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Evaluating Parents and Prediciting Performance of Synthetic Alfalfa Varieties

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EVALUATING PARENTS AND PREDICTING PERFORMANCE OF SYNTHETIC ALFALFA VARIETIES

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EVALUATING PARENTS
AND PREDICTING PERFORMANCE
OF SYNTHETIC ALLELE VARIETIES

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June 1955

Agricultural Research Service
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EVALUATING PARENTS AND PREDICTING PERFORMANCE OF SYNTHETIC ALFALFA VARIETIES

By Thad H. Busbice and Ramzy Y. Gurgis¹

ABSTRACT

One hundred random clones from 'Cherokee' alfalfa (*Medicago sativa* L.) were evaluated by self- (S_1), topcross-, and clonal-progeny tests. Clonal progenies were most effective, topcross progenies moderately effective, and S_1 progenies the least effective in predicting first-cross yield. Forage yield was mostly independent of self-fertility. Nine clones were selected for yielding ability based on the progeny tests. The nine clones, their S_1 families, the diallel set of single-cross families from the nine clones, and the Syn 1 and Syn 2 generations of 10 synthetic varieties from the nine clones were evaluated. The best single-cross family yielded 150 %; the best Syn 1 yielded 132 %; and the best Syn 2 yielded 116 % of 'Cherokee'. The predicted yield of the best synthetic possible among the nine clones in the equilibrium generation (Syn 4 and beyond) was 109 % of 'Cherokee'. The Syn 2 yields were predicted with 94 %, 91 %, and 85 % accuracy (as measured by regression analysis) from formulas based on diallel-cross yields, general-combining-ability yields, and clonal yields, respectively, coupled with S_1 family yields and coefficients of inbreeding. The coefficients of inbreeding alone could account for more than 80 % of the variation among Syn 2 varieties. The negative effect of inbreeding and gene recombination on advanced generations was apparent. Only a few of the 502 synthetic varieties possible from the 9 selected clones were predicted to outyield 'Cherokee' in the equilibrium generation. The prediction formulas will allow one to determine with reasonable accuracy (1) the number of clones to include in a synthetic variety, (2) the parents that are likely to produce the best possible variety, and (3) the quantity that the variety will yield in the generation the farmer plants. **KEY WORDS:** breeding, breeding *Medicago sativa* L., heterosis, inbreeding depression, *Medicago sativa* L., plant breeding.

INTRODUCTION

Alfalfa (*Medicago sativa* L.) varieties presently grown in areas where alfalfa has long been adapted appear to be only slightly superior in yield potential to the older varieties of those areas. This is true in spite of intensive breeding efforts made to improve forage yield. Most small

gains in adapted populations have been attributable to specific improvements in pest resistance, rather than to the lifting of an apparent genetically-imposed yield barrier. In addition, many varieties have shown great promise in the early generations of breeding only to turn out to be disappointingly mediocre upon final testing in advanced generations.

Several papers have been published on breeding methods, progeny tests, and predicted advance from selection. Most have suggested that

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certain important gains would result if certain steps were followed. Yet, there are conflicting findings in the literature, and the combined efforts of alfalfa breeders have failed to make any substantial improvement in forage yield.

In this paper, we demonstrate methods of predicting the yield of synthetic varieties based on common progeny tests and reveal some of the difficulties associated with attempts to breed higher yielding alfalfa.

Tysdal et al. proposed the polycross as an effective way to evaluate parents for breeding potential (28).² Tysdal and Crandall reported that some single-cross and polycross families yielded 20% to 26% more forage than check varieties (26). Tysdal et al. stressed selection for self-sterility, stating that 10% of an unselected population would be highly self-sterile (28). Tysdal and Crandall reported that the polycross progenies of "self-sterile" clones yielded 106% of "self-fertile" ones, resulting from a negative correlation of -0.40 between forage yield and self-fertility (26). In contrast, Wilsie reported that self-fertility was mostly independent of forage yield (29).

Bolton recommended that parents be evaluated by both the S_1 and polycross-progeny tests, the S_1 for undesirable segregation and the polycross for combining ability (1). As a final evaluation he recommended the diallel cross.

Davis suggested improving synthetic varieties by selecting clones based on the polycross progeny of S_1 lines (10). Davis and Panton observed that the variation between the polycross progenies was less than half of that among S_1 progenies and suggested that the polycross progenies would be of limited value in selecting superior parents (11). S_1 progenies were found to be excellent predictors of two-clone combinations. In contrast, Johnson concluded that S_1 progeny testing had not been effective for improving forage yield (19).

Carnahan and Miller reported that the experimental synthetics based on polycross-progeny tests yielded up to 115% of the check, concluding that such tests were effective in determining merit of potential parents (9). Hill et al. concluded that selection for forage yield on the basis of polycross tests would always be more effective than selection based on clonal tests (18).

The terms "Syn 0," "Syn 1," "Syn 2," and so forth were introduced into the literature by Tysdal et al. to describe the parents, the first generation of random mating, the second generation of random mating, and so forth of a synthetic variety (28).

Tysdal and Crandall found that the four- and five-clone synthetic varieties selected on the basis of polycross-progeny tests yielded up to 116% of the check (26). They reported that the Syn 2 generation yielded about the same as the Syn 1. Graumann and Matlock reported synthetic-variety yields of 120% to 125% of the check in the Syn 1 generation, but this yield was reduced to 110% in advanced generations, with most of the change coming in the Syn 2 (14). Two-clone synthetics tended to be more productive than multiple-clone synthetics in the Syn 1, but this advantage was lost in subsequent generations. Kehr et al. reported that the mean forage yields of the multiple-clone synthetics were 107%, 104%, 102%, and 101% of the checks for Syn 1, Syn 2, Syn 3, and Syn 4 generations, respectively (21). For two-clone synthetics the relative yields were 108%, 98%, 100%, and 100%. Individual synthetics varied greatly in the four generations, causing Kehr et al. to conclude that each new synthetic would have to be tested in the different generations to be able to select the best for a commercial variety.

Pearson and Elling reported that Syn 2 yields could not be accurately predicted from diallel-cross yields (23). However, there was a positive relationship between the general combining abilities of the clones and their synthetic varieties. Syn 2 yields were definitely inferior to Syn 1 yields. Theurer and Elling reported that the yield of a given synthetic could not be accurately predicted from single-cross data (25).

Busbice et al. expressed disappointment in the lack of progress made from selection based on polycross- and S_1 progeny tests (7). They stressed the importance of genotype \times environment interactions on both selection procedures and variety tests and emphasized the lack of concrete evidence on the selection method and experimental precision required to improve alfalfa yields.

Dudley et al. predicted a 9.3% gain in yield from selecting the upper 10% of 'Cherokee' alfalfa (12), an increase comparable to that predicted by Kehr and Gardner for 'Ranger' alfalfa (20).

² Italic numbers in parentheses refer to items in "Literature Cited" at the end of this paper.

Hanson et al. reported yield increases of up to 120% of the check from 11 generations of phenotypic recurrent selection for vigor in the field (17). With subsequent selection in the laboratory for characters other than vigor, yield decreased sharply. Relaxation of selection pressure for vigor was considered the probable cause of this decrease.

Rotili and Zannone have shown that selfing and subsequent selection at the partly inbred level is important in improving genetic worth (24). They suggested that synthetic varieties could be improved by combining four selected inbred clones.

Kehr and Gardner stressed the importance of nonadditive gene action and recommended reciprocal recurrent selection to improve alfalfa yield (20).

Tysdal et al. postulated that a definite ceiling in the yield of synthetic varieties exists at a level below that attainable by F_1 hybrids (28). They suggested that hybrid vigor be used commercially by producing double crosses from self- and sib-sterile single crosses. Bolton (1) outlined an alternative plan to that proposed by Tysdal et al. (28) in which the S_1 families of selected self-fertile plants would be combined to produce single crosses. Kehr and Gardner reported that two-thirds of the genetic variance in 'Ranger' alfalfa was nonadditive and suggested the use of commercial hybrids for the greatest yield improvement (20). Similar conclusions were made by Dudley et al. for 'Cherokee' alfalfa (12). Bradner and Childers suggested a 30% to 40% gain in forage yield from hybrid varieties utilizing male sterility (2).

MATERIALS AND METHODS

Experiment 1

In the spring of 1966, 400 seedlings of 'Cherokee' alfalfa were transplanted into an isolated area near Raleigh, N.C., for cross-pollination by natural bee colonies. Plants were spaced 30.5 cm apart both within and between rows to form a square crossing-block. One hundred plants chosen at random from the crossing-block were given the designations NC200, NC201, . . . , NC299. In the fall, topcross seed and stem cuttings were taken from each plant. The stems were used to vegetatively propagate each plant, and the clones were self-pollinated in the greenhouse during the winter. In the spring of 1967, we returned to the crossing-block and measured

forage yield on the original plants.

In the summer of 1967, we established a field experiment near Clayton, N.C., to compare topcross progeny, self-progeny, and clonal cuttings of the 100 random 'Cherokee' clones. Ten of the clones were nearly self-sterile, and so their self-progenies could not be tested. Seedlings and rooted cuttings were started in the greenhouse in the summer and transplanted into the field in September according to a split-plot design. Main plots were topcross, self-, or clonal populations, and subplots were families or clones. The experiment was replicated four times. A subplot was 10 plants in a row. Both plant-to-plant and row-to-row distances were 30.5 cm. Rows of similarly spaced plants of 'Cherokee' were planted on the borders of the experiment to reduce border effect, and the field was limed and fertilized according to recommendations based on soil analysis.

During 1968 and 1969, forage yield was measured on three dates each year: recovery-plant height was measured 18 days after the first and second harvest in both years, and plant counts were made at the beginning and end of the experiment. The yield was adjusted by the beginning plant count to remove error from establishment variation.

Experiment 2

Nine clones were selected for further study based on forage yield averaged over their topcross progeny, self-progeny, and clonal progeny in experiment 1. They represented the 'best' 10% of the self-fertile component of 'Cherokee' alfalfa. Single crosses were made among the nine clones according to the diallel design, and seeds from the reciprocals within a single cross were bulked. Also, selfed seed were produced on each clone, and each clone was vegetatively propagated.

