11
Cabbage Breeding

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In the United States, cabbage is the most economically important member of the genus *Brassica* (Table 11.1). However, less cabbage is being consumed in recent years, principally because consumers now have a wider range of vegetables from which to choose.

Per capita consumption of cabbage in this country decreased from 23 lb in 1940 to around 11 lb in the mid-1970s. About 9 lb were eaten as fresh cabbage, primarily as coleslaw, and approximately 2 lb were consumed as sauerkraut (*41*).

From 1974 to 1978 the major fresh-market cabbage production states (based on aver-

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TABLE 11.1. Acreage, Yield Production, and Value of Cabbage Grown for Fresh Market and Processing in the United States[a]

Year	Harvested acres	Yield per acre (cwt)	Production (1000 cwt)	Value ($1000)
1920[b]	121,670	178	21,672	19,167
1930[b]	160,790	134	21,482	20,024
1940[b]	191,410	140	26,800	15,149
1950[b]	176,630	181	31,931	31,573
1960[b]	134,610	190	25,545	45,476
1970	107,930	220	23,744	81,973
1978	96,100	246	24,575	163,888

[a]After U.S. Department of Agriculture (*40*).
[b]After U.S. Department of Agriculture (*41*).

age harvested acres) were Texas, 17,920; Florida, 16,920; New York, 11,880; California, 8400; North Carolina, 7320; Wisconsin, 5280; New Jersey, 4360; Michigan, 4260; and Ohio, 3180 (see Table 11.2).

Processing cabbage (for sauerkraut) is primarily produced in New York, Wisconsin, and Ohio (*40*). Cabbage for coleslaw is produced in most parts of the country, but in the winter much of it comes from cabbage produced and stored in New York because it is whiter than winter-grown southern cabbage. It is also less juicy and therefore makes better coleslaw. Cabbage for fresh market is produced in norther states in the summer and in southern states in the winter. Texas and Florida are the major centers for winter production. Cabbage is also an important crop in the northern European countries, and in the USSR, Japan, China, and Australia. Cabbage breeding occurs to some extent in all these countries, but Holland and Japan are the major breeding centers.

ORIGIN AND GENERAL BOTANY

Historical evidence indicates that modern hard-head cabbage cultivars are descended from wild non-heading brassicas originating in the eastern Mediterranean and in Asia Minor. The ancient Greeks held these early forms of cabbage in high regard and believed that they

TABLE 11.2. Acreage (1974–1978) by Season and Production of States Producing over 3000 Acres of Cabbage Annually[a]

State	Harvest season				Total production (1000 cwt)
	Winter	Spring	Summer	Fall	
California	2640	2620	1480	1660	1907
Florida	9720	5480	—	1720	4167
Michigan	—	—	2480	1780	722
New Jersey	—	780	2300	1280	890
New York	—	—	3460	8420	4482
North Carolina	—	2100	3120	2100	1108
Ohio	—	440	1200	1540	950
Texas	8780	3560	—	5580	3887
Wisconsin	—	—	3040	2240	2009

[a]After U.S. Department of Agriculture (*40*).

were a gift from the gods. The Celts and, later, the Romans disseminated cabbage throughout Europe. In fact, the Latin name *Brassica* is derived from the Celtic word *bresic,* meaning cabbage. Over a period of centuries, hard-headed cabbage types evolved in northern Europe, while loose-heading, heat-resistant types developed further south (*38*).

Cabbage was first introduced into the Americas when the French explorer Jacques Cartier planted seed in Canada on his third voyage in 1541. Because cabbage was such a commonly grown vegetable throughout northern Europe, the earliest colonists brought seed to America, where the Indians also adopted the crop.

Most of the cultivars grown in the United States today are descended from types originally grown in Germany, Denmark, or the Low Countries. Round-headed types are older than flat or egg-shaped cultivars, which apparently did not evolve until as late as the seventeenth or eighteenth century (*38*). Because cabbage is easily stored for 2 or 3 months, it was an especially popular winter vegetable in the northern United States until well into the present century, when modern transportation and refrigeration made it possible to obtain other fresh vegetables the year around.

Cabbage, *Brassica oleracea* L. var. *capitata,* belongs to the Cruciferae or mustard family. Broccoli, cauliflower, Brussels sprouts, collards, kale, and kohlrabi are all readily intercrossed members of this species.

During the early growth and development of the cabbage plant, the first leaves expand and unfold, forming what is commonly referred to as the frame. Once the frame has been produced, the newly expanding leaves only partially unfold, forming the shell or outer skin of the head. Next, the growing point increases in size, while the core and stem enlarge in diameter and become a storage area for essential nutrients. Finally, the head is filled with a number of sessile fleshy leaves. Under favorable growing conditions, the inner leaves can exert sufficient pressure at maturity to cause the head to burst or crack open. Usually the crack occurs at the top or along one side of the head, but in the case of short-cored cultivars the split often occurs at the base of the head.

