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INBREEDING ALFALFA, *MEDICAGO SATIVA* L., BY SELFING, SIB-MATING, AND BACKCROSSING

by

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INTRODUCTION

Utilization of hybrid vigor in alfalfa breeding programs has long been considered a desirable goal. However, the rapid decline of vigor and fertility upon selfing has prevented the development of productive inbred lines of alfalfa. Although several studies have been conducted to examine vigor and fertility responses during inbreeding, understanding of the genetic mechanisms involved remains unclear. Attempts to propagate highly self-sterile but cross-fertile non-inbred clonal lines vegetatively met with limited success, and were not economically feasible for hybrid seed production.

Since the late 1950's, research workers at Iowa State University have initiated several investigations to gain a better understanding of fertility relationships in alfalfa. Results of these studies have shown that some problems related to vigor and fertility encountered with straight selfing may be partially overcome, or at least delayed, by slower forms of inbreeding, such as sib-mating and backcrossing. In the most recent study, sib-mating for a limited number of generations appeared to maintain a greater level of heterozygosity for fertility and incompatibility factors than did selfing. Results from this and earlier studies indicated that more information was needed to adequately assess the desirability of sib-mating and backcrossing as breeding procedures for developing inbred or partially inbred lines of alfalfa. Recent discovery of a presumed cytoplasmic male-sterility system in alfalfa gives added impetus for breeders to obtain information relative to the feasibility of developing inbred lines for hybrid combinations.

This study was undertaken with the following primary objectives: (1) to determine the effects of sib-mating over a period of several generations on fertility and vigor of alfalfa; (2) to determine the effects of backcrosses among various levels of inbreeding on fertility in alfalfa; and (3) to evaluate the feasibility of sib-mating and backcrossing as procedures for the production of inbred, or at least partially inbred, lines of alfalfa.

REVIEW OF LITERATURE

The literature pertaining to the present study has been recently and thoroughly reviewed by Aycock (1966), Williams (1964), and Lantican (1961). Consequently, this review will emphasize recent developments and review briefly the studies most pertinent to a consideration of present concepts concerning inbreeding and fertility in alfalfa.

Considerable controversy exists relative to inheritance patterns in alfalfa. Somatic chromosome numbers of 16 and 32 have been observed repeatedly, and establish conclusively that the basic number is eight (Bolton, 1962). Many early workers assumed that alfalfa was either a diploid or allopolyploid and they expected disomic segregation. Ledingham (1940) and Julén (1944) presented cytological evidence for autotetraploidy. Oldemeyer and Brink (1953) substituted a haploid complement (n=8) from diploid _Medicago falcata_ for one of two homologous sets of chromosomes in _M. media_ without impairing fertility. This substitution indicates that cultivated alfalfas are autotetraploid. Sprague (1959) observed that interspecific and tri-species hybrids of three diploid _Medicago_ species, _sativa_, _falcata_, and _gaetula_, displayed regular meioses. Therefore, these three appear to be genetic variants of the same polymorphic species. Lesins (1957) and Stanford and Clement (1958) studied dihaploids and concluded that _M. sativa_ is essentially autotetraploid and that tetrasomic inheritance should be the rule.

Until 1951, data from genetic studies with alfalfa were interpreted largely by disomic ratios. Stanford (1951) was the first to demonstrate a definite case of tetrasomic inheritance. In a study of purple versus white flower color, he classified segregants in the critical F_3 generation and noted that the observed values fit a tetrasomic ratio. Since that time, several workers have proposed tetrasomic inheritance for various traits in alfalfa, including Davis (1956), Markus and Wilsie (1957), and Busbice and Wilsie (1966b, 1966c). Disomic inheritance has not been proved conclusively to the exclusion of tetrasomic inheritance. Since tetrasomic inheritance is common in alfalfa, the question is not one of autotetraploidy versus allotetraploidy, but whether alfalfa is a true autotetraploid or a segmental allopolyploid (Bolton, 1962).

Medicago is a naturally cross-pollinated species. Tysdal et al. (1942) observed 89.1 percent crossing when yellow or white flowered plants were used as female testers with purple flowered male parents. Other workers, including Knowles (1943), Bolton (1948), and Kehr and LaBerge (1966), noted that the amount of cross pollination varied with the materials used, planting arrangement, and environment. Lesins (1961) questioned the results from early studies because most of the testers were inbreds and few tester plants were included in these experiments. He suggested the use of male sterile plants as testers for the amount of cross pollination. His calculation method involved a comparison of the number of flowers cross-pollinated to the number available for pollination. In one study the proportion of pods formed varied from 8 to 44 percent. He noted that this method saved time and labor because no progeny of the recessive testers must be grown.

Ordinarily, for alfalfa seed to be formed following either self- or cross-pollination, tripping of the flower must occur. Whether tripping is required for seed set was long a topic of controversy. It was maintained by Hay (1925) and Carlson (1928) that considerable seed set occurred without tripping. Kirk and White (1933) discussed autogamy in alfalfa and pointed out that pollination occurs when plants are in the early bud stage, and that tripping is not required to effect fertilization. In contrast, Knowles (1943) and Tysdal (1940, 1946) maintained that very few pods are formed without tripping. Armstrong and White (1935) reported that tripping of the staminal column against the standard petal ruptures the stigmatic membrane, releasing the stigmatic fluid, thus inducing pollen germination. According to White (1949), the accumulated evidence establishes the fact that tripping is almost obligatory for seed setting.

Despite being primarily cross-pollinated, alfalfa also can be selfed. However, it has been known since the work of Piper et al. (1914) that seed production is much lower following selfing than crossing. Knowles (1943) measured self- and cross-fertility of random plants and self-fertile selections of Grimm alfalfa. From self-pollinations these groups set an average of 0.56 and 1.56 seeds/flower, respectively, but 3.70 and 4.60 seeds/flower when crossed. Bolton (1948) obtained 1.58 seeds/flower selfed but 5.54 seeds/flower crossed, and other workers have reported similar results. The range in self-fertility generally is greater than that observed after crossing, and both the range and the amount of self-fertility decline more rapidly upon inbreeding. Wilsie (1951) observed a range in self-fertility from 0.12 to 1.84 seeds/flower selfed, and later reported a range of 0.0 to 4.0 seeds/flower selfed from a population of 437 hybrid plants (1958a).

Causes for the reduced seed-set following selfing compared with crossing have been considered by several investigators. Quantity of pollen and relative germinability under a wide range of environmental conditions were implicated by Engelbert (1932). Bolton and Fryer (1937) added differential rates of pollen tube growth to these factors, but also stated that no single feature of the pollen could wholly explain the extreme differences in fertility between plants they classed as "steriles" and "fertiles". They found lower pollen viability among the "steriles", and noted two classes of sterile pollen. One type appeared normal but failed to germinate, while the other grains appeared clear and empty. Seasonal variations in pollen viability were not observed in experiments conducted by Sexsmith and Fryer (1943). They concluded that seasonal differences in seed set could not, therefore, be attributed to changes in pollen viability.

Brink and Cooper (1936) and Rotar and Kehr (1963) investigated pollen abortion in relation to seed set and agronomic performance. It was concluded by Brink and Cooper (1936) that the amount of aborted pollen was probably not a limiting factor in seed production. Rotar and Kehr (1963) observed that self-fertility was not correlated significantly with irregularities at meiosis, micronuclei per quartet, or agronomic characteristics. Miller and Schonhorst (1968) reported that the percentage pollen germination was independent of pollen tube length, self-fertility, and the number of racemes, flowers, pods, or seeds produced.

The number of ovules/ovary is an important factor in determining the potential number of seeds a given plant may produce. Martin (1914) found that the number of ovules/ovary ranged from 12 to 18 in tetraploid alfalfa. A range of 8 to 14 ovules/ovary was noted by Cooper (1935) and Barnes and Cleveland (1963b) reported 6 to 17 in diploid and tetraploid plants. It was concluded by Barnes and Cleveland (1963b) that ovule number in diploid alfalfa was controlled by four genes. Three genes (Ov_1, Ov_2, and Ov_3) showed complete dominance while the fourth (Ov_4) was incompletely dominant. Genetic effects of all four loci appeared to be additive. Gartner and Davis

(1966) determined that the number of ovules/ovary was not correlated significantly with either the number of seeds/pod or the number of pods set.

Cooper et al. (1937), Brink and Cooper (1938, 1939), and Cooper and Brink (1940) examined several factors that affect seed-set in alfalfa. Cooper et al. (1937) studied the effects of self-pollination and noted that (1) pollen tubes often failed to reach the basal ovules, (2) many ovules were not fertilized even though an abundance of pollen tubes was present, and (3) abortion of fertile ovules was a common occurrence. They also reported that the probability of an ovule being fertilized declined from the apex toward the base of the ovary. The proportion fertilized at each position was less for the low-fertility clones. They observed further that development of the fertilized ovule was much slower in the low seed-setting plants.

A partial self-incompatibility system in alfalfa was described by Brink and Cooper (1939) and Cooper and Brink (1940). Brink and Cooper (1938) reported that in some plants the male gametophytes were less able to effect fertilization in the individual from which they arose than were unrelated male gametophytes. They observed that this partial self-incompatibility resulted largely from the inability of the male gametophyte to make sufficient growth to reach the eggs in the ovary of the same plant. They observed that with selfing few pollen tubes advanced beyond the mid-region of the ovary, whereas, with cross-pollination the tubes usually reached the base. In a series of self-pollinations, pollen tubes were observed to pass directly by the micropyle of unfertilized ovules. They also observed that pollen tubes originating from cross-pollination penetrated the ovarian cavity at a faster rate.

Cooper et al. (1937) and Brink and Cooper (1939) described another factor causing reduced seed-set in alfalfa, somatoplastic sterility. This collapse of the fertilized ovules is particularly common after self-pollination. Brink and Cooper (1939) noted that only one-fifth as many fertile ovules collapsed after crossing as after selfing. They contributed this type of sterility to a differential growth rate of the endosperm following self- and cross-fertilization. Food reserves can be shared equally between the integument and endosperm if parallel growth of these tissues occurs. However, following selfing, the rate of endosperm growth often is so low that the balance shifts in favor of the integument. Hyperplasia then arises, causing collapse of the endosperm and eventual termination of ovule development. Cooper and Brink (1940) concluded that the abortion of fertile ovules may be a manifestation of self-incompatibility per se, or it may be an inbreeding effect. They also calculated that 98 percent of the difference between potential and actual fertility following selfing, and 67 percent of the difference following crossing were attributable to the frequency of fertilization and collapse of fertile ovules during the first six days after fertilization.

It was more recently confirmed by Sayers and Murphy (1966) that the frequency with which fertilization occurs and the incidence of ovule abortion were the two main factors controlling the differential self- and cross-fertility observed among alfalfa clones. In their experiments, pollen tube growth was similar after either self- or cross-pollination. Thus, they reasoned that selfing had a more pronounced effect on the frequency of pollen tube penetration into the ovules than it did on pollen tube growth. They concluded that fertilization and ovule abortion may be controlled to a greater extent by the genotype of the female parent than by the genotype of either the zygote or endosperm.

The term "relational incompatibility" was proposed by Fyfe (1957) to denote the inverse proportionality between the relative fertility of a mating and the extent that the parents are inbred. He believes this phenomenon could be due to an interaction of gametophytes before fertilization (differential ovule penetration), or to interactions within and between gametic complements after fertilization (less ovule abortion following crossing). The term self-incompatibility was considered appropriate only for the reaction between pollen and maternal tissue (less and slower penetration of pollen tubes after selfing). In conclusion, he reasoned that both relational- and self-incompatibility could operate in tandem to reduce seed-set. Barnes and Cleveland (1963a) found that long pollen tube lengths, in vitro, resulted from a long period of sustained growth, rather than fast growth. Pollen grain size had little relationship to pollen tube length. From selfed and crossed progenies, they concluded that pollen tube length was under genetic control. Miller and Schonhorst (1968) recently noted that self-fertility was correlated significantly with pollen tube length. Thus, it seems possible that the self-fertility of inbred lines of alfalfa could be increased by selection for increased pollen tube length.

Numerous studies have shown that various inbreeding schemes result in a rapid loss of vigor and fertility. Kirk (1927) observed that S_1 alfalfa lines were 30 percent lower in seed yield than their S_0 parents. Williams (1931) found that the average seed yield of S_1 plants was 88 percent less than that of the parent clones. Inbred lines were developed to the S_8 generation by Tysdal et al. (1942) with seed yields declining to 62 and 8 percent for the S_1 and S_8 generations, respectively, compared to the open-pollinated parental varieties. Wilsie and Skory (1948) reported a decrease of 84 percent in self-fertility between the first and second selfed generations. Wilsie (1958a) noted that one generation of selfing reduced fertility 80 to 90 percent. An 80 to 90 percent decline in self-fertility fron non-inbred to S_2 and S_3 generations was observed by Koffman (1959). Steuckardt and Dietrich (1968) reported a 50 percent loss in seed production with one generation of selfing.

Kirk (1927) observed that S_1 lines of alfalfa were reduced 19 percent in forage yield. However, a few S_3 lines did not differ significantly from the original open-pollinated strain. In general, delayed maturity was noted in the S_2 lines. According to Wilsie (1966), data from a wide range of alfalfa stocks at Iowa State University have shown an average loss of 30 percent in vigor in the S_1, with a range from zero to 46 percent. S_2 progenies declined about 54 percent and S_3 lines about 46 percent compared to their S_0 parents. Panella and Lorenzetti (1966) reported that forage yield was reduced more with inbreeding than was plant height. In this same study the most severe depression of vigor was noted in Lahontan, the variety with the narrowest genetic base.

Several other effects associated with inbreeding have been reported. Stewart (1934) observed that one generation of selfing gave progenies with significantly lower variability in plant height, plant width, stem diameter, leaflet length and width, blossom color, and foliage color. These results were cited as evidence that alfalfa is much less heterozygous than it commonly is thought to be. Koffman and Wilsie (1961) reported that inbred lines showed more severe winter damage, reduced yield and vigor, more upright growth habit, more apparent leaf disease, lighter foliage color, and smaller crown size than the open pollinated source varieties. Contrary to Stewart's data, they found that variability in expression of growth habit, leaf diseases, and foliage color appeared to increase with inbreeding, with no apparent approach toward true-breeding inbred lines. Progenies with increased levels of inbreeding were reduced in spring vigor, forage yield, seed production, plant height and width, and had delayed maturity in experiments of Aycock and Wilsie (1968).

Several workers have shown that the drastic reductions in vigor and fertility after selfing can be slowed or partially overcome by milder forms of inbreeding. Tysdal and Kisselbach (1944) reported 3.2 and 8.0 seeds/10 flowers from self- and self-plus sib-pollination, respectively. Koffman and Wilsie (1961) observed that sib-mating S_1 plants appeared to postpone loss of self-fertility for one generation. Lantican (1961) found that sib-compatibility was twice as great as self-compatibility for S_1 plants. Backcrossing the S_1 to its S_0 parent was observed to restore fertility far above the levels obtained with selfing or sib-mating. He used S_1 plants only as female parents, and suggested that a possible explanation for the restored fertility could be the greater array of gametes in the S_0 pollen parent, thus avoiding incompatibility. Williams (1964) mated several of Lantican's backcross (S_1 x S_0) lines to their S_1 parents, reciprocally. The BC_2 progeny showed a marked increase in seed-set compared to the selfed BC_1 plants. Reciprocal differences were not observed. This may have been related to the fact that the S_1 and BC_1 plants were inbred and probably did not differ greatly in their gametic arrays. In general, restoration of fertility tended to be associated with the self-fertility of the S_1 and S_0 parents. This suggests that use of highly self-fertile plants as base material for inbreeding would be desirable. Aycock and Wilsie (1967) reported that the drastic decline in fertility following selfing was halved by sib-mating. They noted also that self-fertility in two populations of alfalfa was correlated significantly with sib- and cross-fertility.

Busbice and Wilsie (1966a) point out that inbreeding depression observed in alfalfa usually is greater in the early generations of selfing than is expected for an autotetraploid based on the coefficient of inbreeding (F). They proposed that the loss of allelic interactions which assure a high degree of heterozygosity was responsible for the rapid decline in vigor upon inbreeding. Busbice (1968) further examined this problem and reported that the relationship of seed yield to F of the zygote was non-linear, contrary to the earlier proposal of Fyfe (1957). It was suggested by Busbice (1968) that the inbreeding coefficient of the developing zygote was the primary factor limiting selfed seed production in alfalfa. He concluded that reduced seed yield with inbreeding did not result from a failure of the gametes to unite, but was due to a loss of heterozygosity in the zygote, with resultant lethality.

Procedures and progress in alfalfa breeding have been reviewed by White (1949) and Bolton (1962). Early workers relied on natural or mass selection techniques to obtain improved varieties. It was soon evident, however, that complex characters such as seed and forage yields must be evaluated by progeny testing to achieve progress. Over the years, selfed, maternal line, topcross, polycross, open-pollinated, and diallel cross progeny tests have been used to evaluate clones. Most of the recent varieties are synthetics composed of clones found to be superior in combining ability.

The possibility of producing hybrid alfalfa also has been considered for many years. Tysdal et al. (1942) reported that the mean forage yield of 28 F_1 hybrids was slightly lower than that of three check varieties. However, the ten most productive hybrids yielded 15 percent more than the checks, and one hybrid was 39 percent higher in yield. They noted that specific parental combinations gave yields that were considerably different than anticipated from parental performance. Tysdal and Kisselbach (1944) advocated the use of highly self-sterile but cross-fertile clones with high combining ability to produce F_1 hybrids. They also noted that some double crosses produced by crossing two F_1 hybrids yielded as well as the F_1 hybrid produced from selfed lines. Wilsie and Skory (1948) reported that their lines differed materially in combining ability and suggested the determination of specific combining ability to maximize progress. Wilsie (1958b) obtained an F_1 single-cross that yielded 81 percent more than the better parent. Many observations point to the conclusion that alfalfa exhibits sufficient hybrid vigor to boost forage yields appreciably.

Tysdal and co-workers (1942, 1944) proposed a system for commercial seed production of hybrid alfalfa that is similar to the procedure used in corn. They advocated vegetative propogation of four self-sterile clones to produce two self- and sib-sterile single-crosses, which in turn would combine to form a high yielding double cross. Bolton (1948) proposed the use of non self-tripping, self-fertile plants in the same general scheme, thereby avoiding the necessity of vegetative propogation. Recently, Davis and Greenblatt (1967) have reported apparent cytoplasmic sterility in alfalfa. Use of this sterility system may provide a method for commercial production of various types of hybrids, for example, single crosses, top crosses, or three- and four-way crosses.

Although inbreeding does not seem essential for the development of lines with high combining ability, it does offer advantages for the elimination of undesirable traits and the fixation of desired characters. Lantican (1961), Williams (1964), and Aycock (1966) all have suggested the use of sib-mating and backcrossing to develop inbred lines for the production of commercial hybrids. Highly self-fertile clones should provide an exceptionally desirable base of breeding material and a large number of lines must be evaluated to find the desirable, inbreeding-tolerant types necessary for a successful program.

MATERIALS AND METHODS

Source and Identification of Materials

Source materials for this study were obtained from the S_0 population described previously by Aycock (1966). They traced originally to a commercial seed lot of certified Vernal alfalfa (accession number 2896) obtained in 1963.

To maintain pedigrees and to identify individual clones, the system of Newell and Tysdal (1945) as modified by Aycock (1966) was used. Three main ideas were incorporated into the pedigree numbers used in this study. These were the year of selection, method of progeny derivation, and a serial identification of selections. The letter designations used by Aycock (1966) to identify populations were deleted because only the S_0 (A) population was continued in this study. For example, clone number 62-100-1 was selected in 1966 (designated as 6), as a result of sib-mating (progeny derivation system 2), and was a descendant of the original plant number 100. The number of the first plant in each S_0 cross (100, 102, ..., 198) also was used as the family line number throughout the study. Other numbers used to identify progeny derivation systems were (1) for selfing, (4) for hybridization, and (0) for a non-inbred or commercial variety. Full-sib$_3$ (FS_3) progeny produced by crossing two FS_2 parents were designated 72-102 with the two plants selected as parents for the next cycle of sib-mating numbered 72-102-2 and 72-102-3.

In the selfing series, no pedigrees were maintained because each group of plants in succeeding generations was grown from a composite of seeds from all plants that set seed the preceding year. The plants were numbered consecutively each year (1, 2, 3, ..., n) and the derivation numbers accumulated. For example, S_1 plants selected in 1964 were numbered 41-1, 41-2, etc. and S_5 plants selected in 1968 were designated 811111-1, 811111-2, etc.

Terminology similar to that used by Aycock (1966) was adopted for this study. A plant is defined as being initially started from seed. A clone or clonal line is a plant that has been vegetatively propagated by stem cuttings.

Greenhouse Procedures

Sib-mated population

In September 1966, FS_2 seed from 40 of the 50 original family lines was available. The seed from reciprocal crosses was bulked for each family and planted in a sterilized mixture composed of 2 parts soil, 1 part sand, and 1 part peat in greenhouse flats. Three weeks later, 10 or fewer seedlings from each family were transplanted individually into 4-inch clay pots filled with the same soil mixture. After two more weeks of growth, two plants from each family were selected randomly for use as parents in the sib-mating scheme. The pots were placed randomly on the greenhouse bench except for the restriction that each pair of sib-parents was placed together. Pairs were shifted in position during the crossing period to prevent possible differential effects related to location on the bench. Nutrient solution was prepared by mixing 10g $MgSO_4$, 20g KCl, 20g KNO_3, 30g KH_2PO_4, and 50g $Ca(H_2PO_4)_2$ in 11 liters of distilled water. Ten to twelve ml of the solution were applied to each pot at three-week intervals. To accelerate flowering, the photoperiod was extended to 18 hours per day from December through February with 200-watt incandescent lamps.

