or selection among and within half-sib families (Webel and Lonnquist 1967; Paterniani 1967; Bahadur 1974; Dudley et al. 1975). In all cases, a top fraction of the individuals scored is selected and randomly mated to be selected again.

A restriction in population size introduces the process of genetic drift into the model. The accidental and irreversible fixation of favorable or unfavorable alleles due to sampling fluctuations abruptly stops the possible response to selection at a locus. The probability of fixation of favorable alleles due to a sampling accident increases with allelic frequency. Since the expected frequency of favorable alleles increases with succeeding generations of selection, fixation in later generations increases both the probability of fixing favorable alleles and the gains expected from selection (Robertson 1960). For a given selection intensity, the smaller the population size, the earlier fixation will occur, implying a larger reduction in the total response to selection.

The shape of the response curve depends on how the genotypic variance changes as selection proceeds. Three main sources of changes in genotypic variance are: (a) Finite population size. The expected reduction in variance per generation, due to the fixation of genes because of drift, causes the response curve to be concave downwards (Robertson 1960). (b) Changes in gene frequency. As the gene frequency moves from zero to one, the genotypic variance first increases, then passes through a maximum at a critical frequency and then decreases. A diminishing variance will enhance the concavity of the response curve, while an increasing variance will attenuate or even reverse the shape (Silvela 1980). c) Linkage disequilibrium. In an additive model, selection generates negative linkage disequilibrium (Bulmer 1971) and this implies a reduction in genotypic variance and the corresponding enhancement of the concavity.

Artificial selection enhances inbreeding at neutral loci carrying genes not affecting the character under selection, an effect that increases with selection intensity (Robertson 1961). Plant vigor depression from inbreeding is very noticeable in maize. Selecting for oil content and assuming that genes affecting plant vigor are unrelated to oil genes, one can expect a greater depression in plant vigor as selection intensity increases.

In this work we use the percentage of oil in the maize kernel as a character to check the validity of these theoretical predictions in a natural population.

## Materials and methods

This experiment was initiated in 1963 and conducted at the Urbana Campus of the University of Illinois. The initial population was the open-pollinated variety, Armel's Reid Yellow Dent from Brown County, Illinois. It had been maintained in isolation in relatively large fields and was expected to be in Hardy-Weinberg proportions. Our experiment involved selection for increased oil percentage in the kernel in replicated populations of different sizes (6, 10 and 50 plants), each of which was kept constant throughout the experiment (Table 1). Two different selection pressures were imposed, selecting the kernel with the highest oil content from random samples of 6 and 20 kernels.

The ears were shelled separately and kernels from the central part of the ear were saved for subsequent oil analyses by wide-line nuclear magnetic resonance spectroscopy (Alexander et al. 1967). Six kernels from each ear were analyzed in populations 1, 2 and 3, and 20 kernels from populations 4, 5 and 6. The kernel with the highest oil percentage within each ear was saved for planting. To ensure that population size remained constant, the kernel with the next highest percentage of oil was also saved from each ear and planted in a side plot. In the event the highest percent oil kernel failed to produce a mature plant, the second or alternate plant was used.

At anthesis, tassels were bagged, the pollen was bulked within each population, and careful pollinations were made on each receptive shoot. If the actual number of harvested ears in a population ($N_a$) was smaller than the intended number ($N_b$), the population size was increased in the next cycle by taking a second sample(s) of one or more random ears from the particular family.

We will refer to this scheme of selection as strict within half-sib family selection, to differentiate it from conventional within half-sib family selection, where the individuals with the largest phenotypic deviations from their family means are selected, some families contribute more than one individual, and some families none.

To estimate heritabilities accurately, and only for the first three generations, exactly the same strict procedure was followed with the two kernels with the lowest oil content within each family, forming a low-sister line corresponding to each high line. Heritabilities were estimated as the ratio between the differences in oil contents of high and low progenies over the differences in oil contents of the parents.