Taxonomy

Taxonomy of the *Brassica* is complicated. Figure 11.1 gives the interrelationship of the *Brassica* (*42*) genome designations and chromosome numbers. The following six *Brassica* species, plus *Raphanus sativus,* radish, $2n = 18$, have been intercrossed with difficulty (*17*), requiring embryo culture to obtain F_1 plants: *Brassica nigra* Koch, black mustard, $2n = 16$; *Brassica carinata* Braun, Ethiopian mustard, $2n = 34$; *Brassica juncea* L. Coss, brown mustard, $2n = 36$; *Brassica napus,* swedes, rape, rutabagas, $2n = 38$; *Brassica campestris,* turnip group and Chinese cabbage, $2n = 20$; *Brassica oleracea,* cole crops, $2n = 18$.

The usual objectives of interspecific crosses are to transfer disease resistance (*39*) or cytoplasmic male sterility (*17*). The amphidiploid species (Fig. 11.1) evidently originated in nature from crosses between the elementary species. In meiosis of the amphidiploids, pairing of homologous chromosome bivalents shows a secondary pairing, indicating lack of duplication of chromosomes in different species. In most cases *B. oleracea* has been successfully used only as the pollen parent.

Cytoplasm Terminology

Williams (*51*) has suggested use of the single capitalized letter representing the uncapitalized genome descriptor (Table 11.3) to designate the cytoplasm in which the

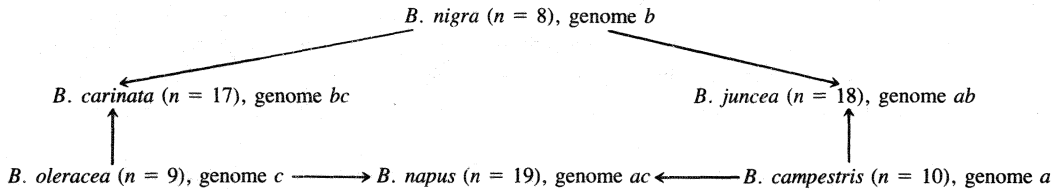

FIGURE 11.1. Relationships of *Brassica* taxa based on chromosome numbers. After U. N. (*39*).

nuclear genes are functioning. Thus, for example, the *B. oleracea* genome is *cc* and its cytoplasm is C. The *B. oleracea* genome in Ogura's radish cytoplasm is designated as R*cc*, *B. campestris* in radish cytoplasm is designated as R*aa*, and *B. juncea* genome in *B. campestris* cytoplasm is designated as A*ab*.

FLORAL BIOLOGY AND CONTROLLED POLLINATION

Flower Development

During differentiation of the flower, the successive development of four sepals, six stamens, two carpels, and four petals occurs. The carpels form a superior ovary with a "false" septum and two rows of campylotropous ovules. When the buds are about 5 mm long, the megaspore in each ovule divides twice, producing four cells, one of which becomes the embryo sac, while the other three abort. The nucellar tissue is largely displaced by the remaining embryo sac; and when the buds open, the ovules mainly consist of the two integuments and the ripe embryo sac.

The androecium is tetradynamous, i.e., there are two short and four long stamens. When the anthers are a few millimeters in length, the pollen mother cells, after meiosis, give rise to the tetrads. The pollen grains are 30–40 μm in diameter and have three germination pores.

TABLE 11.3. Designation of Cytoplasmic and Nuclear Genomes of Agriculturally Important *Brassica* and *Raphanus* Species (with ssp. or var. of *B. campestris*)[a]

Species	ssp. or var.	Cytoplasm	2*n* genome descriptor	Common name
B. nigra	—	B	*bb*	Black mustard
B. oleracea	—	C	*cc*	Cole crops
B. campestris	—	A	*aa*	—
	chinensis		*aa.c*	Pak-choi
	nipposinica		*aa.n*	—
	oleifera		*aa.o*	Turnip rape
	parachinensis		*aa.pa*	Choy sum
	pekinensis		*aa.p*	Chinese cabbage, petsai
	rapifera		*aa.r*	Turnip
	trilocularis		*aa.t*	Sarson
B. carinata	—	BC	*bbcc*	Ethiopian mustard
B. juncea	—	AB	*aabb*	Mustard
B. napus	—	AC	*aacc*	Fodder and oil rape, swede
R. sativus	—	R	*rr*	Radish, daikon

[a]After Williams and Heyn (*51*).

The buds open under pressure of the rapidly growing petals. Opening starts in the afternoon, and usually the flowers become fully expanded during the following morning. The bright-yellow petals become 15–25 mm long and about 10 mm wide. In contrast to those of some other *Brassica* species, the sepals are erect. The anthers open a few hours later, the flowers being slightly protogynous. The flowers are pollinated by insects, particularly bees, which collect pollen and nectar. Nectar is secreted by two nectaries situated between bases of the short stamens and the ovary. Situated outside the bases of each of the two pairs of long stamens is one additional nectary, but these two nectaries are not active (Fig. 11.2).

The flowers are borne in racemes on the main stem and its axillary branches. The inflorescence may attain a length of 1–2 m. The slender pedicels are 1.5–2 cm long (Fig. 11.3).

Seed Development

After fertilization the endosperm develops rapidly, while embryo growth does not start for some days. The embryo is generally still small 2 weeks after pollination. It fills most of the seed coat after 3–5 weeks, by which time the endosperm has been almost completely absorbed. Nutrient reserves for germination are stored in the cotyledons, which are folded together with the embryo radicle lying between them.

