

Backcross Method

The backcross method is used to improve a characteristic of a cultivar for which it is deficient. The term backcrossing refers to the repeated crossing of hybrid progeny back to one of the parents. The parent contributing the genes that control the desired character is called the nonrecurrent or donor parent. Nonrecurrent indicates that the parent is used only once in the backcross procedure and it does not recur. The parent to which the genes are transferred is called the recurrent parent. Recurrent indicates that the parent is used (recurs) repeatedly in the backcrossing procedure.

The value of backcrossing for improvement of crop plants was suggested by Harlan and Pope (1922). They observed that backcrosses had been used for many years in animal breeding to fix desired characters. They indicate that the value of backcrosses for cultivar improvement of small grains had not been fully appreciated.

Harlan and Pope were concerned with the development of barley cultivars with smooth awns, instead of the rough awns that were present on existing cultivars. Imported barley cultivars had smooth awns, but they had objectionable characters, such as black seed. Crosses were made between the smooth-awned barleys and those of the commercially acceptable 'Manchuria' type, but none of the segregates was equal in yield to the 'Manchuria' parent. Harlan and Pope decided to transfer the smooth-awned character to 'Manchuria' by backcrossing. A white, six-rowed, smooth-awned segregate from a previous cross was used as the smooth-awned parent. After only one backcross, they noted that the progeny resembled 'Manchuria' more than observed previously from single-cross populations. The desirable progeny were obtained quickly and inexpensively with a small number of individuals. Subsequent studies in many crop species verified the value of backcrossing for developing improved crop cultivars.

IMPLEMENTATION

The recurrent parent in a breeding program should be a highly acceptable genotype, except for the trait that will be altered by backcrossing. The general principle is that the genotype obtained from backcrossing will not be improved for any character except the one being transferred from the donor parent. If the recurrent parent is inferior for traits in addition to the ones to be purposely altered by backcrossing, it will still be inferior for those traits when backcrossing is completed. Therefore, selection of the recurrent parent is a critical step in a backcrossing program.

The most desirable donor parent is one that has the alleles needed to improve the recurrent parent and that is not seriously deficient in other characters. The overall acceptability of the donor parent can influence the number of backcrosses required to recover the desirable characteristics of the recurrent parent.

The backcrossing procedure used will depend on the genetic control of the character that is to be transferred and the need for progeny testing of individuals to determine their genotype. Backcrossing is simplest when the desired character is controlled by a dominant allele and the character can be evaluated on a single-plant basis before flowering (Fig. 28-1). The following example involves four generations of backcrossing for a single gene controlling disease resistance.

Season 1: F_1 seed is obtained by crossing the susceptible recurrent parent (rr) to the resistant (RR) nonrecurrent parent. All F_1 seeds are Rr .

Season 2: F_1 plants (Rr) are crossed to the recurrent parent (rr) to obtain BC_1F_1 seeds, of which an average of 50 percent are Rr and 50 percent are rr .

Season 3: The BC_1F_1 plants are evaluated before flowering and the susceptible plants (rr) are discarded. The resistant plants (Rr) are crossed to the recurrent parent to obtain BC_2F_1 seeds, of which an average of 50 percent are Rr and 50 percent are rr .

Season 4: The BC_2F_1 plants are evaluated before flowering and susceptible plants (rr) are discarded. The resistant plants (Rr) are crossed to the recurrent parent to obtain BC_3F_1 seeds, of which an average of 50 percent are Rr and 50 percent are rr .

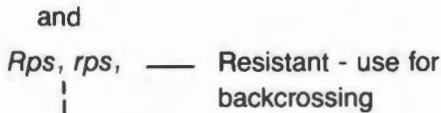
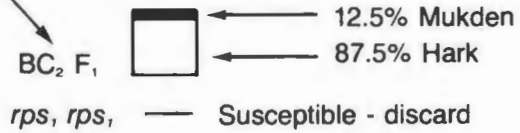
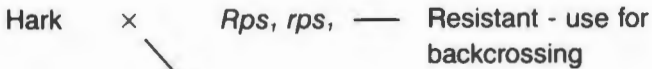
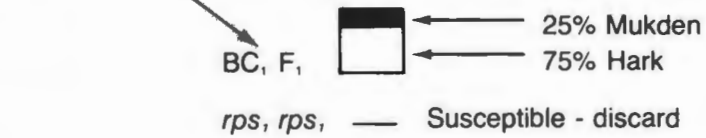
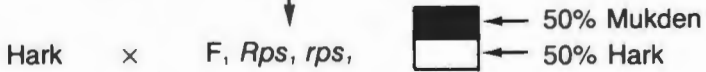
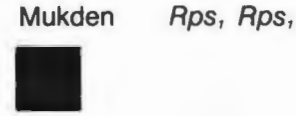
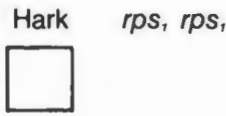
Season 5: BC_4F_1 seeds are obtained in the same manner as described for seasons 3 and 4.