Crow and Kimura (1970) derived a formula to compute the variance effective number $N_{e(v)}$, which is a function of the variance of the number of gametes contributed per individual to the

**Table 1.** Selection pressures (%), population sizes ($N_b$) and number of replicates of the different populations

| Population | % | $N_b$ | Replicates |
|---|---|---|---|
| 1 | 17 | 6 | 5 |
| 2 | 17 | 10 | 4 |
| 3 | 17 | 50 | 2 |
| 4 | 5 | 6 | 5 |
| 5 | 5 | 10 | 4 |
| 6 | 5 | 50 | 2 |

next generation. In our study, each individual contributed a female gamete, while the male gametes, assuming all tassels contributed the same amount of pollen to the bulk, were distributed binomially. The variance of the number of gametes contributed per individual was then $(1-1/N_a)$. Entering this into the variance effective size formula, we obtain $N_{e(v)} = (4/3)\, N_a$.

Follwoing Crow and Kimura (1970), the inbreeding effective size is also $N_{e(i)} = (4/3)\, N_a$. The inbreeding coefficient $F_t$ from generation $t-1$ to $t$ can be then obtained as $F_t = 1/\{2N_{e(i)}\} + F_{t-1}\,\{1-1/(2N_{e(i)})\}$.

The first and second order moments from the first $\{E(\chi)_1, E(\chi^2)_1\}$ and second $\{E(\chi)_2, E(\chi^2)_2\}$ order statistics for random samples of sizes 6 and 20 taken from a standard normal distribution (Sarhan and Greenberg 1962) are

$$E(\chi)_{1,6}=1.27,\ E(\chi)_{2,6}=0.64,\ E(\chi)_{1,20}=1.87,\ E(\chi)_{2,20}=1.41,$$
$$E(\chi^2)_{1,6}=2.02,\ E(\chi^2)_{2,6}=0.69,\ E(\chi^2)_{1,20}=3.76,$$
$$E(\chi^2)_{2,20}=2.14\,.$$

The actual intensities of selection $i$ and second order moments $i_2$ are then,

$$i=\{D\,E(\chi)_1+D'\,E(\chi)_2\}/N_a, \quad i_2=\{D\,E(\chi^2)_1+D'\,E(\chi^2)_2\}/N_a\,.$$

where $D$ and $D'$ are the actual number of normal and alternate plants at harvest.

To develop, for illustrative purposes, a general theoretical model that accounts for the most common schemes of selection in maize (mass selection, within half-sib family selection, between half-sib family selection, and combined selection), let us assume an infinite random mating population, additive gene action, and no genotype-environment interaction. Let $p$, $g$, and $e$ be the phenotypic, genotypic, and environmental deviations of one individual from the overall mean and, considering the population as a set of half-sib families, let $p_b, g_b, e_b$ and $p_w, g_w$, and $e_w$ be the corresponding deviations of the individual between and within families, respectively. We have then $p=p_b+p_w=g_b+e_b+g_w+e_w$ and $g=g_b+g_w$, the four genotypic and environmental components being uncorrelated pairwise. If relative weights are given to the between and within-family components, the phenotypic score of the individual is $y=\chi(g_b+e_b)+g_w+e_w$, where $0\le\chi\le\infty$.

Let $\sigma_{gy}$ be the covariance between $g$ and $y$. Standard theory shows that $\sigma^2_{g_w}=(\frac{3}{4})\,\sigma^2_g$ and $\sigma^2_{g_b}=(\frac{1}{4})\,\sigma^2_g$ (Falconer 1964), and the response to selection ($\Delta$) is the product of the selection differential $(i\,\sigma_y)$ times the regression of $g$ on $y$ (Kempthorne 1957). Then,

$$\Delta = i\,\frac{\sigma_{gy}}{\sigma_y} = i\,\frac{\chi\,\sigma^2_{g_b}+\sigma^2_{g_w}}{\sqrt{\chi^2\,(\sigma^2_{g_b}+\sigma^2_{e_b})+(\sigma^2_{g_w}+\sigma^2_{e_w})}} = i\,\frac{\sigma^2_g}{4}\,\frac{\chi+3}{\sqrt{\chi^2\,\sigma^2_{p_b}+\sigma^2_{p_w}}} \tag{1}$$