Each of the 40 pairs of clones was crossed reciprocally in the late winter and spring of 1966-67. Since fertility generally was low, more than 100 flowers were crossed on most plants. All crosses could not be made during the same period because the time of flowering varied among plants. To make a cross, the standard petal of each flower used as a female was cut off at the base. The flowers were then tripped and the pollen was collected in a small paper boat. Excess pollen was removed from the stigmas with a vacuum pump. Pollen was transferred to the plants used as females immediately after emasculation. A tag with the number of flowers crossed, the date of the cross, and the parents involved was placed on the completed raceme.

Self-fertility also was determined for each plant used as a sib-parent. More than 100 flowers were tripped artificially for most plants. Selfing was accomplished by pressing the flat end of a toothpick on the keel, and drawing the tip across the exposed stigma of the tripped flower. Each raceme was again tagged with the appropriate information.

In four to five weeks, the mature pods were harvested and threshed. The total number of well-filled seeds was counted and divided by the total number of flowers crossed or selfed to determine the self- and sib-fertility indices for each plant.

Because of the extremely low seed-set, crossing was extended late into the spring to obtain adequate amounts of seed for the next cycle of sib-mating for the largest possible number of family lines. This delay prevented transplanting the progeny to the field and necessitated the establishment of plants from seed the following fall. Similar procedures were used in succeeding winter seasons for the FS_3 and FS_4 sib-matings, with the exception that replicates of the crosses were made during succeeding intervals of two or three weeks each to provide more precise analysis of the data. In the winters of 1967-68 and 1968-69, florescent lights were added to enhance plant growth during cloudy weather.

Selfed population

Inbreeding by straight selfing also was accomplished for comparison with the sib-mated progenies. In the fall of 1966, a composite of S_3 seed was formed by combining a maximum of five seeds from each S_2 plant. If less than five seeds were produced on a plant, all were included in the composite.

Greenhouse techniques were the same as those used for the sib-mated plants. Since many plants bloomed poorly or not at all, several were repotted from the field in October 1966, and selfed the following winter.

A composite of S_4 seed was formed similarly in October 1967, except ten seeds/plant were included. Some S_4 plants also were repotted and selfed the following winter. The S_5 composite formed in October 1968 included five seeds or less from each plant.

Backcross populations

In the winter of 1966-67, 18 FS_1 family lines were selected for use as parents in the first type of backcross (BC-1). The families were grouped into three classes according to their relative sib-fertility indices, high (1.5-2.6), medium (0.8-1.0), and low (0.1-0.2). One random FS_2 parent in each family was then backcrossed reciprocally to one of its randomly selected FS_1 parents. All plants were handled like those being sib-mated or selfed.

In the winter of 1968-69, four additional types of backcrosses were made. Twelve of the 18 FS_1 family lines selected for the first backcross were also selected for crossing with their FS_4 descendents in the second type of backcross (BC-2). The same 12 FS_4 plants used in BC-2 were selected for backcrossing to their non-inbred (S_0) parent in the third type of backcross (BC-3). Because of difficulties in vegetative propagation and sterility of certain plants, only 16, 9, and 8 crosses were made for the BC-1, BC-2, and BC-3 populations, respectively.

In the fourth and fifth types of backcrosses, S_3 and S_5 plants derived from the straight selfing procedure were backcrossed to a selected group of S_0 clones. The S_3 clones were grouped into four classes on the basis of their self-fertility indices, high (0.15-0.35), medium (0.05-0.10), low (0.030-0.040), and very low (0.000-0.005). The S_0 clones were similarly grouped into four classes, high (1.40-1.60), medium (0.70-1.00), low (0.50-0.60), and very low (0.10-0.30). Two sets of S_3 clones, consisting of one clone from each relative fertility class, were then crossed with a set of S_0 clones developed similarly. As in the first and second types of backcrosses, some matings were not completed, but 33 crosses and reciprocals were made. In the fifth type of backcross, six S_5 plants (all medium or lower in fertility) were crossed with five of the S_0 clones used in the BC-4 matings, giving a total of 30 crosses plus reciprocals.

Analysis of Greenhouse Data

Data for sib_3-fertility, BC-1 fertility, self-fertility of the sib-parents, and self-fertility of the plants in the straight selfing series were based on one replicate of 100 or more flowers per cross and reciprocal, or per self. Analyses of variance appropriate to the randomized complete block design were performed for the sib_4- and sib_5-fertility indices. The mean squares for crosses were partitioned into components for families (F), reciprocals (R), and families by reciprocals (F x R). Fertility indices were based upon 25 to 50 flowers/cross and reciprocal in each of two or three replicates.

Fertility data for the BC-2 (FS_4 x FS_1) and BC-3 (FS_4 x S_0) populations were analyzed in the manner used for the sib-fertility indices. Fertility indices were based upon two replicates of 25 to 50 flowers/cross and reciprocal. Backcross fertility indices involving selfed lines were also analyzed like the data for sib-families except that mean squares for crosses were divided into components attributable to among S_0 clones, among S_3 or S_5 plants, reciprocal effects, and a residual source of variation. BC-4 fertility indices were based upon 25 flowers/cross and reciprocal in two replicates and BC-5 estimates were made from three replicates of 10 flowers/cross and reciprocal.

Heritability estimates for sib- and self-fertility were calculated in standard units by the procedure described by Frey and Horner (1957). Phenotypic correlations between self- and sib-fertility were calculated for each generation using the mean fertility indices of each sib-family.

Field Procedures

Since the materials used in this study were obtained from the investigations conducted by Aycock (1966), where the field experiments were numbered 1 and 2, my experiments were numbered 3 and 4 to maintain the sequence and facilitate record-keeping.

Experiment 3

In April 1967, progenies representing nine levels of inbreeding were available. Seeds were planted individually in peat cups arranged in wooden flats in the greenhouse. On May 16-17, 1967, seedlings of 60 entries (5 to 10/level of inbreeding) were space planted in a field nursery at the Iowa State University Agronomy Farm near Ames. Five plants/entry were transplanted in plots arranged in a randomized complete block design with three replicates. Plants were spaced at 24-inch intervals within rows spaced 40 inches apart. In August 1967, the nursery was overseeded with creeping red fescue to facilitate weed control. In March 1968, 200 pounds/acre of 0-20-20 fertilizer was applied as a topdressing.

The agronomic characters studied in Experiment 3 are listed in Table 1. Fall and spring vigor were scored visually on a 1-9 scale. Yield was recorded in pounds/plant (green weight), and plant height, width, and longest stem were measured in inches. Days to bloom were determined as the number of days from first harvest until the first open flower appeared on each plant. Flowering occurred between 29 and 51

Table 1. Agronomic characters measured in Experiments 3 and 4

Character	Unit of measure	Date scored or measured	
		Experiment 3	Experiment 4
Fall vigor	1-9[a]	October 11, 1967	---
Spring vigor	1-9[a]	May 3, 1968	May 7, 1969
Yield	Pounds/plant	June 6-7, July 23-24, August 28, 1968	June 16-17, 1969
Days to bloom	Days from first cutting	July 1968	July-August 1969
Plant height,			
summer	Inches	July 19, 1968	July 23-24, 1969
fall	Inches	October 14, 1968	October 7, 1968
Plant width,			
summer	Inches	July 20, 1968	July 23-24, 1969
fall	Inches	October 14, 1968	October 7, 1968
Growth habit,			
summer	Height/width	July 1968	July 1969
fall	Height/width	October 1968	October 1968
Longest stem	Inches	---	July 25, 1969

[a] 1 = most vigorous, 9 = least vigorous.

days after harvest. A few plants in the S_3 progenies did not bloom, and the means for these families are therefore atypically low. Growth habit was calculated by dividing plant height by plant width. Therefore, a value of 0.8-1.0 indicates that the plant was upright, whereas a value approaching 0.1-0.2 indicates a relatively prostrate growth habit. All data were obtained on individual plants, but the analyses of variance were computed using plot means. Entry numbers and pedigrees of the progenies included in Experiment 3 are listed in Table 2. For some progenies, seed supplies were limited and germination was poor. As a result, seeds from several plants were sometimes pooled to form composite entries. Entries 344 and 345 were established from stem cuttings of different S_3 clones.

Experiment 4

In the spring of 1968, a second field experiment was established at Ames using seedlings transplanted from the greenhouse. Eighty-one entries representing 11 levels of inbreeding were arranged in a partially balanced lattice design with three replicates. Experimental procedures for this experiment were the same as those described for Experiment 3. Agronomic characters measured in Experiment 4 are presented in Table 1. Entry numbers and pedigrees for the progenies are listed in Table 2. Several entries were again formed from composites of seed because the amount per entry was often limited.

Table 2. Entry numbers and pedigrees for progenies in Experiments 3 and 4

Experiment 3		Experiment 4	
Entry no.	Pedigree	Entry no.	Pedigree
	S_0 progenies		S_0 progenies
301	A30-5	401	A30-10
302	A30-6	402	A30-11
303	A30-7	403	A30-12
304	A30-8	404	A30-13
305	A30-9	405	A30-14
	S_1 progenies		S_1 progenies
306	A30-178	406	A30-104
307	A30-170	407	A30-118
308	A30-101	408	A30-137
309	A30-167	409	A30-147
310	A30-148	410	A30-150
311	A30-115	411	A30-156
312	A30-129	412	A30-166
313	A30-195	413	A30-180
314	A30-151	414	A30-188
		415	A30-198
	S_2 progenies		S_2 progenies
315	A511-3	416	A511-6
316	A511-8	417	A511-9
317	A511-28	418	A511-8
318	A511-29	419	A511-13
319	A511-21	420	A511-17
320	A511-23	421	A511-21
321	A511-13	422	A511-29
322	A511-15	423	A511-30
	F_1 progenies		S_3 progenies
323	A30-120 x 121		
324	A30-112 x 113	424-28	6111-1 to 40[a]

---

[a] Composite.

Table 2. (Continued)

Experiment 3		Experiment 4	
Entry no.	Pedigree	Entry no.	Pedigree
	F_1 progenies (continued)		S_4 progenies
325	A30-130 x 131	429	71111-2
326	A30-104 x 105	430	71111-3
327	A30-100 x 101	431	71111-24
328	A30-122 x 123	432	71111-1 to 13[a]
329	A30-186 x 187	433-35	71111-14 to 40[a]
330	A30-136 x 137		
			S_5 progenies
	FS_1 progenies		
		436	811111-41
331	A44-128-5 x 128-1	437	811111-44
332	A44-130-5 x 130-10	438	811111-1 to 24[a]
333	A44-126-6 x 126-4	439	811111-25 to 45[a]
334	A44-190-1 x 190-10	440	811111-53 to 63[a]
335	A44-164-7 x 164-2		
336	A44-170-8 x 170-7		F_1 progenies
337	A44-178-5 x 178-6		
338	A44-194-1 x 194-8	441	A30-108 x 109
339	A44-182-3 x 182-6	442	A30-114 x 115
		443	A30-138 x 139
	FS_2 progenies	444	A30-142 x 143
		445	A30-166 x 167
340	A52-134-1 x 134-2	446	A30-174 x 175
341	A52-190-3 x 190-2	447	A30-176 x 177
342	A52-124-1 x 124-7	448	A30-190 x 191
343	A52-104-8 x 104-9	449	A30-196 x 197
	S_3 progenies		FS_1 progenies
344-45	Stem cuttings from 15 S_3 clones	450	A44-108-7 x 108-10
		451	A44-118-1 x 118-2
		452	A44-124-1 x 124-8
	FS_3 progenies	453	A44-134-1 x 134-2
		454	A44-136-9 x 136-10
346	62-128-1 x 128-2	455	A44-158-7 x 158-9
347	62-182-1 x 182-2	456	A44-154-3 x 154-10
348	62-164-1 x 164-2	457	A44-180-3 x 180-5
349	62-134-1 x 134-2	458	A44-184-4 x 184-6
350	62-172-1 x 172-2		

Table 2. (Continued)

Experiment 3		Experiment 4	
Entry no.	Pedigree	Entry no.	Pedigree
	FS$_3$ progenies (continued)		FS$_2$ progenies
351	62-102-1 x 102-2	459-63	Composite formed from:
352	62-108-1 x 108-2		
353	62-116-1 x 116-2		
354	62-158-1 x 158-2		A52-102-6 x 102-1
355	62-166-1 x 166-2		A52-108-7 x 108-4
			A52-116-8 x 116-10
	BC-1 progenies		A52-122-2 x 122-6
			A52-132-7 x 132-4
356	62-136-1 x A52-136-7		A52-164-5 x 164-8
357	62-164-1 x A52-164-8		A52-166-6 x 166-9
358	62-102-1 x A52-102-1		A52-178-7 x 178-4
359	62-134-1 x A52-134-1		A52-188-7 x 188-4
360	62-112-1 x A52-112-7		A52-192-1 x 192-6
			FS$_3$ progenies
		464	62-104-1 x 104-2
		465	62-106-1 x 106-2
		466	62-122-1 x 122-2
		467	62-124-1 x 124-2
		468	62-154-1 x 154-2
		469	62-158-1 x 158-2
		470	62-162-1 x 162-2
		471	62-182-1 x 182-2
		472	62-192-1 x 192-2
			FS$_4$ progenies
		473	72-106-2 x 106-5
		474	72-112-1 x 112-5
		475	72-116-1 x 116-5
		476	72-128-5 x 128-7
		477	72-132-1 x 132-2
		478	72-144-4 x 144-7
		479	72-162-4 x 162-8
		480	72-164-1 x 164-4
		481	72-166-5 x 166-6

Analysis of Field Data

Experiments 3 and 4

Analyses of variance appropriate to the randomized complete block design assuming fixed effects were calculated for the agronomic traits measured in Experiments 3 and 4. The mean squares for entries were partitioned to estimate the variation among progenies within each level of inbreeding. Eight and ten individual degree of freedom comparisons, designed to test differences among various levels of inbreeding, were made in Experiments 3 and 4, respectively.

Phenotypic correlations among all characters were calculated for each group of progenies in each experiment on a plot mean basis. Correlation coefficients were calculated by the formula

$$r_p = \frac{\Sigma\, xy}{\sqrt{\Sigma x^2 \Sigma y^2}}$$

where $\Sigma\, xy$, $\Sigma\, x^2$, and $\Sigma\, y^2$ were the sum of cross products, sum of squares for X, and sum of squares for Y, respectively.

Degree of Inbreeding

The inbreeding coefficient (F) was calculated for each generation by the procedure of Malecot as outlined by Kempthorne (1957). The formula used to calculate F under self-fertilization was

$$F_n = 1/6\left[1 + 2\alpha + (5 - 2\alpha)F_{n-1}\right]$$

where F_n is the probability of two genes selected at random at a locus being identical by descent in any given generation, and α is the probability of double reduction. For full-sib progenies, F values were determined by the formula

$$F_n = 1/6 \left[4r_{xy} + 2\alpha + 2(1 - \alpha)F_{n-1}\right]$$

where r_{xy} is the coefficient of parentage (relationship of the two parents producing the progeny) and F_n and α are the same as described previously. The inbreeding coefficients for backcross progenies were calculated by the formula

$$F_n = 1/6 \left[4r_{xy} + (F_x + F_y)\right]$$

where r_{xy} is the relationship of the two parents mated in the backcross, and F_x and F_y are the inbreeding coefficients of the parents X and Y, respectively. F_n and α retain their same definitions.

For all calculations of F, three assumptions were made. These were: (1) $\alpha = 0$, (2) the S_0 parental clones that were randomly selected in 1963 were unrelated ($r_{xy} = 0$), and (3) the S_0 parental clones were non-inbred ($F = 0$).

RESULTS

Greenhouse Studies

Fertility of sib-mated population

Mean fertility indices for the sib_3, sib_4, and sib_5 populations are presented in Table 3. Individual plant data used for calculating these indices are listed for reference in Appendix Tables 25, 26, and 27. Average sib-fertility declined 70 percent between the third (FS_2) and fifth (FS_4) generations of sib-mating. Sib-fertility of the FS_4 progenies was 97 percent less than that of their non-inbred (S_0) parents. Since the inbreeding coefficient concomitantly increased to only $F = 0.277$, it appears that factors other than inbreeding depression per se must also be contributing to the decline of fertility in alfalfa. The allelic constitution at loci affecting compatibilities of the sib-parents also may be changing rapidly in the populations as generations are advanced.

Table 3. Mean self- and sib-fertility indices and inbreeding coefficients (F) for sib-mated progenies

Generation	Fertility index		F
	Self-fertility	Sib-fertility	
FS_2	0.312	0.294	0.153
FS_3	0.331	0.175	0.218
FS_4	0.196	0.086	0.277

The analysis of variance mean squares for FS_2 fertility indices are shown in Table 4. Highly significant differences were observed among families, with mean sib-fertility ranging from zero to nearly one seed/flower. Although reciprocal effects were not tested for significance, they were small in most families and appeared to be of little importance.

Table 4. Analysis of variance mean squares for FS_2 fertility indices, winter 1966-67

Source of variation	D.F.	M.S.
Families	39	0.1369**
Error	40	0.0359
C.V. (%)		(64.5)

**Significant at the 1 percent level of probability.

Mean squares for the FS_3 and FS_4 fertility indices are presented in Table 5. Significant differences were again noted among families in each generation. Reciprocal effects were not significant in either the FS_3 or FS_4 generation. The lack of significance may have been a result, at least in part, of the random assignment of plants as parents within each family. Examination of the data in Appendix Tables 26 and 27 reveals that reciprocal differences occurred within certain families in each generation. The reciprocal crosses in five FS_3 families and four FS_4 families differed significantly at the .05

Table 5. Analyses of variance mean squares for FS_3 and FS_4 fertility indices, winter 1967-68 and 1968-69, respectively

	Sib_4-fertility		Sib_5-fertility	
Source of variation	D.F.	M.S.	D.F.	M.S
Crosses	59	0.1067**	49	0.0483**
Families (F)	29	0.1674**	24	0.0848**
Reciprocals (R)	1	0.0008	1	0.0194
F x R	29	0.0496**	24	0.0131*
Error	59	0.0234	99	0.0077
C.V. (%)		(87.3)		(101.5)

*,**In this table and in all succeeding tables, one and two asterisks will refer to significant differences at the 5 and 1 percent levels of probability, respectively.

or .01 levels of probability. The data indicate that whether plants were used as either male or female parents of crosses usually was not important in the expression of sib-fertility. However, the significant family x reciprocal interaction indicates that there were instances within some families where plants did not perform the same in reciprocal crosses. As an extreme example, plant 72-128-7 appeared to be female sterile. When used as a male parent in crosses, seed set resulted, but seed was not obtained when this plant was used as the female parent or when it was selfed.

Frequency distributions of the means of sib-mated families for sib-fertility are shown in Table 6. The proportions of families having mean fertility indices of 0.20 or less were

Table 6. Percent of full-sib family means included in various sib- and self-fertility classes

Fertility index	Sib-fertility			Self-fertility		
	FS_2	FS_3	FS_4	FS_2	FS_3	FS_4
0.00 - 0.10	37.5	50.0	80.0	27.5	31.3	52.0
0.11 - 0.20	12.5	22.0	12.0	20.0	12.5	12.0
0.21 - 0.30	12.5	9.4		17.5	18.8	12.0
0.31 - 0.40	17.5	3.1		7.5	9.4	4.0
0.41 - 0.50	2.5	6.2	8.0	10.0	9.4	8.0
0.51 - 0.60				2.5		4.0
0.61 - 0.70	10.0	3.1		2.5	3.1	4.0
0.71 - 0.80	2.5				6.3	
0.81 - 0.90		3.1		2.5		
0.91 - 1.00	5.0			7.5		
1.01 - 2.00		3.1		2.5	6.3	4.0
2.01 - 3.00					3.1	
Total no. of families	(40)	(32)	(25)	(40)	(32)	(25)

50, 72, and 92 percent, respectively, for the FS_2, FS_3, and FS_4 generations. While only one or two families in each generation had fertility indices of zero, other families produced no progeny because the plants did not bloom or had abnormal flowers that prevented crossing. Some families were discontinued because losses during germination and early growth left less than the two plants required for sib-mating. The ranges in sib-fertility among families were similar for the FS_2 and FS_3 generations, but the range declined nearly 50 percent in the FS_4 matings. After five generations of sib-mating, only two of the original 50 families had sib-fertility indices greater than 0.2. In contrast, all S_0 families had cross-fertility indices greater than 0.5 and the range extended to 4.5 seeds/flower (Aycock, 1966). Since the FS_4 families had an inbreeding coefficient of only $F = 0.277$, the data indicate that the development of highly inbred lines by sib-mating may be limited by the necessity for an extremely large number of families in the initial population.