Fruit

The fruits of cole crops are glabrous siliques, 4–5 mm wide and sometimes over 10 cm long, with two rows of seeds lying along the edges of the replum (false septum, an outgrowth of the placenta). A silique contains 10–30 seeds. Three to four weeks after the opening of its flower the silique reaches its full length and diameter. When it is ripe, the two valves dehisce. Separation begins at the attached base and works toward the unattached end, leaving the seeds attached to the placentas. Physical force ultimately separates the seeds, usually by the pushing of the dehisced siliques against other plant parts by the wind or by threshing operations (Fig. 11.4).

Male Sterility

A number of recessive mutations monogenic (*5,9,11,24,34*) for male sterility have been reported, but it was not until Pearson (*28*) crossed *B. nigra* with broccoli that cytoplasmic

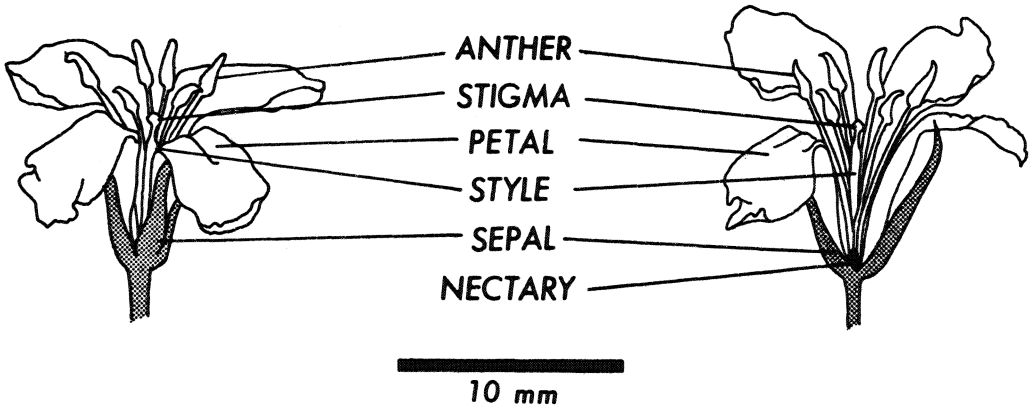

FIGURE 11.2. Floral parts of a cabbage flower.

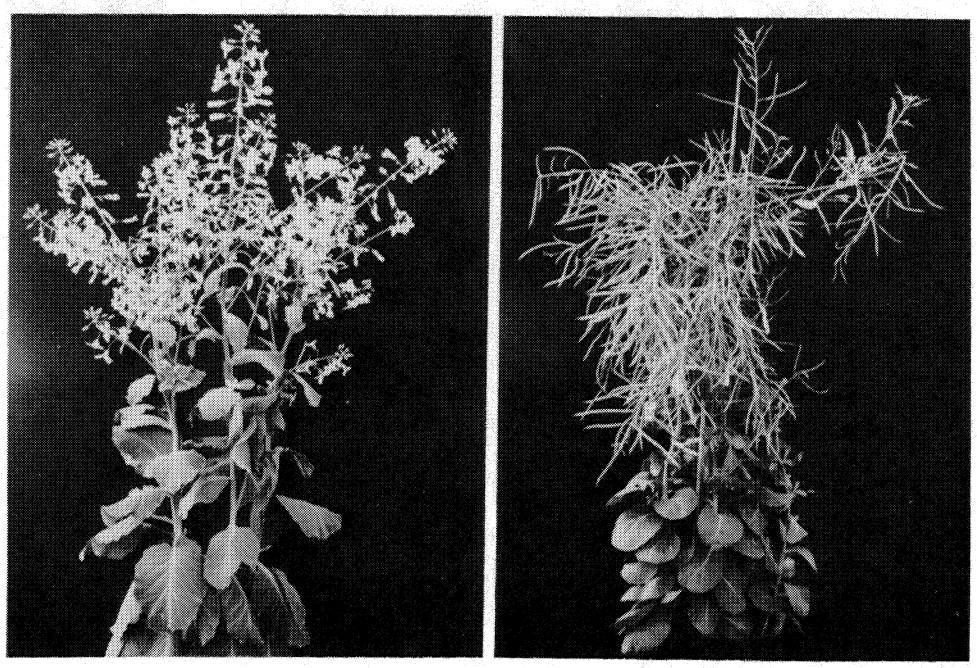

FIGURE 11.3. Cabbage plant in bloom (left) and with developed pods (right).