and this expression is maximized for

$$\chi = \frac{\sigma^2_{p_w}}{3\,\sigma^2_{p_b}}\,. \tag{2}$$

If in Eq. (1) we enter for $\chi$ the values 0, 1, $\infty$ and $\frac{\sigma^2_{p_w}}{3\,\sigma^2_{p_b}}$, we obtain the corresponding responses for conventional within half-sib family selection $\Delta_w = i\,\frac{3}{4}\,\frac{\sigma^2_g}{\sigma_{p_w}}$, mass selection $\Delta_m = i\,\frac{\sigma^2_g}{\sigma_p}$, between half-sib family selection $\Delta_b = i\,\frac{1}{4}\,\frac{\sigma^2_g}{\sigma_{p_b}}$ and combined selection,

$\Delta_c = i\,\frac{\sigma^2_g}{4}\sqrt{\frac{1}{\sigma^2_{p_b}}+\frac{9}{\sigma^2_{p_w}}}$, which will be the maximum.

Lush (1947) developed these equations with an extra term accounting for the finite size of the families. However, analysis of the oil content of a kernel with nuclear magnetic resonance spectroscopy is done in seconds, a very large number of individuals can be analyzed, and family sizes of 100 or more individuals can easily be achieved, a size large enough for our equations to be practically valid.

For strict within half-sib family selection, every family contributes the best individual to the selected group and, although the response is similar to $\Delta_w$, it only differs from $\Delta_w$ in that the intensity of selection, for the same number of individuals scored, would be smaller. If $N_f$ and $N_k$ are the number of families and the number of individuals per family, respectively, the intensity of selection for the strict method would be that corresponding to the expected standard value of the best individual from a sample of $N_k$, whereas for the conventional method, the intensity of selection would be the average expected standard value of the best $N_f$ individuals from a sample of $N_f\,N_k$, which is larger. The response with combined selection $\Delta_c$ will always be the largest, but for particular values of $\chi$ it will be very similar to some of the other responses. For $\frac{\sigma^2_{p_w}}{3\,\sigma^2_{p_b}}$ being very large or very small, $\Delta_c$ will be larger but very close to $\Delta_b$ and $\Delta_w$, respectively. For $\frac{\sigma^2_{p_w}}{3\,\sigma^2_{p_b}}=1$, $\Delta_c$ will be identical to $\Delta_m$. For example, in a hypothetical case with $\sigma^2_{e_b}=\sigma^2_{e_w}=0$, $\chi=1$, and combined selection will be equivalent to mass selection as it should be for an ideal character with heritability one.

It should be emphasized that, because between half-sib family selection drastically reduces the effective population size, the smaller the weight given to the between family component in the phenotypic score, the larger the expected effective size will be. As the environmental variance within half-sib families $\sigma^2_{e_w}$ decreases, $\chi$ also decreases. For instances in which nondestructive analysis of single kernels can be conducted, as happens in our study, $\sigma^2_{e_w}$ must be very small. Actually it would be very difficult to imagine two environments more similar than those of two contiguous kernels in the same cob. Therefore, the expected effective population size will be larger with combined selection based on kernels within an ear than with combined selection based on plants within a row.

The theoretical expectations given below refer to a diploid, additive, single locus model with two alleles per locus in a finite random mating population. Let $q$, $u$, $\mu=2qu$ and $\sigma^2_g=2q(1-q)\,u^2$ be the gene frequency, the gene effect, the mean, and the genotypic variance in the original population assumed to be in Hardy-Weinberg proportions, respectively.