Season 6: The BC_4F_1 plants are evaluated before flowering and the susceptible plants (rr) are discarded. The resistant plants (Rr) are self-pollinated and the BC_4F_2 seeds are harvested at maturity.

Season 7: The BC_4F_2 plants on the average are 25 percent RR , 50 percent Rr , and 25 percent rr . The plants are evaluated before flowering, the susceptible plants (rr) are discarded, and the resistant plants (RR and Rr) are self-pollinated. The seed from each BC_4F_2 plant is harvested separately.

Recurrent parent - susceptible

Donor parent - resistant



Multiple backcrosses

Hark with $Rps, Rps,$

Figure 28-1 Schematic representation of transferring a gene from one cultivar to another by backcrossing. The donor parent 'Mukden' has resistance to race 1 of phytophthora rot (*Phytophthora megasperma* var. *sojae*) to which 'Hark' is susceptible. When backcrossing is completed, 'Hark' should have almost 100 percent of its original genes and also the gene for resistance to phytophthora rot. (Courtesy of Fehr, 1978.)

Season 8 + : Each BC_4F_2 plant is progeny tested before flowering, and segregating progeny from Rr plants are discarded. Plants from BC_4F_2 individuals that are homozygous resistant RR are self-pollinated. During season 8 and subsequent seasons, the BC_4F_2 families are evaluated for important characters in comparison with the recurrent parent. The desirable ones are selected and bulked to replace the recurrent parent.

Some desired characters that are controlled by a dominant allele cannot be evaluated until after flowering is completed. In such cases, the procedure just described for a dominant character evaluated before flowering must be altered. One procedure that can be used is the following.

Season 1: F_1 seed is obtained by crossing the susceptible recurrent parent (rr) to the resistant nonrecurrent parent (RR). All F_1 seeds are Rr .

Season 2: F_1 plants are crossed to the recurrent parent (rr) to obtain BC_1F_1 seeds, of which an average of 50 percent are Rr and 50 percent are rr .

Season 3: The BC_1F_1 plants are crossed to the recurrent parent. The character is evaluated before harvest, and susceptible plants and their BC_2F_1 seeds are discarded. The resistant plants (Rr) and their BC_2F_1 seeds (50 percent Rr and 50 percent rr on the average) are saved.

Seasons 4 and 5: The procedure described for season 3 is used to obtain BC_3F_1 and BC_4F_1 seeds.

Season 6: The BC_4F_1 plants are self-pollinated. The character is evaluated before harvest and susceptible plants are discarded. The BC_4F_2 seeds from resistant plants are harvested.

Season 7: The BC_4F_2 plants (25 percent RR , 50 percent Rr , and 25 percent rr on the average) are self-pollinated. The character is evaluated before harvest and susceptible plants are discarded. The seeds from each resistant BC_4F_2 plant (RR and Rr) are harvested separately.

Season 8 + : Seeds from each resistant BC_4F_2 individual are planted and the plants in each row are self-pollinated. Rows segregating for the character are discarded. Selfed seeds from homogeneous resistant rows are harvested.

During season 8 and subsequent seasons, the resistant BC_4F_2 families are evaluated for important characters in comparison with the recurrent parent. The desirable ones are selected and bulked to replace the recurrent parent.

When the desired character is controlled by a recessive allele, a progeny test must be included in the backcrossing procedure. A progeny test also must be used when the character cannot be evaluated in the environment where the backcross is made, regardless if a dominant or recessive allele controls the desired phenotype. The following example describes the transfer of a recessive allele (r) in the shortest possible time when a progeny test is required to determine the genotype of a backcross progeny.