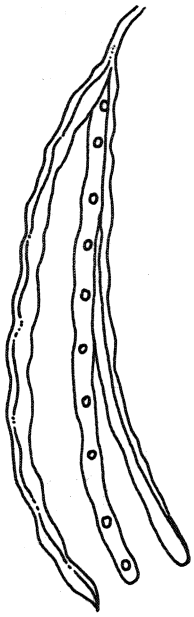

FIGURE 11.4. A dehisced silique showing seeds along the edges of the replum.

male sterility, designated N*ps/ps*, was obtained in *B. oleracea* and developed in cabbage. Unfortunately, this system was complicated by petaloidy and lack of development of the nectaries, giving a male sterile that was unattractive to bees. These problems were being solved through backcrossing and selection, when an easier-to-use cytoplasmic male sterility was obtained. This occurred when Bannerot (*4*) crossed a cytoplasmic male-sterile radish (R cytoplasm) from Ogura (*26*) with cabbage. In the BC_4 generation he obtained normal plants with $2n = 18$ that were totally male sterile, the flowers having only empty pollen grains or vestigial anthers. Male-sterile plants had the problem of pale or white cotyledons and also of pale-yellow leaves during plant development, accentuated at low temperatures. These problems are cytoplasmically inherited, and various attempts to overcome them are being made via cell fusion, with the hope of retaining the factor for sterility and eliminating the factor for pale leaves and low temperature sensitivity. If these attempts are not successful, it is doubtful that R cytoplasm-based male sterility can be used successfully, at least in the more temperate climates. In contrast to the cytoplasmic steriles produced with *B. nigra* cytoplasm, many cultivars of which had fertility-restoring genes, all the fertile *B. oleracea, B. campestris,* and *B. napus* genotypes tested on R cytoplasm have carried only *ms* genes. All brassicas apparently have no fertility-restoring genes for the R cytoplasm type of sterility and act as maintainers. Thus, any *B. oleracea* plant can be combined with R cytoplasm to produce a sterile plant. Restorer genes are present in radish. Obtaining a male-sterile version of an inbred line only requires converting any source plant with R cytoplasm to that inbred genotype by backcrossing. The inbred line will always be a B line (fertile maintainer) for the male sterile. The recurrent inbred parent must be selected for self-compatibility, or a closely selected OP line heterozygous for several *S* alleles can be used as a B line. Figure 11.5 shows flowers of an R-cytoplasmic male-sterile A line and its maintainer B line. Racemes of these plants are shown in Fig. 11.6. Petals of the male-sterile flowers are smaller than those of fertile flowers. Fortunately, nectaries are usually normal in male-sterile flowers with R cytoplasm, and bees usually work these sterile flowers.

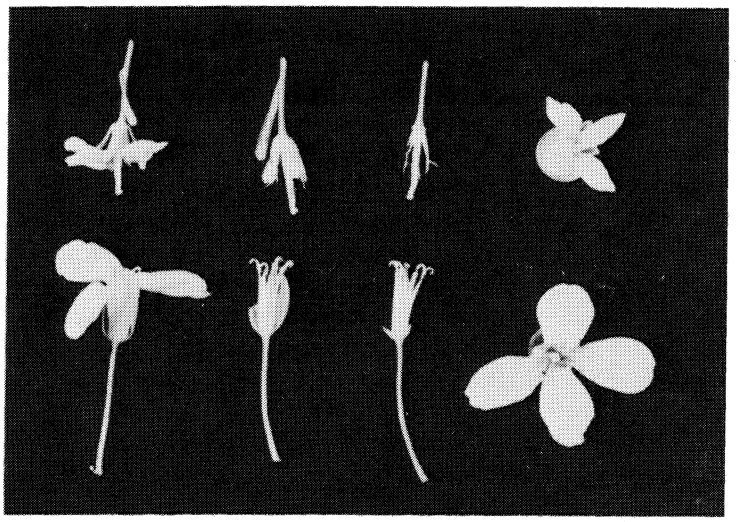

FIGURE 11.5. Male-fertile and -sterile flowers showing normal stamens (below) and vestigial stamens (above).

FIGURE 11.6. Racemes from a cytoplasmic male-sterile A line (left) and the fertile maintainer B line (right).

The R cytoplasm of the male-sterile radish has also been combined with *B. campestris* and *B. napus* to obtain cytoplasmic male sterility in these species.

Self-Incompatibility

Cabbage flowers must be cross-pollinated. Depending on the cultivar, a few to most plants are self-incompatible. Few seeds will be set following self-pollination. Pollination in the field must be by insects because the sticky pollen is not windblown. In the greenhouse or with proper protection in the field, the pollination can be done by hand. The pollen is viable and will achieve fertilization and seed set in most cross-pollinations, excluding that small percentage for which the incompatibility specificity of the plant functioning as female is the same as the incompatibility specificity of the pollen. Maximum seed set does not occur in self-pollinations, because there are identical incompatibility specificities in both the stigma (female) and pollen (male). When the male and female *S*-allele specificities are identical, self-incompatibility acts to prevent the pollen from germinating on and growing into the stigma or style. By this mechanism, self-incompatibility prevents self-fertilization. The self-incompatibility phenomenon also prevents fertilization in crosses between plants of identical genotypes, and in crosses between plants of near identical genotype when dominance or codominance conditions the identical expression of incompatibility specificities. No such barrier inhibits pollen germination and penetration on stigmas of plants of nonidentical *S*-allele genotype, which therefore have different incompatibility specificities.