For mass selection, assuming for the sake of simplicity that $\sigma_p=1$, the expected total increase over $t$ generations is (Robertson 1960)

$$\Delta_{m,t} = 2\,N\,i\,\sigma^2_g\,(1-A^t) \tag{3}$$

where $N$ is the population size and $A=1-1/(2N)$. For $t=1$, Eq. (3) equals the response to mass selection given above as it should. The rate of response $R$ is

$$R_{m,t} = \Delta_{m,t+1} - \Delta_{m,t} = i\,\sigma^2_g\,\{1-1/(2N)\}^t\,. \tag{4}$$

$R_{m,t}$ decreases as $t$ increases, showing that Eq. (3) gives a response curve concave downwards. For infinite population size, Eq. (3) becomes $R_{m,t}=t\,i\,\sigma^2_g$, which is a straight line. Equation (3) does not take into account the concavity due to changes in $\sigma^2_g$, since it was derived ignoring terms in $u^3$. Unless $u$ is extremely small, Eq. (3) is only close to correct for the first few generations. In other words, Eq. (4) implies that, with infinite population size, the response to selection is constant $\Delta_m=i\,\sigma^2_g$ generation after generation, and with finite population size the response is reduced each generation by a factor of $1-1/(2N)$.

**Table 2.** Estimates of the total phenotypic variance $\hat{\sigma}_p^2$ and its components ($\hat{\sigma}_{p_b}^2$ between families, $\hat{\sigma}_{p_w}^2$ within families)

| Year | Component | Population |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
|  |  | 1 | 2 | 3 | 4 | 5 | 6 |
| 1963 | $\hat{\sigma}_{p_b}^2$ | 0.07 ± 0.03 | 0.14 ± 0.04 | 0.14 ± 0.03 | 0.27 ± 0.08 | 0.11 ± 0.03 | 0.16 ± 0.02 |
|  | $\hat{\sigma}_{p_w}^2$ | 0.24 ± 0.03 | 0.23 ± 0.02 | 0.27 ± 0.02 | 0.26 ± 0.02 | 0.30 ± 0.01 | 0.27 ± 0.01 |
|  | $\hat{\sigma}_p^2$ | 0.31 ± 0.04 | 0.37 ± 0.04 | 0.41 ± 0.04 | 0.53 ± 0.08 | 0.41 ± 0.03 | 0.43 ± 0.02 |
| 1964 | $\hat{\sigma}_{p_b}^2$ | 0.25 ± 0.09 | 0.25 ± 0.08 | 0.22 ± 0.04 | 0.14 ± 0.05 | 0.34 ± 0.09 | 0.28 ± 0.04 |
|  | $\hat{\sigma}_{p_w}^2$ | 0.40 ± 0.05 | 0.42 ± 0.04 | 0.43 ± 0.03 | 0.41 ± 0.02 | 0.44 ± 0.02 | 0.49 ± 0.02 |
|  | $\hat{\sigma}_p^2$ | 0.65 ± 0.10 | 0.67 ± 0.09 | 0.65 ± 0.05 | 0.55 ± 0.05 | 0.78 ± 0.09 | 0.77 ± 0.04 |
| 1965 | $\hat{\sigma}_{p_b}^2$ | 0.25 ± 0.09 | 0.14 ± 0.05 | 0.29 ± 0.05 | 0.21 ± 0.07 | 0.25 ± 0.07 | 0.25 ± 0.02 |
|  | $\hat{\sigma}_{p_w}^2$ | 0.30 ± 0.03 | 0.33 ± 0.03 | 0.38 ± 0.02 | 0.42 ± 0.03 | 0.35 ± 0.02 | 0.35 ± 0.01 |
|  | $\hat{\sigma}_p^2$ | 0.55 ± 0.09 | 0.47 ± 0.06 | 0.67 ± 0.05 | 0.63 ± 0.08 | 0.60 ± 0.07 | 0.60 ± 0.02 |

If we extend Eq. (3) to the next order of approximation in $u^3$ we obtain (Silvela 1980)

$$\begin{aligned} \Delta_{m,t} = {} & i\,\sigma_g^2\,\frac{1-A^t}{1-A} + \Bigg[\frac{1-A^t B^t}{1-A\,B}\,\frac{i_2-1}{2} \\ & + \left[\frac{A^t-A^t B^t}{A-A\,B} - \frac{1-A^t B^t}{1-A\,B}\right] \cdot \frac{i^2 A}{A-1}\Bigg]\,\sigma_g^2\,(1-2q)\,u \end{aligned} \tag{5}$$

where $B=(1-1/N)$. For infinite population size, Eq. (5) becomes

$$\Delta_{m,t} = t\,i\,\sigma_g^2 + \left(\frac{1}{2}\right) t\,i\left[\frac{i_2-1}{i} + t\,i - i\right]\sigma_g^2\,(1-2q)\,u \tag{6}$$