From the 9 clones, 502 synthetic varieties having 2 or more parents were possible. We produced the Syn 1 and Syn 2 generations of 10 of these synthetics: three two-clone synthetics, three four-clone synthetics, three six-clone synthetics, and the nine-clone synthetic. Of the three synthetics in a set of two-, four-, or six-clone synthetics, one was based on the highest clonal yields in experiment 1 among the nine clones, the second was based on the highest self-progeny yields, and the third was based on the highest

topcross-progeny yields in experiment 1 among the nine clones.

The Syn 1 generation of each synthetic was produced by mixing together equal numbers of seed from each single cross that constituted the variety. The Syn 2 generation of each synthetic was produced by mating plants chosen at random from the Syn 1 generation.

To produce a two-clone Syn 2, 30 crosses were made between 60 full sibs from the single cross that formed the Syn 1. Ten seeds were required from each cross, and they were bulked.

To produce a four-clone Syn 2, 10 plants were chosen at random from each of the 6 single crosses that formed the Syn 1. The resulting 60 plants were paired at random, and 30 crosses were made. A record of parentage was maintained and the frequencies of full-sib, half-sib, and unrelated matings were recorded to allow the precise computation of the coefficient of inbreeding of the Syn 2 generation. Ten seeds were required from each cross, and they were bulked.

To produce a six-clone Syn 2, 4 plants were chosen at random from each of the 15 single crosses that formed the Syn 1. The resulting 60 plants were paired at random to produce 30 crosses. As with the four-clone Syn 2 plants, the parentage of the these plants was maintained to allow the precise computation of the coefficient of inbreeding of the Syn 2 generation. Ten seeds were required from crossing each pair, and they were bulked.

To produce the nine-clone Syn 2, 2 plants were chosen at random from each of the 36 single crosses that formed the Syn 1. The resulting 72 plants were paired at random to produce 36 paired crosses. Seven seeds were required from each pair, and they were bulked. Again, a record of parentage was maintained to allow the precise computation of the coefficient of inbreeding of the Syn 2 generation.

To represent an unselected 'Cherokee' population, 30 clones were chosen at random from the 90 self-fertile clones and paired to produce 15 random crosses. The crosses were maintained separately, but when considered together they represented the unselected check variety. They were considered to be the best standard on which to measure progress from selection, because they were produced without selfing from the self-fertile component of 'Cherokee,' making them directly comparable with the single crosses and

the synthetics.

In producing all crosses, the standard petal was removed from unopened flowers, and emasculation was made by using a vacuum. Pollen was transferred to the stigma immediately after emasculation, caution being taken to prevent contamination. The detail employed in producing the crosses and the synthetics allowed a minimum of genetic drift from the finite population size, prevented selfing, and provided a precise basis for computing the coefficient of inbreeding for each Syn 2.

In 1971, the 9 clones, their self-families, their single-cross families from the diallel, the Syn 1 and Syn 2 generations of the 10 synthetic varieties, and the 15 paired crosses from the random 'Cherokee' clones, along with 3 check varieties, were established at two locations. The checks were 'Cherokee', 'Apalachee', and 'Team'. Seedlings and cuttings were started in the greenhouse in the summer and transplanted into the fields in early September.

Location 1 near Raleigh, N.C., has a clay-loam topsoil over a clay subsoil, and location 2 near Clayton, N.C., has a sand-loam topsoil over a clay subsoil. Both locations were well drained. Fertilizer and lime were applied according to recommendations based on soil analysis.

The experiment was replicated nine times in a randomized block design at both locations, but at the second location one replication failed to become established because a corner of it was temporarily flooded from a rain soon after transplanting. Over the 2 locations there were 17 replications. Plot size and plant spacing were the same as in experiment 1.

Plots were harvested four times at both locations in 1972 and 1973, but one of the harvests in 1973 (the third growth period) was not recorded because a hailstorm had damaged the foliage at one location. Recovery-plant height was measured 18 days after the first and second harvest at both locations in both years, and plant counts were taken at the beginning and end of the experiment. To remove error from establishment variation, forage yield was adjusted by the beginning-stand count. A small portion of the data has been presented elsewhere (5, 15).

THEORETICAL CONSIDERATIONS

The Coefficient of Inbreeding

A synthetic variety, in its simplest definition,

is one that is multiplied from generation to generation by random mating or by conditions approximating random mating. Often such a variety is initiated by intermating a small number of selected parents. When only a few parents are intermated, relatives mate in advanced generations, resulting in some inbreeding. Inbreeding changes from generation to generation until an equilibrium is reached, reducing heterozygosity and the productivity of the variety.

The coefficient of inbreeding can be computed for any generation of a synthetic variety (3). In experiment 2 the parental clones were selected from the variety 'Cherokee' and were considered to be noninbred ($F_0=0$), unrelated, and autotetraploid. The synthetics were produced in the absence of selfing. Under these conditions the formulas developed by Busbice simplify to

$$F_1=0, \quad (1)$$

$$F_2=[1-(1/3)^{(2-1)}]/4n=1/6n, \quad (2)$$

$$\text{and } F_t=[1-(1/3)^{(t-1)}]/4n, \quad (3)$$

where F_1 , F_2 , and F_t are the coefficients of inbreeding for the Syn 1, Syn 2, and Syn t generations, respectively, and n is the number of parents. Inbreeding at equilibrium is $1/4n$.

The coefficient of inbreeding is conditioned by the probabilities of two individuals picked at random from a synthetic generation being full sibs, half sibs, or having no parents in common. These probabilities are a property of n , such that $2/[n(n-1)]$, $[4(n-2)]/[n(n-1)]$, and $[(n-2)(n-3)]/[n(n-1)]$ are the probabilities of mating individuals with two, one, or zero parents in common, respectively, in one generation to produce the next. When the generation is large, actual matings closely approximate the theoretical expectations. However, in experiment 2, the Syn 1 was relatively small: only 60 to 72 plants were mated to produce the Syn 2. In these synthetics the actual frequencies of mating plants with two, one, or zero parents in common deviated slightly from the theoretical expectations. We computed the coefficients of inbreeding of the Syn 2 plants based on both the actual matings and theoretical expectations (table 1). Those based upon the actual matings were, of course, the most accurate.

Predicting Yield of Synthetic Varieties Based on the Coefficient of Inbreeding

One cannot breed and test all possible synthetics from a set of potential parents. To ef-

TABLE 1.—Coefficients of inbreeding for the Syn 2 generation of several synthetics based on theoretical expectations of random mating in a large population and on actual matings in experiment 2.

Synthetics	F_2	
	Theoretical ¹	Actual ²
2-clone Syn 2:		
(1, 2)	0.083	0.083
(4, 6)	.083	.083
(2, 9)	.083	.083
4-clone Syn 2:		
(1, 2, 3, 9)	.042	.040
(1, 4, 5, 6)	.042	.035
(1, 2, 7, 9)	.042	.033
6-clone Syn 2:		
(1, 2, 3, 7, 8, 9)	.028	.026
(1, 2, 3, 4, 5, 6)	.028	.031
(1, 2, 4, 5, 7, 8)	.028	.025
9-clone Syn 2 (1, 2, . . . , 9)	.019	.017

¹ Based on expectations of random mating in a large population.

² Based on matings in experiment 2.

ficiently breed synthetic varieties, one must be able to predict the yield of such varieties from a knowledge of the genetic potential of the parents and the dynamics of variety synthesis. Three questions must be resolved by the breeder: (1) How many parents should be included to form the variety? (2) Which parents should be used, and how can they be evaluated for genetic potential? (3) How well will the variety yield in the generation the farmer plants? Prediction equations based on the coefficient of inbreeding can be used to answer these questions.

The yield of a synthetic variety can be expressed as

$$Y_t=A+B(1-F_t), \quad (4)$$

where Y_t —the yield in generation t ($t=0, 1, 2, \dots, t$), A —the yield of the variety if it were inbred to homozygosity, B —the yield attributable to heterozygosity, when there is no inbreeding in the synthetic generation, and F_t —the coefficient of inbreeding of general t (4). This formula describes a linear relationship between the yield and the coefficient of inbreeding. Since the value of F_t can be computed for any synthetic variety, the problem of predicting yield centers on estimating values of A and B .

A procedure has been published showing how A and B can be estimated from parental and first-cross yields, when the parents are inbred

(4). However, alfalfa and many other forage crops are usually bred from noninbred and unrelated parents. When such parents are mated to form a synthetic variety, there is no inbreeding in the parental and first-cross generations ($F_0=F_1=0$), and these generations cannot be used to estimate the values of A and B . Thus, we are concerned with how to predict yields in advanced generations of varieties developed from noninbred and unrelated parents. In this instance, one can use self- and single-cross-family yields to approximate the values of A and B . The relationships are

$$Y_1 = A + B \quad (5)$$

and $S_{1 \text{ avg}} = A + B' (1 - F_{S_1}), \quad (6)$

where Y_1 = the yield of the Syn 1 generation (the average of the possible single crosses among the noninbred and unrelated parents), $S_{1 \text{ avg}}$ = the average S_1 family yields of the parents, and F_{S_1} = the coefficient of inbreeding of an S_1 family. B' differs from B in some undetermined amount. B is the yield attributable to heterozygosis in the Syn 1 generation and directly relates to the combining abilities among the parents. B' is the yield attributable to heterozygosis in the parents. At best, one can assume that B' approximates B , and one can solve for A and B in terms of S_1 and single-cross yields:

$$A \approx Y_1 - [(Y_1 - S_{1 \text{ avg}}) / F_{S_1}], \quad (7)$$

and $B \approx (Y_1 - S_{1 \text{ avg}}) / F_{S_1}. \quad (8)$

Substituting these approximate values of A and B , we have

$$Y_t = Y_1 - [F_t (Y_1 - S_{1 \text{ avg}}) / F_{S_1}], \quad (9)$$

and when the species is diploid,

$$Y_t = Y_1 - 2F_t (Y_1 - S_{1 \text{ avg}}), \quad (10)$$

and when the species is autotetraploid,

$$Y_t = Y_1 - 6F_t (Y_1 - S_{1 \text{ avg}}). \quad (11)$$

When no selfing occurs in producing the Syn 2 generation, formula 9 further simplifies, regardless of ploidy level, to

$$Y_2 = Y_1 - [(Y_1 - S_{1 \text{ avg}}) / n]. \quad (12)$$

The yield of a synthetic variety in equilibrium is of particular interest to the plant breeder. A diploid variety may be in equilibrium in the

Syn 2, but several generations of seed increase (four or more for practical purposes) are required for an autopolyploid variety to reach equilibrium. Varieties planted by farmers are usually near equilibrium. Under the assumption that the parents are noninbred, unrelated, and that no selfing occurs in producing the variety, predicted equilibrium yield is

$$Y_e = Y_1 - [(2k - 1) (Y_1 - S_{1 \text{ avg}}) / kn], \quad (13)$$

where k is one-half the ploidy number. For autotetraploids such as alfalfa, this simplifies to

$$Y_e = Y_1 - [3 (Y_1 - S_{1 \text{ avg}}) / 2n]. \quad (14)$$

In diploids $Y_e = Y_2$.

