Inbreeding

Inbreeding represents the mating of individuals that are more closely related than individuals mated at random in a population. The most extreme form of inbreeding is the mating of an individual to itself by self-pollination. Less extreme forms of inbreeding also play an important role in plant breeding.

CONSEQUENCES OF INBREEDING

The mating of related individuals increases homozygosity by bringing together identical alleles at a locus. Homozygosity permits the expression of recessive alleles that may have been masked by a dominant allele in the parents. When the recessive alleles are less favorable than dominant ones, the overall desirability of individuals decreases. This reduction in performance is referred to as inbreeding depression.

There are major differences among species for the amount of inbreeding depression that is expressed. In self-pollinated species such as wheat and oat, inbreeding depression is minimal and homozygous genotypes are used as cultivars for crop production. In some cross-pollinated diploid species such as maize, homozygous genotypes can be produced readily, but their performance is lower than that of the hybrid cultivars used in commercial production. Inbreeding depression is so severe in some cross-pollinated polyploid species, such as alfalfa, that homozygous genotypes do not survive.

PURPOSES OF INBREEDING

One important purpose of inbreeding is the development of genotypes that can be maintained through multiple generations of seed production. Self-pollinated

cultivars are reproduced for many generations without changes in their genetic composition. Reliable production of inbred commercial hybrid seed of a species is dependent on the availability of inbred parents whose genotype can be maintained.

Inbreeding has been used to reduce the frequency of deleterious recessive alleles in genotypes that serve as parents of a synthetic or a vegetatively propagated cultivar. One selfed generation may permit the expression and subsequent elimination of deleterious alleles without excessive inbreeding depression occurring in lines selected for use as parents for population development.

Inbreeding increases the genetic variability among individuals in a population. Greater genetic variability among inbred progeny can increase the effectiveness of selection and the amount of genetic improvement in a breeding program (Chap. 17).

INBREEDING IN DIPLOID SPECIES

The degree of relationship among individuals was described by Wright (1921,1922) as the coefficient of inbreeding (F). Later, Malecot (1948) defined the coefficient of inbreeding as the probability that two alleles at a locus are identical by descent. The value of F for a population describes the average level of homozygosity present.

A close relationship has been found in diploid species between the coefficient of inbreeding and the degree of inbreeding depression. A review of experimental data in maize led Hallauer and Miranda (1981) to conclude that (a) there was a linear relationship between percentage of homozygosity and performance of quantitative characters, (b) the method of inbreeding made no practical difference in the performance of lines at a comparable level of inbreeding, (c) the decrease in performance associated with a reduction in the level of heterozygosity was adequately described by the additivity of unlinked loci, and (d) the effects of epistasis on inbreeding depression did not seem to be important.

Four mating systems used to increase homozygosity in a breeding population are self-pollination, full-sib mating, half-sib mating, and backcrossing (Fig. 8-1). Self-pollination occurs when male and female gametes from the same individual unite to produce seed. Full-sib mating represents the crossing of pairs of individuals in a population. Half-sib mating occurs when individual plants are fertilized by random pollen from the population. Backcrossing is a mating scheme in which individuals in a population are crossed to one of their parents in successive generations.

The changes in homozygosity (F) with different inbreeding methods in a diploid species are calculated in Table 8-1. The F value for the F_2 generation is defined as 0. The percentage of homozygosity associated with each generation of backcrossing depends on the level of inbreeding of the recurrent parent. A noninbred recurrent parent ($F = 0$) refers to an F_2 population or its equivalent, and an inbred recurrent parent ($F = 1$) is a completely homozygous individual.
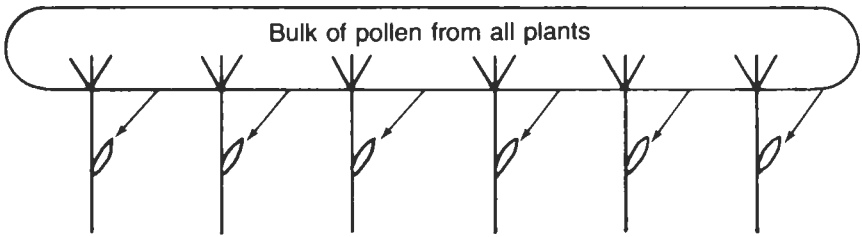
Self-pollination