This is not a straight line but a convex curve if $q<1/2$ (the genotypic variance increases with selection) or a concave one if $q>1/2$ (the genotypic variance decreases with selection). That is, in Eq. (5), the concavity due to the first term is enhanced if $q>1/2$ and attenuated or even reversed if $q<1/2$.

Equation (5) is also an approximation, but closer to the correct value than is Eq. (3). The exact response curve can be obtained by a matrix method (Hill 1969) and for 10 generations, Eq. (5) is very close to correct values even for $u=0.10$ (Silvela 1980).

For multiple loci and assuming statistical independence between loci and no epistasis, the total response would be the sum over all loci

$$\begin{aligned} \Delta_{m,t} = {} & i\,[\Sigma\,\sigma_g^2]\,\frac{1-A^t}{1/2\,N} + \Bigg[\frac{1-A^t B^t}{1-A\,B}\,\frac{i_2-1}{2} \\ & + \left[\frac{A^t-A^t B^t}{A/N} - \frac{1-A^t B^t}{1-A\,B}\right]\frac{i^2 A}{1/2\,N}\Bigg] \times [\Sigma\,\sigma_g^2\,(1-2q)\,u] \end{aligned} \tag{7}$$

In Eq. (7) $i$, $i_2$ and $N$ are known and $\Sigma\,\sigma_g^2$ is the total genotypic variance or the heritability in the original population. The only unknown term is $\Sigma\,\sigma_g^2\,(1-2q)\,u$, which therefore can be estimated by fitting the equation to the data. Estimates other than zero would suggest, depending on their size and sign, relatively large $u$ values and high or low average original frequencies.

These formulae may be used for within-family selection substituting $N_{e(v)}$ for $N$.

## Results and discussion

The average estimate of the strict within half-sib family heritability obtained from the high and low sister families and their progenies, over the first three generations with 22 replicates per generation, is $h_w^2 = 0.60 \pm 0.03$. The estimates of the total, between and within half-sib family phenotypic variances, over the same period of time, are $\hat{\sigma}_p^2 = 0.56 \pm 0.03$, $\hat{\sigma}_{p_b}^2 = 0.21 \pm 0.02$, and $\hat{\sigma}_{p_w}^2 = 0.35 \pm 0.02$ (Table 2). Estimates of the total genotypic variance and the environmental variances between and within half-sib families are $\hat{\sigma}_g^2 = 0.27 \pm 0.01$, $\hat{\sigma}_{e_b}^2 = 0.14 \pm 0.03$ and $\hat{\sigma}_{e_w}^2 = 0.15 \pm 0.02$. In common ear-to-row or modified ear-to-row selection schemes, the within half-sib family environmental variance (variance between plants in a row instead of variance between kernels in an ear) is considerable larger than the between half-sib family environmental variance (variance between row means). Here, in the strict scheme, the two estimates are equal, and this is probably because the environmental differences between kernels in the same ear are very small.

Entering these estimates into Eqs. (1) and (2), we get the expected responses for the four conventional selection methods: $\Delta_b = 0.15\,i$, $\Delta_w = 0.34\,i$, $\Delta_m = 0.36\,i$, and $\Delta_c = 0.37\,i$. For the strict scheme used in our experiment, the expected response would be $\Delta_{ws} = 0.34\,i'$, $i'$ being smaller than $i$. Thus, combined selection would be more effective than any of the other methods. However, these responses refer to the first generation of selection. The long-term response, as obtained from Eq. (3), is theoretically proportional to the product $N\,i$, $N$ representing the effective population size. The effective size increases as the weight given to the between-family component decreases. In our case, the weight for combined selection is $\chi_c = 0.56$ and the weight for mass selection is $\chi_m = 1.00$ and, therefore, the effective size for combined selection is expected to be larger than $N$. The effective size for the strict scheme is the largest and equal to $\frac{4}{3}\,N$. However, in a practical breeding program of, e.g. 200 plants with 100 kernels analyzed per ear, the population size would be very large and the detrimental effects of the finite size would only be noticeable after a very large number of generations. Combined