In formulas 12 and 13 we have considered selfing to be absent in the production of synthetic varieties. In experiment 2, selfing was prevented by emasculation, but under field pollination some selfing may occur. Selfing increases inbreeding and slows the approach to equilibrium (3). An estimate of the frequency of selfing can be included in the computation of F_t as shown by Busbice (3), and a prediction including inbreeding due to selfing can be made using formula 9.

All these formulas are based on single-cross yields from the diallel design. The diallel is rarely used by the breeder when the number of parents to be evaluated is large, because of the very large number of single crosses required when each parent is mated to all others under test. The diallel is of practical use for predicting yield only when the number of parents to be evaluated is small, usually less than 15. When the number of parents is large, a method of evaluation more efficient than the diallel cross is needed. The polycross or clonal test provides such a method, although both are less precise than the diallel-cross method.

Yields from either polycross or clonal tests, coupled with an S_1 progeny test, can be used to predict yield, by means of the same logic already presented. With polycross yields, the essential relationships are

$$Y_t = A + B(1 - F_t), \quad (15)$$

$$S_{1 \text{ avg}} = A + B' (1 - F_{S_1}), \quad (16)$$

and $GCA_{\text{avg}} = A' + B''. \quad (17)$

Y_t and $S_{1 \text{ avg}}$ have already been defined. GCA is the average general combining abilities (average polycross-progeny yields) of the parents entering the synthetic. A' is the yield attribut-

able to homozygosity, and B'' is the yield attributable to heterozygosity in the polycross progenies. Together A' and B'' measure the general combining ability of the parents entering the synthetic. At best A' approximates A , and B' and B'' approximate B . Under these assumptions one can solve for A and B in terms of S_1 and polycross-progeny yields. When the parents are noninbred and unrelated,

$$Y_t = GCA_{avg} - [F_t (GCA_{avg} - S_{1\ avg}) / F_{S_1}]. \quad (18)$$

For an alfalfa synthetic variety produced without selfing, it follows that

$$Y_2 = GCA_{avg} - [(GCA_{avg} - S_{1\ avg}) / n] \quad (19)$$

$$\text{and } Y_c = GCA_{avg} - [3 (GCA_{avg} - S_{1\ avg}) / 2n]. \quad (20)$$

A similar set of equations based on clonal yields would be as follows:

$$Y_t = Y_0 - [F_t (Y_0 - S_{1\ avg}) / F_{S_1}], \quad (21)$$

$$Y_2 = Y_0 - [Y_0 - S_{1\ avg}) / n], \quad (22)$$

and

$$Y_c = Y_0 - [3 (Y_0 - S_{1\ avg}) / 2n], \quad (23)$$

where Y_0 is the average of the clonal yields of the parents entering the synthetic.

Notice that the importance of the S_1 progeny yields in these formulas decreases as n increases. Probably, these prediction methods will have their greatest utility when n is small (fewer than 10). Also, there may be a change in the yield in advanced generations caused by gene recombination that is independent of inbreeding. The prediction formulas will not account for such a change, particularly when n is large. When parents have been selected for high combining ability, yield will likely decrease in advanced generations from gene recombination alone.

It should be obvious that we have not developed a precise method of predicting yield of synthetic varieties. Instead we have attempted to present practical methods based upon common ways of progeny testing. Because of the large number of synthetic combinations that can be made from relatively few potential parents, one may need a computer to solve the prediction equations. The computer can be programed to rank the predicted yields of all possible synthetics and print the results and parental identities of only the best 20 or 30. Also the computer can be programed

to predict the best 2-, 4-, . . . , n -parent synthetic from a collection of several hundred parents that have been progeny tested. From these predictions the plant breeder can judge which parents should be included in the variety he will produce and ultimately market.

It should be emphasized that, although the formulas presented thus far are based on a linear relationship between the yield and the coefficient of inbreeding, genetic theory does not maintain that the relationship must always be linear. Wright demonstrated that in diploids the rate of decline in vigor is proportional to the decline in heterozygosity when dominant and partially dominant gene action is responsible for heterosis (30). Also, Kempthorne concluded that in diploids, if there are no epistatic effects, such as dominance \times dominance, dominance \times dominance \times dominance, and so forth, the yield is linearly related to the coefficient of inbreeding in spite of the fact that there may be epistasy (22). This limited theory suggests linearity, but there is evidence that the relationship of both seed and forage yield of alfalfa to the coefficient of inbreeding may be exponential.

We suggest the following exponential relationship as a possibility for alfalfa

$$Y_t = e^{\alpha + \beta(1 - F_t)}. \quad (24)$$

The prediction equations would have the following logarithmic form:

$$\ln Y_t = \ln Y_1 - 6F_t (\ln Y_1 - \ln S_{1\ avg}). \quad (25)$$

RESULTS

Experiment 1

The plants became established soon after transplanting, and most grew well for the duration of the experiment. Loss of stand occurred in some entries, with the greatest loss occurring in the S_1 families. (See final stand count in table 2). We observed anthracnose disease caused by *Colletotrichum trifolii* in the summer, and some stand loss may have occurred from this disease.

Inbreeding depressed the vigor of the S_1 families (table 2). The average S_1 forage yield was 64% of the clonal yield, which agrees closely with other reports on inbreeding depression in alfalfa (6). The average topcross forage yield was 78% of the average clonal yield, suggesting that some selfing may have occurred in the topcross crossing-block.

(Continued on page 11.)

∞ TABLE 2.—*Forage yield of the original plants and their clonal, topcross, and S₁ progenies; recovery-plant height and final stand count of the progenies; and the self-fertility of the clones*

Entry	Dry-forage yield (g)				Recovery-plant height ¹ (cm)						Final stand count (plants/subplot)			Self-fertility of clone (seed-flower)
	Original plant ²	Progeny ³			After 1st cutting			After 2d cutting			Topcross	S ₁	Clonal	
		Topcross	S ₁	Clonal	Topcross	S ₁	Clonal	Topcross	S ₁	Clonal				
Self-fertile clones:														
NC 201	36	831	627	792	43.0	41.1	45.6	40.8	36.1	39.6	7.00	6.50	8.00	1.41
NC 202	8	614	320	447	39.0	32.0	40.9	38.9	33.3	37.0	7.25	3.00	7.25	.26
NC 203 ¹	14	965	950	1,393	42.1	38.8	48.5	44.9	38.3	44.5	9.00	6.50	9.75	1.27
NC 204	42	818	608	821	39.5	38.4	43.6	41.0	38.8	38.9	5.00	3.00	.75	.63
NC 205	56	697	693	1,266	42.1	42.1	48.8	40.5	35.6	43.4	7.75	4.00	9.00	.51
NC 206	11	854	677	917	45.0	42.6	49.0	42.0	36.4	45.6	6.50	3.00	2.75	1.44
NC 207	14	763	423	588	43.0	35.8	37.3	40.4	31.1	33.6	7.50	5.25	8.25	1.13
NC 208	(³)	603	364	432	39.4	34.4	41.6	39.3	31.5	34.0	8.75	3.00	4.50	.49
NC 209	28	643	477	1,014	41.9	37.9	44.1	39.6	32.8	40.0	6.00	2.00	7.25	.39
NC 210 ¹	25	835	732	1,246	40.3	42.7	53.6	37.4	34.9	44.5	9.25	6.50	9.25	.49
NC 211	45	555	382	797	41.1	34.3	39.1	37.4	34.4	38.0	7.00	4.75	10.00	.65
NC 212	8	541	169	365	39.4	31.0	37.5	37.9	23.6	37.6	7.50	.25	6.00	.10
NC 213	17	726	729	974	40.3	39.0	42.9	37.8	34.6	39.4	9.25	7.00	8.75	.50
NC 214	48	637	597	1,044	41.8	37.9	46.5	40.8	36.1	42.8	7.25	3.75	9.50	.89
NC 215	11	601	240	346	40.6	35.5	36.5	41.6	32.5	38.6	7.25	2.50	5.25	1.03
NC 216	22	525	203	588	37.8	31.9	38.0	35.8	28.0	34.0	7.25	3.00	10.00	.66
NC 217	42	456	419	452	41.4	35.8	39.9	38.9	32.4	34.0	4.50	4.25	3.50	.44
NC 218	11	988	323	502	43.5	38.6	41.1	42.3	33.5	38.1	8.00	3.25	5.75	.34
NC 221	53	817	588	1,164	39.9	41.0	42.5	36.8	28.5	35.9	5.00	.25	1.75	.61
NC 222	36	866	924	955	40.9	46.3	44.9	43.8	39.5	41.4	7.75	7.00	7.75	1.46
NC 223	20	699	400	882	41.3	35.3	40.6	41.5	34.8	39.9	9.00	5.75	8.75	.76
NC 224	48	710	800	970	40.9	39.0	43.4	39.4	34.3	40.4	7.50	7.00	8.75	1.86
NC 225	8	733	606	741	40.4	37.9	42.1	38.6	34.8	36.6	9.25	8.50	8.50	.90
NC 226	17	727	617	1,093	42.5	38.5	45.3	41.3	36.1	40.9	8.25	6.00	9.50	.73
NC 227 ¹	34	858	877	1,044	45.4	40.6	43.5	39.0	36.4	38.9	8.50	6.75	8.25	1.28
NC 228 ¹	(³)	922	699	1,178	42.4	38.0	45.6	41.5	35.1	42.9	8.25	7.25	9.00	.50
NC 229	25	621	741	1,090	40.0	36.1	41.3	41.0	35.0	40.5	8.00	8.50	9.50	1.59
NC 230	42	903	622	1,195	40.3	37.6	44.4	42.8	36.0	43.6	8.50	5.50	9.50	.58
NC 231	28	734	689	904	42.3	43.6	42.6	40.9	34.9	39.3	8.50	5.75	8.00	.50
NC 232	11	733	678	845	43.3	39.3	40.4	41.3	37.1	42.6	8.75	7.50	9.25	1.50
NC 233	59	776	664	952	40.8	37.1	43.0	39.4	36.0	39.9	5.25	2.50	6.00	1.23
NC 235	31	852	660	1,084	43.1	38.4	45.9	39.4	33.4	41.0	8.75	6.50	9.75	1.31
NC 236 ¹	56	915	857	1,088	43.3	39.8	41.5	40.4	36.5	40.9	9.25	8.75	9.00	1.03
NC 237	31	586	492	921	40.0	35.5	46.8	38.8	33.1	40.3	6.75	7.25	5.75	1.25
NC 238	36	817	770	1,124	40.0	34.8	39.0	41.0	33.9	43.8	6.25	1.50	4.75	1.75