Full-sib mating

Half-sib mating

Bulk of pollen from all plants
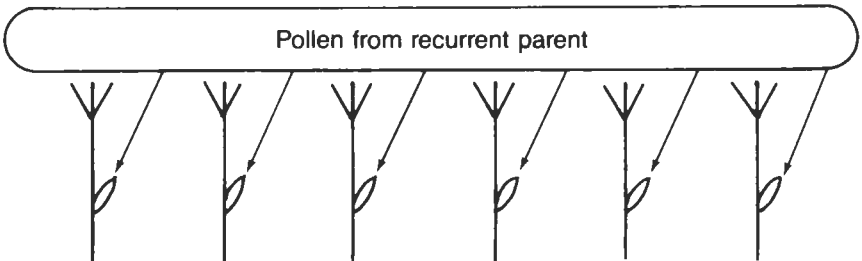

Backcrossing

Pollen from recurrent parent
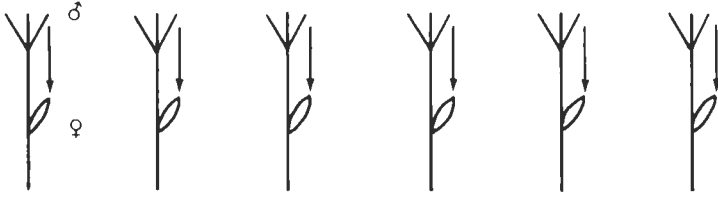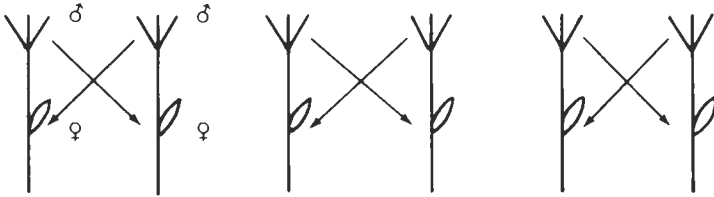
Figure 8-1 Four methods of inbreeding a population of plants with maize used as the example. The pollen of maize is produced in the tassel and the eggs are present in the ear. For each method of inbreeding, one or more seeds from each individual in a population is used collectively to plant the next generation.

Table 8-1 Calculation of Coefficients of Inbreeding for Five Methods of Inbreeding in a Diploid Species*

Generation of Inbreeding†	Self-Pollination	Full-Sib	Half-Sib	Backcrossing—Recurrent parent	
				Inbred ($F = 1$)	Noninbred ($F = 0$)
	$F = \frac{1}{2}(1 + F')$	$F = \frac{1}{4}(1 + 2F' + F'')$	$F = \frac{1}{8}(1 + 6F' + F'')$	$F = \frac{1}{2}(1 + F')$	$F = \frac{1}{4}(1 + 2F')$
1	$\frac{1}{2}(1 + 0) = \frac{1}{2}$	$\frac{1}{4}(1 + 2 \cdot 0 + 0) = \frac{1}{4}$	$\frac{1}{8}(1 + 6 \cdot 0 + 0) = \frac{1}{8}$	$\frac{1}{2}(1 + 0) = \frac{1}{2}$	$\frac{1}{4}(1 + 2 \cdot 0) = \frac{1}{4}$
2	$\frac{1}{2}(1 + \frac{1}{2}) = \frac{3}{4}$	$\frac{1}{4}(1 + 2 \cdot \frac{1}{4} + 0) = \frac{3}{8}$	$\frac{1}{8}(1 + 6 \cdot \frac{1}{8} + 0) = \frac{7}{32}$	$\frac{1}{2}(1 + \frac{1}{2}) = \frac{3}{4}$	$\frac{1}{4}(1 + 2 \cdot \frac{1}{4}) = \frac{3}{8}$
3	$\frac{1}{2}(1 + \frac{3}{4}) = \frac{7}{8}$	$\frac{1}{4}(1 + 2 \cdot \frac{3}{8} + \frac{1}{4}) = \frac{1}{2}$	$\frac{1}{8}(1 + 6 \cdot \frac{7}{32} + \frac{1}{8}) = \frac{39}{128}$	$\frac{1}{2}(1 + \frac{3}{4}) = \frac{7}{8}$	$\frac{1}{4}(1 + 2 \cdot \frac{3}{8}) = \frac{7}{16}$
4	$\frac{1}{2}(1 + \frac{7}{8}) = \frac{15}{16}$	$\frac{1}{4}(1 + 2 \cdot \frac{1}{2} + \frac{3}{8}) = \frac{19}{32}$	$\frac{1}{8}(1 + 6 \cdot \frac{39}{128} + \frac{7}{32}) = \frac{195}{512}$	$\frac{1}{2}(1 + \frac{7}{8}) = \frac{15}{16}$	$\frac{1}{4}(1 + 2 \cdot \frac{7}{16}) = \frac{15}{32}$