**Table 3.** Percent oil per generation for the different populations averaged over replicates ($C$ – population, $N_b$ – size, % – selection pressure)

| Generation | $C$<br>$N_b$<br>% | 1<br>6<br>17% | 2<br>10<br>17% | 3<br>50<br>17% | 4<br>6<br>5% | 5<br>10<br>5% | 6<br>50<br>5% |
|---|---|---|---|---|---|---|---|
| 1963 | | 4.66±0.09 | 4.80±0.04 | 4.70±0.00 | 4.75±0.03 | 4.85±0.13 | 4.75±0.05 |
| 1964 | | 4.56±0.10 | 4.47±0.10 | 4.50±0.00 | 4.80±0.19 | 4.80±0.04 | 4.75±0.05 |
| 1965 | | 5.18±0.17 | 5.12±0.15 | 5.30±0.00 | 5.58±0.16 | 5.80±0.12 | 5.80±0.00 |
| 1966 | | 5.38±0.12 | 5.42±0.22 | 5.50±0.10 | 6.00±0.13 | 6.32±0.22 | 6.30±0.20 |
| 1967 | | 5.49±0.32 | 5.45±0.37 | 5.44±0.26 | 6.09±0.36 | 6.43±0.23 | 6.41±0.32 |
| 1968 | | 5.48±0.49 | 6.02±0.37 | 5.75±0.08 | 6.25±0.27 | 6.82±0.35 | 6.94±0.18 |
| 1969 | | 5.67±0.30 | 6.06±0.26 | 6.05±0.13 | 6.55±0.23 | 7.03±0.31 | 7.34±0.16 |
| 1970 | | 6.03±0.34 | 6.55±0.27 | 6.53±0.11 | 6.86±0.19 | 7.43±0.25 | 8.00±0.32 |
| 1971 | | 5.51±0.54 | 6.36±0.35 | 6.34±0.14 | 7.12±0.30 | 7.01±0.26 | 7.69±0.37 |
| 1972 | | 5.75±0.20 | 6.14±0.28 | 6.51±0.15 | 7.67±0.44 | 7.40±0.69 | 8.37±0.40 |
| 1973 | | 6.00±0.31 | 5.81±0.23 | 6.66±0.06 | 7.29±0.20 | 8.68±0.42 | 8.43±0.32 |

**Table 4.** Overall selection responses calculated as the regression of percent oil on generation number (generation intervals 0–10, 0–5, 5–10) and realized heritabilities ($Rh^2$) for the different populations ($C$ – population, $N_b$ – size, % – selection pressure)

| Population | | | Response | | | $Rh^2$ |
|---|---|---|---|---|---|---|
| $C$ | $N_b$ | % | 0–10 | 0–5 | 5–10 | |
| 1 | 6 | 17 | 0.13±0.02 | 0.20±0.05 | 0.07±0.05 | 0.27±0.08 |
| 2 | 10 | 17 | 0.17±0.04 | 0.27±0.06 | −0.03±0.07 | 0.29±0.03 |
| 3 | 50 | 17 | 0.22±0.02 | 0.24±0.05 | 0.17±0.04 | 0.31±0.01 |
| 4 | 6 | 5 | 0.28±0.02 | 0.34±0.05 | 0.25±0.05 | 0.25±0.02 |
| 5 | 10 | 5 | 0.33±0.04 | 0.44±0.06 | 0.29±0.11 | 0.27±0.04 |
| 6 | 50 | 5 | 0.39±0.03 | 0.47±0.06 | 0.29±0.06 | 0.34±0.03 |