See footnotes at end of table.

TABLE 2.—*Forage yield of the original plants and their clonal, topcross, and S₁ progenies; recovery-plant height and final stand count of the progenies; and the self-fertility of the clones—Continued*

Entry	Dry-forage yield (g)				Recovery-plant height ¹ (cm)						Final stand count (plants/subplot)			Self-fertility of clone (seed-flower)
	Original plant ²	Progeny ³			After 1st cutting			After 2d cutting			Topcross	S ₁	Clonal	
		Topcross	S ₁	Clonal	Topcross	S ₁	Clonal	Topcross	S ₁	Clonal				
Self-fertile clones:—Continued														
NC 239	31	715	635	1,065	38.9	37.9	50.5	40.6	35.1	45.1	6.25	3.50	8.00	.48
NC 240 ⁺	28	980	523	1,302	42.8	35.0	48.6	39.5	33.3	40.6	8.75	6.25	8.75	1.24
NC 241	17	480	287	290	40.1	32.6	39.6	37.0	26.9	28.6	7.75	2.50	6.75	.83
NC 242	20	867	504	838	43.3	34.6	39.6	42.3	32.5	41.1	6.75	1.50	7.00	1.01
NC 243	62	757	806	1,289	43.9	38.8	45.0	38.9	38.0	41.3	8.75	6.75	5.50	1.61
NC 244	17	678	636	921	38.1	39.5	43.9	38.1	33.6	41.6	7.50	3.50	8.00	1.66
NC 245	28	706	737	1,174	40.4	39.3	43.4	37.5	31.9	39.6	8.25	6.25	8.00	.33
NC 246	104	617	647	980	38.0	37.8	42.8	36.8	33.0	38.6	4.50	3.25	8.50	1.80
NC 247	50	889	732	1,335	39.1	37.6	44.8	40.8	35.0	39.4	9.00	4.25	7.00	.72
NC 248	14	751	536	1,042	39.9	38.4	43.9	38.0	34.9	41.3	7.75	6.75	7.50	.60
NC 249	14	642	629	506	43.4	38.8	37.0	38.3	36.1	37.1	5.00	7.25	2.00	1.15
NC 250	36	685	629	1,292	42.5	36.9	41.1	42.1	34.4	37.4	6.50	2.75	5.75	.20
NC 251	25	733	505	1,215	40.5	39.5	46.6	38.9	36.1	43.1	8.25	3.75	8.50	.58
NC 252	36	720	328	818	43.6	33.1	38.5	36.9	26.4	35.0	6.50	4.25	9.00	.76
NC 253	22	725	550	780	38.3	37.9	44.0	38.6	34.9	37.9	7.50	4.75	9.25	1.15
NC 254	14	663	544	776	42.9	35.5	42.5	40.3	34.5	42.9	8.25	7.00	7.50	.33
NC 255	11	882	311	640	40.1	29.5	38.0	39.8	26.9	33.8	6.75	.25	.25	.33
NC 256	34	728	469	764	40.4	34.0	39.9	39.3	32.6	37.8	7.75	2.00	6.75	.54
NC 257	39	873	702	944	44.0	40.3	43.1	41.4	38.1	42.8	8.75	7.50	8.25	1.84
NC 258	25	890	499	789	42.4	33.0	41.1	41.1	34.3	41.5	9.50	6.00	6.75	.64
NC 259	31	868	720	1,042	41.1	38.5	46.5	41.3	37.0	40.4	8.75	8.75	8.00	.32
NC 260	34	1,182	1,058	1,234	42.6	41.0	43.0	43.1	41.1	45.8	9.75	7.50	5.50	1.28
NC 261	39	803	790	1,074	39.1	40.6	41.3	39.8	35.9	39.3	7.00	6.25	9.75	1.29
NC 263	17	882	461	850	43.6	38.5	45.5	40.6	32.3	41.9	7.75	4.00	8.25	1.00
NC 264	39	867	619	1,139	45.4	42.5	47.5	43.5	38.6	45.9	6.75	2.50	7.75	.85
NC 265	28	619	217	581	41.3	36.5	43.9	38.6	31.0	37.4	7.75	2.75	7.00	.59
NC 266	36	620	651	911	42.6	46.0	47.3	38.1	37.1	45.6	7.75	6.75	9.50	.92
NC 267	28	738	349	711	44.8	35.1	39.3	39.1	36.1	41.1	8.00	3.75	6.25	.50
NC 268	14	702	425	644	38.9	34.9	41.1	39.4	32.9	38.5	5.75	2.50	5.25	2.82
NC 270	25	727	435	893	42.3	31.6	42.5	43.0	34.6	43.8	9.00	7.25	9.00	2.11
NC 271	45	702	456	698	40.6	29.9	37.4	36.9	27.1	32.8	6.50	3.25	7.75	.49
NC 272	50	859	705	1,282	38.0	38.0	46.0	43.1	35.8	42.6	8.75	6.25	8.50	.90
NC 273	64	734	691	1,016	39.9	40.6	44.9	42.1	32.5	43.0	7.75	4.50	9.25	1.52
NC 275	17	896	784	876	42.0	41.9	42.4	38.8	38.1	39.1	8.00	6.00	8.00	.48
NC 276	22	624	397	886	38.0	32.0	42.9	38.3	28.8	38.3	7.75	3.75	8.50	1.10

TABLE 2.—*Forage yield of the original plants and their clonal, topcross, and S₁ progenies; recovery-plant height and final stand count of the progenies; and the self-fertility of the clones—Continued*

Entry	Dry-forage yield (g)				Recovery-plant height ¹ (cm)						Final stand count (plants/subplot)			Self-fertility of clone (seed-flower)
	Original plant ²	Progeny ³			After 1st cutting			After 2d cutting			Topcross	S ₁	Clonal	
		Topcross	S ₁	Clonal	Topcross	S ₁	Clonal	Topcross	S ₁	Clonal				
Self-fertile clones:—Continued														
NC 277	36	709	506	993	44.1	40.6	49.1	39.8	34.5	39.0	7.50	4.75	9.25	2.08
NC 278	36	550	299	532	42.5	32.4	39.3	38.3	28.4	33.1	6.75	1.25	5.00	1.23
NC 279	31	893	737	1,053	39.9	42.0	46.1	39.8	33.0	42.3	9.50	1.75	8.00	1.13
NC 280	14	671	504	334	39.6	41.0	29.3	37.8	33.6	27.0	7.25	3.25	6.25	.18
NC 281	36	796	627	1,058	41.3	43.4	46.8	42.6	36.4	43.1	8.25	6.00	6.75	1.62
NC 282	14	725	488	450	40.3	38.0	40.8	38.9	35.1	37.0	5.75	.25	.75	.41
NC 283	64	818	565	1,123	43.0	41.4	49.5	38.9	36.9	40.1	6.75	1.25	3.00	1.14
NC 284	17	608	293	590	38.4	34.6	37.9	38.6	30.3	34.9	7.00	2.25	8.25	.77
NC 285 ⁴	31	858	818	1,279	43.1	41.9	49.0	42.9	37.4	41.4	6.75	8.50	9.25	.84
NC 286	25	784	518	1,213	43.3	38.8	48.9	40.0	36.6	43.6	8.50	7.25	8.75	.79
NC 287 ⁴	56	917	999	1,066	44.8	37.4	42.0	41.0	35.5	41.5	8.00	8.50	8.75	.87
NC 289	42	607	658	842	42.4	40.3	42.0	40.6	35.8	40.9	8.00	5.00	9.25	1.49
NC 290	25	667	699	948	41.1	39.9	45.1	40.5	35.8	43.5	6.25	3.75	7.25	.54
NC 292	22	666	777	972	40.5	38.6	46.0	40.8	35.8	43.5	7.50	5.50	8.00	.11
NC 293	14	819	617	873	40.8	37.9	41.3	41.4	34.5	41.3	8.25	6.75	8.00	1.17
NC 294	81	861	848	1,226	44.9	43.3	46.3	43.3	37.4	44.8	6.75	3.75	4.50	1.08
NC 295	42	924	676	947	46.3	39.5	42.5	43.9	37.0	43.5	8.25	6.00	8.75	.58
NC 296 ⁴	25	1,071	926	1,387	43.1	43.5	47.0	43.4	37.5	46.8	9.50	5.25	9.00	.21
NC 297	25	857	730	1,251	40.1	38.1	44.9	40.9	37.5	44.1	9.25	6.50	8.00	1.03
NC 299	14	655	259	447	41.8	35.9	37.8	40.9	33.4	39.0	7.50	4.50	8.00	.61
Average self-fertile clones	30.7	758	590	917	41.5	37.9	43.2	40.1	34.3	40.1	7.61	4.79	7.35	.93
Self-sterile clones:														
NC 200	25	901	...	894	41.8	...	41.0	39.8	...	40.1	8.75	...	4.50	.04
NC 219	50	786	...	786	40.6	...	45.4	41.4	...	43.3	9.25	...	7.00	.02
NC 220	8	645	...	740	41.9	...	38.1	39.9	...	39.8	8.00	...	8.00	0
NC 234	56	962	...	1,061	38.5	...	39.8	39.8	...	48.6	8.75	...	8.75	.07
NC 262	31	621	...	434	39.5	...	31.3	37.3	...	30.3	7.50	...	6.75	0
NC 269	11	511	...	196	35.9	...	19.9	35.9	...	17.5	5.5025	.29
NC 274	17	866	...	857	40.1	...	39.4	41.4	...	39.0	7.50	...	6.25	.02
NC 288	45	907	...	1,200	43.8	...	43.5	43.0	...	44.4	9.00	...	8.25	.67