Incompatibility Specificities

The incompatibility specificities of cabbage are controlled by one locus, called the *S* gene. About 50 alleles, S_1, S_2, S_3, . . . , S_{50}, each giving one specificity, have been identified. Thus, homozygous *S*-allele genotypes S_1S_1, S_2S_2, S_3S_3, etc., have incompatibility specificities of S_1, S_2, S_3, etc., for both their stigma (female) and pollen (male) reproductive organs. Most cabbage plants have heterozygous *S*-allele genotypes because of the cross-fertilization enforced by the self-incompatibility. The two *S*-alleles of heterozygous plants complicate the expression of incompatibility specificities. The incompatibility specificities for *S*-allele heterozygous cabbage plants are complicated because control of the pollen specificity is by the sporophyte, the whole (diploid) plant, rather than by the individual (haploid) pollen grain. These complications of the sporophytic control of incompatibility of pollen are more easily comprehended after understanding the simpler gametophytic control of pollen specificity. Therefore, the next section describes gametophytic incompatibility, as it occurs in *Petunia,* alfalfa, clovers, and many fruit trees (*22*). The subsequent section will return to the sporophytic incompatibility of cabbage.

Gametophytic Incompatibility

Self-incompatibility has gametophytic control when the haploid *S*-allele genotype of each pollen grain (male gamete) exactly indicates that gamete's expressed incompatibility specificity. For a heterozygous S_1S_2 plant, meiosis will give haploid male gametes of S_1 and S_2 genotypes in about a 1 : 1 proportion. Therefore, 50% of the pollen grains will have S_1 specificity and 50% will have S_2 specificity. Determination of whether the gametophytically controlled pollen grain will function compatibly or incompatibly in any given self- or cross-pollination requires an answer to only one question: Does the *S* allele (haploid genotype) conferring specificity on the pollen grain also occur in the female flower? If not, the pollination will be compatible; if so, whether the female plant is homozygous or heterozygous, the pollination will be incompatible. (These relationships for compatible and incompatible pollinations for gametophytic incompatibility are illustrated later in Table 11.5)

Sporophytic Incompatibility

For sporophytic incompatibility, we must ask: Does the *S* allele given to the pollen grain by meiosis also occur in the female flower of this pollination? However, this only gives a partial answer as to whether the pollination will be incompatible or compatible. If no, then the pollination will be compatible; if yes, the pollination may be compatible or incompatible, depending on answers to the following further questions that must be asked separately but jointly considered for the plant functioning as male and for the plant functioning as female:

1. Is the male plant homozygous for one or heterozygous for two *S* alleles? If heterozygous, which of the following four levels of interaction between the two *S* alleles characterizes the incompatibility specificity of the pollen: dominance, codominance, mutual weakening, or intermediate activity?
2. Is the female plant homozygous for one or heterozygous for two *S* alleles? If heterozygous, which of the following four levels of interaction between the two *S* alleles characterizes the incompatibility specificity of the female organ

TABLE 11.4. S-Allele Interactions in Heterozygous Genotypes with Sporophytic Incompatibility

Dominance	$S_1 < S_2$
Codominance	$S_1 = S_2$
Mutual weakening	No action by either allele
Intermediate gradations	0–100% activity by each allele

(stigma): dominance, codominance, mutual weakening, or intermediate activity (Table 11.4)?

Knowing in advance whether a pollination will be compatible or incompatible requires knowing whether either or both plants are homozygous, whether the two *S* alleles of a plant that is heterozygous interact with dominance, codominance, mutual weakening, or intermediate activities, and which of the alleles is dominant and which recessive (Table 11.4).

For a cabbage plant that is homozygous, only one *S* allele is designated for incompatibility specificity, but the intensity of expression may be weak, intermediate, or strong. When two plants that are homozygous are cross-pollinated, the question that must be asked is the same one as for the gametophytic system: Is the same *S* allele present in both plants? However, it is usually not known if either plant is homozygous. Therefore, determination of the incompatibility/compatibility of all cabbage pollinations—whether the plant is used as male or female, and whether one or both plants are homozygous—ultimately depends on asking all the questions that must be asked for all plants that are heterozygous for *S* alleles.

Assaying Self-incompatibility

The procedure first developed for quantifying self-incompatibility was to count the number of seeds that develop to maturity after each specific self- or cross-pollination. One disadvantage is the 60-day time duration between pollination and seed maturity. A second disadvantage is that subsequent to expressions of compatibility or of weak incompatibility, the numbers of seeds developing and ultimately reaching maturity may also be reduced by disease, water shortage, high temperature, or other stresses. Thus, seed counts at maturity often do not strictly reflect the intensity of expressed compatibility/incompatibility.

Ability of the fluorescent microscope to display readily those pollen tubes that have penetrated the style provides a direct measure of incompatibility that can be completed within 12–15 hr. However, it is adequate and more convenient in a large breeding program to pollinate on day 0. The pollinated flowers are then collected 16–30 hr later (day 1). On the same day, the excised ovaries are then softened in 60% NaOH and placed in aniline blue for staining. At about 48 hr (day 2) after pollination, the stigma and style are squashed on a microscope slide. The aniline blue stain accumulates in the pollen tubes and fluoresces when irradiated with ultraviolet light. Therefore, with appropriate light filters, under a fluorescent microscope, the tubes are visible, whereas the background of stylar tissues is largely unseen. Penetration of the style by none or a few tubes indicates incompatibility, penetration by many tubes indicates compatibility, and penetration by intermediate numbers indicates intermediate strength of the expressed incompatibility/compatibility (Figs. 11.7 and 11.8). In facilitating a breeding program, the