Table 3 also includes the mean self-fertility indices for the FS_2, FS_3, and FS_4 parents. Self-fertility data for the individual sib-parents are shown in Appendix Tables 28, 29, and 30. Average self-fertility indices were similar for the FS_2 and FS_3 generations, but considerably lower for the FS_4 parents. The proportions of family means included in various self-fertility classes are shown in Table 6. The percentages of families with mean self-fertility indices less than 0.2 were 47, 44, and 64 for the FS_2, FS_3, and FS_4 generations, respectively. These indices represent a decline of 70 to 80 percent from the self-fertility of the S_0 parents. Although the data were not analyzed statistically, fertility indices presented for individual entries in Appendix Tables 28, 29, and 30 show differences of more than one seed/flower selfed among family means in each generation. Differences of similar magnitude also were observed between individual members of some families in the FS_2 and FS_3 generations. The data further indicate that individual families differed in their response to inbreeding during the three generations of sib-mating. Many families continually declined in fertility, some increased during the three generations, and still others exhibited no definite trend. Since the self-fertility levels for all three generations generally were quite low, it is possible that too few flowers were selfed to adequately determine the true fertility indices. At the low levels of fertility, environmental effects undoubtedly exerted a stronger influence on fertility than they did in earlier generations.

Fertility of selfed population

Mean self-fertility indices and inbreeding coefficients for each generation of selfing are shown in Table 7. Self-fertility data for the individual S_3, S_4, and S_5 plants included in the straight selfing scheme are presented in Appendix Tables 31, 32, and 33, respectively. Data presented in Table 7, plus that reported by Aycock (1966) for earlier generations, show that self-fertility declined drastically between the S_0 and S_3 generations. Mean self-fertility of the S_3 plants was 95 percent lower than that of the S_0 parents, and 67 percent of the S_3 plants either did not bloom or failed to set seed during the first winter that selfing was attempted. Therefore, despite efforts to maintain a random sample of lines, a strong selection for self-fertility resulted. Tables 7 and 8 show that both the mean and the range of self-fertility indices were markedly greater in the S_4 as opposed to the S_3 generation. Relatively fewer S_4 plants had a fertility index of zero than

Table 7. Mean fertility indices and inbreeding coefficients (F) for selfed populations

Generation	Self-fertility index	F
S_3	0.038	0.421
S_4	0.181	0.518
S_5	0.108	0.598

Table 8. Percentage of selfed plants included in various self-fertility classes

Self-fertility index	Generation		
	S_3	S_4	S_5
0.0	28.3	21.8	43.1
0.01 - 0.05	53.5	34.6	19.5
0.06 - 0.10	6.8	23.6	15.6
0.11 - 0.15	4.5		3.9
0.16 - 0.20	2.3	7.3	2.0
0.21 - 0.30	2.3	1.8	3.9
0.31 - 0.40	2.3	1.8	2.0
0.41 - 0.50			2.0
0.51 - 0.60			2.0
0.61 - 0.70		1.8	2.0
0.71 - 0.80		1.8	2.0
1.00 - 2.00		5.5	2.0
Total number of plants	(44)	(55)	(51)

did their S_3 parents (Table 8). However, the proportion of S_5 plants that failed to produce seed increased sharply in comparison with both the S_3 and S_4 generations. Many of the S_3 and S_4 generation plants were so poor in vigor that they either did not bloom or failed to produce seed during the first winter. Some of these plants were observed to be slightly self-fertile after they were repotted from the field and selfed again the following winter. Consequently, some S_5 plants with fertility indices of zero might be expected to exhibit some self-fertility if evaluated again after growth in the field for a summer. Although the levels of fertility generally were very low in all three generations, five and two plants in the S_4 and S_5 generations, respectively, exhibited self-fertility indices comparable to those of the S_0 parents.

In summary, inbreeding by straight selfing was accompanied by much greater reductions in vigor and self-fertility than were observed with the sib-mating procedure. This decline was not entirely unexpected, however, because the inbreeding coefficient increases more rapidly with straight selfing. However, in the S_3 generation, the inbreeding coefficient was only $F = 0.421$, whereas self-fertility had declined 95 percent from the S_0 value. As suggested for the sib-mated populations, genetic factors for incompatibility also may have affected the self-fertility values of the selfed populations; and homozygosity for these factors should be obtained even more rapidly with selfing.

Fertility of backcross populations

Backcross-fertility indices for individual crosses in the five types of backcross populations are presented in Tables 34 to 38 in the Appendix, and mean fertility values for the different populations are listed in Table 9. In general, the inverse relationship between fertility and the inbreeding coefficient was similar to that shown previously for the selfed and sib-mated progenies. However, backcrosses involving selfed lines exhibited greater fertility relative to their respective F values than did those involving sibbed progenies. Although both selfed and sibbed progenies were subjected to some unavoidable selection for fertility, a larger proportion of selfed plants failed to produce seed each generation. Therefore, the selfed lines included in backcrosses may have been more highly selected for fertility than were the sibbed lines. More importantly, since the selfed lines were grown from a composite of seeds in each generation, the relationship between the selected plants and the S_0 clones may have been less than that of the pedigreed sib-progenies. If segregation was occurring for incompatibility factors, the selfed lines may have contained fewer loci with alleles in common with their S_0 parents than the sibbed progenies which were maintained in direct family lines. Within each group of backcrosses, involving either selfed lines or

Table 9. Fertility indices and inbreeding coefficients (F) of backcross populations

Backcross			
Designation	Description	Backcross-fertility index	F
BC-1	(FS_2 x FS_1)	0.414	0.206
BC-2	(FS_4 x FS_1)	0.310	0.227
BC-3	(FS_4 x S_0)	0.648	0.130
BC-4	(S_3 x S_0)	0.720	0.237
BC-5	(S_5 x S_0)	0.487	0.266

sib-mated progenies, fertility declined as F increased.

The analyses of variance mean squares for the fertility indices of backcrosses involving sib-progenies are shown in Tables 10 and 11. In the first type of backcross (FS_2 x FS_1), differences among families were highly significant. The magnitude of these differences can be seen in Table 34 of the Appendix, where family means show a range of 0.2 to 1.2 seeds/flower crossed. Although differences shown for reciprocal crosses were not tested statistically, they were usually small for the BC-1 population. However, fertility was higher in 11 of the 16 backcrosses when the more inbred (FS_2) clone was the male parent.

Although fertility of the BC-1 crosses did not approach that of the less inbred (FS_1) parent, a reversal of the trend shown previously in the selfed and sibbed populations for low

Table 10. Analysis of variance mean squares for fertility indices of backcross-1 involving sib-progenies, winter 1966-67

Source of variation	D.F.	M.S.
Families	15	2.469**
Error	16	0.051
C.V. (%)		(54.7)

Table 11. Analyses of variance mean squares for fertility indices of backcrosses-2 and -3 involving sib-progenies, winter 1968-69

	BC-2 fertility		BC-3 fertility	
Source of variation	D.F.	M.S.	D.F.	M.S
Crosses	17	0.4228**	15	1.0325**
Families (F)	8	0.8068**	7	1.7044**
Reciprocals (R)	1	0.0820	1	1.0617**
F x R	8	0.0813	7	0.3564
Error	17	0.0636	15	0.1660
C.V. (%)		(81.4)		(42.3)

fertility indices to be associated with high values of F was observed in the BC-1 data.

The data indicate that backcrossing inbred sib-progenies to their immediate parents may delay loss of fertility while concomitantly increasing F. However, the difference in fertility observed between the FS_2 parent (0.294) and the BC-1 cross (0.414) may be too small to affect a breeding program significantly. Determination of the self- and cross-fertility indices of BC_1 progenies should be useful for examining the feasibility of this procedure.

Analyses of variance mean squares of the fertility indices for the backcross-2 (FS_4 x FS_1) and backcross-3 (FS_4 x S_0) populations are presented in Table 11. Highly significant differences were observed among crosses and among families in the BC-2 and BC-3 matings. As shown with the first type of backcross, the BC-2 data did not indicate a significant effect for reciprocal crosses. As observed in the BC-1 crosses, fertility was higher in a majority of the crosses, however, when the more inbred (FS_4) clone was the male parent. Williams (1964) observed a similar lack of reciprocal differences in backcrosses involving S_1 x (S_1 x S_0) parents and postulated that when both parents were inbred, their gametic arrays may be similar. In my backcrosses, both parents were more inbred than those used by Williams and were members of the same family line. Therefore, common genetic incompatibility factors may have limited the amount of fertility restoration. The Family x Reciprocal interaction was not significant in either the BC-2 or BC-3 matings, indicating that the different families responded similarly in relation to reciprocal effects in the crosses made in this study.

Contrary to the results for the BC-1 and BC-2 populations, reciprocal differences were highly significant for the third type of backcross (FS_4 x S_0). Mean fertility indices were 0.841 and 0.477 seed/flower for crosses with the FS_4 parent as the male and female parent, respectively. In six of the eight crosses, higher fertility again resulted when the non-inbred plant was the female parent. These results confirm those of Lantican (1961), who observed that backcrosses of S_1 x S_0 lines showed significant reciprocal effects. Data from these two studies indicate that reciprocal effects are likely to occur when one parent of a backcross is non-inbred and the other parent has been selfed or sib-mated.

Analyses of variance of the fertility indices for backcrosses involving selfed progenies are shown in Table 12. Data for the BC-4 (S_3 x S_0) matings show significant differences among S_3 parents, S_0 parents, and for reciprocal effects. Fertility was again greater when the more inbred clone was the male parent. Residual effects, comprised partly of parent x reciprocal interactions, also were significant. Data presented in Appendix Table 37 show that the S_3 clones responded differently when mated to various S_0 parents. In crosses involving S_3 clone, 6111-3, for example, fertility was considerably greater in all crosses when it was mated as the female parent. Conversely, for clone 6111-4, fertility was much greater in all crosses when it was the male parent. Other S_3 clones gave varying results in crosses to different S_0 parents.

Table 12. Analysis of variance mean squares for fertility indices of backcrosses-3 and -4 involving selfed lines, winter 1968-69

	BC-4 fertility (S_3 x S_0)		BC-5 fertility (S_5 x S_0)	
Source of variation	D.F.	M.S.	D.F.	M.S.
Crosses	65	1.0265**	59	0.5181**
Among S_3 or S_5 clones	10	2.4665**	5	2.4440**
Among S_0 clones	5	0.7858**	4	0.2217
Reciprocals	1	1.5020**	1	2.3575**
Residual	49	0.7475**	49	0.3082*
Error	65	0.1686	118	0.2131
C.V. (%)		(57.0)		(94.8)

In the fifth type of backcross (S_5 x S_0), differences among S_5 plants and reciprocal crosses were highly significant (Table 12). Mean fertility indices again were greater when the more inbred plants were the male parents. Similar to the BC-4 matings, S_5 plants also responded differently when mated to different S_0 parents (Appendix Table 38). Clones 811111-3 and 811111-7 had greater fertility in all crosses when they were used as male rather than female parents. Conversely, fertility indices of matings involving clone 811111-12 were greater when it was mated as the female. Clone 811111-35 appeared to be female-sterile, and other S_5 clones gave varying responses when mated to different S_0 parents. The failure of S_5 plants to respond similarly in crosses with the different

S_0 parents undoubtedly contributed appreciably to the significance shown for the residual source of variation.

Relative fertility designations of individual clones mated to produce the BC-4 and BC-5 backcross populations are shown in Appendix Table 39. Mean fertility indices measured in the two types of backcross populations, grouped according to relative fertility of their parental lines, are presented in Table 13. In general, relative fertility of the backcross populations paralleled the fertility classifications of the more inbred parents. Surprisingly, fertility indices of the backcrosses usually were inversely related to those of the S_0 parents. These data suggest that the S_0, S_3, and S_5 lines used in this study had incompatibility factors in common. When two lines that were relatively high in self-fertility were crossed, the resulting backcross fertility often was low. Conversely, when a cross was made between two lines that were low in self-fertility, but perhaps contained different incompatibility factors, the resulting backcross fertility was high. Armstrong (1952) observed a similar trend in crosses among related and unrelated F_1 plants and concluded that fertility was restored in crosses between two highly sterile parents because they possessed different sterility factors. Similarly, sterility was thought to be retained in other crosses because the parents had the same sterility factors.

Table 13. Mean fertility indices of backcrosses grouped according to the relative self-fertility of the parents, winter 1968-69

	Relative fertility[a]								
	S_3 parents (BC-4)					S_5 parents (BC-5)			
Relative fertility	High	Medium	Low	Very low	Mean	Medium	Low	Very low	Mean
S_0 parents									
High	0.966	0.810	0.580	0.484	0.710	0.818	0.379	0.199	0.465
Medium	1.383	0.555	0.884	0.252	0.769	0.694	0.550	0.279	0.508
Low	1.816	0.945	0.798	0.249	0.952	0.723	0.509	0.441	0.558
Mean	1.388	0.770	0.754	0.328	0.810	0.745	0.479	0.306	0.510

[a] Mean fertility indices used to determine relative fertility ratings of the parents are shown in Appendix Table 39.

Phenotypic correlations and heritability

Phenotypic correlations between self- and sib-fertility for each generation are shown in Table 14. The correlations were similar and highly significant for the three generations of sib-mating. These relatively large, positive coefficients indicate that self- and sib-fertility were closely related in the family lines used in this study.

Table 14. Phenotypic correlations of sib-fertility with self-fertility

	Generation		
	Sib_3-fertility	Sib_4-fertility	Sib_5-fertility
Self-fertility	0.731**	0.740**	0.743**
No. of families	(40)	(32)	(25)

Broad sense heritability estimates for self- and sib-fertility are presented in Table 15. Except for sib-fertility in the FS_3-FS_4 generations, the estimates are moderately high for both types of fertility. These estimates indicate that selection for either self- or sib-fertility, or both, as generations are advanced should enable the breeder to improve the general level of fertility in alfalfa breeding populations. Recently, Villegas and Wilsie (1969) reported an increase in self-fertility of 30 to 40 percent per generation during two

Table 15. Heritability estimates of self- and sib-fertility cycles of recurrent selection in alfalfa.

	Heritability (%)	
Generations	Self-fertility	Sib-fertility
FS_1 and FS_2	54.3	45.8
FS_2 and FS_3	48.9	47.2
FS_3 and FS_4	50.0	13.9

Both the mean and the range of self-fertility were observed to increase during each cycle.

Field Studies

Experiment 3

Mean performance of the various generations of progenies are presented in Table 16, with the analysis of variance mean squares for each agronomic trait shown in Table 17. Data for individual entries within each generation are listed in Table 40 of the Appendix. Highly significant differences among entries were observed for all agronomic characters studied. Variation among progenies within each generation generally increased as the progenies become more inbred, whether by sib-mating or selfing. For most attributes, the S_2, FS_2, and FS_3 generations showed the greatest variability among progenies. The S_0 progenies did not differ significantly for any character.

Table 16. Generation mean performance of progenies for agronomic characters measured in Experiment 3, 1967-68

	Generations								
Character	S_0 (0.000)[a]	S_1 (0.167)	S_2 (0.306)	S_3 (0.421)	F_1 (0.000)	FS_1 (0.083)	FS_2 (0.153)	FS_3 (0.218)	BC-1 (0.267)
Fall vigor (1-9)	5.1	5.2	6.9	6.7	4.1	5.3	5.6	5.4	5.8
Spring vigor (1-9)	4.7	5.7	7.4	7.3	3.5	4.9	5.2	5.8	6.4
Total yield (lb./plant)	2.27	1.47	0.78	0.93	2.81	2.06	1.82	1.53	1.36
Days to bloom	30.8	32.1	37.4	34.2	30.5	32.1	32.0	33.5	34.1
Plant height (in.)									
summer	27.4	24.1	19.0	20.4	27.2	25.7	25.8	25.2	24.5
fall	11.2	9.8	7.0	7.6	12.3	10.4	10.2	10.6	11.5
Plant width (in.)									
summer	27.1	21.7	15.5	19.9	28.1	23.6	24.0	22.9	20.6
fall	17.2	14.7	10.9	11.1	18.5	16.0	14.7	14.0	14.1
Growth habit									
summer	1.07	1.17	1.40	1.12	1.01	1.15	1.13	1.19	1.35
fall	0.68	0.69	0.66	0.73	0.69	0.67	0.70	0.78	0.86

[a] Inbreeding coefficient (F).

Table 17. Analyses of variance for agronomic characters measured in Experiment 3

Source of variation	D.F.	Mean squares Fall vigor	Spring vigor	Total yield
Replications	2	5.58**	2.04*	0.08
Entries	59	3.74**	5.78**	1.57**
S_0 progenies	4	0.29	0.28	0.07
S_1 progenies	8	1.66**	1.51*	0.30**
S_2 progenies	7	2.26**	1.76**	0.41**
S_3 progenies	1	0.03	4.86**	0.50*
F_1 progenies	7	3.36**	3.14**	1.40**
FS_1 progenies	8	1.28*	0.55	0.41**
FS_2 progenies	3	2.19**	0.90	0.38*
FS_3 progenies	9	4.01**	3.34**	0.58**
BC-1 progenies	4	1.46	1.56*	0.21
(S_0,F_1) vs (others)	1	45.75**	123.93**	39.08**
S_0 vs F_1	1	9.48**	13.37**	2.70**
(S_1,S_2,S_3) vs (FS_1,FS_2,FS_3)	1	14.08**	49.62**	13.94**
S_1 vs (S_2,S_3)	1	37.21**	41.90**	6.15**
S_2 vs S_3	1	0.22	0.10	0.11
FS_1 vs (FS_2, FS_3)	1	0.77	9.90**	3.30**
FS_2 vs FS_3	1	0.42	3.42*	0.70*
BC-1 vs (Selfs, Sibs)	1	0.15	3.05*	0.22
Error	179	0.55	0.61	0.11
C.V. (%)		(13.6)	(14.2)	(19.4)

Mean squares						
Days to bloom	Plant height		Plant width		Growth habit	
	summer	fall	summer	fall	summer	fall
15.08*	19.18*	13.09**	5.01	9.79*	0.002	0.018
29.29**	35.57**	18.80**	78.31**	32.61**	0.153**	0.074**
4.80	2.51	2.73	9.44	2.47	0.014	0.018
20.14**	14.62**	9.24**	47.27**	24.30**	0.115**	0.038**
48.70**	25.94**	19.04**	54.27**	27.08**	0.312**	0.060**
12.91	9.88	4.33	62.08*	0.00	0.045	0.012
4.42	8.41	8.19**	57.31**	22.86**	0.052	0.079**
11.99**	10.25*	8.30**	34.47**	20.21**	0.090*	0.046**
25.98**	60.82**	34.88**	40.51*	15.44**	0.180**	0.102**
13.90**	25.59**	16.90**	56.36**	20.29**	0.138**	0.076**
24.47**	4.64	17.47**	10.30	15.62**	0.111*	0.260**
269.30**	79.06**	138.72**	1264.83**	505.26**	1.105**	0.043*
0.51	0.07	9.86**	8.87	14.54*	0.031	0.000
106.48**	101.53**	131.23**	623.36**	146.82**	0.290*	0.053**
304.63**	68.50**	99.24**	404.66**	194.93**	0.406**	0.001
46.75**	2.00	1.87	91.35**	0.07	0.379**	0.021
15.63	0.25	0.04	2.10	50.38**	0.010	0.114**
18.69*	0.64	1.31	10.09	4.69	0.028	0.052*
4.12	1.56	54.09**	7.50	0.33	0.276*	0.324**
4.39	4.76	1.33	12.22	2.68	0.043	0.008
(6.4)	(9.0)	(11.3)	(15.4)	(11.1)	(17.6)	(12.3)

This was not unexpected, however, as each S_0 progeny was comprised of a random sample of plants from the original base population, the variety Vernal. The F_1 progenies exhibited significant variation for several characters. Examination of the individual progeny means in Appendix Table 40 indicates that much of the variation was due to entry 329, which performed considerably poorer than the other F_1 progenies for the characters that exhibited significant differences. The variation among S_3 progenies was less often significant than was the variation among S_1 or S_2 progenies. The lack of significant variation among S_3 progenies may have been related in part to the procedure of progeny selection. Since a composite of genotypes was used to form each S_3 progeny, and plot means were used in the analyses, significant differences among progenies might not be expected.

For most characters, the largest source of variation was the comparison between inbred and non-inbred progenies (S_0 and F_1 vs others). This difference was not unexpected, and serves to confirm considerable data illustrating the large decline in growth and vigor observed with inbreeding. A second major difference observed for all attributes was the superiority of sib-mated progenies relative to selfed lines. This comparison indicates that sib-mating at least delays the drastic decline in vigor noted with selfing. The inbreeding coefficients of the sib-mated progenies used in this study, however, are considerably smaller than those of the selfed lines. It remains to be determined whether vigor can be maintained in sib-progenies that have comparatively high inbreeding coefficients.

The S_1 progenies were superior to the S_2 and S_3 lines for most characters measured in Experiment 3. Differences for this comparison were highly significant for all characters, except fall growth habit. In contrast, the means for S_2 versus S_3 progenies usually did not differ significantly. However, the data in Table 16 show that the S_3 progenies were significantly earlier in maturity, greater in summer width, and less erect in summer growth habit than the less-inbred S_2 lines. These data indicate that selection pressures occurred for some attributes in the S_2 generation which reversed the usual depressing effects of inbreeding.