TABLE 2.—*Forage yield of the original plants and their clonal, topcross, and S₁ progenies; recovery-plant height and final stand count of the progenies; and the self-fertility of the clones*—Continued

Entry	Dry-forage yield (g)				Recovery-plant height ¹ (cm)				Final stand count (plants/subplot)		Self-fertility of clone (seed-flower)	
	Original plant ²	Progeny ³			After 1st cutting		After 2d cutting		Topcross	S ₁		
		Topcross	S ₁	Clonal	Topcross	S ₁	Topcross	S ₁				
Self-sterile clones:—Continued												
NC 291	14	778	...	579	40.5	...	33.9	40.8	8.00	...	7.00	.01
NC 298	36	652	...	890	37.6	...	41.9	37.9	8.75	...	6.00	.05
Average self-sterile clones												
	29.3	763	...	801	40.0	...	37.4	39.7	8.10	...	6.28	.12
LSD 0.05 (all entries) ...												
		201	234	284	(⁶)	5.35	4.71	3.99	2.23	2.58	2.40	...
LSD 0.01 (all entries) ...												
		264	308	374	(⁶)	7.04	6.20	5.25	2.94	3.39	3.16	...

¹ Plant height is the average of measurements taken 18 days after harvest in both years.

² Yield of the originating field at the first harvest in the spring following the year of establishment.

³ Annual yield per subplot, averaged over 2 years.

⁴ Selected for further study in experiment 2.

⁵ Died.

⁶ No significance.

The progeny yields varied greatly (table 2). Topcross yields ranged from 456 to 1,182 g; S₁ yields ranged from 169 to 1,058 g; and clonal yields ranged from 196 to 1,393 g. The genotypic variance among clonal-progeny yields was double that among S₁ progeny yields, and five times that among topcross-progeny yields (table 3). The genotypic variance among clonal progeny represented the total genetic variance of the 'Cherokee' population. The genotypic variance among S₁ families was expected to be less than that among the clones because of inbreeding depression. If all clones were depressed at the same rate, the effect of this depression on the variance among S₁ families would be simply one of coding. Under this situation the genotypic variance among S₁ progeny yields would be (0.64)² of such variance among clonal-progeny yields. This computed value of 0.41 compares closely with the actual value of 0.47. This does not mean that all clones are depressed at the same rate, but it does indicate that the reduced S₁ variance was largely a manifestation of inbreeding depression. The variance among topcross-progeny yields also may have been reduced some by inbreeding. But the greatest reduction in the genotypic variance among topcross-progeny yields was due to the averaging effects of the common male parentage, that is, a random sample of pollen from the 'Cherokee' population.

Inbreeding depression for recovery-plant height was much less pronounced than that for forage yield, only 12% and 14% on the average for S₁ families after the first and second cuttings, respectively (table 2). The genotypic variance for recovery-plant height among S₁ families was reduced from that among clonal progeny, largely reflecting the effect of inbreeding depression (table 3). Such variance among topcross families for recovery-plant height was almost nonexistent, again demonstrating the averaging effect of the common male parentage.

Because the purpose of progeny testing was to measure the breeding potential of parents, the covariances and correlations among the progeny types were of interest. The genotypic covariances between clonal and progenies and self-progenies were consistently larger than the genotypic covariances between clonal and topcross, and between self-progenies and topcross progenies (table 4). Also, the phenotypic correlation between the clonal progenies and self-progenies was slightly larger than such correlations involv-

TABLE 3.—*Estimates of genotypic and error variances for several characters associated with 3 progeny types from 90 self-fertile 'Cherokee' plants*

Variable	Genotypic variance			Error variance		
	Topcross	S_1	Clonal	Topcross	S_1	Clonal
Forage yield g/subplot	12,024	29,651	63,606	42,026	56,897	84,017
Recovery after 1st cut cm	-0.69	8.47	11.85	36.33	29.74	23.10
Recovery after 2d cut cm	1.69	7.45	10.93	16.53	19.44	23.58
Final stand count plants/subplots	0.79	4.13	4.18	2.57	3.42	2.96

TABLE 4.—*Estimates of genotypic and error covariances between 3 types of progeny, for several characters based on the analysis of covariances of 90 self-fertile 'Cherokee' plants*

Variable	Genotypic covariance			Error covariance		
	Clones-topcross	Clones-self	Topcross-self	Clones-topcross	Clones-self	Topcross-self
Forage yield g/subplot	21,013	38,721	14,836	-3,784	-1,387	1,946
Recovery after 1st cut cm	1.14	7.29	1.99	1.65	-0.07	0.81
Recovery after 2d cut cm	4.33	8.13	3.56	0.03	-2.57	-0.26
Final stand count plants/subplot	1.37	2.65	1.46	0.02	-0.13	-0.09

ing topcross progenies (table 5). The phenotypic correlations of 0.57, 0.60, and 0.74 for forage yield between progeny types were much higher than similar ones reported by Johnson (19) and Busbice et al. (5), and slightly larger than those reported by Davis (10).

The relatively high phenotypic correlations between progeny types for yield, plant height, and stand count (table 5) suggest that all three progeny types are partial estimators of each other, and that all three would be partly successful in the evaluation of parents for breeding potential. Genetic correlations that may be computed from data in tables 3 and 4 suggest the same thing. It is quite possible that clonal progeny would be the most efficient and topcross progeny the least efficient for evaluating parents, because the genotypic variance was the greatest among clonal progeny and the least among topcross progeny, relative to their respective error variance (table 3). However, this conclusion must be accepted tentatively because theory relating heritability to the variance and covariance of clonal progeny, topcross progeny, and self-progeny has not been established. (Data from experiment 2 relate to the effectiveness of selection).

Original-plant yield was positively correlated with clonal- and S_1 progeny yields, but it was essentially uncorrelated with topcross yields (table 5). Although the relationships in this study were not large, the positive correlations

indicate that for the greatest plant-breeding efficiency, phenotypic selection should precede progeny testing as suggested by Carnahan and Miller (9).

The self-fertility of clones was slightly correlated with yield and plant height, but most of the coefficients were nonsignificant at the 5% level (table 5). These correlations, based on the 90 self-fertile clones, suggest a small positive relationship between self-fertility and general vigor. Yield and plant-height data on the 10 self-sterile clones tend to support this contention, in that the mean of the self-sterile clones was slightly less than that of the self-fertile clones (table 2). Even so, the relationship is not of sufficient magnitude as to have much effect on selection procedures. This is in agreement with the findings of Wilsie (29).

The great variation among progenies suggests that selection within the 'Cherokee' variety would be highly effective in improving the yield of hybrid and synthetic varieties. Clones NC203, NC296, NC285, NC287, NC236, NC227, NC228, NC210, and NC240 were selected for study in experiment 2 and given the code numbers 1, 2, 3, 4, 5, 6, 7, 8, and 9, respectively.

Experiment 2

As in experiment 1, the plants became established soon after transplanting, and most grew exceptionally well for the duration of the experiment. Stand loss during the experiment was

TABLE 5.—*Phenotypic correlations between several characters and progeny types*¹

Character and progeny type	Dry-forage yield (g)			Recovery-plant height (cm)						Final stand count (plants/subplot)			Self-fertility of clone (seed/flower)
	Topcross	S ₁	Clonal	After 1st cutting			After 2d cutting						
				Topcross	S ₁	Clonal	Topcross	S ₁	Clonal				
Dry-forage yield (g) :													
Original plant	0.09	0.37	0.42	0.09	0.25	0.26	0.03	0.19	0.17	—0.26	—0.01	0.03	0.23
Topcross60	.57	.39	.40	.36	.58	.51	.50	.40	.32	.01	.06
S ₁74	.24	.68	.47	.44	.71	.59	.27	.56	.19	.22
Clonal19	.50	.71	.39	.54	.70	.30	.40	.32	.14
Recovery plant height (cm)—													
After 1st cutting:													
Topcross30	.18	.40	.37	.32	.14	.27	.02	.06
S ₁54	.33	.69	.51	.12	.33	.11	.12
Clonal30	.48	.70	.17	.27	.23	.13
After 2d cutting:													
Topcross58	.60	.29	.27	.08	.14
S ₁67	.24	.55	.13	.19
Clonal33	.38	.27	.20
Final stand count													
(plants/subplot) :													
Topcross57	.55	— .03
S ₁51	.19
Clonal12

¹ Correlation coefficients greater than 0.21 are significant at 0.05 levels, 88 *df*. Correlation coefficients greater than 0.27 are significant at 0.01 level, 88 *df*.

generally small, with the greatest loss occurring in the S_1 families (table 6).

The ranking of the nine clones in experiment 2 changed from that in experiment 1 for all characters. (Compare appropriate entries in tables 2 and 6.) This was also true for the S_1 families. This changing of rank was expected because the nine clones were grouped in experiment 1 at the upper range of the distribution. The data from experiment 2 were considered to be more accurate than those from experiment 1 because of the greater replication in experiment 2.