*F = coefficient of inbreeding; F' = coefficient of previous generation; F'' = coefficient of second generation removed.
Source: Hallauer and Miranda, 1981.

†$F = 0$ for the F_2 generation or for noninbred plants of a random-mated population. Generation 1 is the first generation after the F_2.

Self-pollination and backcrossing to an inbred parent are the most extreme forms of inbreeding, followed by full-sib mating (Table 8-1). Homozygosity will be achieved eventually under all systems of inbreeding except backcrossing to a noninbred parent. With a noninbred parent, the inbreeding coefficient can reach a maximum of 0.5.

Variation in the approach to homozygosity among the self, full-sib, half-sib, and backcross systems of mating is associated with differences in the opportunity for identical alleles to come together. A slower fixation of undesirable alleles allows more opportunities for selection during inbreeding. In the choice of a system of inbreeding, the importance of selection must be weighed against the length of time required to attain the desired level of homozygosity.

INBREEDING DEPRESSION IN AN AUTOPOLYPLOID SPECIES

The coefficient of inbreeding for an autotetraploid species undergoing self-pollination was described by Kempthorne (1957) as

$$F = \tfrac{1}{8} [1 + 2\alpha + (5 - 2\alpha) F']$$

where F = probability that two alleles at a locus are identical by descent

α = probability of double reduction, which results in gametes that have alleles from sister chromatids

F' = coefficient of inbreeding for preceding generation

When a random-mated population is inbred one generation by self-pollination, the coefficient of inbreeding becomes $\tfrac{1}{8}$ if $\alpha = 0$. F' equals 0 because the coefficient of inbreeding in a random-mated population is zero.

$$F = \tfrac{1}{8} \{1 + 2(0) + [5 - 2(0)] \, 0\} = \tfrac{1}{8}$$

The change in the coefficient of inbreeding by self-pollination in an autotetraploid is illustrated in Fig. 8-2. Four identical alleles at a locus are required to achieve homozygosity in an autotetraploid compared with only two in a diploid; therefore, homozygosity is achieved less rapidly in an autotetraploid.

Inbreeding depression in autopolyploids has been found to exceed that predicted by the coefficient of inbreeding. In alfalfa, an autotetraploid species, the decrease in forage yield with one generation of self-pollination has been twice as large as that predicted by the percentage increase in homozygosity (Aycock and Wilsie, 1968) (Fig. 8-3). This response to inbreeding has been attributed to a decrease in favorable interactions among multiple alleles at a locus.