Differences among the generations of full-sib progenies usually were much smaller than those among the selfed generations. The FS_1 progenies had significantly greater spring vigor, yield, and fall plant width, and were more prostrate in growth habit than the FS_2 and FS_3 lines. Similarly, the FS_2 progenies were superior to the FS_3 plants in spring vigor and yield, earlier in maturity, and less erect in growth habit. These data indicate that sib-mating has a definite advantage compared with selfing for the development of relatively vigorous, agronomically desirable lines of alfalfa that are partially inbred.

Experiment 4

Means for the various generations of progenies for all characters are shown in Table 18, with individual entry means presented in Appendix Table 41. Analyses of variance mean squares for all traits measured in Experiment 4 are shown in Table 19.

In general, the results of this experiment confirmed the findings of Experiment 3. The mean squares attributable to entries were highly significant for all traits. Variation among progenies again increased as the progenies became more highly inbred. For most characters, the greatest variation was observed among the S_4, S_5, FS_3, and FS_4 progenies, and the least variability usually occurred among the S_0, F_1, and FS_2 progenies. Because of poor germination, seedlings from ten families were composited for planting the five entries of the FS_2 generation. This procedure probably contributed to the lack of significant variation among FS_2 progenies. Variability among S_3 progenies also was small, again possibly due to the composite structure of each entry. Conversely, the chief differences among S_4 and S_5 progenies were between the entries formed from a composite of seeds versus those formed from a single plant (Table 2 and Appendix Table 41). Since seed production was very low for most entries, only the progeny from plants with high self-fertility could be included as separate entries. These highly selected entries performed much better than did those formed by compositing the seed from

Table 18. Generation mean performance of progenies for agronomic characters measured in Experiment 4, 1968-69

Character	Generations			
	S_0 (0.000)[a]	S_1 (0.167)	S_2 (0.306)	S_3 (0.421)
Spring vigor (1-9)	3.2	5.4	7.4	7.5
Yield (lb./plant)	1.81	1.10	0.51	0.56
Days to bloom	28.4	29.0	33.4	37.1
Plant height (in.)				
fall	16.4	14.4	13.4	11.7
summer	23.8	23.4	21.6	20.1
Plant width (in.)				
fall	28.9	26.7	20.3	18.6
summer	33.6	27.9	19.2	18.0
Growth habit				
fall	0.60	0.57	0.70	0.65
summer	0.75	0.92	1.31	1.25
Longest stem (in.)	34.3	29.4	23.9	21.9

[a] Inbreeding coefficient (F).

Generations						
S_4 (0.518)	S_5 (0.598)	F_1 (0.000)	FS_1 (0.083)	FS_2 (0.153)	FS_3 (0.218)	FS_4 (0.277)
7.6	6.7	3.0	3.7	5.6	6.1	6.5
0.52	0.85	1.94	1.59	1.08	1.01	0.77
38.4	33.7	27.1	29.3	28.4	32.4	32.8
10.7	12.6	17.4	15.7	16.2	14.8	13.9
19.2	19.7	23.2	23.1	23.8	24.4	21.6
18.8	22.9	29.2	27.6	24.3	23.9	23.6
16.8	22.5	33.1	32.0	27.7	26.1	24.7
0.59	0.59	0.63	0.61	0.68	0.66	0.62
1.33	0.99	0.74	0.76	0.92	0.98	0.98
21.3	24.8	35.5	34.3	30.4	29.3	27.9

Table 19. Analyses of variance for agronomic characters measured in Experiment 4

Source of variation	D.F.	Mean squares		
		Spring vigor	Yield	Days to bloom
Replications	2	2.78*	0.57*	63.68**
Entries	80	10.89**	0.98**	58.08**
S_0 progenies	4	1.86*	0.19	1.72
S_1 progenies	9	3.67**	0.23**	28.53**
S_2 progenies	7	1.50*	0.11	89.52**
S_3 progenies	4	1.11	0.12	26.38**
S_4 progenies	6	5.37**	0.45**	32.15**
S_5 progenies	4	7.49**	0.78**	25.06**
F_1 progenies	8	1.12	0.08	9.51
FS_1 progenies	8	3.55**	0.11	13.65*
FS_2 progenies	4	3.50**	0.26*	1.67
FS_3 progenies	8	7.54**	0.80**	19.05**
FS_4 progenies	8	1.61*	0.32**	24.33**
(S_0,F_1) vs (others)	1	325.81**	32.97**	824.69**
S_0 vs F_1	1	0.27	0.17	16.27
(Selfs) vs (Sibs)	1	87.26**	7.29**	373.21**
(S_1,S_2) vs (S_3,S_4,S_5)	1	25.37**	1.13**	835.48**
S_1 vs S_2	1	53.27**	4.65**	170.65**
S_3 vs (S_4,S_5)	1	0.84	0.11	4.22
S_4 vs S_5	1	7.15**	0.93**	187.04**
(FS_1,FS_2) vs (FS_3,FS_4)	1	90.19**	6.31**	310.95**
FS_1 vs FS_2	1	37.05**	2.58**	6.79
FS_3 vs FS_4	1	1.89	0.78**	1.47
Error	160	0.70	13.73	6.04
C.V. (%)		(14.9)	(26.9)	(7.8)

Mean squares						
Plant height		Plant width		Growth habit		Longest stem
summer	fall	summer	fall	summer	fall	
44.55**	1.68	73.78*	48.95**	0.07	0.038*	41.50*
24.36**	25.07**	126.82**	63.81**	0.26**	0.049**	89.69**
5.40	6.01*	3.32	10.36	0.01	0.018	8.02
27.37**	10.26**	28.60	24.67**	0.08	0.023**	13.41
2.74	15.13**	55.45**	25.47*	0.54**	0.129**	3.26
3.01	8.93**	18.42	5.58	0.09	0.027*	1.79
23.57**	7.50**	48.18**	17.82	0.33**	0.027**	35.39**
8.64	32.81**	158.04**	69.38**	0.28**	0.011	102.12**
21.06**	10.27**	8.64	25.79**	0.04	0.025**	20.68*
21.17**	14.67**	12.22	27.77**	0.01	0.042**	10.30
2.38	2.16	22.25	5.18	0.05	0.008	5.69
28.78**	19.68**	63.04**	51.47**	0.07	0.043**	66.33**
28.54**	40.39**	36.91*	53.48**	0.17**	0.137**	37.48**
56.41**	358.05**	2721.81**	1122.11**	2.86**	0.005	1975.59**
3.54	10.11*	2.38	0.56	0.01	0.007	14.19
208.62**	252.95**	1861.21**	445.62**	2.83**	0.021	1607.08**
237.50**	145.41**	717.02**	404.21**	0.33*	0.011	528.18**
43.86*	15.50**	1020.37**	535.90**	2.08**	0.254**	407.56**
5.43	0.50	15.30	39.52*	0.04	0.036**	8.20
2.34	30.77**	281.73**	148.13**	0.97**	0.001	112.73**
2.45	52.86**	606.33**	164.26**	0.64**	0.002	443.32**
3.99	2.07	181.52**	106.73**	0.25*	0.061**	147.56**
103.34**	14.38**	27.31	1.22	0.00	0.017	26.63
7.52	1.91	15.15	9.53	0.06	0.008	8.16
(12.2)	(9.6)	(15.0)	(12.7)	(25.2)	(14.8)	(9.9)

progenies of several plants with low self-fertility indices.

As in Experiment 3, highly significant differences for all characters except fall growth habit were shown between the non-inbred (S_0 and F_1) and inbred progeny means. Although F_1 progenies generally were slightly superior to the S_0 progenies, the differences were significant only for fall plant height (5 percent probability level). Sib-mated progenies again were significantly better than selfed progenies for all characters except fall growth habit.

Performance of S_1 and S_2 lines was significantly better than that of the S_3, S_4, and S_5 progenies for all characters except fall growth habit, and the S_1 progenies were significantly superior to the S_2 progenies for all attributes. Differences between the S_3 lines and the average of the S_4 and S_5 progenies generally were small and most often were not significant. The S_5 progenies usually were superior to the S_3 and S_4 lines and were equal or superior to the S_2 lines for several traits. Inspection of the individual entry means in Appendix Table 41 shows that the superiority of S_5 progenies over the other selfed generations was due largely to the performance of entries 436 and 437. These two highly self-fertile lines, 71111-41 and 71111-44, performed consistently better than the entries that were constituted by compositing seed of several plants, particularly in yield and spring vigor. Their performance indicates that it may be possible to develop inbred lines of alfalfa that have acceptable vigor and fertility, albeit at a very low frequency.

Average performance of the FS_1 and FS_2 progenies was significantly better than that of the FS_3 and FS_4 lines for all traits except summer height and fall growth habit. For most characters, the FS_1 progenies were superior to the FS_2 lines. In contrast, performance of the FS_3 and FS_4 progenies was similar, except for days to bloom and plant height.

Phenotypic correlations

Phenotypic correlations among all characters measured in Experiments 3 and 4 are shown for the different types of progenies in Tables 20 to 24. Correlation coefficients were calculated from plot means with a range of 13 to 28 degrees of freedom for r values among characters for different levels of inbreeding. Negative correlation values for associations of other characters with either fall or spring vigor represent positive relationships because of the method of scoring vigor (1 = best; 9 = poorest). Considerable variation often existed among estimates for a given pair of characters among the different types of progenies and between the two years. Some of the variation in estimates between years was caused by a considerable amount of lodging in Experiment 4. The larger, taller, less inbred progenies were lodged more severely than the smaller, more highly inbred lines. Therefore, correlations involving plant shape were more subject to error in Experiment 4, particularly for the less inbred generations. In general,

Table 20. Phenotypic correlations among agronomic characters measured on S_0 progenies (upper diagonal) and F_1 progenies (lower diagonal) in Experiments 3 and 4

	Fall vigor[a]	Spring vigor	Yield[b]	Days to bloom
Fall vigor	--- ---	0.18[d] ---[e]	0.74** ---	-0.09 ---
Spring vigor	0.77** ---	--- ---	-0.13 -0.92**	-0.70** 0.26
Yield	-0.54** ---	-0.91** -0.60**	--- ---	0.23 -0.57**
Days to bloom	0.36 ---	0.56 0.04	-0.64** 0.12	--- ---
Plant height, summer	-0.79** ---	-0.95** 0.17	0.09 0.03	-0.62** 0.61**
Plant height, fall	-0.30 ---	0.19 0.25	-0.38 -0.08	-0.23 0.32
Plant width, summer	-0.59** ---	-0.91** 0.07	0.95** 0.12	-0.60** 0.50**
Plant width, fall	-0.57** ---	-0.85** -0.22	0.83** 0.67**	-0.55** -0.12
Growth habit, summer	0.47* ---	0.83** -0.11	-0.89** 0.09	-0.49* 0.17
Growth habit, fall	0.31 ---	0.82** 0.32	-0.91** -0.39*	0.54** 0.34
Longest stem	--- ---	--- 0.09	--- -0.21	--- 0.08

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[a] Measured in Experiment 3 only.

[b] Total of 3 cuttings in Experiment 3; one cutting only in Experiment 4.

[c] Measured in Experiment 4 only.

[d] Experiment 3, 1967-68.

[e] Experiment 4, 1968-69.

Plant height		Plant width		Growth habit		Longest stem^c
summer	fall	summer	fall	summer	fall	
-0.50	-0.40	0.38	0.38	-0.82**	-0.50	---
---	---	---	---	---	---	---
-0.55*	-0.60*	-0.29	0.00	-0.26	-0.26	---
0.02	-0.61*	0.35	-0.40	-0.13	-0.37	-0.70**
0.17	-0.60*	0.45	0.20	-0.46	-0.47	---
0.29	-0.57*	-0.02	0.29	0.12	0.50	0.78**
0.67**	-0.87**	0.82**	0.16	-0.18	-0.78**	---
-0.48	-0.40	-0.60**	-0.31	0.01	-0.21	-0.44
---	-0.41	0.20	-0.60*	0.45	-0.12	---
---	0.62*	0.32	-0.65**	0.13	0.82**	0.54*
-0.13	---	-0.91**	-0.28	0.51	0.94**	---
0.38	---	-0.35	-0.04	0.28	0.90**	0.99**
0.92**	0.17	---	0.44	-0.70**	-0.95**	---
-0.24	0.09	---	0.25	-0.22	-0.24	-0.35
0.08	-0.00	0.83**	---	-0.69**	-0.58*	---
0.01	0.17	0.13	---	-0.18	-0.68**	-0.23
-0.81**	0.23	-0.97**	-0.73**	---	0.73**	---
0.83**	0.25	-0.69**	0.04	---	0.26	0.27
-0.76**	0.63**	-0.80**	-0.76**	0.79**	---	---
0.39*	0.82**	-0.07	-0.67**	0.27	---	0.83**
---	---	---	---	---	---	---
-0.24	0.42*	0.66**	0.06	-0.44**	0.19	---

Table 21. Phenotypic correlations among agronomic characters measured on FS$_1$ progenies (upper diagonal) and FS$_2$ progenies (lower diagonal) in Experiments 3 and 4

	Fall vigor[a]	Spring vigor	Yield[b]	Days to bloom
Fall vigor	--- ---	0.10[d] ---[e]	-0.06 ---	-0.14 ---
Spring vigor	0.80** ---	--- ---	-0.75** -0.78**	0.16 -0.49**
Yield	-0.56 ---	-0.88** -0.81**	--- ---	-0.01 0.66**
Days to bloom	0.32 ---	-0.74** -0.65**	-0.97** -0.20	--- ---
Plant height, summer	-0.11 ---	0.38 0.14	-0.24 -0.27	0.28 0.43
Plant height, fall	-0.36 ---	-0.05 -0.29	0.08 0.17	-0.22 0.08
Plant width, summer	-0.74** ---	-0.88** -0.78**	0.95** 0.73**	-0.85** -0.65**
Plant width, fall	-0.78** ---	-0.88** -0.46*	0.87** 0.88**	-0.82** 0.07
Growth habit, summer	0.42 ---	0.88** 0.67**	-0.84** -0.67**	0.81** 0.66**
Growth habit, fall	0.09 ---	0.36 -0.00	-0.37 -0.10	0.21 0.01
Longest stem	--- ---	--- -0.22	--- -0.28	--- -0.67**

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[a] Measured in Experiment 3 only.

[b] Total of 3 cuttings in Experiment 3; one cutting only in Experiment 4.

[c] Measured in Experiment 4 only.

[d] Experiment 3, 1967-68.

[e] Experiment 4, 1968-69.

Plant height		Plant width		Growth habit		Longest stem^{c}
summer	fall	summer	fall	summer	fall	
0.46*	-0.54**	-0.11	-0.53**	0.22	-0.09	---
---	---	---	---	---	---	---
-0.62**	0.35	-0.65**	-0.20	0.48*	0.50**	---
-0.14	0.48*	-0.48*	-0.49**	0.37	0.59**	-0.77**
0.18	-0.54**	0.89**	0.28	-0.83**	-0.72**	---
0.18	-0.24	0.46*	0.63**	-0.31	-0.47*	0.72**
-0.38	-0.36	-0.12	0.40*	-0.04	-0.56**	---
0.43*	0.30	0.63**	-0.05	-0.04	0.23	0.76**
---	-0.32	0.18	-0.38	0.13	-0.04	---
---	0.38	0.65**	-0.11	0.79**	0.33	0.63**
0.87**	---	-0.34	0.27	0.27	0.67**	---
0.63*	---	-0.00	-0.40*	0.58**	0.90**	-0.10
0.01	0.49	---	0.40*	-0.92**	-0.71**	---
-0.61*	-0.37	---	0.16	0.10	-0.07	0.75**
0.03	0.49	1.00**	---	-0.55**	-0.53**	---
-0.50	-0.07	0.59*	---	-0.35	-0.78**	-0.12
0.71**	0.29	-0.69*	-0.67*	---	0.70**	---
0.80**	0.42	-0.96**	-0.64*	---	0.60**	0.10
1.00**	0.90**	0.05	0.06	0.68*	---	---
0.24	0.90**	-0.18	-0.18	0.21	---	-0.12
---	---	---	---	---	---	---
0.01	0.71**	0.32	0.25	-0.21	0.14	---

Table 22. Phenotypic correlations among agronomic characters measured on FS$_3$ progenies (upper diagonal) in Experiments 3 and 4 and FS$_4$ progenies (lower diagonal) in Experiment 4 only

	Spring vigor	Yield[a]	Days to bloom
Fall vigor[c]	0.91**[d] ---[e]	-0.84** ---	0.24 ---
Spring vigor	--- ---	-0.93** -0.95**	0.48** 0.69**
Yield	 -0.79**	--- ---	-0.57** -0.60**
Days to bloom	 0.46*	 -0.38	--- ---
Plant height, summer	-0.35*	0.08	0.02
Plant height, fall	-0.64**	0.33	-0.31
Plant width, summer	-0.67**	0.62**	-0.79**
Plant width, fall	-0.15	0.10	-0.19
Growth habit, summer	0.40*	-0.58**	0.65**
Growth habit, fall	-0.31	0.01	-0.07
Longest stem	-0.40*	0.21	-0.86**

---

[a] Total of 3 cuttings in Experiment 3; one cutting only in Experiment 4.

[b] Measured in Experiment 4 only.

[c] Measured in Experiment 3 only.

[d] Experiment 3, 1967-68.

[e] Experiment 4, 1968-69.

Plant height		Plant width		Growth habit		Longest stem [b]
summer	fall	summer	fall	summer	fall	
-0.62**	-0.69**	-0.72**	-0.55**	0.46*	-0.25	---
---	---	---	---	---	---	---
-0.74**	-0.62**	-0.66**	-0.51**	0.38*	-0.17	---
-0.26	-0.35	-0.80**	-0.92**	0.76**	0.40*	-0.56**
0.73**	0.66**	0.85**	0.72**	-0.53**	0.03	---
0.20	0.35	0.73**	0.93**	-0.70**	-0.44*	0.53**
-0.63**	-0.53**	-0.43	-0.35	0.07	-0.30	---
0.09	-0.01	-0.70**	-0.73**	0.88**	0.62**	-0.21
---	0.74**	0.64**	0.23	0.10	0.55**	---
---	0.77**	0.46*	0.34	-0.11	0.41*	0.81**
	---	0.50	0.57**	-0.07	0.64**	---
0.37	---	0.55**	0.38	-0.36	0.58**	0.68**
		---	0.79**	-0.79**	-0.17	---
-0.14	0.47	---	0.78**	-0.89**	-0.17	0.80**
			---	-0.73**	-0.24	---
-0.75**	-0.04	0.28	---	-0.78**	-0.51**	0.57**
				---	0.58**	---
0.51**	-0.26	-0.86**	-0.49**	---	0.38	-0.48*
					---	---
0.64**	0.78**	0.12	-0.63**	0.16	---	0.11

0.01	0.65**	0.71**	0.14	-0.57**	0.40*	---

Table 23. Phenotypic correlations among agronomic characters measured on S_1 progenies (upper diagonal) and S_2 progenies (lower diagonal) in Experiments 3 and 4

	Fall vigor[a]	Spring vigor	Yield[b]	Days to bloom
Fall vigor	--- ---	0.32[d] ---[e]	0.00 ---	-0.33 ---
Spring vigor	0.37 ---	--- ---	-0.81** -0.64**	0.22 -0.17
Yield	-0.39 ---	-0.99** -0.81**	--- ---	-0.69** 0.36
Days to bloom	0.51* ---	-0.78** 0.31	-0.71** -0.64**	--- ---
Plant height, summer	0.20 ---	-0.39 0.28	0.32 -0.55**	-0.45* 0.24
Plant height, fall	-0.81** ---	-0.35 -0.15	0.33 0.21	-0.60** -0.41*
Plant width, summer	-0.32 ---	-0.79** -0.58**	0.79** 0.91**	-0.56** -0.70**
Plant width, fall	-0.88** ---	-0.57** 0.19	0.58** 0.65**	-0.54** -0.66**
Growth habit, summer	0.49* ---	0.49* 0.41	-0.54** -0.81**	0.23 0.68**
Growth habit, fall	0.01 ---	0.18 0.12	-0.28 -0.37	-0.36 0.30
Longest stem	--- ---	--- -0.60**	--- -0.63**	--- -0.39

---

[a] Measured in Experiment 3 only.

[b] Total of 3 cuttings in Experiment 3; one cutting only in Experiment 4.

[c] Measured in Experiment 4 only.

[d] Experiment 3, 1967-68.

[e] Experiment 4, 1968-69.