The average S_1 forage yield was 77% of the clonal yield and 62% of the average diallel-cross yield. The values were 90% and 84%, respectively, for recovery after first cutting, and 89% and 85%, respectively, for recovery after second cutting. These measures of inbreeding depression based on the diallel cross did not differ greatly from those obtained in experiment 1. However, in experiment 2, the clonal yield was much less than the average diallel-cross yield

(table 6). Both populations were noninbred and the cause of this difference was not apparent. Hanson has noted that clones propagated from stem cuttings do not have taproots and that they may perform differently from plants started from seed (16). This may account for some of the differences observed between clonal and diallel-cross yields.

The average Syn 1 performance was similar to the average diallel-cross performance (table 6). The average Syn 2 performance was much less than the Syn 1 performance, demonstrating the negative effects of inbreeding and recombination on the advanced generations of the synthetic varieties.

The average performance of the random single crosses was almost identical to the 'Cherokee' variety (table 6). These crosses provided the standard on which response to selection was measured.

Significant differences in forage yield occur-
(Continued on page 17.)

TABLE 6.—*Forage yield, recovery-plant height, and final stand count of 9 selected clones, their S_1 and diallel single-cross families, synthetic varieties from the selected clones, random single-cross families from 30 unselected clones, and check varieties*

Entry	Dry-forage yield ¹ (g)	Recovery-plant height ² (cm)		Final stand count (plants/subplot)
		After 1st cutting	After 2d cutting	
Clone:				
1	821	40.6	39.3	8.53
2	648	39.6	41.9	6.35
3	683	38.8	36.9	8.29
4	680	37.6	40.3	8.65
5	938	39.1	40.5	8.71
6	599	37.9	36.7	4.88
7	989	41.9	44.9	7.00
8	556	40.0	42.0	6.53
9	670	38.4	38.3	6.24
Average	731	39.3	40.1	7.24
S ₁ family:				
1	588	37.7	37.5	7.29
2	429	35.1	36.1	4.65
3	521	36.8	35.8	6.24
4	398	33.1	35.0	6.59
5	491	34.9	34.8	8.53
6	409	34.2	34.6	3.82
7	522	36.6	37.3	6.29
8	360	36.9	37.6	5.24
9	410	33.8	32.9	6.35
Average	459	35.5	35.7	6.11

See footnotes at end of table.

TABLE 6.—*Forage yield, recovery-plant height, and final stand count of 9 selected clones, their S₁ and diallel single-cross families, synthetic varieties from the selected clones, random single-cross families from 30 unselected clones, and check varieties—Continued*

Entry	Dry-forage yield ¹ (g)	Recovery-plant height ² (cm)		Final stand count (plants/subplot)
		After 1st cutting	After 2d cutting	
Diallel single cross:				
1×2	892	41.1	42.2	7.41
1×3	962	43.1	42.6	8.47
1×4	858	41.4	41.5	7.88
1×5	1,068	41.9	41.9	8.94
1×6	925	42.8	40.8	6.94
1×7	1,016	42.8	42.4	8.12
1×8	970	42.8	43.6	7.94
1×9	909	43.0	39.9	8.12
2×3	935	43.4	43.3	7.88
2×4	870	41.0	41.3	8.24
2×5	870	40.4	40.4	7.35
2×6	997	43.5	43.4	8.65
2×7	1,018	41.6	43.3	7.41
2×8	713	41.2	42.8	6.12
2×9	896	42.1	41.6	8.47
3×4	785	40.9	42.1	7.24
3×5	1,065	42.7	42.9	8.76
3×6	915	43.3	41.4	8.35
3×7	1,035	43.8	43.3	7.88
3×8	883	43.9	43.4	8.29
3×9	968	42.4	42.6	8.06
4×5	892	40.9	40.7	7.76
4×6	874	41.6	42.4	7.06
4×7	806	40.6	41.5	7.29
4×8	720	41.4	43.3	7.29
4×9	729	41.0	39.2	7.24
5×6	1,028	43.4	42.4	9.00
5×7	1,077	41.4	43.0	9.53
5×8	925	43.1	41.1	8.71
5×9	899	41.0	39.3	8.59
6×7	977	42.9	42.4	7.35
6×8	791	42.9	42.1	8.06
6×9	834	42.3	39.5	8.06
7×8	856	43.1	45.9	7.65
7×9	825	41.5	40.2	7.65
8×9	825	42.4	41.1	8.41
Average	906	42.2	42.0	7.95
<hr/>				
2-clone Syn 1:				
(1,2)	892	41.1	42.2	7.41
(4,6)	874	41.6	42.4	7.06
(2,9)	896	42.1	41.6	8.47
4-clone Syn 1:				
(1,2,3,9)	862	42.6	40.6	7.94
(1,4,5,6)	823	41.3	40.4	8.41
(1,2,7,9)	901	40.7	40.9	7.88
6-clone Syn 1:				
(1,2,3,7,8,9)	949	42.8	42.4	7.65

See footnotes at end of table.

TABLE 6.—*Forage yield, recovery-plant height, and final stand count of 9 selected clones, their S_i and diallel single-cross families, synthetic varieties from the selected clones, random single-cross families from 30 unselected clones, and check varieties—Continued*

Entry	Dry-forage yield ¹ (g)	Recovery-plant height ² (cm)		Final stand count (plants/subplot)
		After 1st cutting	After 2d cutting	
6-clone Syn 1—Continued				
(1,2,3,4,5,6)	922	41.3	41.6	8.24
(1,2,4,5,7,9)	869	41.3	41.1	7.88
9-clone Syn 1 (1,2, . . . , 9)	878	40.7	40.4	8.06
Average	887	41.6	41.4	7.74
2-clone Syn 2:				
(1,2)	586	37.6	38.4	6.88
(4,6)	536	36.7	37.4	6.35
(2,9)	539	37.9	37.8	6.29
4-clone Syn 2:				
(1,2,3,9)	768	40.8	39.5	7.76
(1,4,5,6)	815	40.6	39.5	7.00
(1,2,7,9)	832	41.1	40.6	7.29
6-clone Syn 2:				
(1,2,3,7,8,9)	767	40.9	41.5	7.53
(1,2,3,4,5,6)	817	39.9	40.0	7.59
(1,2,4,5,7,9)	763	40.2	40.0	7.06
9-clone Syn 2 (1,2, . . . ,9)	775	40.0	40.1	7.71
Average	720	39.6	39.5	7.15
Random single cross:				
NC283 × NC206	736	42.9	41.5	5.76
NC247 × NC239	804	41.6	41.1	7.35
NC279 × NC204	538	39.0	39.9	4.47
NC208 × NC240	858	42.0	40.3	8.24
NC235 × NC259	843	40.9	39.5	7.59
NC229 × NC248	870	41.0	40.2	6.59
NC276 × NC252	658	34.9	36.6	6.12
NC245 × NC213	746	39.1	38.5	5.71
NC225 × NC299	713	40.6	41.2	8.53
NC255 × NC297	778	41.4	40.8	8.06
NC237 × NC268	581	37.1	37.6	5.65
NC236 × NC254	560	40.3	41.3	7.71
NC294 × NC286	730	40.9	39.9	8.41
NC222 × NC242	818	39.7	43.6	7.35
NC293 × NC278	573	39.5	39.4	4.76
Average	720	40.1	40.1	6.82
'Team'	712	40.1	38.1	5.76
'Apalachee'	773	43.8	42.7	5.94
'Cherokee'	718	40.4	40.6	6.56
Average	730	41.4	40.5	6.21
Mean (all entries)	783	40.5	40.4	7.34
LSD 0.05 (entry × location)	144	2.1	2.8	1.82
LSD 0.01 (entry × location)	190	2.8	3.7	2.40

¹ Annual yield per subplot, averaged over 2 years and 2 locations.

² Plant height was taken 18 days after harvest, averaged over 2 years and 2 locations.

TABLE 7.—*Estimates of genotypic (σ_T^2), genotype \times location-interaction (σ_{TL}^2), and error (σ_E^2) variances for four characters associated with the several populations described in table 6.*

Population	Forage yield			Recovery after 1st cut			Recovery after 2nd cut			Final stand count		
	σ_T^2	σ_{TL}^2	σ_E^2	σ_T^2	σ_{TL}^2	σ_E^2	σ_T^2	σ_{TL}^2	σ_E^2	σ_T^2	σ_{TL}^2	σ_E^2
Combined over populations	¹ 26,216	¹ 2,319	52,788	¹ 5.3	¹ 0.5	12.3	¹ 4.8	¹ 0.7	22.2	¹ 0.86	¹ 0.60	2.23
Clones	¹ 18,320	¹ 5,887	46,446	² 1.2	.8	10.0	¹ 6.1	.9	14.4	² 1.14	¹ 1.15	2.27
S_1 families	² 3,192	2,016	46,805	² 1.7	.3	23.5	— .07	² 2.9	39.9	² .81	¹ 1.98	2.73
Diallel single crosses	¹ 6,740	¹ 2,244	55,344	² .6	.2	10.0	² 1.3	.3	19.8	.19	¹ 1.28	2.28
Syn 1 varieties	— 57	— 560	51,439	.3	— .1	9.9	— .2	0	23.3	.12	— .09	2.04
Syn 2 varieties	¹ 12,361	340	45,737	² 2.0	.3	11.6	.7	.5	22.4	¹ 1.12	.05	2.24
Random single crosses	¹ 9,276	¹ 4,423	48,751	¹ 3.0	¹ 1.3	12.0	² 2.1	.4	18.5	¹ 1.32	¹ 1.68	2.12
Check varieties	— 964	112	62,835	² 2.6	.3	9.9	² 2.4	1.0	21.4	— .38	¹ 1.85	2.07

¹ Significant at 0.01 level.

² Significant at 0.05 level.

red among clones, S_1 families, diallel single-cross families, Syn 2 varieties, and random single crosses (table 7). The variation among S_1 families was significant, but it was small compared to the genotypic variances among clones and single crosses. Only small and insignificant differences for yield occurred among Syn 1 varieties and among check varieties.