The change in percentage of homozygosity in autotetraploids as measured by the coefficient of inbreeding does not take into account changes in the number of loci with two, three, or four different alleles (Chap. 4). The number of different alleles at a locus is considered a factor in the expression of inbreeding depression by autopolyploids. Busbice and Wilsie (1966) described in detail the theoretical
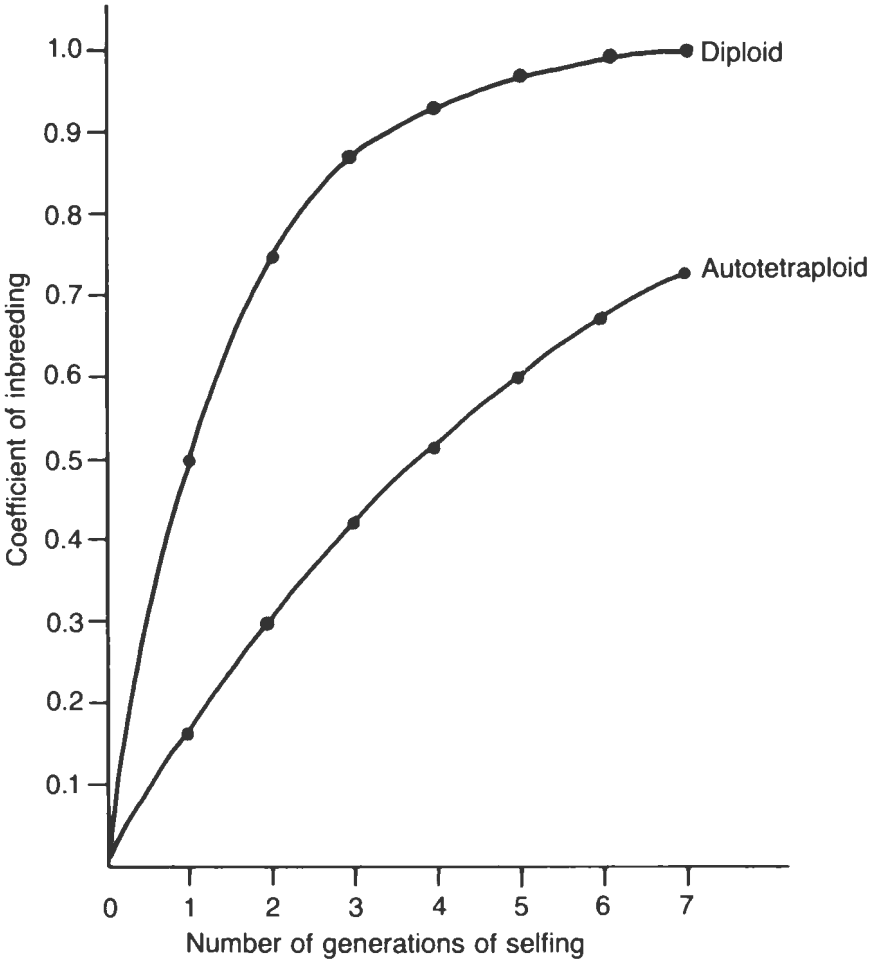
Figure 8-2 Relationship of the coefficient of inbreeding and the number of generations of self-pollination in a diploid and an autotetraploid species.

basis for considering intralocus interactions in predicting the change in performance of autotetraploid alfalfa associated with inbreeding. They defined the genotypic values (G) for loci with one, two, three, or four alleles ($abcd$) by the additive value of alleles and allelic interactions. First-order interactions involve two alleles (ab), second-order interactions involve three alleles (abc), and third-order interactions involve all four alleles.

$$G_{abcd} = a + b + c + d + (ab) + (ac) + (ad) + (bc) + (bd) + (cd)$$
$$+ (abc) + (abd) + (acd) + (bcd) + (abcd)$$
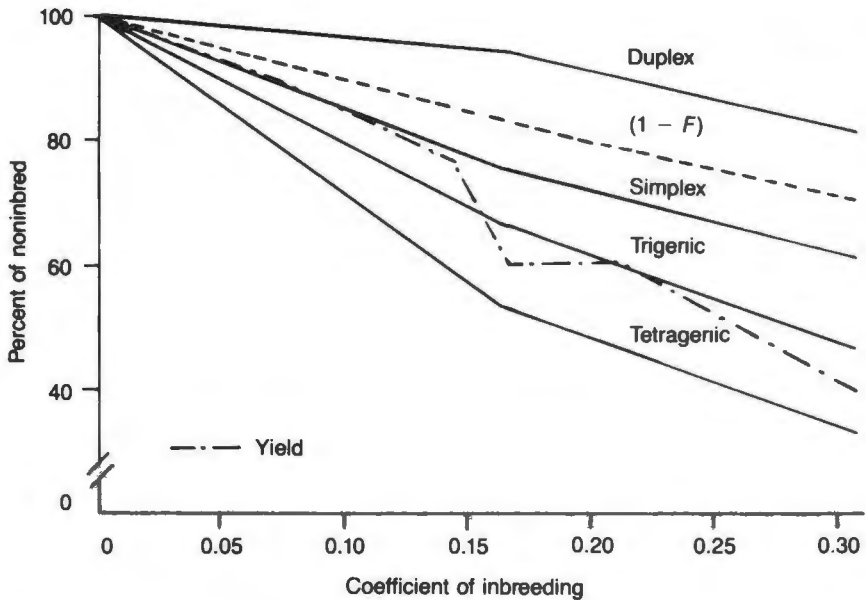$$G_{aabc} = a + a + b + c + (ab) + (ac) + (bc) + (abc)$$