major advantage of the fluorescent microscope is availability of the incompatibility data and attendant conclusions within 2 days, as compared to the 60 days required for seed counts, or the 20–40 days if developing seeds are counted. With the assay completed and conclusions available within 48 hr, additional pollinations can be specifically planned to verify a conclusion, to test a seemingly erroneous conclusion, or to further other breeding objectives directly by accepting the conclusions. This early acceptance facilitates moving on to work with other populations, inbreds, or objectives. Using these procedures, the breeder has knowledge about the expressed incompatibility while sufficient flowers remain to maximize use of the conclusions. Seed set data provide this information only after most of the cabbage plants have finished flowering. With the use of the fluorescent microscope plus improved understanding of the sporophytic incompatibility system (*47*), homozygous *S*-allele genotypes can be identified in 1–3 weeks. This contrasts to the 3 years usually required when only seed set data have been used.

Identifying *S*-Allele Genotypes

Developing cabbage inbred lines that have all possible desirable horticultural and disease resistance characteristics, plus homozygosity for a single *S* allele, is an essential step in developing the inbreds to be used as parents in producing seed of hybrid cabbage cultivars. As a first step, plants from open-pollinated cultivars or hybrid populations should be individually selected for their disease resistance, head solidity, head size, short core, leaf color, and other desirable horticultural characteristics. This directed selection, when accompanied by the usual open- and cross-pollination, will most often result in random selection with respect to the *S* alleles present within the source population.

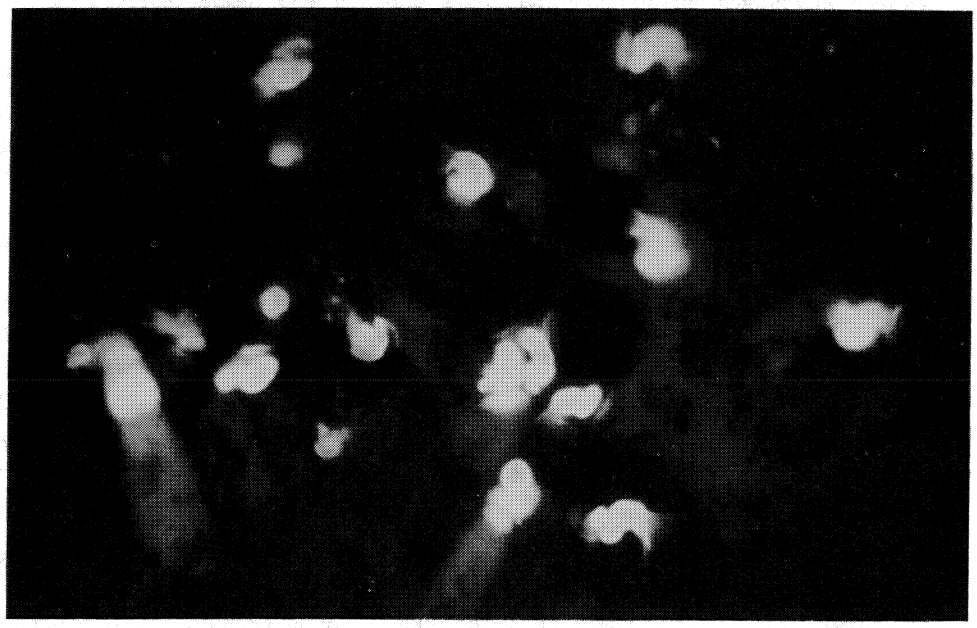

FIGURE 11.7. Fluorescent-microscope view of pollen grains with very short pollen tubes and strong fluorescence (callose formation) indicates incompatibility. The papillae are very faintly fluorescent and therefore barely visible. Nonfluorescing stigma tissues are not visible.

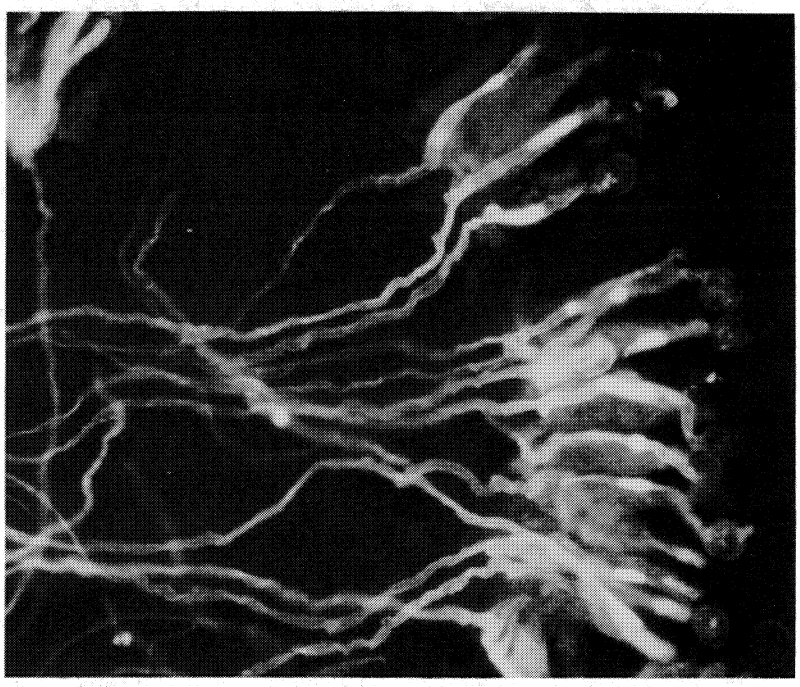

FIGURE 11.8. Fluorescent-microscope view of pollen grains on the papillae of a cabbage stigma, with very long pollen tubes extending beyond the papillae and downward into the style. The numerous long pollen tubes that fluoresce because they contain callose indicate compatibility. The papillae are faintly fluorescent, and nonfluorescing stigma and stylar tissues that are present are not visible.