- Season 1:* F_1 seed is obtained by crossing the susceptible recurrent parent (RR) to the resistant nonrecurrent parent (rr). All of the F_1 seeds are Rr .
- Season 2:* F_1 plants are crossed to the recurrent parent (RR) to obtain BC_1F_1 seeds, of which an average of 50 percent are Rr and 50 percent are RR .
- Season 3:* It is not possible to differentiate between the Rr and RR individuals because all have the dominant character. To complete the backcrossing in the fewest seasons, each BC_1F_1 plant is crossed to the recurrent parent to obtain BC_2F_1 seeds and is self-pollinated to obtain BC_1F_2 seeds for progeny testing.
- Season 4:* The BC_1F_2 seeds are used to progeny test each BC_1F_1 plant before the BC_2F_1 individuals begin flowering. BC_1F_1 plants that are homozygous susceptible (RR) will have all susceptible progeny. The BC_1F_2 progeny from heterozygous BC_1F_1 plants will segregate for resistant (rr) and susceptible plants. BC_2F_1 progeny from homozygous susceptible BC_1F_1 plants (RR) are all susceptible and are discarded. The BC_2F_1 progeny from heterozygous BC_1F_1 plants are crossed to the recurrent parent to obtain BC_3F_1 seeds and are self-pollinated to obtain BC_2F_2 seeds for progeny testing.
- Season 5:* The BC_2F_2 seeds are used to progeny test each BC_2F_1 plant before the BC_3F_1 individuals begin flowering. BC_3F_1 progeny from homozygous susceptible BC_2F_1 plants (RR) are all susceptible and are discarded. The BC_3F_1 progeny from heterozygous BC_2F_1 plants (Rr) are on the average 50 percent Rr and 50 percent RR . The BC_3F_1 plants are crossed to the recurrent parent to obtain BC_4F_1 seeds and are self-pollinated to obtain BC_3F_2 seeds for progeny testing.
- Season 6:* The BC_3F_2 seeds are used to progeny test each BC_3F_1 plant before their BC_4F_1 begin flowering. BC_4F_1 progeny from homozygous susceptible BC_3F_1 plants (RR) are all susceptible and are discarded. The BC_4F_1 plants obtained from crosses on heterozygous BC_3F_1 plants (Rr) are, on the average, 50 percent Rr and 50 percent RR , and all of them are self-pollinated. Each BC_4F_1 plant is harvested separately.
- Season 7:* Each BC_4F_1 plant is progeny tested. The progeny from homozygous susceptible BC_4F_1 plants (RR) are all susceptible and the family is discarded. The BC_4F_2 progeny from heterozygous BC_4F_1 plants (Rr) segregate for resistant (rr) and susceptible ($R-$) plants. If the progeny test can be completed before pollination, only the homozygous resistant (rr) plants are self-pollinated. If the character cannot be evaluated until after flowering, progeny from all BC_4F_1 plants are self-pollinated. The resistant BC_4F_1 plants are identified before harvest and the seed from each is kept separate.
- Season 8+:* During season 8 and subsequent seasons, the resistant BC_4F_2 families are evaluated for important characters in comparison with the recurrent parent. The desirable ones are selected and bulked to replace the recurrent parent.

The procedure as outlined must be modified slightly when used for situations in which the character cannot be evaluated in the same environment where the backcrosses are made. In seasons 4 to 6, the progeny test with BC_xF_2 seeds are conducted in the environment where the character can be evaluated, and the BC_xF_1 plants are grown in a separate environment where the backcrosses are made. The progeny test determines which BC_xF_1 plants should be used for crossing (seasons 4 and 5) or self-pollinated (season 6). In season 7, the BC_4F_2 progeny from heterozygous BC_4F_1 plants are self-pollinated and harvested separately. In season 8, each BC_4F_2 plant is progeny tested and only those that are homozygous for resistance (RR for a dominant allele or rr for a recessive allele) are saved. During season 8 and subsequent seasons, the progeny from homozygous resistant BC_4F_2 plants are evaluated for performance relative to the recurrent parent.

When a progeny test is required to determine the presence of the desired allele during backcrossing, the test can be conducted in one season and backcrossing in another. The procedure eliminates crosses on individuals that do not possess the allele, but increases the number of seasons required to complete the backcrosses. The following example is for transfer of resistance to disease controlled by a recessive allele. It is assumed that resistance cannot be evaluated until after pollination is completed and that four backcrosses will be used.

Season 1: F_1 seed is obtained by crossing the susceptible recurrent parent (RR) to the resistant nonrecurrent parent (rr). All of the F_1 seeds are Rr .

Season 2: F_1 plants are crossed to the recurrent parent (RR) to obtain BC_1F_1 seeds, of which an average of 50 percent are Rr and 50 percent are RR .

Season 3: The BC_1F_1 plants are self-pollinated, and seed from each is harvested separately.

Season 4: BC_1F_2 progeny from each BC_1F_1 plant are grown in a row, plants are self-pollinated, resistant plants (rr) are identified within segregating rows, and the seed from resistant BC_1F_2 plants is harvested.

Season 5: Progeny from the homozygous resistant (rr) BC_1F_2 plants are crossed to the recurrent parent (RR) to obtain BC_2F_1 seeds (Rr).

Season 6: The BC_2F_1 plants are crossed to the recurrent parent to obtain BC_3F_1 seeds, of which an average of 50 percent are Rr and 50 percent are RR .

Season 7: The BC_3F_1 plants are self-pollinated, and seed from each is harvested separately.

Season 8: BC_3F_2 progeny from each BC_3F_1 plant are grown in a row, plants are self-pollinated, resistant plants (rr) are identified within segregating rows, and the seed from resistant BC_3F_2 plants is harvested.

Season 9: Progeny from the homozygous resistant (rr) BC_3F_2 plants are crossed to the recurrent parent to obtain BC_4F_1 seeds (Rr).

Season 10: The BC_4F_1 plants are self-pollinated to obtain BC_4F_2 seed (25 percent RR , 50 percent Rr , and 25 percent rr on the average).

Season 11: BC₄F₂ plants are self-pollinated and the resistant ones are harvested individually.

Season 12 + : During season 12 and subsequent seasons, the resistant BC₄F₂ families are evaluated for important characters in comparison with the recurrent parent. The desirable ones are selected and bulked to replace the recurrent parent.