Plant height		Plant width		Growth habit		Longest
summer	fall	summer	fall	summer	fall	stem^c
-0.13	-0.85**	-0.10	-0.64**	-0.06	-0.12	---
---	---	---	---	---	---	---
-0.68**	-0.44*	-0.49**	0.17	0.17	-0.66**	---
-0.18	-0.01	-0.22	0.10	0.10	-0.03	0.05
0.29	-0.35	0.76**	0.28	-0.64**	-0.67**	---
-0.03	0.38*	0.66**	0.51	-0.57**	-0.05	0.62**
0.27	0.28	-0.52**	-0.17	-0.66**	0.40	---
-0.47**	0.04	0.37*	0.15	-0.60**	0.05	0.31
---	-0.20	0.17	0.07	0.23	-0.28	---
---	0.53**	0.07	-0.40*	0.66**	0.62**	0.84**
0.11	---	-0.30	0.58**	0.26	0.40	---
0.39	---	0.16	0.09	0.28	0.73**	0.39
0.64**	0.48	---	0.58**	-0.91**	-0.37**	---
0.67**	0.20	---	0.39*	-0.69**	-0.10	0.76**
0.02	0.86**	0.66**	---	-0.43*	-0.51*	---
-0.62**	-0.00	0.87**	---	-0.61**	-0.59**	0.49**
0.19	-0.45*	-0.71**	-0.70**	---	0.74**	---
0.79**	0.11	-0.49*	-0.92**	---	0.61**	-0.03
0.38	0.40	-0.09	-0.08	0.90**	---	---
0.75**	0.69**	-0.50*	-0.68**	0.76**	---	0.05
---	---	---	---	---	---	---
-0.19	0.53**	-0.63**	0.37	-0.40*	0.16	---

Table 24. Phenotypic correlations among agronomic characters measured on S_3 and S_4 progenies (upper diagonal) and S_5 progenies (lower diagonal) in Experiment 4, 1968-69

	Spring vigor	Yield	Days to bloom
Spring vigor	--- ---	-0.23[a] -0.28[b]	0.96** 0.36
Yield	-0.98**[c]	--- ---	-0.12 0.18
Days to bloom	0.80**	-0.87**	--- ---
Plant height, summer	-0.73**	0.66**	-0.37
Plant height, fall	0.94**	0.92**	-0.82**
Plant width, summer	-0.94**	0.96**	-0.75**
Plant width, fall	0.96**	0.95**	-0.88**
Growth habit, summer	0.88**	-0.91**	0.71**
Growth habit, fall	-0.34	0.29	-0.25
Longest stem	-0.96**	0.99**	-0.84**

---

[a] S_3 progenies.

[b] S_4 progenies.

[c] S_5 progenies.

Plant height		Plant width		Growth habit		Longest
summer	fall	summer	fall	summer	fall	stem
0.22 -0.91**	-0.66** -0.23	-0.80** -0.97**	-0.70** -0.35	0.99** 0.66**	-0.27 0.17	-0.04 -0.90**
-0.89** 0.49*	0.23 -0.44*	-0.15 0.27	-0.06 0.35	-0.27 -0.35	0.28 -0.70**	-0.70** 0.37
0.14 0.01	-0.62* 0.22	-0.69** -0.23	-0.62* 0.57**	0.91** 0.08	-0.29 -0.37	-0.29 -0.08
--- ---	-0.55* 0.22	0.18 0.93**	0.34 0.57**	0.25 -0.65**	-0.68** -0.37	0.80** 0.96**
0.51	--- ---	0.47 0.08	0.01 0.33	-0.67** -0.02	0.87** 0.63**	-0.11 0.19
0.78**	0.79**	--- ---	0.83** 0.27	-0.85** -0.69**	-0.02 -0.26	0.73** 0.94**
0.74**	0.89**	0.89**	--- ---	-0.73** -0.05	-0.47 -0.51*	0.74** 0.40
-0.81**	-0.69**	-0.99**	-0.86**	--- ---	-0.25 0.14	-0.33 -0.63**
-0.17	0.62**	0.05	0.22	0.10	--- ---	-0.50 -0.28
0.67**	0.87**	0.98**	0.92**	-0.94**	0.20	--- ---

the magnitude of the coefficients and the frequency of significance increased as the populations became more highly inbred.

Certain characters were associated closely among most types of progenies in both experiments. Yield and spring vigor usually were highly and significantly correlated. Yield was often correlated positively with summer height and width and usually was correlated negatively with fall growth habit and days to bloom. In addition to its association with high yield, good spring vigor usually was associated with relatively few days to bloom, good plant width and height during the summer, and long central stems. Most of the other pairs of characters usually were not correlated significantly or varied considerably in their association among levels of inbreeding or between years.

DISCUSSION

General fertility of the alfalfa population used in this study continued to decline as generations were advanced, regardless of the type of inbreeding procedure used. The relative decline in fertility per generation was not as great as that reported by Aycock (1966) for earlier generations of inbreeding within the same base population.

As discussed by Bartlett and Haldane (1934), the theoretical decline in fertility upon inbreeding should be less for a tetraploid species than a diploid. They estimated that 3.8 generations of selfing and 8.7 generations of sib-mating are required to reduce heterozygosity by one-half. Data from this and many other studies have repeatedly shown that both self- and cross-fertility and agronomic desirability in alfalfa decline much more rapidly upon inbreeding than would be expected from theoretical considerations of the inbreeding coefficient alone. Aycock (1966) concluded that the low frequency of quadrivalents per cell reported by Atwood and Grun (1951) precluded the possibility that double reduction was increasing the proportion of homozygous loci more rapidly than normally expected.

Cooper and Brink (1940) and Sayers and Murphy (1966) found that the frequency of fertilization and the incidence of pollen abortion were the two main factors controlling differential fertility between self- and cross-fertilization. Cooper and Brink (1940) reported that 98 percent of the difference between potential and actual fertility following self-pollination, and 67 percent of the difference following cross-pollination were caused by these two factors, which they termed partial self-incompatibility and post-fertilization ovule abortion. Since their determinations were made upon S_1 plants only, it would be desirable to determine the percent fertile and aborted ovules within more advanced levels of inbreeding. Sayers and Murphy (1966) concluded that abortion of fertilized ovules was not necessarily an effect of inbreeding, since a high degree of abortion also occurred after crossing. This indicates that the collapse of fertilized ovules and the resulting loss of fertility may be manifestations of an incompatibility system, per se, in alfalfa.

Barnes and Cleveland (1963c) observed that male parents with long pollen tubes were able to fertilize a greater proportion of the ovules in an ovary than were those with short pollen tubes. In one study, they obtained 69 percent greater seed set in crosses involving a parent with long pollen tubes. Barnes and Cleveland (1963b) also determined that ovule number was controlled by four genes in diploid alfalfa. Although the relationships of these two factors to the partial-incompatibility system is unknown, it should be possible to increase seed set or delay loss of fertility during inbreeding by selection for increased ovule number and increased pollen tube length.

Although the FS_4 families (F = 0.277) were only slightly less inbred than the S_2 plants (F = 0.306), their mean self-fertility index was three times larger than that of the selfed lines. However, the mean self-fertility of FS_2 families (F = 0.153) was only slightly greater than that of S_1 lines (F = 0.167). Therefore, the value of sib-mating, as opposed to selfing, as a procedure for maintaining greater self-fertility seems rather limited. Since the advantage of sib-mating appears to be greater at advanced levels of inbreeding, selfing for a few generations followed by sib-mating, as proposed by Lantican (1961), may be the most effective procedure for the development of highly inbred lines of alfalfa.

Inbreeding by continuous sib-mating gave a rapid decline in sib-fertility. Mean sib-fertility of the FS_4 families relative to the S_0 generation (97 percent decline) was similar to the mean self-fertility of S_2 lines relative to the S_0 parents (93 percent decline). Apparently the rates of fixation of genetic factors for self-incompatibility with straight selfing and for sib-incompatibility with continuous sib-mating were similar and were quite rapid with both systems of inbreeding. The data indicate that development of highly homozygous lines of tetraploid alfalfa by continuous sib-mating would be rather difficult to accomplish.

It is important to note that mean self-fertility was greater than mean sib-fertility for the FS_2, FS_3, and FS_4 progenies. Although selfed lines were not sib-mated in this study, both Lantican (1961) and Busbice (1968) observed greater sib-fertility than self-fertility among S_1 lines. Therefore, despite the relatively high correlations between self- and sib-fertility shown for the different levels of inbreeding in my studies and those of McAllister (1950), Wilsie (1951), and Aycock (1966), certain genetic factors for incompatibility must be operating independently to determine self- and cross-fertility in these generations.

Reciprocal differences were small and nonsignificant for the fertility indices obtained in all sib-matings and in all backcrosses between two inbred parents. These results confirm those of Williams (1964), who obtained no reciprocal differences in fertility indices when both parents of a cross were partially inbred.

In all five types of backcross populations, fertility indices were higher when the less inbred line was the female parent, and they were significantly greater in backcross types 3, 4, and 5 when non-inbred plants were used as the female parents. Whitehead and Davis (1954) reported similar reciprocal differences in parental cross-compatibility and F_1 self-compatibility and noted that fertility of parental crosses was highly correlated with self-fertility of the female parent. They postulated that differences in fertility among parental clones and their crosses resulted from the formation of different numbers of highly functional ovules. Busbice (1968) observed small reciprocal differences in fertility when S_1 lines were backcrossed to their S_0 parents, with greater mean fertility resulting when the female parent was non-inbred. He developed a non-linear regression equation relating the fertility of several kinds of crosses to the inbreeding coefficients of the male and female parents and the developing zygote, and found that the level of inbreeding of the female parent was the most important component of the equation. Several workers, including Whitehead and Davis (1954), Koffman (1959), and Rotar and Kehr (1963) have observed that fertility in alfalfa is not correlated with percentage of viable pollen. Busbice (1968) suggested that inbreeding in the developing zygote was the primary factor limiting the production of selfed seed in alfalfa.

Data from the backcross-1 population (FS_2 x FS_1) indicate that it may be possible to maintain fertility and concomitantly increase the value of F. Proportionately greater levels of fertility were restored in backcrosses involving two inbred lines than when only one parent was inbred. However, greater actual fertility resulted in backcrosses to non-inbred parents. Therefore, if backcrossing is used to maintain acceptable levels of fertility during the development of partially inbred lines of alfalfa, it appears that the line used as the female in crosses should be non-inbred and related to the male parent. One limitation to this procedure is the fact that the maximum inbreeding coefficient obtainable in a backcross involving sib-progenies and their non-inbred parents is F = 0.333, when the sib-progeny is completely inbred (F = 1.0). Since most inbred parents would have an F value considerably less than 1.0, the inbreeding coefficient of the backcross progeny would seldom exceed 0.30.

The decline observed for the expression of agronomic characters as plants become more highly inbred was less severe than the concomitant reduction in self- and cross-fertility. However, the two agronomic characters exhibiting the most rapid decline upon inbreeding were those most important to an alfalfa breeder, vigor and forage yield. The lack of vigor in highly inbred progenies also makes them more susceptible to winter injury, insect damage, and pathogens that incite various diseases.

Busbice and Wilsie (1966a) postulated that a high frequency of loci containing three or four different alleles was responsible for the rapid decline in vigor observed upon inbreeding. The multiple allelic series assure a high degree of heterozygosity at loci with three (trigenic) or four (tetragenic) different alleles, but the heterozygosity diminishes rapidly upon inbreeding. They further postulated that three types of interactions may occur at a locus; first, second, and third order involving two, three, and four alleles, respectively. Assuming that second and third order interactions were relatively unimportant, forage yield data of Tysdal et al. (1942) fit the predicted losses of first order interactions for tetragenic and trigenic loci better than those for duplex or simplex loci. Busbice and Wilsie (1966a) therefore concluded that tetragenic and trigenic loci were important in determining the extent of inbreeding depression, and conversely, for the expression of heterosis. Aycock (1966) observed that the declines in forage yield and spring vigor upon inbreeding were most closely related to the theoretical loss of interactions from tetragenic and trigenic loci. In contrast, plant height, plant width, and days to flower exhibited much smaller declines upon inbreeding and more closely approximated the theoretical losses of interactions from simplex and duplex loci. The data of Aycock (1966) thus supported the hypothesis of Busbice and Wilsie (1966a) that yield and spring vigor are controlled primarily by a series of tetragenic and trigenic loci, but plant height and width and days to bloom appear less complex in their inheritance. Aycock (1966) observed that the decline in seed production with successive generations of inbreeding was greater than that for other agronomic characters and greater than the theoretical losses of first order interactions for all types of loci. He reasoned, therefore, that this provided additional evidence to support the hypothesis that fertility in alfalfa also is affected by genetic systems for incompatibility.

Means for the five agronomic characters measured in my experiments and self-fertility indices were superimposed upon the theoretical losses of first order interactions calculated by Busbice and Wilsie (1966a). These data are presented graphically in Figures 1 and 2. Data from Experiments 3 and 4 were combined and the mean self-fertility indices were obtained from my greenhouse studies and those of Aycock (1966). All data are presented as percent of the non-inbred (S_0) clones. The data encompass a more extended range of F values than were evaluated by Aycock (1966) and provide additional support for the hypothesis of Busbice and Wilsie (1966a). Although the values for all agronomic characters tended to decline more slowly as generations of inbreeding were advanced, the results generally are in agreement with those of Aycock (1966). The rate of decline for yield was similar to the theoretical losses of interactions proposed for tetragenic and trigenic loci, but the generation means for summer plant height and days to bloom were associated more closely with the duplex curve. Summer width declined at a rate intermediate to the other agronomic characters, and appeared to be most closely associated with the theoretical simplex and duplex curves. Compared with the results of Aycock (1966), spring vigor declined at a slightly slower rate, but summer plant width declined more rapidly as levels of inbreeding advanced.

Self-fertility declined more rapidly than the agronomic characters and the theoretical losses of first order interactions from all types of loci. Similar to the seed production data of Aycock (1966), these results indicate that

Figure 1. Mean spring vigor, yield, and self-fertility indices for various levels of inbreeding superimposed on the theoretical losses of first-order interactions from four types of loci as computed by Busbice and Wilsie (1966a)

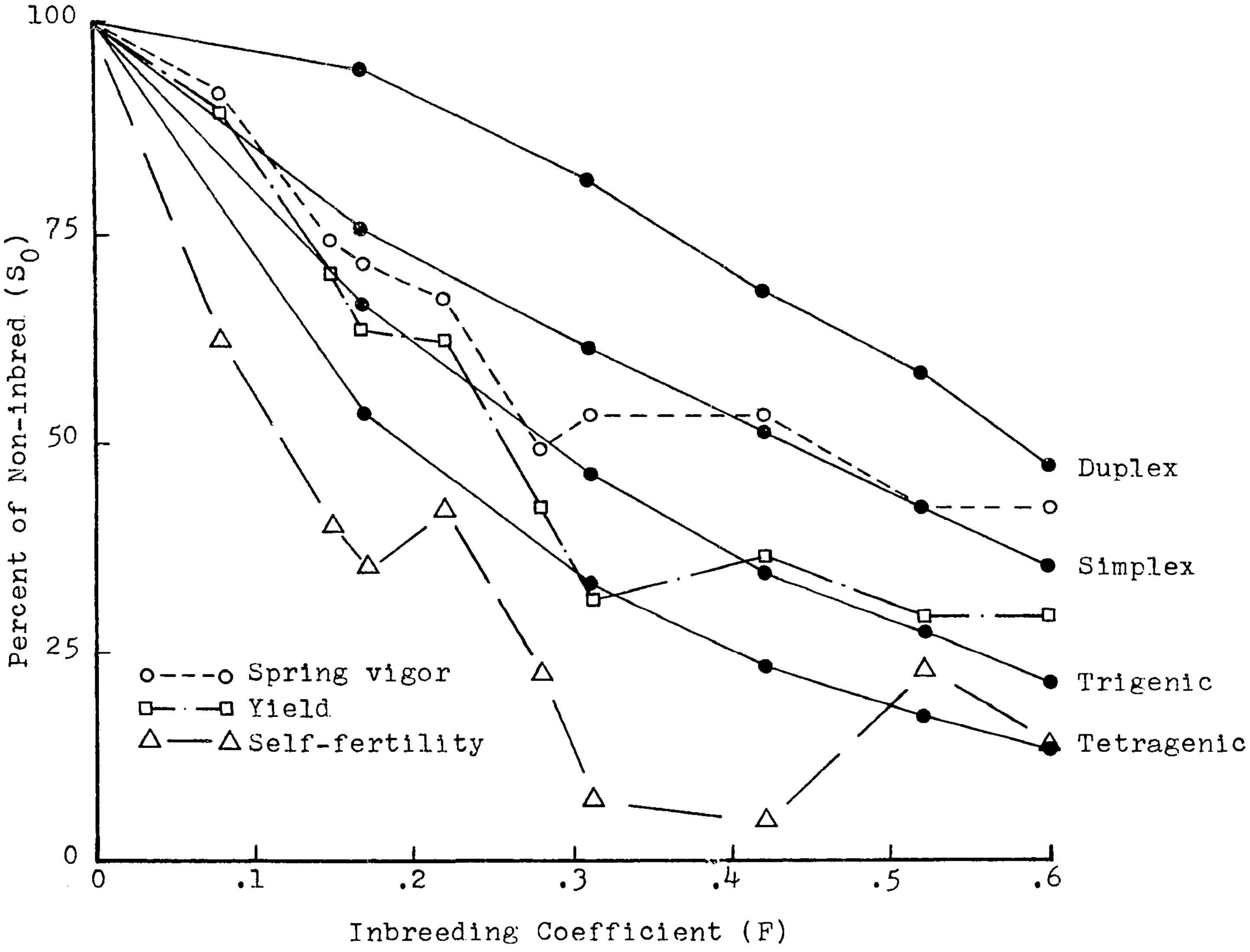
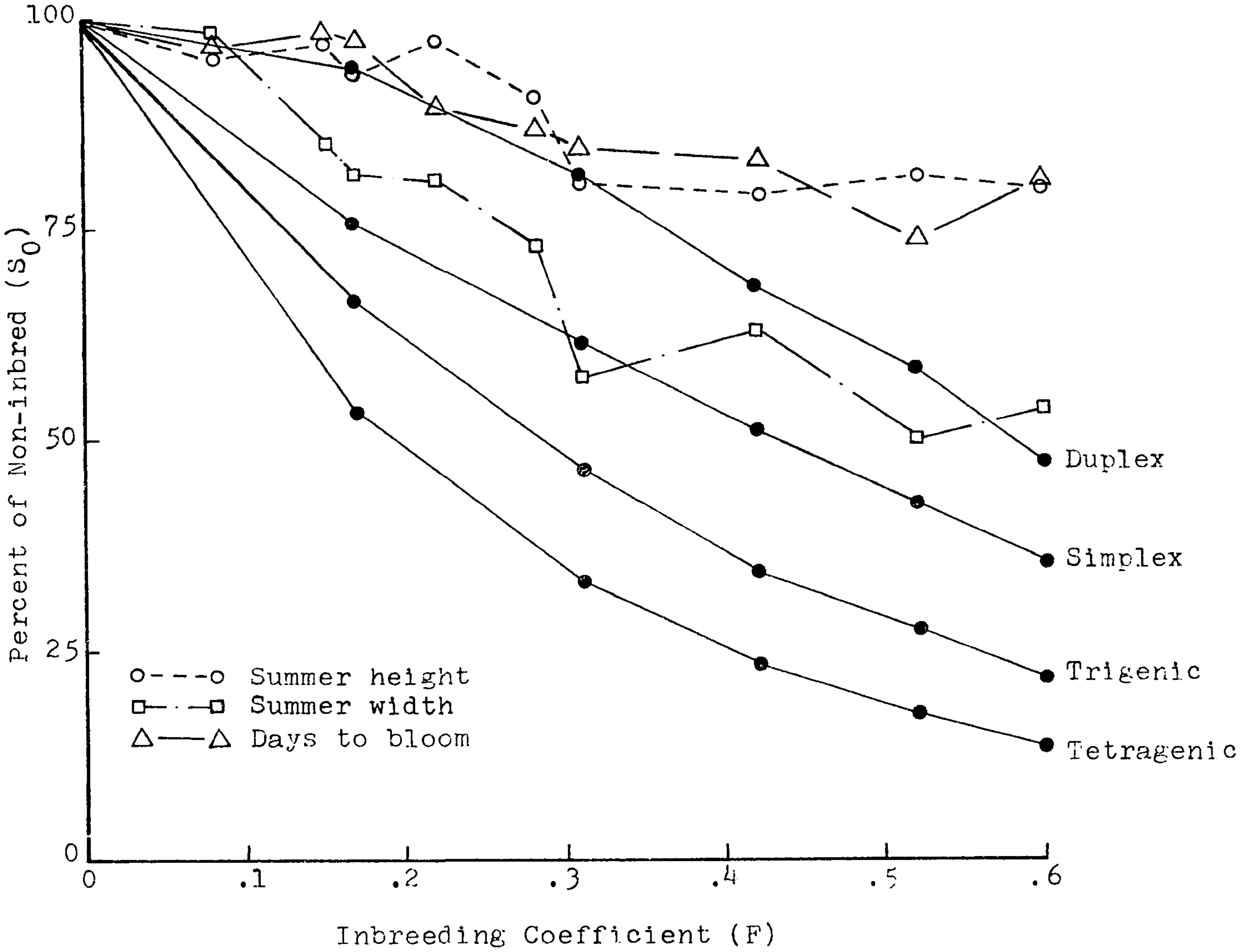

100
75
50
25
0
Percent of Non-inbred (S_0)
0
.1
.2
.3
.4
.5
.6
Inbreeding Coefficient (F)
o----o Spring vigor
□—·—□ Yield
△——△ Self-fertility
Duplex
Simplex
Trigenic
Tetragenic

Figure 2. Mean summer plant height and width and days to bloom for various levels of inbreeding superimposed on the theoretical losses of first-order interactions from four types of loci as computed by Busbice and Wilsie (1966a)


100
75
50
25
0
Percent of Non-inbred (S_0)
0
.1
.2
.3
.4
.5
.6
Inbreeding Coefficient (F)
○---○ Summer height
□-·-□ Summer width
△—△ Days to bloom
Duplex
Simplex
Trigenic
Tetragenic

factors other than inbreeding must be contributing to the loss of fertility in these generations.

