THEORETICAL APPROACH FOR THE CHOICE OF PARENTS AND THEIR NUMBER TO DEVELOP A HIGHLY PRODUCTIVE SYNTHETIC VARIETY IN MAIZE

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Synopsis. The equation to predict yields of synthetic varieties developed from a fixed set of inbred lines or open-pollinated varieties was derived based on GARDNER-EBERHART genetic model. The procedure to the choice of parents to form a highly yielding synthetic variety was devised. "WRIGHT's formula" was proved to be applicable to the both situations where parents might be either homozygous or heterozygous. The factors influencing yields of synthetic varieties were discussed.

Introduction

Breeding synthetic varieties of maize for grain or silage is of considerable value to Japan. Due to the agricultural situation that the net income of farmers from maize production is rather low in comparison with other crops such as rice and vegetables, F_1 hybrid maize like double cross may not be commensurated to the value of the expected crop.

Synthetic varieties have advantage over F_1 hybrids in that yearly crosses need not be made and farmers can depend on their own seed.

Many promising synthetic varieties have been developed in most of the countries since the idea was first suggested by HAYES and GARBER (1919). ALLARD (1960) in his book on principles of plant breeding has presented one chapter on synthetic varieties covering the review of work done till 1960. GARDNER and EBERHART (1966) presented a model for the estimation of genetic effect from diallel cross and related populations of a fixed set of random mating varieties with arbitrary gene frequencies at all loci assuming diploid inheritance, two alleles per locus, and no epistasis. The model can be used even when parents may be homozygous lines. The GARDNER-EBERHART model was applied to the analysis of maize crosses involving genetically diverse races by CASTRO, GARDNER, and LONNQUIST (1968), and the evaluation of

synthetic varieties by HALLAUER and EBERHART (1966), and HALLAUER and SEARS (1968). GILMORE (1969) showed that the degree of inbreeding of parent lines had no effect on the expected yield of synthetics, and that "WRIGHT's formula" could be used to predict yields of synthetics when parent lines of low inbreeding were used.

One of the great importance in the procedures to develop a highly productive synthetic variety may be the determination of parent lines to go into the 'synthetic variety. The objectives of this paper is to determine from a fixed set of inbred lines or open-pollinated varieties which one and how many should be chosen to form the synthetic variety that will give high yield.

Theoretical Analysis

1. GARDNER and EBERHART (1966) suggested that based on their genetic model the mean of varieties (V_i), varieties selfed (V^s_i), variety crosses (C_{ij}), variety crosses selfed (C^s_{ij}), and variety crosses random mated (C^r_{ij}) could be expressed as follows;

$$V_i = u + a_i + d_j$$

$$V^s_i = u + a_i + \frac{1}{2}d_i$$

$$C_{ij} = u + \frac{1}{2}(a_i + a_j) + \frac{1}{2}(d_i + d_j) + h_{ij}$$

$$C^s_{ij} = u + \frac{1}{2}(a_i + a_j) + \frac{1}{4}(d_i + d_j) + \frac{1}{2}h_{ij}$$

$$C^r_{ij} = u + \frac{1}{2}(a_i + a_j) + \frac{1}{2}(d_i + d_j) + \frac{1}{2}h_{ij} \dots (A)$$

where u represents the mean of random inbred

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lines from all varieties, a_i and a_j the contribution of homozygous loci to the i th and j th varieties, d_i and d_j the contribution of heterozygous loci to the i th and j th varieties, and h_{ij} heterosis parameter which is due to difference in gene frequencies in the i th and j th varieties and to dominance. H_{ij} is expressed when varieties i and j are crossed.

The equation A is equal to the mean of a syn-2 generation of a synthetic variety derived from two parent varieties, and also equal to the advanced generation of the synthetic variety if there is no change in gene frequency by selection, mutation, and migration.