GENETIC CONSIDERATIONS

Selection of the Female Parent

The cytoplasm of plant cells is obtained from the female gametes. Therefore, the cytoplasm of lines derived by backcrossing will be determined by the plants used as females in the initial cross and subsequent backcrosses. This is particularly important when cytoplasmic-genetic male sterility is used for hybrid seed production. Male-fertile inbred lines with normal cytoplasm and nonrestorer genes (B lines) are converted to sterile cytoplasm (A lines) so they can be used as the male-sterile female parent in a cross. In such a backcrossing program, a male-sterile line with sterile cytoplasm and nonrestorer genes is used as the female parent for the initial cross. The hybrid plants from the initial cross and all subsequent backcrosses will be male-sterile because they have the sterile cytoplasm.

If recovery of the cytoplasm of the nonrecurrent parent is desirable, even though cytoplasmic male sterility is not involved, the nonrecurrent parent must be used as the female parent in the initial cross. In all subsequent backcrosses, the recurrent parent must be used as the male.

The cytoplasm of the recurrent parent can be obtained in lines derived from backcrossing by using the recurrent parent as the female in the initial cross or in any of the backcross generations.

Probability of Transferring the Desired Genes

The probability of recovering desired genes during backcrossing depends on the expected frequency of individuals possessing the genes and the number of individuals available. It is possible to calculate the number of seeds or plants needed to have a given probability of success in recovering the desired genes.

Sedcole (1977) provided four methods for calculating the total number of plants needed to obtain one or more that have the desired genes for a given probability of success. The methods varied in the accuracy of the estimates and the complexity of the calculation. Using the most precise and complex method, he developed a table that can be used to determine the number of plants needed for most situations that would be encountered in backcrossing (Table 28-1).

Table 28-1 Total Number of Plants Needed to Obtain Required Number with Desired Genes

p^*	q^\dagger	r (Number of Plants to Be Recovered)								
		1	2	3	4	5	6	8	10	15
0.95	$\frac{3}{4}$	3	5	6	8	9	11	14	17	25
	$\frac{1}{2}$	5	8	11	13	16	18	23	28	40
	$\frac{1}{3}$	8	13	17	21	25	29	37	44	62
	$\frac{1}{4}$	11	18	23	29	34	40	50	60	84
	$\frac{1}{8}$	23	37	49	60	71	82	103	123	172
	$\frac{1}{16}$	47	75	99	122	144	166	208	248	347
	$\frac{1}{32}$	95	150	200	246	291	334	418	500	697
	$\frac{1}{64}$	191	302	401	494	584	671	839	1002	1397
0.99	$\frac{3}{4}$	4	6	8	9	11	13	16	19	27
	$\frac{1}{2}$	7	11	14	17	19	22	27	33	45
	$\frac{1}{3}$	12	17	22	27	31	35	44	52	71
	$\frac{1}{4}$	17	24	31	37	43	49	60	70	96
	$\frac{1}{8}$	35	51	64	77	89	101	124	146	198
	$\frac{1}{16}$	72	104	132	158	182	206	252	296	402
	$\frac{1}{32}$	146	210	266	318	368	416	508	597	809
	$\frac{1}{64}$	293	423	535	640	739	835	1020	1198	1623

* p = probability of recovering r plants with the desired genes.

† q = frequency of plants with desired genes.

Source: Sedcole, 1977.

For situations not covered by Table 28-1, Sedcole (1977) indicated that a reasonably reliable method of calculating the number of plants needed can be obtained from the equation

$$n = \frac{[2(r - 0.5) + z^2(1 - q)] + z[z^2(1 - q)^2 + 4(1 - q)(r - 0.5)]^{\frac{1}{2}}}{2q}$$

where n = total number of plants necessary

r = required number of plants with desired genes

q = frequency of plants with desired genes

p = probability of recovering required number of plants with desired genes

z = value that is function of probability (p).

The value of z is 1.645 for $p = 0.95$ and 2.326 for $p = 0.99$. Sedcole provided the following example, which assumes that $r = 15$, $q = 1/64$, and $p = 0.95$, ($z = 1.645$).

$$n = \frac{\left[2(14.5) + 1.645^2 \left(\frac{63}{64} \right) \right] + 1.645 \left[1.645^2 \left(\frac{63}{64} \right)^2 + 4 \left(\frac{63}{64} \right) (14.5) \right]^{\frac{1}{2}}}{2(1/64)}$$

$$n = 1420$$

Germination percentage must be considered when determining the number of seeds needed to provide a certain number of plants. The equation is

$$\text{Number of seeds} = \frac{\text{number of plants needed}}{\text{germination percentage}}$$

For example, if 100 plants are required and the germination percentage is 80 percent, the calculation is

$$\text{Number of seeds} = \frac{100}{0.80} = 125$$

Calculations involved in backcrossing will be illustrated here by making the calculations associated with the transfer of a desired character (disease resistance) that is controlled by a single recessive allele.