Figure 8-3 Comparison of the yield of alfalfa for various levels of inbreeding and the theoretical loss of first-order interactions from a tetragenic, trigenic, duplex, and simplex locus. (Courtesy of Aycock and Wilsie, 1968.)

$$G_{aabb} = a + a + b + b + (ab)$$
$$G_{aaab} = a + a + a + b + (ab)$$
$$G_{aaaa} = a + a + a + a$$

If intralocus interactions contribute to the performance of an individual, a reduction in the frequency of tetragenic and trigenic loci could cause inbreeding depression that would not be accounted for by the increase in the frequency of homozygous loci. Self-pollination of a tetragenic locus would produce one-sixth tetragenic, two-thirds trigenic, and one-sixth duplex loci. This would decrease substantially the frequency of intralocus interactions with no increase in frequency of homozygous loci.

Because of their multiallelism, autopolyploid species can accumulate a greater number of masked deleterious recessive alleles than diploid species. The uncovering of accumulated deleterious alleles during selfing may contribute to the greater degree of inbreeding depression expressed in autopolyploids than is predicted by the coefficient of inbreeding.

INBREEDING IN SMALL POPULATIONS

The need for progeny evaluation and recombination in recurrent selection programs often necessitates the use of population sizes of 200 individuals or less.

Closed populations are commonly utilized so that the effects of a specific selection method can be determined.

The amount of heterozygosity lost each generation in a random-mated population can be influenced by the population size. In populations of monoecious diploid plants undergoing random mating, including self-pollination, heterozygosity decreases by approximately $\frac{1}{2}N$ each generation, where N is the number of unrelated individuals in the population that are mated. In populations in which self-pollination is prevented, the decrease in heterozygosity each generation is approximated by $1/(2N + 1)$.

Effective population size, N_e, is a relative measure of the number of parents used to form a breeding population. It does not represent the number of individuals from a population that are tested in a recurrent selection program. Effective population size is dependent on the level of inbreeding of the parents that are mated and the number of gametes contributed to the next generation by each sex (Hallauer and Miranda, 1981). The general equation for calculating the effective population size is

$$N_e = \frac{4N_m N_f/(N_m + N_f)}{1 + F_p}$$

where N_m = number of male parents

N_f = number of female parents

F_p = coefficient of inbreeding of parents

Table 8-2 Expected Levels of Inbreeding with Varying Effective Population Sizes for Populations Undergoing Recurrent Selection by Evaluation and Recombination of $S_{0:1}$ lines ($F_p = 0$) or $S_{1:2}$ lines ($F_p = 0.5$)

| Cycle of Selection | Inbreeding of Population (F) | | | | | |
| | 20 Parents | | 30 Parents | | 40 Parents | |
	$S_{0:1}(20^*)$	$S_{1:2}(13.3)$	$S_{0:1}(30)$	$S_{1:2}(20)$	$S_{0:1}(40)$	$S_{1:2}(26.7)$
1	0.05	0.08	0.03	0.05	0.02	0.04
2	.10	.14	.06	.10	.05	.07
3	.14	.20	.09	.14	.07	.10
4	.18	.25	.12	.18	.10	.14
5	.22	.31	.15	.22	.12	.17
6	.25	.35	.18	.26	.14	.20
7	.29	.40	.20	.29	.16	.23
8	.32	.44	.23	.32	.18	.26
9	.35	.48	.26	.36	.20	.28
10	.39	.52	.28	.39	.22	.31
20	.62	.76	.48	.62	.39	.52
40	0.86	0.94	0.73	0.86	0.63	0.77

*Effective population size (N_e). $N_e = 2N/(1 + F_p)$, where N is the number of parents recombined and F_p is the coefficient of inbreeding of the parents recombined.

Source: Hallauer and Miranda (1981).

When equal numbers of males and females contribute the same number of gametes to the next generation, such as occurs when selfed lines are used for mating, the equation becomes

$$N_e = \frac{2N}{1 + F_p}$$

where N is the number of individuals that are mated.

The implications of effective population size on population improvement by recurrent selection have been analyzed by several authors, as summarized by Hallauer and Miranda (1981). In brief, inbreeding in a population increases as the effective population size decreases (Table 8-2). As inbreeding increases, genetic variability among individuals within the population is reduced, which results in lower genetic gain from recurrent selection (Chap. 17).

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