**Table 5.** Inbreeding coefficients (×100) at different generations and average actual population sizes and intensities of selection for the different populations. ($C$ – population, $N_b$ – size, % – selection pressure)

| $C$ | $N_b$ | % | Generations | | | | | | Average | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1963 | 1965 | 1967 | 1969 | 1971 | 1973 | $N_a$ | $i$ |
| 1 | 6 | 17 | 0 | 12 | 29 | 40 | 52 | 62 | 4.54 | 1.06 |
| 2 | 10 | 17 | 0 | 8 | 18 | 26 | 34 | 44 | 7.40 | 1.06 |
| 3 | 50 | 17 | 0 | 2 | 4 | 6 | 8 | 10 | 38.00 | 1.07 |
| 4 | 6 | 5 | 0 | 14 | 32 | 41 | 56 | 77 | 4.13 | 1.70 |
| 5 | 10 | 5 | 0 | 8 | 19 | 28 | 37 | 55 | 6.70 | 1.71 |
| 6 | 50 | 5 | 0 | 2 | 4 | 6 | 8 | 10 | 39.10 | 1.72 |

selection would then be expected to be more efficient than any other scheme from the very first generation onwards.

Even for small population sizes, combined selection is expected to be more efficient than strict selection, the one with the largest effective size, for a considerable number of generations. For example, assuming a population size of six and a proportion selected 1 : 6 in the strict scheme, it would be a proportion 6 : 36 in the combined case. The corresponding intensities of selection and responses, obtained from Eq. (3), would be $i' = 1.27$, $\Delta_{ws} = 6.91\,\{1 - 0.94^t\}$ and $i = 1.45$, $\Delta_c = 1.07\,N_c \left\{1 - \left(1 - \frac{1}{2N_c}\right)^t\right\}$, where $N_c$ is the variance effective population size. For $N_c = 6$, $\Delta_c$ will be larger than $\Delta_{ws}$ for the first 32 generations of selection, and since we expect $N_c$ to be larger than six, 32 is just a lower limit for the number of generations during which combined selection would be more effective than strict selection.

One of the most conspicuous features of selection experiments is the increase in response with $N$ and $i$, something that appears clear from Tables 3 and 4. The long-term responses to selection estimated from Eqs. (3) and (5), are expected to depend on the product $N\,i$. Population 3 would be expected to eventually produce a higher percentage of oil than populations 4 and 5. The realized heritabilities (Table 4), calculated as the regression of generation means on the cumulative selection differentials, and the inbreeding coefficients (Table 5) imply a higher plateau of the response curves in population 3 than in populations 4 and 5.

The vigor depression of populations 1, 2, 4 and 5 in the field was apparent from 1970 through 1973, especially for populations 1 and 4. Plant appearance was poor at harvest and, in most replicates, one or more normal and alternate plants either did not produce ears or were missing, to the point that in 1972 and 1973 two replicates in population 4 were completely lost.

These losses due to vigor depression are to be expected in maize when the inbreeding coefficient reaches high levels. Populations 4, 5 and 6 were selected at a standardized selection intensity of 1.71 and populations 1, 2 and 3 with an intensity of 1.06. As a result of these differences in selection intensity, a higher rate of inbreeding is expected in populations 4, 5 and 6 than in populations 1, 2 and 3 for all traits not related to oil content (Robertson 1961). The following predictions can be made for populations 4, 5 and 6, as compared with populations 1, 2 and 3: (a) inbreeding will be higher in populations 4, 5 and 6 due to more intense selection; (b) when the populations reach high inbreeding levels, the probability that a kernel planted does not develop into a viable plant will be higher because of this higher inbreeding; (c) the actual number of plants at harvest, $N_a$, will be expected to be smaller; (d) the calculated coefficients of inbreeding, which increase in inverse proportion to $N_a$, will be larger.

These generalizations hold in all possible comparisons in Table 5 without a single exception. The differences between the two groups of populations would be expected to widen as the number of generations increases. These results suggest increased inbreeding due to higher selection intensity.