Data from the population of Vernal alfalfa used in this study indicate that the possibilities for development of agronomically desirable inbred lines by sib-mating, backcrossing, or a combination of both, are rather limited. Inbreeding by continuous sib-mating was accompanied by rapid declines in fertility and vigor. Backcrossing partially inbred progenies to parents with lower amounts of inbreeding failed to restore fertility to a level near the less-inbred parent. However, some families exhibited relatively stable self- and sib-fertility over the latter generations of sib-mating, after showing a rather sharp decline in the FS_2 generation. Therefore, if a large base population was established and rigid selection for fertility was practiced in the early generations of sib-mating, partially inbred lines might be obtained that would be sufficiently fertile and vigorous to be included in alfalfa breeding programs.

SUMMARY AND CONCLUSIONS

This study was undertaken to determine the effects of inbreeding by continued sib-mating and by various types of backcrosses on fertility and agronomic characters in alfalfa. Materials were obtained from the S_0 (A) population of Aycock (1966) and traced originally to the variety, Vernal. Self-, sib-, and backcross-fertility indices were expressed as ratios of the number of seeds produced to the number of flowers manipulated. Fertility indices were determined during the winter months in the greenhouse and agronomic characters were measured in spaced plant field nurseries.

As generations of inbreeding were advanced, fertility declined much more rapidly with straight selfing than with sib-mating, but fertility relative to the non-inbred parents was not greatly different for the two types of progenies at comparable levels of inbreeding. Sib-mating appeared more advantageous than straight selfing in the maintenance of self-fertility at the higher levels of inbreeding. Mean self-fertility was greater than mean sib-fertility for the parents in each generation of sib-mating. These differences suggest that different loci govern the expression of self- and sib-fertility in alfalfa.

Differences in fertility attributable to reciprocal crosses were small and non-significant in all sib-matings and in all types of backcrosses made between two inbred parents.

However, in all types of backcrosses, fertility was greater when the less inbred plant was mated as the female parent.

Fertility indices for reciprocal crosses were significantly different for backcrosses between inbred progenies and their related non-inbred parents. Backcross fertility indices appeared to be more closely related to the fertility of the female rather than the male parent.

Self- and sib-fertility indices of the sib-parents were correlated significantly in all generations of sib-mating. Heritability estimates also were moderately high for sib- and self-fertility, except for sib-fertility estimated from the FS_3-FS_4 generations. These associations indicate that plant breeders should be able to select effectively for improved self- or sib-fertility, or both, in populations of alfalfa.

In general, the performance for agronomic characters declined less rapidly upon inbreeding than did fertility. However, forage yield and spring vigor, which are most important to alfalfa breeders, declined more rapidly than the other agronomic traits.

Variability among progenies for agronomic characters generally increased as generations of inbreeding were advanced. Variations among S_2, S_4, S_5, FS_3, and FS_4 progenies usually were large, but differences among S_0 and F_1 progenies were small for most attributes and usually did not exceed the 1 or 5 percent levels of probability.

Sib-mated progenies were superior to selfed progenies for all characters measured in Experiments 3 and 4, except fall growth habit. However, inbreeding coefficients of the sib-mated progenies were considerably lower, and it remains to be determined whether vigor can be maintained in sib-progenies that are highly inbred.

The declines for yield and spring vigor with inbreeding were similar to the losses of first order interactions at tetragenic and trigenic loci postulated by Busbice and Wilsie (1966a). Plant height and width and days to bloom declined at rates similar to those postulated for losses of interactions at duplex or simplex loci.

Self-fertility declined more rapidly than any of the theoretical rates proposed for losses of interactions, suggesting that a genetic system for self-incompatibility also is contributing to the drastic depression observed upon inbreeding.

The development of agronomically desirable inbred lines of alfalfa by sib-mating and/or backcrossing would be difficult. However, a few partially inbred progenies were obtained that appear to posses sufficient vigor and fertility to warrant their inclusion in alfalfa breeding programs.

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APPENDIX

Table 25. Sib-fertility of FS$_2$ progenies, winter 1966-67

Cross	Total flowers crossed	Total seeds set	Sib-fertility index	
			Cross	Family[a]
62-100-1 x 62-100-2	16	0	0.000	
62-100-2 x 62-100-1	26	0	0.000	0.000
62-102-1 x 62-102-2	120	35	0.292	
62-102-2 x 62-102-1	143	30	0.210	0.251
62-104-1 x 62-104-2	232	77	0.332	
62-104-2 x 62-104-1	258	46	0.178	0.255
62-106-1 x 62-106-2	106	13	0.123	
62-106-2 x 62-106-1	150	37	0.247	0.185
62-108-1 x 62-108-2	158	30	0.190	
62-108-2 x 62-108-1	136	80	0.588	0.389
62-112-1 x 62-112-2	104	4	0.038	
62-112-2 x 62-112-1	70	14	0.200	0.119
62-116-1 x 62-116-2	164	73	0.445	
62-116-2 x 62-116-1	212	52	0.245	0.345
62-118-1 x 62-118-2	91	12	0.132	
62-118-2 x 62-118-1	143	3	0.031	0.081
62-120-1 x 62-120-2	90	19	0.211	
62-120-2 x 62-120-1	68	15	0.221	0.216
62-122-1 x 62-122-2	241	29	0.120	
62-122-2 x 62-122-1	186	89	0.478	0.299
62-124-1 x 62-124-2	135	49	0.363	
62-124-2 x 62-124-1	146	208	1.425	0.894
62-126-1 x 62-126-2	127	4	0.031	
62-126-2 x 62-126-1	104	4	0.038	0.035
62-128-1 x 62-128-2	164	80	0.488	
62-128-2 x 62-126-1	132	41	0.311	0.399
62-130-1 x 62-130-2	32	3	0.094	
62-130-2 x 62-130-1	37	2	0.054	0.074

---

[a] Mean of reciprocal crosses.

Table 25. (Continued)

Cross	Total flowers crossed	Total seeds set	Sib-fertility index	
			Cross	Family[a]
62-132-1 x 62-132-2	145	1	0.007	
62-132-2 x 62-132-1	90	5	0.055	0.031
62-134-1 x 62-132-2	90	46	0.511	
62-134-2 x 62-132-1	103	74	0.718	0.615
62-136-1 x 62-136-2	179	68	0.380	
62-136-2 x 62-136-1	200	64	0.320	0.350
62-138-1 x 62-138-2	157	20	0.127	
62-138-2 x 62-138-1	146	9	0.062	0.095
62-144-1 x 62-144-2	96	18	0.187	
62-144-2 x 62-144-1	124	15	0.121	0.154
62-146-1 x 62-146-2	75	1	0.013	
62-146-2 x 62-146-1	74	13	0.176	0.094
62-148-1 x 62-148-2	34	0	0.000	
62-148-2 x 62-148-1	43	0	0.000	0.000
62-154-1 x 62-154-2	47	17	0.362	
62-154-2 x 62-154-1	80	30	0.375	0.368
62-158-1 x 62-158-2	113	141	1.248	
62-158-2 x 62-158-1	122	86	0.705	0.976
62-160-1 x 62-160-2	142	4	0.028	
62-160-2 x 62-160-1	80	1	0.012	0.020
62-162-1 x 62-162-2	174	191	1.097	
62-162-2 x 62-162-1	125	74	0.592	0.845
62-164-1 x 62-164-2	114	68	0.596	
62-164-2 x 62-164-1	156	107	0.686	0.641
62-166-1 x 62-166-2	184	161	0.875	
62-166-2 x 62-166-1	187	101	0.540	0.707
62-170-1 x 62-170-2	99	7	0.071	
62-170-2 x 62-170-1	130	5	0.038	0.055
62-172-1 x 62-172-2	157	29	0.185	
62-172-2 x 62-172-1	140	38	0.271	0.228

Table 25. (Continued)

Cross	Total flowers crossed	Total seeds set	Sib-fertility index	
			Cross	Family^a
62-176-1 x 62-176-2	235	7	0.030	
62-176-2 x 62-176-1	293	7	0.024	0.027
62-178-1 x 62-178-2	68	23	0.338	
62-178-2 x 62-178-1	124	4	0.032	0.185
62-180-1 x 62-180-2	101	29	0.287	
62-180-2 x 62-180-1	142	15	0.106	0.196
62-182-1 x 62-182-2	224	102	0.455	
62-182-2 x 62-182-1	194	40	0.206	0.331
62-184-1 x 62-184-2	159	1	0.006	
62-184-2 x 62-184-1	163	14	0.086	0.046
62-186-1 x 62-186-2	112	48	0.429	
62-186-2 x 62-186-1	48	3	0.062	0.245
62-188-1 x 62-188-2	118	20	0.169	
62-188-2 x 62-188-1	102	8	0.078	0.124
62-190-1 x 62-190-2	85	24	0.282	
62-190-2 x 62-190-1	45	4	0.089	0.186
62-192-1 x 62-192-2	141	113	0.801	
62-192-2 x 62-192-1	129	58	0.450	0.625
62-196-1 x 62-196-2	89	2	0.022	
62-196-2 x 62-196-1	123	3	0.024	0.023
62-198-1 x 62-198-2	150	10	0.067	
62-198-2 x 62-198-1	83	0	0.000	0.033
Grand totals	10125	2978		
Grand mean			0.294	
L.S.D. (.05)			0.54	
(.01)			0.72	

Table 26. Sib-fertility of FS_3 progenies, winter 1967-68

Cross	Total flowers crossed	Total seeds set	Sib-fertility index	
			Cross	Family[a]
72-102-2 x 72-102-3	90	13	0.144	
72-102-3 x 72-102-2	109	7	0.064	0.104
72-104-4 x 72-104-5	106	0	0.000	
72-104-5 x 72-104-4	92	0	0.000	0.000
72-106-2 x 72-106-5	132	69	0.523	
72-106-5 x 72-106-2	90	1	0.011	0.267
72-108-1 x 72-108-4	116	10	0.086	
72-108-4 x 72-108-1	103	4	0.039	0.062
72-112-1 x 72-112-5	114	8	0.070	
72-112-5 x 72-112-1	101	26	0.257	0.163
72-116-1 x 72-116-5	110	41	0.373	
72-116-5 x 72-116-1	109	59	0.541	0.457
72-118-1 x 72-118-5	82	1	0.012	
72-118-5 x 72-118-1	51	0	0.000	0.006
72-120-1 x 72-120-3	69	1	0.014	
72-120-3 x 72-120-1	65	11	0.169	0.091
72-122-1 x 72-122-3	120	13	0.108	
72-122-3 x 72-122-1	151	12	0.079	0.093
72-124-2 x 72-124-4	104	27	0.260	
72-124-4 x 72-124-2	76	2	0.026	0.143
72-126-2 x 72-126-4	92	1	0.019	
72-126-4 x 72-126-2	82	1	0.012	0.015
72-128-5 x 72-128-7	136	63	0.463	
72-128-7 x 72-128-5	98	0	0.000	0.231
72-132-1 x 72-132-2	63	4	0.063	
72-132-2 x 72-132-1	162	23	0.142	0.102
72-134-1 x 72-134-2	94	20	0.213	
72-134-2 x 72-134-1	104	3	0.029	0.121

---

[a] Mean of reciprocal crosses.

Table 26. (Continued)

Cross	Total flowers crossed	Total seeds set	Sib-fertility index	
			Cross	Family[a]
72-136-1 x 72-136-2	104	1	0.010	
72-136-2 x 72-136-1	46	2	0.043	0.026
72-138-1 x 72-138-2	86	25	0.297	
72-138-2 x 72-138-1	71	15	0.211	0.254
72-144-1 x 72-144-2	69	9	0.130	
72-144-2 x 72-144-1	85	26	0.306	0.218
72-154-2 x 72-154-5	116	15	0.129	
72-154-5 x 72-154-2	97	6	0.062	0.095
72-158-2 x 72-158-8	16	5	0.312	
72-158-8 x 72-158-2	48	7	0.146	0.229
72-162-4 x 72-162-8	111	56	0.491	
72-162-8 x 72-162-4	104	109	1.048	0.769
72-164-1 x 72-164-4	112	102	0.911	
72-164-4 x 72-164-1	131	105	0.801	0.856
72-166-5 x 72-166-6	79	9	0.114	
72-166-6 x 72-166-5	93	64	0.688	0.401
72-170-8 x 72-170-9	104	3	0.029	
72-170-9 x 72-170-8	102	3	0.029	0.029
72-172-4 x 72-172-5	90	8	0.089	
72-172-5 x 72-172-4	122	12	0.098	0.093
72-176-2 x 72-176-3	125	0	0.000	
72-176-3 x 72-176-2	107	0	0.000	0.000
72-180-5 x 72-180-8	67	0	0.000	
72-180-8 x 72-180-5	86	1	0.012	0.006
72-182-4 x 72-182-6	113	9	0.080	
72-182-6 x 72-182-4	102	14	0.137	0.108
72-184-3 x 72-184-6	110	1	0.009	
72-184-6 x 72-184-3	96	2	0.021	0.015

Table 26. (Continued)

Cross	Total flowers crossed	Total seeds set	Sib-fertility index	
			Cross	Family[a]
72-186-3 x 72-186-6	103	1	0.010	
72-186-6 x 72-186-3	105	0	0.000	0.005
72-188-2 x 72-188-6	118	16	0.136	
72-188-6 x 72-188-2	103	10	0.097	0.116
72-192-3 x 72-192-6	95	1	0.010	
72-192-6 x 72-192-3	105	14	0.133	0.071
72-198-2 x 72-198-7	51	7	0.137	
72-198-7 x 72-198-2	30	0	0.000	0.068
Grand totals	6162	1079		
Grand mean			0.175	
L.S.D. (.05)			0.31	
(.01)			0.41	

Table 27. Sib-fertility of FS_4 progenies, winter 1968-69

Cross	Total flowers crossed	Total seeds set	Sib-fertility index	
			Cross	Family[a]
82-102-2 x 82-102-3	81	2	0.025	
82-102-3 x 82-102-2	85	1	0.012	0.018
82-106-1 x 82-106-2	95	5	0.053	
82-106-2 x 82-106-1	55	6	0.109	0.081
82-108-2 x 82-108-3	47	2	0.043	
82-108-3 x 82-108-2	54	0	0.000	0.021
82-112-2 x 82-112-3	89	3	0.034	
82-112-3 x 82-112-2	73	4	0.055	0.044
82-116-2 x 82-116-3	65	2	0.031	
82-116-3 x 82-116-2	92	6	0.065	0.048
82-120-1 x 82-120-2	84	2	0.024	
82-120-2 x 82-120-1	79	0	0.000	0.012
82-122-1 x 82-122-2	103	10	0.097	
82-122-2 x 82-122-1	94	1	0.011	0.054
82-124-1 x 82-124-2	124	64	0.516	
82-124-2 x 82-124-1	124	46	0.371	0.443
82-128-1 x 82-128-3	87	1	0.011	
82-128-3 x 82-128-1	81	3	0.037	0.024
82-132-1 x 82-132-2	87	1	0.012	
82-132-2 x 82-132-1	92	1	0.011	0.011
82-134-1 x 82-134-2	88	2	0.023	
82-134-2 x 82-134-1	82	2	0.024	0.023
82-138-1 x 82-138-2	66	1	0.015	
82-138-2 x 82-138-1	70	19	0.271	0.143
82-144-2 x 82-144-3	90	8	0.089	
82-144-3 x 82-144-2	97	5	0.051	0.070
82-154-1 x 82-154-2	71	1	0.014	
82-154-2 x 82-154-1	72	0	0.000	0.007

---

[a] Mean of two crosses.

Table 27. (Continued)

Cross	Total flowers crossed	Total seeds set	Sib-fertility index	
			Cross	Family[a]
82-158-2 x 82-158-3	96	29	0.302	
82-158-3 x 82-158-2	92	53	0.576	0.439
82-162-1 x 82-162-2	71	5	0.070	
82-162-2 x 82-162-1	69	21	0.304	0.187
82-164-2 x 82-164-3	82	1	0.012	
82-164-3 x 82-164-2	93	6	0.064	0.038
82-166-2 x 82-166-3	61	0	0.000	
82-166-3 x 82-166-2	62	0	0.000	0.000
82-170-1 x 82-170-2	89	2	0.022	
82-170-2 x 82-170-1	83	1	0.012	0.017
82-172-1 x 82-172-2	77	0	0.000	
82-172-2 x 82-172-1	92	1	0.011	0.005
82-182-1 x 82-182-2	105	7	0.067	
82-182-2 x 82-182-1	113	4	0.035	0.051
82-184-2 x 82-184-3	88	0	0.000	
82-184-3 x 82-184-2	63	0	0.000	0.000
82-188-1 x 82-188-2	55	0	0.000	
82-188-2 x 82-188-1	100	1	0.010	0.005
82-192-1 x 82-192-2	87	1	0.011	
82-192-2 x 82-192-1	91	3	0.033	0.022
82-198-1 x 82-198-2	85	15	0.176	
82-198-2 x 82-198-1	60	10	0.167	0.171
Grand totals	4141	358		
Grand mean			0.086	
L.S.D. (.05)			0.14	
(.01)			0.19	

Table 28. Self-fertility of FS_2 plants, winter 1966-67

Plant	Total flowers selfed	Total seeds set	Self-fertility index Plant	Self-fertility index Family[a]
62-100-1	136	1	0.007	
62-100-2	132	0	0.000	0.003
62-102-1	162	91	0.562	
62-102-2	147	34	0.231	0.397
62-104-1	425	9	0.021	
62-104-2	165	2	0.012	0.016
62-106-1	135	45	0.333	
62-106-2	152	11	0.072	0.202
62-108-1	163	55	0.337	
62-108-2	140	84	0.600	0.468
62-112-1	128	49	0.383	
62-112-2	115	46	0.400	0.391
62-116-1	201	154	0.766	
62-116-2	195	1	0.005	0.385
62-118-1	154	22	0.143	
62-118-2	62	1	0.016	0.079
62-120-1	169	106	0.627	
62-120-2	116	20	0.172	0.399
62-122-1	362	94	0.260	
62-122-2	179	29	0.162	0.211
62-124-1	132	85	0.644	
62-124-2	166	48	0.289	0.466
62-126-1	132	2	0.015	
62-126-2	123	24	0.195	0.105
62-128-1	159	61	0.384	
62-128-2	140	12	0.086	0.235
62-130-1	25	2	0.080	
62-130-2	109	3	0.028	0.054

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[a] Mean of two plants.

Table 28. (Continued)

Plant	Total flowers selfed	Total seeds set	Self-fertility index	
			Plant	Family[a]
62-132-1	165	0	0.000	
62-132-2	145	1	0.007	0.003
62-134-1	205	275	1.342	
62-134-2	149	167	1.121	1.231
62-136-1	126	94	0.746	
62-136-2	134	157	1.172	0.959
62-138-1	142	25	0.176	
62-138-2	148	21	0.142	0.159
62-144-1	115	12	0.104	
62-144-2	63	16	0.254	0.179
62-146-1	161	3	0.019	
62-146-2	147	30	0.204	0.111
62-148-1	136	11	0.081	
62-148-2	137	1	0.007	0.044
62-154-1	131	30	0.229	
62-154-2	161	56	0.348	0.288
62-158-1	110	64	0.582	
62-158-2	153	74	0.484	0.533
62-160-1	124	17	0.137	
62-160-2	116	2	0.017	0.077
62-162-1	126	107	0.849	
62-162-2	133	136	1.022	0.935
62-164-1	143	251	1.755	
62-164-2	159	37	0.233	0.994
62-166-1	175	47	0.269	
62-166-2	181	262	1.448	0.858
62-170-1	198	8	0.040	
62-170-2	213	56	0.263	0.151
62-172-1	157	63	0.401	
62-172-2	152	11	0.072	0.236

Table 28. (Continued)

Plant	Total flowers selfed	Total seeds set	Self-fertility index	
			Plant	Family[a]
62-176-1	150	3	0.020	
62-176-2	174	4	0.023	0.021
62-178-1	178	20	0.112	
62-178-2	152	4	0.026	0.069
62-180-1	135	22	0.163	
62-180-2	146	23	0.158	0.160
62-182-1	203	87	0.429	
62-182-2	313	26	0.083	0.256
62-184-1	184	4	0.022	
62-184-2	115	1	0.009	0.015
62-186-1	119	7	0.059	
62-186-2	167	64	0.383	0.221
62-188-1	153	84	0.549	
62-188-2	145	11	0.076	0.312
62-190-1	116	53	0.457	
62-190-2	123	46	0.374	0.415
62-192-1	115	4	0.035	
62-192-2	186	146	0.785	0.410
62-196-1	155	58	0.374	
62-196-2	120	0	0.000	0.187
62-198-1	133	19	0.143	
62-198-2	116	2	0.017	0.080
Grand totals	12227	3813		
Grand mean			0.312	

Table 29. Self-fertility of FS_3 plants, winter 1967-68

Plant	Total flowers selfed	Total seeds set	Self-fertility index	
			Plant	Family[a]
72-102-2	124	21	0.169	
72-102-3	115	23	0.200	0.184
72-104-4	172	0	0.000	
72-104-5	146	0	0.000	0.000
72-106-2	105	0	0.000	
72-106-5	156	65	0.417	0.208
72-108-1	33	0	0.000	
72-108-4	71	2	0.028	0.014
72-112-1	134	33	0.246	
72-112-5	138	43	0.312	0.279
72-116-1	166	68	0.410	
72-116-5	194	201	1.036	0.723
72-118-1	145	3	0.021	
72-118-5	141	15	0.106	0.063
72-120-1	123	17	0.138	
72-120-3	110	22	0.200	0.169
72-122-1	134	50	0.373	
72-122-3	156	43	0.276	0.324
72-124-2	136	29	0.213	
72-124-4	163	113	0.693	0.453
72-126-2	160	15	0.094	
72-126-4	101	14	0.139	0.116
72-128-5	150	113	0.753	
72-128-7	146	0	0.000	0.376
72-132-1	147	9	0.061	
72-132-2	193	65	0.337	0.199
72-134-2	127	54	0.425	
72-134-9	155	73	0.471	0.448

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[a] Mean of two plants.