Individual plants selected as described above will usually be heterozygous for two *S* alleles, S_1S_2, S_2S_{26}, or S_1S_{49}, for example. Each selected individual plant must next be selfed by bud pollination (self-pollination is discussed later in this chapter) for maintenance and seed increase. Simultaneously, open flowers on the plant should also be selfed. The resultant seed set or pollen tube penetration from the open flowers will be used to measure intensity of the self-incompatibility of the selected plant. If compatible or weakly compatible, all resultant seed for this plant may be discarded. For selfing, neither the buds nor flowers need be emasculated. Outcrosses with other flowers must be totally avoided since they would result in a false indication of compatibility for plants that are actually incompatible. Also, care should be taken to see that no outcrosses occur during the bud pollinations, because identification of *S*-allele genotypes is relatively easy and efficient in populations carrying precisely two *S* alleles that have segregated into all three possible genotypic combinations. Three or more *S* alleles in the population make the task nearly impossible. Therefore, the I_1 generation (first generation of inbreeding) from selfing an *S*-allele heterozygous plant is by far the most effective population for identifying *S*-allele genotypes. This population will contain the three genotypes, S_aS_a, S_aS_b, S_bS_b, for example, in a 1 : 2 : 1 ratio. There will be no other genotypes if no outcrossing is permitted. (This genotype labeling is used because it will not be known if either of the two possible alleles in the I_1 population represents S_1, S_2, S_3, . . . , or S_{50}. S_a and S_b are tentative assignments to be used until a specific numerical *S*-allele designation is assigned.)

A group of 11 plants from an I_1 population provides a 95% probability of having at least one plant of each of the three genotypes (two homozygous and one heterozygous). Identifying a plant of each of these three *S*-allele genotypes requires incompatible/compatible interpretations from a series of reciprocal pollinations between subsets of two of the 11 I_1 sibling plants. The next several paragraphs show, in fact, that the efficient procedure is to begin by reciprocally crossing a series of individual I_1 plants to each of two other individual I_1 plants. This procedure is continued until the three different (all possible) genotypes of three plants become simultaneously evident. Thus, the three possible genotypes will each be represented by one of the three I_1 plants. On the assumption that each I_1 plant is self-incompatible, i.e., that mutual weakening does not apply, the incompatible/compatible expectations for these reciprocal pollinations are presented in Table 11.5. The expectations come from knowledge that dominance or codominance occurs in the pollen and also in the stigma (the two sexual organs), giving four sexual organ × *S*-allele interactions, designated types I, II, III, IV, as summarized in Table 11.5. It is assumed that each *S*-allele heterozygote will belong to one of these four types. This assumption will usually be valid and the interpretation is then straightforward from Table 11.5.

When the above assumption is not valid, the heterozygote will be of a type intermediate to the extreme types I, II, III, IV. Such intermediate types will lack strong dominance or codominance in the heterozygote. Intermediate activities in the heterozygote by both *S* alleles constitute mutual weakening. This weakening in the *S*-allele heterozygote is specific for given pairs of *S* alleles. Such mutual weakening is indicated when many of the reciprocal crosses between I_1 plants give intermediate seed sets or penetrations of pollen grains into the stigmas that indicate neither definite incompatibility nor definite compatibility. Rather, *S*-allele action intermediate to these extremes is evidence. Also, repeats of the identical pairs of reciprocal crosses will sometimes indicate near incompatibility and sometimes near compatibility. Thus, the compatible/incompatible interpretations are more variable than usual.

Intermediate *S*-allele interactions with mutual weakening of both *S*-allele activities in the heterozygote do not permit rapid and efficient identification of *S*-allele genotypes of the individual I_1 plants. Also, one or both *S*-allele homozygotes is likely to have weak intensity of self-incompatibility. More seriously, the mutual weakening will prevent use of the two *S* alleles in a moderately uniform single-cross F_1 as is essential for producing the strongly desired three- and four-way hybrid cultivars. For these reasons, an I_1 population should be discarded after determining that the *S*-allele interaction in the heterozygote involves mutual weakening. The only merit that could justify keeping any plants from such I_1 populations is the presence of one or more rare but valuable characteristics.