2. The mean of a three-variety synthetic variety: The synthetic variety, in general, can be developed by following way (cf. LONNQUIST, 1961). Three parent varieties, e.g., V_1 , V_2 , and V_3 are crossed in all combinations among the varieties, and equal numbers of seeds of each of the resulting variety crosses are mixed to provide a syn-1 generation of the synthetic variety. The mixed seeds are planted in an isolation block to allow to undergo random mating or a crossing nursery to random mate by hand pollination without permitting selfing to occur. In making up a syn-2 generation of the synthetic variety, equal numbers of seeds are taken from each of the harvested ears to provide a balanced synthetic variety for planting the following year.

Therefore, the mean of the mixed population of the variety crosses (a syn-1 generation) can be expressed as follows;

$$\begin{aligned} C_{123} &= \frac{1}{3} (C_{12} + C_{13} + C_{23}) \\ &= \frac{1}{3} \left[u + \frac{1}{2} (a_1 + a_2) + \frac{1}{2} (d_1 + d_2) + h_{12} \right. \\ &\quad \left. + u + \frac{1}{2} (a_1 + a_3) + \frac{1}{2} (d_1 + d_3) + h_{13} \right. \\ &\quad \left. + u + \frac{1}{2} (a_2 + a_3) + \frac{1}{2} (d_2 + d_3) + h_{23} \right] \\ &= u + \frac{1}{3} (a_1 + a_2 + a_3) + \frac{1}{3} (d_1 + d_2 + d_3) \\ &\quad + \frac{1}{3} (h_{12} + h_{13} + h_{23}) \end{aligned}$$

The mean of the syn-2 generation of the synthetic variety derived from the mixed population can be expressed as follows by considering the frequencies of all possible mating types in the syn-1 generation.

$$\begin{aligned} C_{123}^r &= \frac{1}{9} (C_{12} \cdot C_{12} + C_{13} \cdot C_{13} + C_{23} \cdot C_{23} + 2 C_{12} \cdot C_{13} \\ &\quad + 2 C_{12} \cdot C_{23} + 2 C_{13} \cdot C_{23}) \end{aligned}$$

$$\begin{aligned} &= \frac{1}{9} \left[u + \frac{1}{2} (a_1 + a_2) + \frac{1}{2} (d_1 + d_2) + \frac{1}{2} h_{12} \right] \\ &+ \frac{1}{9} \left[u + \frac{1}{2} (a_1 + a_3) + \frac{1}{2} (d_1 + d_3) + \frac{1}{2} h_{13} \right] \\ &+ \frac{1}{9} \left[u + \frac{1}{2} (a_2 + a_3) + \frac{1}{2} (d_2 + d_3) + \frac{1}{2} h_{23} \right] \\ &+ \frac{2}{9} \left[u + \frac{1}{2} a_1 + \frac{1}{4} (a_2 + a_3) + \frac{1}{2} d_1 \right. \\ &\quad \left. + \frac{1}{4} (d_2 + d_3) + \frac{1}{4} (h_{12} + h_{13} + h_{23}) \right] \\ &+ \frac{2}{9} \left[u + \frac{1}{2} a_2 + \frac{1}{4} (a_1 + a_3) + \frac{1}{2} d_2 \right. \\ &\quad \left. + \frac{1}{4} (d_1 + d_3) + \frac{1}{4} (h_{12} + h_{13} + h_{23}) \right] \\ &+ \frac{2}{9} \left[u + \frac{1}{2} a_3 + \frac{1}{4} (a_1 + a_2) + \frac{1}{2} d_3 \right. \\ &\quad \left. + \frac{1}{4} (d_1 + d_2) + \frac{1}{4} (h_{12} + h_{13} + h_{23}) \right] \\ &= u + \frac{1}{3} (a_1 + a_2 + a_3) + \frac{1}{3} (d_1 + d_2 + d_3) \\ &\quad + \frac{2}{9} (h_{12} + h_{13} + h_{23}) \quad \dots\dots (B) \end{aligned}$$