Season 1: Crosses are made between the nonrecurrent (*rr*) and the recurrent (*RR*) parents. The number of F_1 seeds that should be obtained will depend on the number of hybrid plants required in season 2 for crossing to obtain the required number of BC_1F_1 seeds. We will assume that the BC_1F_1 seeds can be obtained on one F_1 plant and that the germination percentage for F_1 seeds is 80 percent. The minimum number of F_1 seeds that should be obtained is

$$\frac{1 \text{ } F_1 \text{ plant}}{0.80} = 2 \text{ } F_1 \text{ seeds}$$

Therefore, at least two F_1 seeds should be obtained in season 1.

Season 2: F_1 plants (*Rr*) are crossed to the recurrent parent (*RR*) to obtain BC_1F_1 seeds, of which an average of 50 percent are *Rr* and 50 percent are *RR*. How many BC_1F_1 seeds should be obtained? The answer is a function of (a) the number of heterozygous BC_1F_1 plants that are desired for crossing in season 3, (b) the probability of success required for obtaining the desired number of heterozygous BC_1F_1 plants, and (c) the germination percentage. We will assume that three heterozygous BC_1F_1 plants are desired and that the probability of success is 99 percent. When $p = 0.99$, $r = 3$, and $q = \text{frequency of } Rr \text{ individuals} = 1/2$, the number of BC_1F_1 plants that should be available in season 3 is 14 (Table 28-1). With a germination percentage of 80 percent, the number of BC_1F_1 seeds required is $14/0.80 = 18$ seeds.

Season 3: Each BC_1F_1 plant (*Rr* or *RR*) is crossed to the recurrent parent to obtain BC_2F_1 seeds. How many BC_2F_1 seeds should be obtained on each plant? The answer is a function of (a) the number of heterozygous BC_2F_1 plants that are desired for crossing in season 4, (b) the probability of success required, and (c) the germination percentage. We will assume that two heterozygous BC_2F_1 plants are desired from each heterozygous BC_1F_1 plant and that the probability of success is 95 percent. If a heterozygous BC_1F_1 plant (*Rr*) is crossed to the recurrent parent, the fre-

quency of heterozygous (Rr) BC_2F_1 seeds is $1/2$. When $p = 0.95$, $r = 2$, and $q = 1/2$, the number of BC_2F_1 plants required is eight. With a germination percentage of 80 percent, the number of BC_2F_1 seeds required from each BC_1F_1 plant is $8/0.80 = 10$ seeds.

Season 4: BC_1F_2 seeds are used to progeny test each BC_1F_1 plant. How many BC_1F_2 plants should be grown to evaluate adequately the genotype of each BC_1F_1 individual? Each heterozygous Rr plant will have progeny that segregate, on the average, $3/4$ susceptible (RR or Rr) and $1/4$ resistant (rr). The number of BC_1F_2 plants that should be grown will depend on the minimum number of resistant plants that must be found in the progeny and the probability of success. When $p = .99$, $r = 2$, and $q = 1/4$, the number of plants is 24. With a germination percentage of 80 percent, the number of BC_1F_2 seeds that should be planted for the progeny test is $24/0.80 = 30$.

The illustrations presented thus far have used characters controlled by a single gene. If two or more genes control a character, the number of plants required each backcross generation to transfer the desired genes successfully increases substantially. For example, assume that the desired character is controlled by dominant alleles at two loci. The initial cross between the nonrecurrent parent $AABB$ and the recurrent parent $aabb$ provides heterozygous F_1 plants $AaBb$. When the F_1 plants are crossed to the recurrent parent, how many BC_1F_1 plants must be obtained to be 99 percent sure that three plants have both dominant alleles? The frequency of AB gametes from the F_1 plants is $1/4$, which is the frequency of $AaBb$ plants expected in the BC_1F_1 . When $p = 0.99$, $q = 1/4$, and $r = 3$, the number of BC_1F_1 plants required is 31 (Table 28-1). In contrast, obtaining the same number of heterozygous BC_1F_1 individuals for a single gene would require only 14 plants.

Recovery of Genes from the Recurrent Parent

The objective of backcrossing is to recover the genes of the recurrent parent, except for the ones being transferred from the donor parent. The average rate of recovery depends on the amount of selection for characteristics of the recurrent parent that is practiced during backcrossing, and the effect of linkage.

In the absence of selection and linkage, the average percentage of genes from the recurrent parent increases each backcross by one-half of the percentage of germplasm of the nonrecurrent parent that was present in the previous backcross generation (Table 28-2). The general equation for average recovery of the recurrent parent is $1 - (1/2)^{n+1}$, where n is the number of backcrosses to the recurrent parent. For the initial cross, $n = 0$; for the first backcross, $n = 1$; and so forth.