The selection responses given in Tables 3 and 4, which are the best estimates of the averages over generations, show that the response curves are not linear but concave. Whether the concavity differs from that expected from Eq. (3) has been investigated fitting Eq. (7) to the data in each replicate. We used as effective size $N_{e(v)} = 4/3\ N_a$, and for $N_a$ and $i$ the averages over the 10 generations. The data were standardized dividing by the original phenotypic standard deviation $\sigma_{p_w}$, and $\sigma_g$ was estimated by the original within half-sib family heritability. All the estimates of $\Sigma\ \sigma_g^2\ (1-2\ q)\ u$ (21 because one replicate was lost accidentally at the beginning of the experiment) were negative with a mean of $-0.073 \pm 0.011$. The assumption that all individuals contribute equally to the pollen bulk is unlikely and the actual effective population size might have been considerable smaller. The estimate of $\Sigma\ \sigma_g^2\ (1-2q)\ u$, entering $\frac{N_a}{2}$ for $N_a$ in Eq. (7), is $-0.070 \pm 0.018$. These results suggest that, if this enhancement of the concavity is due to additive genes, their original frequency was, on the average, high. However, unpublished experimental data point to a negative correlation between oil content and yield. This negative relationship suggests that past selection for yield in Reid Yellow Dent would have caused the frequencies of many, if not most, alleles favoring high oil to be low rather than high, prior to any artificial selection for high oil.

Falconer (1964) stated: "It should be noted, however, that the drawing of conclusions from the results of experiments in the field of quantitative genetics is to some extent a matter of personal judgment". The consistency of negative estimates indicates that in all cases the response curves are more concave than would be expected from Eq. (3) alone. This may be due to other reasons if one were to use other models. Dominance genes at low frequencies would also give slower-than-expected responses (Silvela 1980). In unselected populations, neither inbreeding depression with selfing nor heterosis when two inbreds are crossed are encountered, and this suggests additive genetic control of the oil percentage in the kernel. Although Dudley (1977) reported dominance effects for oil content in corn, it should be noted that he worked with strains selected over 76 generations. The strains evaluated by Dudley (1977) were more divergent in oil content (0.5% – 18.5%) than those strains evaluated in the present study. Dudley (1977) suggested that dominance is relatively unimportant for oil production.

Another possible explanation for the pronounced concavity found is perhaps the generation of negative linkage disequilibrium, which reduces the heritability and the response to selection. Bulmer (1971) estimated that in some cases the reduction could be as large as 20%.

The realized heritabilities decreased with reductions in population size (Table 4). Variation in selection intensity had little effect on the realized heritability. Frankham et al. (1968) found that the realized heritabilities for the number of abdominal bristles in *Drosophila melanogaster*, after 12 generations of selection, increased as selection intensity decreased. Hanraham et al. (1973) selected mice for post-weaning weight and did not find differences in realized heritabilities due to different intensities of selection. Their selection pressures, however, were very low (25% and 50%) compared to Frankham's (10%, 20%, 40% and 80%) or to ours (5% and 17%).

The following conclusions can be drawn: (1) The results are in good qualitative agreement with the general theory, expressed by Robertson's Eq. (3) that relates effective population size and selection intensity to response over generation time. Responses increase with $N$ and $i$, and the results suggest that a change in $N$ can be compensated with a change in $i$ in the opposite direction and vice versa. (2) The results are also consistent with extended theory showing that artificial selection causes inbreeding to be higher than expected on the effective population size by itself. (3) Standard breeding theory, however, does not provide a full explanation of the shape of the response curve found. In our case, without exception, all the responses were more concave downwards than expected from theoretical models in their simpler form. These models do not take into account changes in genetic variance as selection proceeds or the generation of negative linkage disequilibrium. Both factors could account for the observed response curves in our experiment. (4) In agreement with general theory, combined selection is expected to be more efficient than any other conventional selection method. If the combined procedure is based on selection between kernels within an ear, it would even be more efficient than the normal combined procedure based on selection between plants in a row.

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