3. The mean of a four-variety synthetic variety: By the similar consideration as 2, the mean of the mixed population of variety crosses of four varieties (a syn-1 generation) is

$$\begin{aligned} C_{1234} &= \frac{1}{6} (C_{12} + C_{13} + C_{14} + C_{23} + C_{24} + C_{34}) \\ &= u + \frac{1}{4} (a_1 + a_2 + a_3 + a_4) + \frac{1}{4} (d_1 + d_2 + d_3 \\ &\quad + d_4) + \frac{1}{6} (h_{12} + h_{13} + h_{14} + h_{23} + h_{24} + h_{34}) \end{aligned}$$

The mean of the syn-2 generation of the synthetic variety derived from the mixed population is

$$\begin{aligned} C_{1234}^r &= u + \frac{1}{4} (a_1 + a_2 + a_3 + a_4) + \frac{1}{4} (d_1 + d_2 + d_3 \\ &\quad + d_4) + \frac{2}{16} (h_{12} + h_{13} + h_{14} + h_{23} + h_{24} + h_{34}) \\ &\quad \dots\dots (C) \end{aligned}$$

4. The extension to the mean of n-variety synthetic variety: The mean of a mixed population of variety crosses of n varieties (a syn-1 generation) can be expressed as follows;

$$\begin{aligned} C_{123\dots n} &= \frac{1}{nC_2} (C_{12} + C_{13} + \dots + C_{n-1,n}) \\ &= u + \frac{1}{n} (a_1 + a_2 + a_3 + \dots + a_n) \\ &\quad + \frac{1}{n} (d_1 + d_2 + d_3 + \dots + d_n) \\ &\quad + \frac{1}{nC_2} (h_{12} + h_{13} + \dots + h_{n-1,n}) \end{aligned}$$

The mean of the syn-2 generation of the

synthetic variety derived from the mixed population can be expressed as follows ;

$$C^{r_{123\dots n}} = u + \frac{1}{n} (a_1 + a_2 + a_3 + \dots + a_n) \\ + \frac{1}{n} (d_1 + d_2 + d_3 + \dots + d_n) \\ + \frac{2}{n^2} (h_{12} + h_{13} + \dots + h_{n-1 \cdot n}) \dots\dots (D)$$

5. **The relation of the equation D to "WRIGHT's formula":** From 4,

$$C^{r_{123\dots n}} = C_{123\dots n} - \frac{2}{n^2(n-1)} (h_{12} + h_{13} + \dots + h_{n-1 \cdot n})$$

Now from the GARDNER-EBERHART model, $V_1 = u + a_1 + d_1$, $V_2 = u + a_2 + d_2$, $C_{12} = u + \frac{1}{2} (a_1 + a_2) + \frac{1}{2} (d_1 + d_2) + h_{12} = \frac{1}{2} (V_1 + V_2) + h_{12}$. Therefore $h_{12} = C_{12} - \frac{1}{2} (V_1 + V_2)$. Similarly

$h_{13} = C_{13} - \frac{1}{2} (V_1 + V_3)$, ..., and $h_{n-1 \cdot n} = C_{n-1 \cdot n} - \frac{1}{2} (V_{n-1} + V_n)$. By substituting C_{ij} 's and V_i 's for h_{ij} 's in the formulae above mentioned, we have

$$C^{r_{123\dots n}} = C_{123\dots n} - \frac{1}{n} \left[\frac{2}{n^2(n-1)} (C_{12} + C_{13} + \dots + C_{n-1 \cdot n}) - \frac{1}{n} (V_1 + V_2 + V_3 + \dots + V_n) \right]$$

Let $\bar{C}_{ij}$ and $\bar{V}_i$ be here

$$\bar{C}_{ij} = \frac{1}{nC_{2 \atop i,j}} \sum_{i < j}^n C_{ij} = \frac{2}{n(n-1)} (C_{12} + C_{13} + \dots + C_{n-1 \cdot n}) = C_{123\dots n}$$

$$\bar{V}_i = \frac{1}{n} \sum_{i=1}^n V_i = \frac{1}{n} (V_1 + V_2 + V_3 + \dots + V_n) \\ (i, j = 1, 2, 3, \dots, n)$$