The term average recovery is used because within each backcross generation there is a range among plants for the number of genes from the recurrent parent that they possess. This variation among plants is reflected by the frequency of

Table 28-2 Average Recovery of Genes from Recurrent Parent During Backcrossing

Generation	Percentage of Parentage	
	Recurrent	Nonrecurrent
F ₁	50	50
BC ₁ F ₁	75	25
BC ₂ F ₁	87.5	12.5
BC ₃ F ₁	93.75	6.25
BC ₄ F ₁	96.875	3.125
BC ₅ F ₁	98.4375	1.5625

individuals in each generation that are homozygous for the genes of the recurrent parent. The general equation used (Allard, 1960) is

$$\text{Proportion of homozygous individuals} = \left(\frac{2^m - 1}{2^m} \right)^n$$

where m is the number of backcrosses to the recurrent parent and n is the number of genes for which the recurrent and nonrecurrent parents had different alleles (number of heterozygous loci). For the initial cross, $m = 0$; for the first backcross, $m = 1$; and so forth.

If the nonrecurrent and recurrent parents have different alleles at 10 loci, only 0.1 percent of the BC₁F₁ plants, 6 percent of the BC₂F₁, and 26 percent of the BC₃F₁ will be homozygous for the 10 alleles of the recurrent parent (Table 28-3). The remainder of the plants will have varying frequencies of the 10 alleles; consequently, there can be considerable variation in the phenotype of plants, especially in the early generations. Selection of plants for backcrossing that resemble the recurrent parent can increase the rate of recovery of its genes. For that reason, it is useful to obtain more than the minimum number of plants needed to be certain the desired genes are present. For example, if the frequency of plants with the desired genes is $q = 1/2$ and the probability of success is $p = 0.95$, a minimum of five plants is needed to obtain the desired genes. If 40 backcross individuals are obtained, approximately 15 should have the desired genes. Se-

Table 28-3 Percentage of Individuals Homozygous for Alleles of Recurrent Parent in Different Backcross Generations

Number of Genes with Different Alleles	Backcross Generation					
	1	2	3	4	5	6
	----- % -----					
1	50	75	88	94	97	98
2	25	56	77	88	94	97
5	3	24	51	72	85	92
10	0.1	6	26	52	73	85

lection among the 15 plants for those most like the recurrent parent can hasten the recovery of genes from the recurrent parent.

Effect of Linkage on Recovery of Genes of the Recurrent Parent

The impact of linkage on recovery of genes of the recurrent parent was discussed in the original paper on backcrossing by Harlan and Pope (1922). They noted that backcrossing provides a good opportunity for crossing over to occur between the desired genes from the nonrecurrent parent and undesirable ones linked to them. Assume that resistance to disease (*R*) is linked to an undesirable gene (*d*) in the nonrecurrent parent and that the recurrent parent has the alleles *rD*. For recovering the desired *RD* gamete, a crossover between *Rd* is effective in the heterozygous genotype $\frac{Rd}{rD}$, but not in the homozygous individuals $\frac{Rd}{Rd}$ or $\frac{rD}{rD}$. In each backcross generation, *Rd* gametes from the backcross progeny are united with *rD* gametes from the recurrent parent to produce $\frac{Rd}{rD}$ individuals. In contrast, selfing in a population reduces the percentage of heterozygous individuals, thereby reducing the possibility of effective crossing over.

Allard (1960) indicated that the probability of eliminating an undesirable gene linked to the desired one could be expressed by the equation

$$1 - (1 - p)^{m+1}$$

where *p* is the recombination fraction between the linked genes and *m* is the number of backcrosses. For example, if the recombination fraction were 0.10, the probability of eliminating the undesirable gene without selection during five backcrosses would be

$$1 - (1 - 0.10)^{5+1} = 0.47$$

Table 28-4 Effect of Linkage on Probability of Eliminating Undesirable Gene (*b*) Linked to Desirable Gene (*A*)*

Recombination Fraction	Probability that Undesirable Gene Will Be Eliminated	
	With 5 Backcrosses	With Selfing
0.50	0.98	0.50
0.20	0.74	0.20
0.10	0.47	0.10
0.02	0.11	0.02
0.01	0.06	0.01
0.001	0.006	0.001

*It is assumed that selection is practiced for *A* but not for *b*.

Source: Allard, 1960.

The probability of eliminating an undesirable gene b linked to a desirable gene A by selfing and backcrossing when no selection is practiced is provided in Table 28-4.

Retaining the Heterogeneity of the Recurrent Parent

Inbred lines of self- and cross-pollinated crops generally have some genetic heterogeneity, even though it may not be readily visible. If it is considered important to retain the heterogeneity in the backcross-derived cultivar, a large number of plants from the recurrent parent should be used during the last backcross. The number that should be used is not fixed; however, 30 generally is considered a minimum.

Backcrossing for Quantitative Characters

The ease and success of backcrossing is influenced by (a) the number of genes controlling a character and (b) the role of the environment on expression of the genes. As the number of genes increases, the proportion of the desired genotypes decreases. As the proportion of a desired genotype decreases, the number of plants that must be grown to recover that genotype increases. This can be understood by examining Table 28-1 for different proportions of q . Therefore, one problem associated with backcrossing for quantitative characters is the large population size that must be used.

A second difficulty with backcrossing for quantitative characters is the influence of environment on expression of the desired genes. Success in backcrossing is dependent on the ability to identify the desirable genotypes in each generation. When the environment has a large influence on expression of the character, such identification can be difficult.