In general, the same pattern of variation occurred for recovery-plant height and final stand count as for forage yield, but fewer significant differences were observed (table 7). The highly significant differences among check varieties for recovery-plant heights was an exception. 'Apalachee' is noted for its rapid recovery after cutting, and it exceeded 'Cherokee' and 'Team' in this characteristic.

Except for recovery-plant height of S_1 families, the experimental errors were homogenous for all populations (table 7). With this exception, the combined error for all populations was used to test for genotype \times location interactions. The genotype \times location-interaction mean square from the combined analyses was used to test entry differences. Generally, the genotype \times location interactions were small compared to genotypic differences (table 7).

General combining ability (GCA) was much greater than specific combining ability (SCA) for all characters of the nine selected clones, as measured by the diallel analysis (table 8). This is the same result obtained by Dudley et al. for the unselected 'Cherokee' population (12). Thus, selection did not change the relationship of GCA to SCA. Because GCA was large in respect to SCA, the best synthetic variety should

be obtained, at least in the early generations, by combining clones with high GCA. The ranking of the clones in descending order for forage-yield GCA was 5, 7, 1, 3, 6, 2, 9, 8, and 4. However, the diallel analysis did not provide the answer to how many clones should be included in the synthetic variety. Also, the effect of recombination and inbreeding in advanced generations on the component of nonadditive variance is not defined by the diallel analysis. Kehr and Gardner (20), Dudley et al. (12), and Hill et al. (18) reported a large nonadditive genetic variance in alfalfa.

The forage yield of the single-cross families from the diallel ranged from 99% to 150% of the check. These results show the ease with which alfalfa yield could be improved, if technology for producing hybrid varieties were available. Of course, part of this range was due to environmental components, and the yield advantage of some families may have been exaggerated by the spaced planted condition. Nevertheless, the yield advantage of some single-cross families over the check and the Syn 2 varieties was remarkable.

There were no significant differences among the Syn 1 varieties, but differences among the Syn 2 varieties were highly significant, indicating effects of inbreeding and recombination (table 7). Inbreeding effects accounted for a significant amount of the variation among Syn 2 varieties (table 9). The two-clone synthetics were significantly inferior to the other synthetics. There were no significant differences among two-clone varieties, nor among the four-, six-, and nine-clone varieties. We should point

TABLE 8.—*Estimates of the mean squares and combining-ability components for several characters from the analysis of the diallel cross among the nine selected clones*¹

Source	Character			
	Forage yield	Recovery after 1st cut	Recovery after 2d cut	Final stand count
Mean squares				
General combining ability (GCA)	² 29,453	² 3.075	² 5.756	0.843
Specific combining ability (SCA)	3,563	.408	.892	.360
Error	2,708	.362	.653	.431
Components				
GCA, $-\sum_i g_i^2$	3,821	.388	0.729	0.059
SCA, $-\sum_i \sum_j s_{ij}^2$	855	.046	.239	-.071
Error, σ_e^2/yr	2,708	.362	.653	.431

¹ The diallel cross was analyzed by method 4, model 1 of Griffing (13).

² Significant at a 0.01 level.

TABLE 9.—*Nonorthogonal comparisons of two-, four-, six-, and nine-clone synthetic varieties in the Syn 2 generation for several characters*

Source	df	Mean squares			
		Forage yield	Recovery after 1st cut	Recovery after 2d cut	Final stand count
All varieties	9	¹ 471,799	¹ 83.4	¹ 55.4	² 4.75
Due to regression of yield on the coefficient of inbreeding	1	¹ 3,665,481	¹ 602.4	¹ 396.6	¹ 28.69
Among 2-clone synthetics	2	26,735	13.3	8.6	.90
Among 4-, 6-, and 9-clone synthetics	6	28,775	7.5	16.5	.80
2-clone vs. 4-clone	1	¹ 3,221,591	¹ 601.2	¹ 204.0	¹ 36.27
2-clone vs 4-, 6-, and 9-clone synthetics	1	¹ 4,021,756	¹ 682.2	¹ 379.3	¹ 59.56
Error	1,335	52,788	12.3	22.2	2.23

¹ Significant at 0.01 level.

² Significant at 0.05 level.

out that the 10 synthetics we produced were not necessarily the best or the worst of those possible among the nine clones.

Prediction

It was obvious from the diallel cross (table 6) that selection in experiment 1 was effective in improving single-cross performance. The remaining question is, how effective were the different progeny tests? An answer to this question is attempted in table 10. The 15 random

single crosses are representative of the possible single crosses from 'Cherokee'. The proportion of the variation among these single crosses that can be explained by regression on progeny-test means of the parents is a good measure of the effectiveness of the progeny tests. Topcross and clonal progeny seemed to have been more effective than S_1 progeny for forage yield. This is in agreement with the findings of Johnson (19). Overall, the clonal-progeny test is judged to have

TABLE 10.—*The proportion of the sum of squares within a population that could be explained by linear regression of single-cross or synthetic performance in experiment 2 on progeny-test means from experiment 1*

[Percent]

Characteristic and progeny test	Population from experiment 2			
	15 random single crosses ¹	36 diallel single crosses	10 Syn 1 synthetics	10 Syn 2 synthetics
Forage yield:				
S_1	4.1	0.6	12.1	1.5
Topcross	8.5	.1	4.2	¹ 7.8
Clonal	17.7	.2	13.0	0
S_1 + topcross + clonal	13.7	.8	2.4	3.7
Recovery after 1st cut:				
S_1	18.7	¹ 11.9	1.1	3.5
Topcross	10.2	¹ 4.1	2.5	¹ 25.3
Clonal	24.1	¹ 17.8	14.4	¹ 9.8
S_1 + topcross + clonal	28.1	¹ 25.8	16.8	0
Recovery after 2d cut:				
S_1	43.3	19.0	.3	0
Topcross	65.2	.9	.7	1.3
Clonal	20.3	¹ 14.4	.8	2.6
S_1 + topcross + clonal	44.3	9.6	0	1.6
Final stand count:				
S_1	16.3	15.5	.3	3.2
Topcross	27.7	.1	5.3	10.1
Clonal	9.4	.6	1.1	29.6
S_1 + topcross + clonal	18.4	¹ 10.0	1.8	13.3

¹ Significant at 0.01 level.

been the most effective. The proportion of the random single-cross variations that were explained by regression was small in all cases. Nevertheless, if the r^2 values in table 10 can be considered crude substitutes for heritabilities, they are realistic for such complex characters as forage yield, plant height, and persistence. The fractions are somewhat smaller than the estimates of heritability for the yield and recovery plant height in 'Cherokee' obtained by Dudley et al. (12).

The proportion of the variation among the diallel single crosses and the synthetic varieties that could be explained by regression was generally small and insignificant (table 10). This was expected because the progeny tests in experiment 1 were not precise enough to distinguish among the nine "best" clones in combining ability. Remember that experiment 1 contained only four replications and that the ranking of the nine clones and S_1 families changed in experiment 2 from that in experiment 1.

Data obtained from experiment 2 were used to predict the performance of the Syn 2 varieties (table 11). Of special interest is the finding that

the coefficient of inbreeding alone could account for more than 80% of the variation among the Syn 2 varieties for yield and plant height and 67% for persistence. The coefficient of inbreeding was more effective than any of the progeny tests, including the diallel cross. However, the progeny tests were effective with the single-cross data being the most effective. As in experiment 1, S_1 data were the least effective.

The prediction formulas based on both linear and exponential relationships were highly effective, explaining up to 94% of the variation among Syn 2 varieties for forage yield (table 11). As expected, the prediction formulas using single-cross data were most effective, and those using clonal data the least effective. While the linear and logarithmic functions were about equal in their ability to explain variation among the Syn 2 varieties, the logarithmic function most accurately predicted actual yields (table 12).

Both the linear and logarithmic formulas based on the diallel-cross data overpredicted yields, the linear function by 9% to 10% and the logarithmic function by 5% to 6%. (See

TABLE 11.—*The proportion of the sum of squares among Syn 2 varieties that could be explained by regression of Syn 2 performance on progeny-test data and coefficients of inbreeding (F_2)*

[Percent]

Prediction method	Character			
	Forage yield ¹	Recovery after 1st cut ¹	Recovery after 2d cut	Final stand count
Coefficient of inbreeding:				
$Y_2 = F_2$	86	80	180	67
Progeny-test data:				
$Y_2 = Y_1$	77	37	0	6
$Y_2 = GCA_{avg}$	46	28	137	44
$Y_2 = Y_0$	57	24	223	34
$Y_2 = S_{1 avg}$	32	29	228	34
Simple combinations:				
$Y_2 = (Y_0 + Y_1) / 2$	75	54	223	40
$Y_2 = (Y_0 + S_{1 avg}) / 2$	53	28	132	37
$Y_2 = (Y_1 + S_{1 avg}) / 2$	60	48	221	11
$Y_2 = (Y_0 + Y_1 + S_{1 avg}) / 3$	66	45	130	39
Linear formulas:				
$Y_2 = Y_1 - 6F_2(Y_1 - S_{1 avg})$	94	87	186	58
$Y_2 = GCA_{avg} - 6F_2(GCA_{avg} - S_{1 avg})$	91	83	186	269
$Y_2 = Y_0 - 6F_2(Y_0 - S_{1 avg})$	82	69	176	55
Logarithmic formulas:				
$\ln Y_2 = \ln Y_1 - 6F_2(\ln Y_1 - \ln S_{1 avg})$	94	87	186	62
$\ln Y_2 = \ln GCA_{avg} - 6F_2(\ln GCA_{avg} - \ln S_{1 avg})$..	91	83	186	271
$\ln Y_2 = \ln Y_0 - 6F_2(\ln Y_0 - \ln S_{1 avg})$	85	70	177	60

¹ Significant at 0.01 level.

² Significant at 0.05 level.