Then we have

$$C^{r_{123\dots n}} = \bar{C}_{ij} - \frac{1}{n} (\bar{C}_{ij} - \bar{V}_i) \dots\dots (E)$$

The equation E means that the mean of a syn-2 generation of a synthetic variety derived from n parent varieties can be predicted by the mean of variety crosses in all possible combinations among n varieties subtracted from it one n th of the difference between the means of the variety crosses and the parent varieties under the model. This can be expressed in short as $\hat{F}_2 = \bar{F}_1 - \frac{1}{n} (\bar{F}_1 - \bar{P})$, which is same to that suggested by WRIGHT (1922) for the prediction of the mean of random bred population derived from n homozygous lines, and is commonly called "WRIGHT's formula". He expressed in his paper that "a

random bred stock derived from n inbred families will have $1/n$ th less superiority over its inbred ancestry than first crosses or random bred stock from which the inbred families might have been derived without selection."

The equation E could be used in the both situations where parent populations are heterozygous (open-pollinated varieties) or homozygous (inbred lines) because it is based on GARDNER-EBERHART model in which gene frequencies of parents could be arbitrary.

6. **The determination of parents of a synthetic variety:** In order to determine from a fixed set of parent varieties or inbred lines which one and how many should be chosen to form a synthetic variety which will give high yield, the following procedure is suggested. Firstly, observe the yields of n varieties and their derived populations in the replicated yield trials in one or several environments. If parents are inbred lines, yield data on the inbred lines, single crosses F_1 , and F_2 derived from selfing F_1 are needed. Secondly, estimate genetic constants (u , a 's, d 's, and h 's) by doing the analysis of variance suggested by GARDNER and EBERHART (1966), and then test the adequacy of the model to the obtained data. Thirdly, compute the predicted yields of all possible combinations of synthetic varieties from two, three, four, ..., up to n varieties by substitute the estimated genetic constants into the equation D corresponding to the number of parents. Fourthly, compare the predicted yields of the synthetic varieties from the same and different numbers of parents. Finally, find out the highest yielding synthetic variety and then the parent varieties or inbred lines of the synthetic variety will be determined.

Discussion

Synthetic variety is designated by LONNQUIST (1961) as "open pollinated population derived from the intercrossing of selfed plants or lines and subsequently maintained by routine mass selection procedures from isolated plantings." ALLARD (1960) indicated a similar designation of the term which had come to be used in his book. Some maize breeders, however, seem to call a synthesized population derived from inbred lines as a synthetic variety and from open-pollinated varieties as a composite.

or a composite variety. As it was suggested by GILMORE (1969) and also could be guessed from this analysis, there is no reason to discriminate between synthetic variety and composite because the prediction equation is just same in the both synthesized populations, although the discrimination might be useful in practice in maize breeding. That is why the term synthetic variety is used in the both synthesized populations derived from inbred lines or open-pollinated varieties in this paper.

Regarding with the factors influencing yields of synthetic varieties, from the equation E

$$\begin{aligned} C_{123\dots n}^r &= \frac{1}{n} [(n-1) \bar{C}_{ij} + \bar{V}_i] \\ &= \frac{1}{n} \left(\frac{2}{n} \sum_{\substack{j,i \\ i < j}}^n C_{ij} + \frac{1}{n} \sum_{i=1}^n V_i \right) \\ &= \frac{1}{n^2} \left(2 \sum_{\substack{i,j \\ i < j}}^n C_{ij} + \sum_{i=1}^n V_i \right) \dots\dots (F) \end{aligned}$$

Therefore, as it was pointed out by ALLARD (1960), three factors would affect theoretically on the yield of the mean of a syn-2 generation of a synthetic variety. The three factors are ;

- a. the sum of yields of parent varieties or inbred lines,
- b. the sum of yields of variety crosses or single crosses.
- and c. the number of parent varieties or inbred lines.