Success in the transfer of quantitative characters can be influenced by (a) selection of the recurrent parent, (b) self-pollination, and (c) progeny testing.

1. *Selection of the nonrecurrent parent:* It can be difficult, if not impossible, to completely transfer the desired character as found in the nonrecurrent parent. For that reason, it is helpful whenever possible to choose a nonrecurrent parent that is more extreme for a character than is desired in the backcross-derived lines. For example, assume that the objective is to make a cultivar 10 days earlier in maturity. If a nonrecurrent parent is chosen that reaches maturity only 10 days earlier than the recurrent parent, it may be possible to obtain lines that are 7 or 8 days earlier than the recurrent parent, but extremely difficult to achieve any that are 10 days earlier in maturity. The alternative is to use a nonrecurrent parent that is 20 days earlier in maturity. A breeder can lose half the earliness of the nonrecurrent parent and still reach the desired objective.

As for a qualitative character, the nonrecurrent parent should resemble the recurrent parent as much as possible for all characters except the one being transferred. This may reduce the number of backcross generations required to recover lines with the desirable characteristics of the recurrent parent.

2. *Self-pollination*: The genes controlling the desired character are heterozygous after each backcross, and BCF_1 plants differ by the number of the desired alleles from the nonrecurrent parent that they possess. Because the alleles from the recurrent parent are common to all plants, the variability among BCF_1 plants for the character of interest may be limited. Self-pollination of plants after each backcross increases the number of different genotypes by the formation of individuals homozygous for alleles. Selfed individuals with a high frequency of desired alleles, some in the homozygous condition, should be more readily detected than BCF_1 individuals that have only heterozygous loci. Each generation of self-pollination increases the formation of homozygous loci and the variability among individuals; therefore, selection may be practiced among F_2 plants or those in later generations.
3. *Progeny testing*: Selection on a single-plant basis can be relatively ineffective for characters that are strongly influenced by the environment. A replicated progeny test of selfed individuals can improve the reliability of information about the genetic potential of a single plant and increase the chance of using genotypes for backcrossing that have the highest frequency of the desired alleles. If plants are self-pollinated either manually or naturally during the progeny test, single-plant selection within superior lines can further enhance the selection of superior individuals for backcrossing.

General considerations in transferring a quantitative character are outlined here for an inbred line or cultivar. The goal of the backcrossing program in this example is to improve the protein content of the seed of an inbred line from the present level of 20 percent to the desired level of 25 percent. A nonrecurrent parent is chosen that has 30 percent protein and that resembles the recurrent parent as much as possible for other characteristics.

Season 1: F_1 seeds are obtained by crossing the nonrecurrent (30 percent protein) and recurrent (20 percent protein) parents.

Season 2: The F_1 plants are self-pollinated to obtain F_2 seeds.

Season 3: Plants of the F_2 generation and the recurrent and nonrecurrent parents are grown and harvested separately. Seed of each F_2 plant is evaluated for protein content, and its content is compared with the content of the recurrent and nonrecurrent parents. F_2 plants with the highest seed protein are retained for progeny testing in season 4 as $F_{2,3}$ lines.

Season 4: A replicated test is grown for the $F_{2,3}$ lines that were saved in season 3. The $F_{2,3}$ lines with the highest seed protein content are identified for use as parents in the first backcross during season 5.

Season 5: The F_2 -derived lines with high seed protein content are crossed to the recurrent parent to obtain BC_1F_1 seeds.

Season 6: The BC_1F_1 plants are self-pollinated to obtain BC_1F_2 seeds.

Season 7: Plants of the BC_1F_2 generation and the parents are grown and harvested separately. BC_1F_2 plants with the highest protein are identified for progeny testing in season 8 as $BC_1F_{2:3}$ lines.

Season 8: A replicated test is grown for the $BC_1F_{2:3}$ lines that were saved in season 7. The $BC_1F_{2:3}$ lines with the highest protein content are identified for use as parents in the second backcross during season 9.

Seasons 9–12: The second backcross is made and the progeny evaluated with the procedure used in seasons 5 to 8. All subsequent backcrosses are made and evaluated in the same manner.

After the desired number of backcrosses has been made, the progeny with high protein and the characteristics of the recurrent parent are tested for yield and other important characters.

Lines with the desired characteristics can be bulked and used as an improved version of the recurrent parent.

The procedure adopted for backcrossing a quantitative character will vary with the heritability of the character involved and the importance of time in completing the work.

1. If satisfactory evaluation of the character being transferred can be made on a single-plant basis, the season of replicated progeny testing can be eliminated. If single-plant evaluation is of limited value, replicated progeny tests will be the only method of identifying lines with the desired characteristics.
2. Selection on a single-plant basis within the progeny of F_2 plants may be helpful in identifying segregates that have a superior level of the character.
3. If time is an important consideration, backcrosses can be made on plants or lines during the season of their evaluation. Backcross seed would only be saved from those plants or lines that had the desired characteristic.