TABLE 12.—*Measured and predicted forage yield of 10 synthetic varieties*

[Percent of check]

Varieties	Measured yield		Predicted Syn 2 yield based on—						
			Linear relationship between yield and heterozygosis ¹			Exponential relationship between yield and heterozygosis ²			
	Syn 1 ³	Syn 2	$f(Y_1) \ f(GCA_{avg}) \ f(Y_0)$			$f(Y_1) \ f(GCA_{avg}) \ f(Y_0)$			
2-clone:									
(1,2)	124 (124)	81	97	99	86	94	95	85	
(4,9)	121 (121)	74	89	88	72	83	82	71	
(2,9)	124 (124)	75	91	90	75	85	85	73	
4-clone:									
(1,2,3,9)	120 (129)	107	114	113	91	110	109	90	
(1,4,5,6)	114 (131)	113	117	114	97	113	111	95	
(1,2,7,9)	125 (129)	116	117	115	101	113	112	99	
6-clone:									
(1,2,3,7,8,9)	132 (127)	107	117	117	96	114	114	94	
(1,2,3,4,5,6)	128 (129)	113	117	116	95	114	113	93	
(1,2,4,5,7,9)	121 (126)	106	117	117	103	114	114	102	
9-clone (1,2,...,9)	122 (126)	108	119	119	98	117	117	97	
Average	123 (127)	100	110	109	92	106	105	90	

¹ For linear functions see table 11.

² For logarithmic functions see table 11.

³ The mean of the single crosses entering the synthetic is shown in parenthesis.

averages in table 12.) The formulas based on clonal yield underpredicted. Little can be said about the underprediction, except to note that the clonal progeny failed to yield as much as seedling progeny, possibly because of different root systems.

The diallel-cross progeny were directly comparable to the check and to the Syn 2 varieties, and one can speculate about the overprediction. The logarithmic function was more accurate than the linear one because it could account for the rapid inbreeding depression associated with low levels of inbreeding in alfalfa. Still, the logarithmic function overpredicted. An important reason for the overprediction is that the theory on which the prediction formulas are based fails to account for yield changes attributable to gene recombination independent of inbreeding. These changes are a result, in part, of what Hanson et al. called "relaxation of selection pressure" (17). When parents are highly selected for combining ability, the effects of gene recombination in advanced generations will be negative.

Finally, we come to the questions of which clones should be included in the new synthetic variety and how much will the variety yield in the generation planted by the farmer, usually near equilibrium. The best information we have is based on the logarithmic prediction formulas utilizing single-cross and S_1 progeny yields (table 13). Prediction based on the linear function and the logarithmic function were almost perfectly correlated. None of the two-clone and probably none of the three-clone synthetics (when overprediction is considered) would yield as much as 'Cherokee', supporting the hypothesis that at least four parents are necessary to produce a successful synthetic variety (3, 25).³ Only a small number of the possible 502 synthetics would be expected to exceed 'Cherokee' by 5%, perhaps fewer than 35 when overprediction and

³ Also, W. E. Davies, 1970, The yield in succeeding generations of experimental lucerne synthetics based on varying plant numbers, unpublished report of Fodder Crops Section of Eucarpia (Lusignan).

TABLE 13.—*Ranges and distributions of predicted forage yields of the 502 synthetics possible from the 9 selected clones, at equilibrium*

Prediction formulas and type of synthetic	Range (% of check)	Distribution			
		Number below check	Number exceeding check	Number exceeding check by 10 %	Number exceeding check by 15 %
Linear: ¹					
2-clone	64-93	36	0	0	0
3-clone	81-110	65	19	1	0
4-clone	89-118	46	80	13	1
5-clone	97-119	8	118	36	6
6-clone	103-120	0	84	41	10
7-clone	108-119	0	36	28	6
8-clone	112-117	0	9	9	2
9-clone	115	0	1	1	0
Total		155	347	129	25
Logarithmic: ²					
2-clone	62-89	36	0	0	0
3-clone	75-104	80	4	0	0
4-clone	85-112	91	35	1	0
5-clone	92-114	37	89	5	0
6-clone	99-115	4	80	13	0
7-clone	104-115	0	36	10	0
8-clone	109-114	0	9	5	0
9-clone	112	0	1	1	0
Total		248	254	35	0

¹ $Y_e = Y_1 - [3(Y_1 - S_{1\text{ avg}})/2n]$.

² $\ln Y_e = \ln Y_1 - [3(\ln Y_1 - \ln S_{1\text{ avg}})/2n]$.

experimental error are considered.

The best synthetic variety at equilibrium, based on both the linear- and the logarithmic-prediction formulas, would be the six-clone synthetic from clones 1, 2, 3, 5, 6, and 7. These six clones had the highest GCA in the diallel analysis, and they were among the highest in the S_1 progeny test. According to prediction, this variety would yield 137% of 'Cherokee' in the Syn 1 and 115% of 'Cherokee' at equilibrium. Adjusting for a 6% over-prediction, the new variety would be expected to outyield 'Cherokee' by 9% at equilibrium. This prediction should hold true under the environmental conditions under which the evaluations were made. However, under dense seeding in other years and locations, and with the possibility of some selfing in seed production fields, the yield advantage of the new variety could be much less. When all factors are considered, it is not surprising that many new varieties that hold great promise for improvement during their developmental stages perform disappointingly when they reach the generation intended for commerce.

DISCUSSION

Gene Action

Although some of the literature is conflicting and some reports on breeding methods overly optimistic, a clear interpretation of the breeding behavior of alfalfa is emerging. From the work of Kehr and Gardner (20), Dudley et al. (12), and Hill et al. (18), it is clear that nonadditive gene action is important to the expression of vigor in alfalfa. The extreme sensitivity of alfalfa to inbreeding is another manifestation of nonadditive gene action. Alfalfa responds readily to selection for yield, as measured in the first cross after selection. But most of this response results from nonadditive effects, and the benefits are partly lost in the advanced generations because of gene recombination. Additional vigor is lost in narrow-based synthetics because of inbreeding. Nonadditive gene action in alfalfa is the result of diallelic (digenic), triallelic (trigenic), and tetraallelic (tetragenic or quadrigenic) interactions at a locus, and epistatic interactions between loci. Diallelic interactions in autotetraploids are to a degree passed from parent to offspring by means of the diallelic gamete. Also, epistatic interactions are passed in part from generation to generation through link-

age. But triallelic and tetraallelic interactions arise anew with each new generation. Busbice and Wilsie have postulated that triallelic and tetraallelic loci are essential to the expression of heterosis in alfalfa (8).

Progeny tests that include nonadditive variation (clonal and diallel-cross tests) are more effective than tests that exclude a part of the nonadditive variation (topcross and S_1 tests). Although GCA variance is largely additive, estimates of GCA from diallel and polycross tests successfully rank parents for both nonadditive and additive effects, when specific combining ability is unimportant. The benefit of selection is the greatest in the first cross following such selection. Thereafter, as recombination and possibly some inbreeding rearrange the higher order and largely nonadditive genic interactions, the benefit of selection declines sharply. The advantage that one progeny test may have over another in the Syn 1 declines in the advanced generations as the general benefit of selections declines.

Hybrid Varieties

The highest expression of heterosis in alfalfa resides in single individuals, because all non-inbred autotetraploid hybrid varieties are a mixture of genotypes (6). Theoretically, the highest yielding alfalfa variety would be one produced by vegetatively propagating a single superior clone, but this is impractical. A more practical approach to maximizing heterosis would be the marketing of single-cross, three-way, or double-cross hybrids through the use of cytoplasmic male sterility. From this and other studies reported in the literature, it is clear that synthetic varieties can never achieve the yield and vigor of hybrid varieties.

The marketing of hybrid alfalfa, if the technology can be developed, could substantially improve yield. However, there would be a price to be paid in genetic vulnerability. An exceedingly large store of genes is maintained in our present-day synthetic varieties, both commercial and experimental. Because of this readily available store, alfalfa breeders have been eminently successful in breeding alfalfa resistant to many pests and adapted to many soils and climates. The large-scale marketing of hybrid varieties would ultimately reduce this store of genetic variability.

Synthetic Varieties

Alfalfa breeders have long debated the merits of narrow-based versus broad-based synthetics. This study indicates that one can achieve a small advantage in yield from narrow-based synthetics, that is, synthetics produced from only a few clones. To achieve this advantage one must balance combining ability against inbreeding depression. When fewer than four clones are used to initiate the variety, inbreeding depression in advanced generations probably will overwhelm any increased combining ability available through selection. When as many as 16 unrelated and noninbred clones are combined to initiate the variety, inbreeding is negligible ($\frac{1}{4}n = \frac{1}{4}$), and successful narrow-based synthetics can be formed with fewer than 16 clones. Probably, there would be little advantage to including more than 10 clones in a narrow-based synthetic.

Broad-based synthetics have been successful in commerce. The merit of broad-based synthetics over narrow-based ones has been given as increased stability over environments, but a discussion of the validity of this claim lies outside the scope of this paper. However, the breeding of broad-based synthetics requires less testing for combining ability than does the breeding of narrow-based ones. Simple phenotypic selection can maintain a median level of vigor near that possible from narrow-based synthetics, and a combination of phenotypic selection and strain crossing allows one great flexibility in breeding for adaptation and pest resistance.

The best narrow-based synthetic is based on a unique set of parents. To identify these parents, precise evaluation for combining ability must be made. An evaluation sequence is recommended, beginning with phenotypic selection as recommended by Carnahan and Miller (9). It is not essential to select a large number of plants, provided that several adapted sources of germ plasm are sampled. The theory of inbreeding shows how the mating of relatives leads to inbreeding, and the germ-plasm base of some breeding strains may be narrower than one realizes. Phenotypic selection should be followed by clonal evaluation at more than one location so that the genotype \times environment interaction can be evaluated. After clonal evaluation, the best clones can be selected for S_1 and polycross-progeny testing. If genotype \times environment interaction were important in the clonal test, more

than one location would be required for the S_1 and polycross-progeny tests. In any event, these tests will require a large number of replications for reliability. Plant density may have an effect on reliability, but a discussion on this subject is outside the scope of this paper. Finally, the prediction formulas developed in this paper should be helpful in choosing the right set of clones for the best variety.

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