Table 29. (Continued)

Plant	Total flowers selfed	Total seeds set	Self-fertility index	
			Plant	Family[a]
72-136-5	113	0	0.000	
72-136-6	154	60	0.390	0.195
72-138-1	40	7	0.175	
72-138-6	138	371	2.688	1.431
72-144-4	101	25	0.247	
72-144-7	143	89	0.622	0.434
72-146-5	31	1	0.032	
72-146-8	147	1	0.007	0.019
72-154-2	150	96	0.640	
72-154-5	136	18	0.132	0.386
72-158-2	42	39	0.929	
72-158-8	153	117	0.764	0.846
72-162-4	91	27	0.297	
72-162-8	69	77	1.116	0.706
72-164-1	138	248	1.797	
72-164-4	175	97	0.554	1.175
72-166-5	124	106	0.855	
72-166-6	148	184	1.243	1.049
72-170-8	126	7	0.056	
72-170-9	136	18	0.132	0.094
72-172-4	132	1	0.008	
72-172-5	134	44	0.328	0.168
72-176-2	136	0	0.000	
72-176-3	152	0	0.000	0.000
72-180-5	80	1	0.012	
72-180-8	129	13	0.101	0.056
72-182-4	207	12	0.058	
72-182-6	116	17	0.147	0.102

Table 29. (Continued)

Plant	Total flowers selfed	Total seeds set	Self-fertility index	
			Plant	Family[a]
72-184-3	109	0	0.000	
72-184-6	134	3	0.022	0.011
72-186-3	88	34	0.386	
72-186-6	40	0	0.000	0.198
72-188-2	132	25	0.189	
72-188-6	106	36	0.340	0.264
72-190-1	143	0	0.000	
72-190-5	27	33	0.111	0.055
72-192-3	145	8	0.055	
72-192-6	152	15	0.099	0.077
72-196-1	77	1	0.013	
72-196-3	35	1	0.029	0.021
72-198-2	156	3	0.019	
72-198-7	139	4	0.029	0.024
Grand totals	8765	2900		
Grand mean			0.331	

Table 30. Self-fertility of FS_4 plants, winter 1968-69

Plant	Total flowers selfed	Total seeds set	Self-fertility index	
			Plant	Family[a]
82-102-2	124	0	0.000	
82-102-3	121	2	0.016	0.008
82-106-1	75	2	0.027	
82-106-2	98	18	0.191	0.109
82-108-2	133	8	0.060	
82-108-3	70	1	0.014	0.037
82-112-2	173	40	0.231	
82-112-3	107	18	0.168	0.199
82-116-2	130	86	0.661	
82-116-3	155	44	0.284	0.472
82-120-1	123	1	0.008	
82-120-2	104	3	0.029	0.018
82-122-1	137	18	0.131	
82-122-2	119	3	0.025	0.078
82-124-1	127	96	0.756	
82-124-2	148	86	0.581	0.668
82-128-1	124	1	0.008	
82-128-3	133	25	0.188	0.098
82-132-1	132	1	0.008	
82-132-3	101	2	0.020	0.014
82-134-1	108	26	0.241	
82-134-2	112	11	0.982	0.611
82-138-1	117	64	0.547	
82-138-3	113	66	0.584	0.565
82-144-2	51	5	0.098	
82-144-3	120	1	0.008	0.053
82-154-1	53	47	0.887	
82-154-2	108	3	0.028	0.457

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[a] Mean of two plants.

Table 30. (Continued)

Plant	Total flowers selfed	Total seeds set	Self-fertility index	
			Plant	Family[a]
82-158-2	59	45	0.763	
82-158-3	122	154	1.262	1.012
82-162-1	104	43	0.413	
82-162-2	132	26	0.197	0.305
82-164-2	61	24	0.393	
82-164-3	119	8	0.067	0.230
82-166-2	108	0	0.000	
82-166-3	103	0	0.000	0.000
82-170-1	142	11	0.077	
82-170-2	157	11	0.070	0.073
82-172-1	109	1	0.009	
82-172-2	121	3	0.025	0.017
82-182-1	146	15	0.103	
82-182-2	140	4	0.029	0.066
82-184-2	109	0	0.000	
82-184-3	143	2	0.014	0.007
82-188-1	110	2	0.018	
82-188-2	138	0	0.000	0.009
82-192-1	130	20	0.154	
82-192-2	267	73	0.273	0.213
82-198-1	117	9	0.077	
82-198-3	126	42	0.333	0.205
Grand totals	5975	1171		
Grand mean			0.196	

Table 31. Self-fertility of S_3 plants, winters 1966-67, 1967-68

Plant	Total flowers selfed	Total seeds set	Self-fertility index
6111-1	583	8	0.015
6111-2	279	59	0.211
6111-3	409	129	0.315
6111-4	453	17	0.037
6111-5	388	1	0.003
6111-6	869	0	0.000
6111-7	577	8	0.014
6111-8	472	16	0.034
6111-9	595	29	0.049
6111-10	798	2	0.003
6111-11	360	0	0.000
6111-12	471	11	0.023
6111-13	235	10	0.043
6111-14	207	11	0.053
6111-15	348	1	0.003
6111-16	242	48	0.198
6111-17	204	0	0.000
6111-18	284	26	0.091
6111-19	402	0	0.000
6111-20	391	30	0.077
6111-21	109	0	0.000
6111-22	207	2	0.010
6111-23	206	0	0.000
6111-24	483	73	0.151
6111-25	241	0	0.000
6111-26	243	0	0.000
6111-27	339	2	0.006
6111-28	219	3	0.014
6111-29	244	19	0.078
6111-30	213	1	0.005
6111-31	273	2	0.007
6111-32	205	0	0.000
6111-33	293	0	0.000
6111-34	234	0	0.000
6111-35	241	7	0.029
6111-36	152	1	0.007
6111-38	214	24	0.112
6111-39	289	2	0.007
6111-40	132	0	0.000

Table 31. (Continued)

Plant	Total flowers selfed	Total seeds set	Self-fertility index
6111-42	272	0	0.000
6111-43	207	3	0.014
6111-44	148	1	0.007
6111-45	148	3	0.020
6111-46	126	4	0.032
Grand totals	13955	553	
Grand mean			0.038

Table 32. Self-fertility of S_4 plants, winters 1967-68, 1968-69

Plant	Total flowers selfed	Total seeds set	Self-fertility index
71111-1	213	17	0.080
71111-2	290	12	0.041
71111-3	217	4	0.018
71111-4	115	4	0.035
71111-5	172	0	0.000
71111-6	221	69	0.312
71111-7	187	10	0.053
71111-8	176	6	0.034
71111-9	230	5	0.022
71111-10	103	3	0.291
71111-11	233	4	0.017
71111-12	219	10	0.046
71111-14	241	6	0.025
71111-15	219	16	0.073
71111-16	231	0	0.000
71111-17	266	3	0.011
71111-19	118	1	0.008
71111-20	321	13	0.040
71111-21	318	19	0.060
71111-22	111	6	0.054
71111-23	175	0	0.000
71111-24	322	2	0.006
71111-25	178	7	0.039
71111-26	265	15	0.057
71111-27	197	0	0.000
71111-28	209	12	0.057
71111-29	150	13	0.087
71111-31	179	4	0.022
71111-32	169	27	0.160
71111-34	227	0	0.000
71111-35	196	18	0.092
71111-36	292	9	0.031
71111-37	228	22	0.096
71111-38	203	7	0.034
71111-39	156	0	0.000
71111-40	64	0	0.000
71111-41	250	183	0.732
71111-43	86	2	0.023
71111-44	385	690	1.792
71111-45	261	23	0.088

Table 32. (Continued)

Plant	Total flowers selfed	Total seeds set	Self-fertility index
71111-46	156	2	0.013
71111-47	95	0	0.000
71111-48	64	0	0.000
71111-49	214	244	1.140
71111-50	27	0	0.000
71111-51	247	50	0.202
71111-52	240	56	0.233
71111-53	108	128	1.185
71111-54	463	29	0.063
71111-55	384	10	0.026
71111-56	352	214	0.608
71111-57	252	47	0.186
71111-58	83	2	0.024
71111-59	16	0	0.000
71111-60	69	0	0.000
Grand totals	11163	2024	
Grand mean			0.181

Table 33. Self-fertility of S_5 plants, winter 1968-69

Plant	Total flowers selfed	Total seeds set	Self-fertility index
811111-2	213	1	0.005
811111-3	168	2	0.012
811111-5	206	4	0.019
811111-6	106	8	0.075
811111-7	212	0	0.000
811111-8	202	0	0.000
811111-12	175	22	0.126
811111-13	11	0	0.000
811111-14	249	3	0.012
811111-16	80	15	0.187
811111-17	143	18	0.126
811111-19	206	0	0.000
811111-21	167	12	0.072
811111-22	204	0	0.000
811111-23	130	82	0.631
811111-24	46	0	0.000
811111-26	56	3	0.054
811111-27	183	0	0.000
811111-28	208	0	0.000
811111-29	109	30	0.275
811111-30	224	12	0.054
811111-31	13	1	0.077
811111-33	21	0	0.000
811111-34	118	0	0.000
811111-35	250	0	0.000
811111-36	206	75	0.364
811111-39	42	0	0.000
811111-40	21	0	0.000
811111-41	88	49	0.557
811111-42	236	0	0.000
811111-43	211	1	0.005
811111-44	18	1	0.056
811111-45	209	1	0.005
811111-46	240	117	0.487
811111-49	51	0	0.000
811111-51	109	4	0.037
811111-53	169	231	1.367
811111-55	90	5	0.056
811111-56	115	1	0.009
811111-60	199	49	0.246

Table 33. (Continued)

Plant	Total flowers selfed	Total seeds set	Self-fertility index
811111-66	203	0	0.000
811111-67	226	4	0.018
811111-69	194	0	0.000
811111-71	84	61	0.726
811111-73	204	0	0.000
811111-74	219	0	0.000
811111-75	142	0	0.000
811111-76	54	0	0.000
811111-78	208	10	0.048
811111-80	202	1	0.005
811111-82	166	0	0.000
Grand totals	7606	822	
Grand mean			0.108

Table 34. Backcross-1 (FS_2 x FS_1) fertility indices, winter 1966-67

Backcross	Total flowers crossed	Total seeds set	Backcross fertility index
62-102-1 x 52-102-1	92	34	0.370
52-102-1 x 62-102-1	185	143	0.773
62-106-2 x 52-106-3	148	32	0.216
52-106-3 x 62-106-2	43	7	0.163
62-108-1 x 52-108-7	110	9	0.082
52-108-7 x 62-108-1	126	19	0.151
62-112-1 x 52-112-7	127	12	0.095
52-112-7 x 62-112-1	132	57	0.432
62-118-1 x 52-118-7	70	13	0.186
52-118-7 x 62-118-1	14	0	0.000
62-120-1 x 52-120-4	137	31	0.226
52-120-4 x 62-120-1	170	48	0.282
62-126-1 x 52-126-9	50	1	0.020
52-126-9 x 62-126-1	64	2	0.031
62-128-1 x 52-128-8	114	64	0.561
52-128-8 x 62-128-1	98	18	0.184
62-132-1 x 52-132-4	71	1	0.014
52-132-4 x 62-132-1	52	2	0.039
62-134-1 x 52-134-1	109	13	0.119
52-134-1 x 62-134-1	123	76	0.617
62-136-1 x 52-136-7	140	112	0.800
52-136-7 x 62-136-1	155	164	1.058
62-138-2 x 52-138-3	109	3	0.027
52-138-3 x 62-138-2	188	5	0.027
62-144-1 x 52-144-10	125	33	0.264
52-144-10 x 62-144-1	115	35	0.304
62-162-1 x 52-162-7	115	35	0.304
52-162-7 x 62-162-1	89	104	1.168

Table 34. (Continued)

Backcross	Total flowers crossed	Total seeds set	Backcross fertility index
62-164-1 x 52-164-8	157	215	1.369
52-164-8 x 62-164-1	183	194	1.060
62-176-1 x 52-176-2	102	3	0.029
52-176-2 x 62-176-1	92	7	0.076
Grand totals	3605	1492	
Grand mean			0.414
L.S.D. (.05)			0.68
(.01)			0.93

Table 35. Backcross-2 (FS_4 x FS_1) fertility indices, winter 1968-69

Backcross	Total flowers crossed	Total seeds set	Backcross fertility index
82-102-1 x 52-102-1	74	4	0.054
52-102-1 x 82-102-1	76	4	0.053
82-108-2 x 52-108-7	83	18	0.217
52-108-7 x 82-108-2	69	1	0.015
82-112-2 x 52-112-7	56	0	0.000
52-112-7 x 82-112-2	59	13	0.220
82-128-2 x 52-128-1	54	0	0.000
52-128-1 x 82-128-2	49	0	0.000
82-132-1 x 52-132-4	78	37	0.474
52-132-4 x 82-132-1	90	12	0.133
82-134-2 x 52-134-2	70	4	0.057
52-134-2 x 82-134-2	65	35	0.539
82-144-1 x 52-144-10	55	2	0.036
52-144-10 x 82-144-1	48	2	0.042
82-162-3 x 52-162-7	52	19	0.365
52-162-7 x 82-162-3	61	45	0.738
82-164-1 x 52-164-5	50	64	1.280
52-164-5 x 82-164-1	61	96	1.574
Grand totals	1150	356	
Grand mean			0.310
L.S.D. (.05)			0.53
(.01)			0.73

Table 36. Backcross-3 (FS_4 x S_0) fertility indices, winter 1968-69

Backcross	Total flowers crossed	Total seeds set	Backcross fertility index
82-102-1 x 30-103	54	8	0.148
30-103 x 82-102-1	59	25	0.424
82-108-2 x 30-109	67	40	0.597
30-109 x 82-108-2	56	14	0.250
82-112-2 x 30-113	69	9	0.130
30-113 x 82-112-2	43	18	0.419
82-128-2 x 30-129	59	1	0.017
30-129 x 82-128-2	51	14	0.275
82-134-2 x 30-134	68	3	0.044
30-134 x 82-134-2	53	51	0.962
82-144-1 x 30-145	72	20	0.278
30-145 x 82-144-1	55	86	1.564
82-162-3 x 30-163	44	10	0.227
30-163 x 82-162-3	62	50	0.806
82-164-1 x 30-164	58	143	2.465
30-164 x 82-164-1	66	108	1.929
Grand totals	926	600	
Grand mean			0.648
L.S.D. (.05)			0.87
(.01)			1.20

Table 37. Backcross-4 (S_3 x S_0) fertility indices, winter 1968-69

Backcross	Total flowers crossed	Total seeds set	Backcross fertility index
6111-3 x 30-113	59	179	3.033
30-113 x 6111-3	59	81	1.373
6111-3 x 30-127	58	213	3.672
30-127 x 6111-3	55	22	0.400
6111-3 x 30-134	55	96	1.745
30-134 x 6111-3	54	18	0.333
6111-4 x 30-103	52	0	0.000
30-103 x 6111-4	58	113	1.948
6111-4 x 30-129	54	10	0.185
30-129 x 6111-4	57	125	2.193
6111-4 x 30-163	44	2	0.045
30-163 x 6111-4	64	37	0.578
6111-8 x 30-113	50	19	0.380
30-113 x 6111-8	59	51	0.864
6111-8 x 30-127	49	33	0.674
30-127 x 6111-8	58	28	0.483
6111-8 x 30-134	54	30	0.556
30-134 x 6111-8	57	65	1.140
6111-9 x 30-119	55	4	0.073
30-119 x 6111-9	56	31	0.554
6111-9 x 30-133	60	8	0.133
30-133 x 6111-9	60	17	0.283
6111-9 x 30-176	55	0	0.000
30-176 x 6111-9	55	10	0.182

Table 37. (Continued)

Backcross	Total flowers crossed	Total seeds set	Backcross fertility index
6111-14 x 30-103	58	18	0.310
30-103 x 6111-14	68	76	1.118
6111-14 x 30-129	53	5	0.094
30-129 x 6111-14	58	60	1.035
6111-14 x 30-163	51	19	0.373
30-163 x 6111-14	57	51	0.895
6111-15 x 30-113	46	11	0.239
30-113 x 6111-15	61	35	0.574
6111-15 x 30-127	52	37	0.712
30-127 x 6111-15	55	11	0.200
6111-15 x 30-134	56	1	0.179
30-134 x 6111-15	48	31	0.646
6111-16 x 30-103	55	48	0.873
30-103 x 6111-16	60	119	1.983
6111-16 x 30-129	58	62	1.069
30-129 x 6111-16	54	21	0.389
6111-16 x 30-163	53	62	1.170
30-163 x 6111-16	57	35	0.614
6111-18 x 30-113	64	46	0.719
30-113 x 6111-18	60	98	1.633
6111-18 x 30-127	58	38	0.655
30-127 x 6111-18	62	27	0.436
6111-18 x 30-134	59	26	0.441
30-134 x 6111-18	60	92	1.533

Table 37. (Continued)

Backcross	Total flowers crossed	Total seeds set	Backcross fertility index
6111-20 x 30-119	53	26	0.491
30-119 x 6111-20	54	36	0.667
6111-20 x 30-133	50	24	0.480
30-133 x 6111-20	56	29	0.518
6111-20 x 30-176	50	38	0.760
30-176 x 6111-20	56	17	0.304
6111-24 x 30-119	55	3	0.055
30-119 x 6111-24	56	89	1.589
6111-24 x 30-133	53	15	0.283
30-133 x 6111-24	49	40	0.816
6111-24 x 30-176	52	11	0.212
30-176 x 6111-24	48	32	0.667
6111-33 x 30-103	51	2	0.039
30-103 x 6111-33	49	7	0.143
6111-33 x 30-129	47	2	0.043
30-129 x 6111-33	55	3	0.055
6111-33 x 30-163	50	4	0.080
30-163 x 6111-33	28	2	0.071
Grand totals	3612	2601	
Grand mean			0.720
L.S.D. (.05)			0.82
(.01)			1.09

Table 38. Backcross-5 (S_5 x S_0) fertility indices, winter 1968-69

Backcross	Total flowers crossed	Total seeds set	Backcross fertility index
811111-3 x 30-103	32	5	0.156
30-103 x 811111-3	31	19	0.613
811111-3 x 30-113	30	0	0.000
30-113 x 811111-3	31	8	0.258
811111-3 x 30-127	30	4	0.133
30-127 x 811111-3	32	6	0.187
811111-3 x 30-134	32	1	0.031
30-134 x 811111-3	30	8	0.267
811111-3 x 30-163	32	5	0.156
30-163 x 811111-3	30	39	1.300
811111-7 x 30-103	21	4	0.190
30-103 x 811111-7	20	10	0.500
811111-7 x 30-113	32	6	0.187
30-113 x 811111-7	31	8	0.258
811111-7 x 30-127	31	8	0.242
30-127 x 811111-7	33	11	0.355
811111-7 x 30-134	31	6	0.193
30-134 x 811111-7	31	8	0.267
811111-7 x 30-163	20	3	0.150
30-163 x 811111-7	21	0	0.000
811111-12 x 30-103	32	43	1.387
30-103 x 811111-12	32	34	1.062
811111-12 x 30-113	31	57	1.839
30-113 x 811111-12	32	15	0.469
811111-12 x 30-127	30	63	2.100
30-127 x 811111-12	31	11	0.355

Table 38. (Continued)

Backcross	Total flowers crossed	Total seeds set	Backcross fertility index
811111-12 x 30-134	30	53	1.767
30-134 x 811111-12	31	27	0.871
811111-12 x 30-163	32	44	1.375
30-163 x 811111-12	31	24	0.774
811111-14 x 30-103	32	2	0.062
30-103 x 811111-14	29	27	0.931
811111-14 x 30-113	30	8	0.267
30-113 x 811111-14	31	24	0.774
811111-14 x 30-127	30	9	0.600
30-127 x 811111-14	32	16	0.500
811111-14 x 30-134	33	7	0.212
30-134 x 811111-14	33	31	0.939
811111-14 x 30-163	31	2	0.064
30-163 x 811111-14	30	10	0.300
811111-19 x 30-103	21	0	0.000
30-103 x 811111-19	20	34	1.700
811111-19 x 30-113	31	3	0.097
30-113 x 811111-19	32	22	0.687
811111-19 x 30-127	31	5	0.161
30-127 x 811111-19	29	21	0.724
811111-19 x 30-134	31	2	0.064
30-134 x 811111-19	31	17	0.548
811111-19 x 30-163	21	7	0.333
30-163 x 811111-19	21	3	0.143

Table 38. (Continued)