Number of Backcrosses

The number of backcrosses will depend on (a) the importance of recovering characteristics of the recurrent parent, (b) the amount of selection imposed during backcrossing, and (c) the similarity of the nonrecurrent parent to the recurrent one and (d) the extent of linkage between desirable and undesirable genes. There may be as few as one backcross or more than five.

There usually are at least four backcrosses when it is important that the recovered lines be essentially identical to the recurrent parent except for the characteristic being transferred. This is particularly true when the cultivar derived from backcrossing is given the same name as the recurrent parent, to which a number or letter has been added.

A relatively large number of backcrosses is required when the nonrecurrent parent is markedly inferior to the recurrent parent in one or more characters. Use of plant introductions or wild relatives of the cultivated species as nonrecurrent parents can introduce undesirable characters that require multiple backcrossing before their elimination. Selection can aid in rapid recovery of characteristics of the recurrent parents.

Only one or a few backcrosses are used when the new cultivar does not have to resemble the recurrent parent in all characteristics. Allard (1960) suggested that development of cultivars after only a few backcrosses should be called the backcross pedigree method, instead of backcrossing. He suggested that the term backcrossing be used only when the objective is to recover all of the features of the recurrent parent. The advantage of limited backcrossing is that the possibility exists for identifying segregates that are superior to the recurrent parent for characters other than the one being transferred. The potential for transgressive segregation decreases with each generation of backcrossing.

In transferring quantitative characters, it can be difficult to retain a high level of the desired character through multiple backcrosses. One possibility for reducing the number of backcrosses is to select in each backcross generation for the character being transferred, then evaluate the selected individuals in replicated tests for other important characters. Backcrossing can be discontinued whenever an individual with the desired characteristics is recovered, regardless of the number of backcrosses involved.

Transferring Multiple Characters

It can be desirable to improve a cultivar simultaneously for more than one character. An example is the development of a cultivar that has different genes for disease resistance, sometimes referred to as pyramiding. There are two options for transferring multiple characters: (a) transfer the genes simultaneously in one backcrossing program or (b) transfer the genes in independent backcrossing programs and combine them into one individual at the end.

The problem with transferring several genes simultaneously is the large number of backcross seed that must be obtained to be certain that a genotype with all the desired genes is present. To illustrate, assume that four independent genes for disease resistance, *FHJN*, are to be transferred simultaneously. If a heterozygous individual, *FfHhJjNn*, were backcrossed to the recurrent parent (*ffhhjjnn*), the frequency of an *FfHhJjNn* individual would be $(1/2)^4 = 1/16$. For a 99 percent probability that at least one heterozygous individual would be recovered, 72 backcross progeny would be required (Table 28-1). In contrast, if each gene was transferred independently, the frequency of recovering a heterozygous individual for one gene would be $1/2$. Seven backcross progeny would be required to be 99 percent certain of recovering the heterozygous individual, for a total of $7 \times 4 = 28$ backcross progeny for the four independent backcross programs.

Another potential problem with the simultaneous transfer of multiple char-

acters is the difficulty of evaluating one individual for more than one character at a time. When there are independent backcrossing programs for each character, individuals are only evaluated for one character at a time.

When characters are transferred in independent programs, the procedure for each character is one of those that have already been discussed. After the backcross-derived lines from the independent programs are available, their genes must be combined into a single individual. An example of a procedure to combine four dominant alleles in one individual follows.

Season 1: The following crosses are made: (a) $FFhhggnn \times ffHHggnn$ to obtain $FfHhggnn$ individuals and (b) $ffhhGGnn \times ffhhggNN$ to obtain $ffhhGgNn$ individuals.

Season 2: The F_1 plants from the crosses in season 1 are crossed, $FfHhggnn \times ffhhGgNn$. The frequency of $FfHhGgNn$ individuals would be $(1/2)^4 = 1/16$; therefore, 72 hybrid seeds would be required for 99 percent probability that at least one individual had the desired genotype.

Season 3: Each F_1 plant obtained in season 2 is evaluated for resistance to the four races, and selected $FfHhGgNn$ individuals are self-pollinated.

Season 4: F_2 progeny from self-pollinated $FfHhGgNn$ plants are evaluated and plants resistant to the four races are self-pollinated and harvested separately. The frequency of $F_H_G_N_$ plants among the F_2 progeny is $(3/4)^4 = 81/256 = 32\%$, and the frequency of $FFHHGGNN$ plants is $(1/4)^4 = 1/256 = 0.4\%$.

Season 5: F_3 progeny from selected F_2 plants are grown. Plants within each row are evaluated, and resistant plants are self-pollinated and harvested separately. The frequency of $FFHHGGNN$ F_3 plants has increased through self-pollination.

Season 6: F_4 progeny from selected F_3 plants are grown. Each line is evaluated to identify those homozygous for the four dominant alleles. Such lines are self-pollinated and harvested separately.

Season 7: The $F_{3.5}$ lines are evaluated for important agronomic characters, and self-pollinated seeds of the acceptable ones are bulked to form the backcross-derived line that will replace the recurrent parent.

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