The first two factors mean that in order to form a high yielding synthetic variety it is to be desired to have the parents which are highly productive *per se* and highly combinable each other. In general, open-pollinated varieties are more productive than inbred lines so that open-pollinated varieties would be more preferable than inbred lines for the parents of a high yielding synthetic variety. So far as the number of parents concerned, the yield of a synthetic variety is, as shown by equation F, the product of $1/n^2$ and the quantity twice the sum of all crosses plus the sum of their parents. So the number of parents might have an optimum value corresponding to the yield and combining ability of the parents.

Finally it should be noted that the equation F is the mean of the diallel table made up from n parents, and that the equation is quite equivalent to the GILMORE's (1969) derived from PUNNET square.

Summary

The prediction equation for the yield of a synthetic variety developed from a fixed set (n) of parent component was derived from GARDNER-EBERHART genetic model, in which parent component might be either inbred lines or open-pollinated varieties. By modifying the equation, "WRIGHT's formula" was proved to be applicable when parents were heterozygous as well as homozygous.

The procedure to determine from the n parents which one and how many should be chosen to form a synthetic variety that will give high yield under the model was suggested as follows ; compute the predicted yields of all possible combinations of synthetics developed from two, three, ..., up to n parents by substituting the estimates into the prediction equation corresponding to the number of parents, compare the calculated yields of all of the synthetics, and then find out the highest yielding synthetic variety and its parent inbred lines or varieties.

The factors influencing yields of synthetics, such as yield, combining ability, and number of parents, were discussed.

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トウモロコシにおける高収合成品種育成のための構成系統とその数の決め方に関する理論的解析

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今一組の育種材料(自然受粉品種・自殖系統)が与えられているとき、それらから合成できる全可能組合せの合成品種のなかで、最高収量が期待される合成品種を育成するための、最適構成系統とその数を決定する方法を見出すことを目的とした。

一般に、 n 個の品種を構成系統として合成した合成品種 ($C_{123\cdots n}^r$) の収量の期待式は、GARDNER-EBERHART (1966) の遺伝モデルが成立するときには

$$\begin{aligned} C_{123\cdots n}^r = & u + \frac{1}{n}(a_1 + a_2 + a_3 + \cdots + a_n) \\ & + \frac{1}{n}(d_1 + d_2 + d_3 + \cdots + d_n) \\ & + \frac{2}{n^2}(h_{12} + h_{13} + \cdots + h_{n-1,n}) \end{aligned}$$

で表わされることを明らかにした。ここで u は全供試品種に由来する任意にとった自殖系統の平均値、 a_i, d_i は品種 i の遺伝子に由来する相加的および優性効果、 h_{ij} は品種 i と j とが交雑されたときに生ずるヘテロシス

効果である。

構成系統の決定の具体的手順は次のようである。1. 品種・同自殖・品種間交雑・同自殖・同任意交配の各集団(育種材料が自殖系統のときは、自殖系統・単交雑 F_1 ・同 F_2) の作成と収量試験、2. 分散分析によるモデルの適合性検定と遺伝統計量 (u, a_i, d_i, h_{ij}) の推定、3. えられた遺伝統計量の上式へのあてはめによる全合成品種の期待収量の計算、4. 最高収量が期待される合成品種の選出とその構成系統の決定。

なお上式の変形により、

$$C_{123\cdots n}^r = \frac{1}{n^2} \left(2 \sum_{\substack{i,j \\ i < j}}^n C_{ij} + \sum_{i=1}^n V_i \right)$$

がえられた。この式から、高収合成品種の構成系統としては系統自身が高収(一般的に品種の方が自殖系統より有利)で組合せ能力が高いこと、系統数は多い必要がないことが推論された。