Backcross	Total flowers crossed	Total seeds set	Backcross fertility index
811111-35 x 30-103	21	0	0.000
30-103 x 811111-35	21	20	0.952
811111-35 x 30-113	30	0	0.000
30-113 x 811111-35	29	21	0.724
811111-35 x 30-127	32	0	0.000
30-127 x 811111-35	31	6	0.193
811111-35 x 30-134	31	0	0.000
30-134 x 811111-35	31	17	0.548
811111-35 x 30-163	22	0	0.000
30-163 x 811111-35	21	3	0.143
Grand totals	1740	847	
Grand mean			0.487
L.S.D. (.05)			0.75
(.01)			0.99

Table 39. Relative self-fertility indices of parents mated in the fourth (S_3 x S_0) and fifth (S_5 x S_0) backcrosses, winter 1968-69

Number of clone or plant	Relative fertility	Mean self-fertility
S_0 parents		
30-103	Low	
30-113	Low	0.570
30-127	Medium	
30-129	Medium	0.857
30-134	High	
30-164	High	1.494
S_3 parents		
6111-15	Very low	
6111-33	Very low	0.015
6111-4	Low	
6111-8	Low	0.035
6111-14	Medium	
6111-18	Medium	0.072
6111-3	High	
6111-16	High	0.256
S_5 parents		
811111-7	Very low	
811111-19	Very low	
811111-35	Very low	0.000
811111-14	Low	0.012
811111-3	Medium	
811111-12	Medium	0.126

Table 40. Mean performance of individual progenies within each generation for agronomic characters measured in Experiment 3, 1967-68

Entry number	Fall vigor (1-9)	Spring vigor (1-9)	Total yield (lb./plant)	Days to bloom	Plant height (in.)		Plant width (in.)		Growth habit	
					summer	fall	summer	fall	summer	fall
					S_0 progenies					
301	5.0	4.3	2.37	32.7	28.9	10.0	29.0	16.7	1.08	0.61
302	4.7	5.0	2.08	30.0	27.5	12.4	25.9	16.9	1.12	0.76
303	5.0	4.5	2.23	29.9	27.3	11.9	24.9	16.8	1.15	0.75
304	5.5	5.0	2.46	29.8	26.9	11.3	27.2	16.9	1.01	0.68
305	5.3	4.6	2.22	31.3	26.6	10.6	28.7	18.8	0.99	0.59
Mean	5.1	4.7	2.27	30.8	27.4	11.2	27.1	17.2	1.07	0.68
					S_1 progenies					
306	5.0	4.7	1.90	28.7	26.1	10.1	28.6	19.8	0.94	0.51
307	5.3	4.6	1.89	32.2	26.6	8.1	21.8	11.5	1.25	0.70
308	6.5	6.9	1.03	33.2	23.9	7.8	18.1	10.1	1.30	0.78
309	4.9	6.1	1.39	29.9	21.3	11.7	19.1	14.5	1.20	0.83
310	4.3	5.9	0.99	36.9	23.9	12.5	17.0	16.4	1.47	0.78
311	4.2	5.5	1.45	34.9	26.6	11.3	22.3	16.1	1.22	0.71
312	5.1	6.2	1.57	30.8	20.5	9.6	26.4	15.8	0.83	0.62
313	5.9	5.5	1.55	32.1	24.8	7.6	23.9	14.3	1.07	0.53
314	5.8	5.8	1.45	30.2	23.0	9.5	18.5	13.6	1.27	0.71
Mean	5.2	5.7	1.47	32.1	24.1	9.8	21.7	14.7	1.17	0.69
					S_2 progenies					
315	5.4	7.3	0.83	33.6	18.3	12.5	17.1	15.4	1.10	0.81
316	5.9	7.3	0.84	35.3	17.6	7.4	15.0	13.3	1.22	0.57
317	7.3	6.5	1.24	34.1	17.9	6.4	16.4	10.8	1.12	0.60

Table 40. (Continued)

Entry number	Fall vigor (1-9)	Spring vigor (1-9)	Total yield (lb./plant)	Days to bloom	Plant height (in.)		Plant width (in.)		Growth habit	
					summer	fall	summer	fall	summer	fall
318	6.5	6.7	1.11	34.8	20.7	7.4	18.5	11.9	1.73	0.71
319	7.4	7.6	0.72	39.0	19.9	4.2	13.6	7.6	1.48	0.57
320	7.3	7.0	0.99	38.2	23.1	7.6	22.9	12.8	1.11	0.60
321	8.0	8.4	0.23	37.8	21.2	5.8	11.1	6.7	1.98	0.93
322	7.3	8.7	0.26	46.0	13.4	4.9	9.5	9.1	1.44	0.54
Mean	6.9	7.4	0.78	37.4	19.0	7.0	15.5	10.9	1.40	0.66
				F_1 progenies						
323	5.4	4.7	2.28	31.8	25.3	10.9	23.7	14.9	1.09	0.74
324	2.2	2.9	2.85	30.9	28.5	14.1	29.5	17.8	0.98	0.79
325	3.5	3.0	3.19	30.3	28.2	14.4	31.1	22.7	0.94	0.64
326	3.8	2.6	3.68	29.6	29.1	10.0	30.7	20.3	0.98	0.48
327	4.9	3.4	2.97	31.5	27.1	11.9	30.7	18.5	0.89	0.65
328	3.7	2.7	2.84	30.4	27.3	11.3	28.0	20.0	1.01	0.51
329	5.3	5.4	1.45	31.5	24.3	13.9	19.3	14.5	1.30	1.01
330	4.1	3.1	3.26	28.1	28.1	11.7	31.7	19.1	0.90	0.62
Mean	4.1	3.5	2.81	30.5	27.2	12.3	28.1	18.5	1.01	0.69
				FS_1 progenies						
331	4.2	5.0	2.37	33.4	22.2	10.5	27.2	18.3	0.87	0.60
332	5.0	4.3	2.41	29.5	26.4	12.1	27.7	19.2	0.97	0.65
333	5.1	4.9	1.95	36.6	25.0	9.8	22.4	20.0	1.17	0.50
334	6.2	4.7	2.39	32.1	27.0	7.6	24.1	12.2	1.18	0.64
335	4.9	5.5	1.47	31.6	24.1	13.0	17.4	14.2	1.47	0.92
336	4.7	4.5	1.85	30.9	27.8	11.2	22.3	14.5	1.27	0.77

Table 40. (Continued)

Entry number	Fall vigor (1-9)	Spring vigor (1-9)	Total yield (lb./plant)	Days to bloom	Plant height (in.)		Plant width (in.)		Growth habit	
					summer	fall	summer	fall	summer	fall
337	6.1	5.5	1.56	31.1	24.7	11.2	20.9	15.0	1.22	0.75
338	5.5	4.6	2.32	32.2	25.8	8.9	23.2	15.1	1.15	0.60
339	5.7	4.7	2.24	31.5	27.8	9.5	27.3	15.2	1.05	0.63
Mean	5.3	4.9	2.06	32.1	25.7	10.4	23.6	16.0	1.15	0.67
				FS_2 progenies						
340	5.4	5.1	2.04	30.1	30.7	15.0	27.0	16.5	1.18	0.92
341	6.9	5.8	1.55	33.2	23.8	7.5	20.0	12.1	1.23	0.62
342	5.3	5.4	1.48	35.6	28.1	10.2	21.8	13.5	1.34	0.77
343	5.0	4.5	2.20	29.2	20.6	8.1	27.3	16.7	0.78	0.49
Mean	5.6	5.2	1.82	32.0	25.8	10.2	24.0	14.7	1.13	0.70
				S_3 progenies						
344	6.7	8.2	0.64	32.8	19.1	8.5	16.7	11.1	1.20	0.78
345	6.6	6.4	1.22	35.7	21.7	6.8	23.1	11.1	1.03	0.69
Mean	6.7	7.3	0.93	34.2	20.4	7.6	19.9	11.1	1.12	0.73
				FS_3 progenies						
346	5.1	6.2	1.37	35.7	20.4	10.6	23.7	17.2	0.92	0.65
347	6.2	6.5	1.32	36.1	23.3	7.2	21.7	12.9	1.13	0.56
348	4.5	4.7	2.22	29.9	27.1	11.9	30.5	17.2	0.91	0.70
349	4.2	5.3	1.86	33.2	29.3	13.5	28.9	15.4	1.11	0.91
350	5.5	6.2	1.27	35.7	22.6	7.7	22.1	11.3	1.07	0.70

Table 40. (Continued)

Entry number	Fall vigor (1-9)	Spring vigor (1-9)	Total yield (lb./plant)	Days to bloom	Plant height (in.) summer	Plant height (in.) fall	Plant width (in.) summer	Plant width (in.) fall	Growth habit summer	Growth habit fall
351	7.0	7.7	0.87	34.8	23.5	10.7	16.7	11.5	1.56	0.95
352	6.5	6.2	1.23	33.8	24.3	7.7	18.5	11.1	1.42	0.69
353	6.5	6.2	1.60	31.0	25.5	11.0	23.3	16.1	1.14	0.69
354	3.4	3.8	2.21	33.5	29.3	13.9	24.4	15.9	1.23	0.88
355	5.3	5.5	1.38	31.4	26.9	11.7	19.5	11.3	1.41	1.06
Mean	5.4	5.8	1.53	33.5	25.2	10.6	22.9	14.0	1.19	0.78
				BC-1 progenies						
356	5.5	5.7	1.74	31.1	23.1	8.6	21.1	14.6	1.41	0.61
357	5.2	6.4	1.43	30.9	23.6	12.4	23.0	17.4	1.13	0.72
358	7.0	6.5	1.31	35.3	25.6	12.1	21.3	13.5	1.28	0.90
359	5.7	7.5	1.00	36.4	25.9	14.8	18.1	11.1	1.64	1.35
360	5.7	5.9	1.32	36.7	24.1	9.8	19.6	13.8	1.30	0.72
Mean	5.8	6.4	1.36	34.1	24.5	11.5	20.6	14.1	1.35	0.86
L.S.D.										
(.05)	1.2	1.3	0.54	4.5	3.5	5.9	5.6	2.6	0.34	0.45
(.01)	1.6	1.7	0.71	4.7	4.7	7.8	7.5	3.5	0.44	0.59

Table 41. Mean performance of individual progenies within each generation for agronomic characters measured in Experiment 4, 1968-69

Entry number	Spring vigor (1-9)	Yield (lb./plant)	Days to bloom	Plant height (in.)		Plant width (in.)		Growth habit		Longest stem (in.)
				fall	summer	fall	summer	fall	summer	
				S_0 progenies						
401	4.2	1.41	29.4	14.2	22.4	28.8	33.5	0.50	0.71	31.6
402	3.9	1.72	27.6	16.9	25.3	27.7	34.5	0.63	0.76	34.7
403	2.7	1.98	28.6	17.4	25.1	27.3	33.5	0.69	0.78	35.3
404	2.6	1.90	28.7	17.7	23.1	28.8	31.9	0.63	0.81	35.8
405	2.6	2.03	27.7	15.9	22.9	32.0	34.5	0.53	0.71	34.0
Mean	3.2	1.81	28.4	16.4	23.8	28.9	33.6	0.60	0.75	34.3
				S_1 progenies						
406	4.9	1.23	30.7	17.1	24.3	26.1	26.1	0.69	1.02	30.1
407	3.5	1.31	26.2	11.9	23.7	26.7	29.4	0.46	0.84	29.1
408	7.7	0.78	23.6	14.9	25.1	29.2	27.2	0.53	1.01	30.0
409	4.9	1.01	27.7	15.0	24.9	26.2	25.3	0.59	1.07	28.1
410	5.1	1.27	28.7	16.7	26.5	24.8	28.5	0.69	0.97	29.9
411	5.1	1.03	31.0	13.5	23.9	27.7	27.2	0.50	0.90	26.1
412	6.1	0.69	26.2	12.6	22.3	22.1	22.7	0.58	1.05	26.4
413	5.7	1.45	32.4	13.8	16.4	32.7	29.4	0.43	0.57	32.1
414	6.3	0.80	33.3	12.4	20.6	24.3	29.1	0.57	0.80	30.1
415	5.0	1.42	30.4	16.1	26.2	27.1	34.4	0.61	0.77	32.5
Mean	5.4	1.10	29.0	14.4	23.4	26.7	27.9	0.57	0.92	29.4
				S_2 progenies						
416	7.5	0.45	30.0	14.2	21.4	21.1	20.1	0.67	1.30	23.6
417	7.5	0.49	39.1	9.8	20.5	22.6	20.7	0.44	1.04	2.41

Table 41. (Continued)

Entry number	Spring vigor (1-9)	Yield (lb./plant)	Days to bloom	Plant height (in.)		Plant width (in.)		Growth habit		Longest stem (in.)
				fall	summer	fall	summer	fall	summer	
418	8.6	0.37	33.9	11.8	21.5	20.9	16.8	0.58	1.30	22.0
419	7.9	0.25	42.5	15.5	23.1	15.1	12.5	1.16	2.20	23.8
420	7.8	0.46	27.7	14.7	22.5	21.2	18.7	0.76	1.30	24.7
421	6.8	0.50	36.3	10.7	21.9	16.8	15.5	0.64	1.56	23.0
422	6.4	0.83	28.1	15.5	21.6	23.9	25.7	0.68	0.87	24.9
423	6.9	0.73	29.9	14.5	20.2	21.1	23.6	0.70	0.92	25.1
Mean	7.4	0.51	33.4	13.4	21.6	20.3	19.2	0.70	1.31	23.9
				S_3 progenies						
424	8.2	0.35	40.3	11.6	20.5	16.8	16.1	0.69	1.46	21.8
425	7.7	0.86	38.4	11.5	18.7	17.4	15.2	0.69	1.32	20.6
426	6.6	0.62	33.2	14.6	19.4	19.5	21.3	0.75	0.99	22.1
427	7.7	0.52	38.8	10.0	20.9	19.9	19.4	0.51	1.26	22.6
428	7.3	0.43	34.8	10.9	20.9	19.3	17.9	0.60	1.23	22.3
Mean	7.5	0.56	37.1	11.7	20.1	18.6	18.0	0.65	1.25	21.9
				S_4 progenies						
429	4.6	0.79	35.8	11.7	24.9	21.4	25.3	0.55	0.89	28.0
430	8.1	0.30	34.5	10.5	16.2	15.9	14.5	0.69	1.18	17.3
431	8.3	0.30	43.8	8.7	18.8	21.4	14.8	0.41	1.41	19.7
432	8.2	1.31	40.8	12.8	19.5	20.2	15.0	0.65	1.30	20.8
433	8.3	0.27	36.0	11.6	16.9	19.1	13.8	0.66	1.98	18.8
434	7.8	0.39	39.0	8.6	18.9	15.5	18.2	0.57	1.30	22.0
435	7.9	0.32	37.9	11.2	18.9	18.1	16.1	0.63	1.23	22.3
Mean	7.6	0.52	38.4	10.7	19.2	18.8	16.8	0.59	1.33	21.3

Table 41. (Continued)

Entry number	Spring vigor (1-9)	Yield (lb./plant)	Days to bloom	Plant height (in.)		Plant width (in.)		Growth habit		Longest stem (in.)
				fall	summer	fall	summer	fall	summer	
				S_5 progenies						
436	5.4	1.17	34.5	14.8	21.2	24.7	28.3	0.62	0.78	28.9
437	5.1	1.48	29.2	16.1	19.7	28.0	30.2	0.60	0.68	32.1
438	7.9	0.50	35.7	8.5	20.0	20.0	20.7	0.48	0.98	21.8
439	8.7	0.21	36.5	9.8	16.8	16.1	11.8	0.62	1.47	17.3
440	6.3	0.89	32.9	13.9	20.6	25.7	21.4	0.61	1.05	24.2
Mean	6.7	0.85	33.7	12.6	19.7	22.9	22.5	0.59	0.99	24.8
				F_1 progenies						
441	1.7	2.19	26.5	16.9	20.1	31.4	33.9	0.56	0.68	36.9
442	3.7	2.04	27.2	18.2	25.3	34.3	33.5	0.58	0.79	36.3
443	3.5	1.85	27.3	19.7	20.7	29.1	35.6	0.68	0.59	40.3
444	3.0	1.82	24.5	18.7	24.2	28.1	29.3	0.69	0.92	34.1
445	3.5	1.79	24.6	15.5	19.2	26.1	32.9	0.61	0.59	34.9
446	3.1	2.00	30.0	20.3	27.0	25.6	33.2	0.81	0.84	34.4
447	3.1	1.96	27.7	15.8	22.5	29.3	32.6	0.56	0.72	31.2
448	2.6	2.11	27.1	15.2	24.3	31.9	32.8	0.51	0.80	33.7
449	3.1	1.70	28.9	16.7	25.0	26.7	34.0	0.64	0.77	37.5
Mean	3.0	1.94	27.1	17.4	23.2	29.2	33.1	0.63	0.74	35.5
				FS_1 progenies						
450	4.2	1.41	28.4	17.2	21.1	24.8	28.4	0.69	0.78	32.5
451	4.3	1.48	25.9	11.7	19.1	27.5	29.5	0.46	0.69	32.2
452	3.5	1.60	31.8	17.2	24.4	23.7	33.2	0.74	0.76	35.7

Table 41. (Continued)

Entry number	Spring vigor (1-9)	Yield (lb./plant)	Days to bloom	Plant height (in.)		Plant width (in.)		Growth habit		Longest stem (in.)
				fall	summer	fall	summer	fall	summer	
453	2.6	1.90	30.4	15.3	19.8	32.9	31.6	0.47	0.65	34.5
454	4.5	1.38	26.5	17.1	24.5	26.6	31.5	0.66	0.84	33.6
455	4.6	1.66	29.4	17.9	26.4	29.6	32.1	0.64	0.86	33.9
456	1.3	1.85	30.6	12.5	26.0	30.5	34.5	0.42	0.76	37.8
457	4.2	1.41	28.4	15.6	22.2	28.3	33.5	0.57	0.72	32.7
458	3.9	1.66	31.9	16.9	24.5	24.7	33.7	0.69	0.78	35.9
Mean	3.7	1.59	29.3	15.7	23.1	27.6	32.0	0.61	0.76	34.3
				FS_2 progenies						
459	6.6	0.75	28.8	15.6	24.5	22.7	26.0	0.69	1.03	31.7
460	6.7	1.07	29.4	16.1	23.5	25.3	25.7	0.66	0.97	28.2
461	5.8	0.84	27.6	16.1	23.1	23.3	27.3	0.70	0.90	31.2
462	4.3	1.47	27.8	15.5	22.8	25.9	32.4	0.62	0.72	30.9
463	4.7	1.25	28.5	17.6	24.9	24.3	26.8	0.76	0.99	29.9
Mean	5.6	1.08	28.4	16.2	23.8	24.3	27.7	0.68	0.92	30.4
				FS_3 progenies						
464	6.1	0.83	28.9	12.2	21.3	24.4	27.1	0.51	0.83	26.3
465	4.6	1.51	30.8	13.1	24.8	28.8	27.3	0.48	0.94	29.7
466	9.0	0.28	35.9	10.8	18.5	16.6	15.2	0.67	1.28	18.3
467	3.4	2.04	29.5	15.6	22.8	29.8	31.7	0.56	0.78	32.2
468	6.6	0.86	36.3	15.1	26.9	21.5	24.6	0.72	1.15	33.7
469	5.8	1.24	32.8	19.3	28.0	27.2	26.5	0.74	0.94	31.0
470	5.8	0.80	32.8	16.4	25.6	21.7	26.1	0.83	1.02	28.3

Table 41. (Continued)

Entry number	Spring vigor (1-9)	Yield (lb./plant)	Days to bloom	Plant height (in.)		Plant width (in.)		Growth habit		Longest stem (in.)
				fall	summer	fall	summer	fall	summer	
471	7.3	0.65	32.4	14.9	27.3	22.9	26.4	0.67	1.06	32.1
472	6.7	0.89	32.4	16.7	24.5	22.6	29.9	0.74	0.85	31.9
Mean	6.1	1.01	32.4	14.8	24.4	23.9	26.1	0.66	0.98	29.3
				FS_4 progenies						
473	5.7	1.14	29.1	11.3	24.0	23.8	27.2	0.48	0.91	28.0
474	7.3	0.32	36.2	9.8	19.6	27.3	19.1	0.37	1.35	23.6
475	5.5	1.37	33.1	18.0	22.9	22.1	27.0	0.83	0.89	28.4
476	6.9	0.87	31.0	13.7	17.4	28.5	24.9	0.50	0.70	30.5
477	7.0	0.78	35.3	10.3	18.1	25.0	25.6	0.43	0.81	23.5
478	7.5	0.51	33.7	9.7	22.6	16.9	21.5	0.61	1.16	26.5
479	5.9	0.76	35.3	16.9	24.0	24.3	22.9	0.70	1.10	26.2
480	6.1	0.69	28.0	17.9	19.7	27.5	30.9	0.66	0.68	34.9
481	6.8	0.50	33.1	17.3	26.5	17.3	22.9	1.04	1.22	29.2
Mean	6.5	0.77	32.8	13.9	21.6	23.6	24.7	0.62	0.98	27.9
L.S.D.										
(.05)	1.4	0.47	4.0	4.4	2.2	6.3	5.0	0.40	0.15	4.6
(.01)	1.8	0.63	5.2	5.9	3.0	8.3	6.6	0.53	0.20	6.1