For types II and III, but not for type I or IV, a reciprocal difference is expected from any reciprocal crosses between the recessive *S*-allele homozygous genotype S_aS_a and the heterozygous genotype S_aS_b (from Table 11.5). This reciprocal difference is expected because S_b is dominant to S_a (symbolized by $S_a < S_b$) in either the pollen or stigma for types II and III, but it is not dominant in both sexual organs (Table 11.5). Therefore, observation of a reciprocal difference between any two plants of an I_1 population immediately indicates either type II or III. It also indicates that one of the two I_1 plants is the genotype S_aS_a (recessive) while the other is the heterozygote S_aS_b (with $S_a < S_b$ in either pollen or stigma). The S_aS_a and S_aS_b genotypes cannot be positively assigned to either of the two I_1 plants, until or unless some more reciprocal crosses to these two plants have already been made. Information is essential relative to the incompatibility/compatibility

TABLE 11.5. Expected Incompatible/Compatible Interpretations and Reciprocal Difference Interpretations[a] from Reciprocal Intercrosses among Plants of the Two Homozygous and One Heterozygous *S*-Allele Genotypes for Sexual Organ × S-Allele Interaction, Types I, II, III, and IV

Type of interaction	*S*-allele interaction		Genotype and phenotype[b]	
	Stigma	Pollen	Female	Male
I	Dominance	Dominance	S_aS_a	S_aS_a Inc, $S_a < S_b$ Com, S_bS_b Com
			$S_a < S_b$	Com, Inc, Inc
			S_bS_b	Com, Inc, Inc
II	Codominance	Dominance	S_aS_a	S_aS_a Inc, S_aS_b Com, S_bS_b Com
			$S_a = S_b$	Inc, Inc, Inc
			S_bS_b	Com, Inc, Inc
III	Dominance	Codominance	S_aS_a	S_aS_a Inc, $S_a = S_b$ Inc, S_bS_b Com
			$S_a < S_b$	Com, Inc, Inc
			S_bS_b	Com, Inc, Inc
IV	Codominance	Codominance	S_aS_a	S_aS_a Inc, $S_a = S_b$ Inc, S_bS_b Com
			$S_a = S_b$	Inc, Inc, Inc
			S_bS_b	Com, Inc, Inc

[a]Reciprocal crosses with a reciprocal difference are indicated by dashed arrows and reciprocal crosses without a reciprocal difference by solid arrows.

[b]The *S*-allele phenotype of heterozygotes is indicated by the symbols < and = where < specifies recessive vs. dominant and = indicates codominance. These phenotypes correspond with the described *S*-allele interactions in stigma and pollen. The phenotype for homozygotes always corresponds with the genotype.

of additional reciprocal crosses between the one of these two I_1 plants that is S_aS_a and one of the additional sibling I_1 plants that is S_bS_b. The already achieved tentative assignment of either S_aS_a or S_aS_b (with $S_a < S_b$) makes these two I_1 plants more efficient than any other I_1 plants for continued use toward ultimate identification of the three genotypes. Their use will result in positive genotype assignments after the fewest additional reciprocal crosses. Use of both is required because it is not known which of the two is S_aS_a. Therefore, each of the two I_1 plants should continue to be reciprocally crossed once to each additional I_1 plant if sufficient reciprocal crosses have not already been made. When a pair of reciprocal crosses between either of these two I_1 plants and another I_1 plant gives reciprocal incompatibility, this information is not immediately useful in ascertaining the genotypes. This information will nevertheless be useful for assigning the genotype of the fourth, fifth, or eighth, etc., I_1 plant, after the genotypes of I_1 plants 1, 2, and 3 have been assigned as follows. The S_aS_a and S_aS_b genotypes can be positively assigned to the two I_1 plants giving the reciprocal difference as soon as one of the two (plant 1) is found to have reciprocal compatibility with a third I_1 plant (plant 3). Plant 1 is S_aS_a since it was both

reciprocally compatible with plant 3 (which must therefore be the homozygous dominant S_bS_b), and since it also had a reciprocal difference in crosses with plant 2. Plant 2 therefore must be the heterozygote S_aS_b (with $S_a < S_b$). It is type II if S_aS_b was the female parent in the incompatible cross and the male in the reciprocal but compatible cross (from Table 11.5). It is type III if S_aS_b was the male parent in the incompatible cross and the female in the reciprocal but compatible cross.

With all three of the possible genotypes now identified, the plant with S_aS_a genotype becomes the most efficient for identifying the genotype of all the additional plants. This known genotype S_aS_a will be reciprocally incompatible with an unknown S_aS_a; it will be reciprocally different with an unknown S_aS_b; and it will be reciprocally compatible with a plant of unknown genotype S_bS_b.

With type I there is a dominance for one of the two alleles of the heterozygote in both the pollen and stigma (Table 11.5). Type I, therefore, is indicated when a first I_1 plant is reciprocally compatible with one of a second and third I_1 plant that are reciprocally compatible with each other, while this first I_1 plant is on the contrary reciprocally incompatible with the other of the second and third reciprocally compatible I_1 plants (from Table 11.5). One of the second and third reciprocally compatible I_1 plants is the homozygous recessive genotype (S_aS_a). The second plant is either the heterozyous ($S_a < S_b$) or homozygous dominant (S_bS_b) genotype. The third plant is also either the heterozygous ($S_a < S_b$) or homozygous dominant (S_bS_b) genotype. Within the I_1 generation, there is no way of further differentiating among these three genotypes. In the I_2 generation all plants from the homozygous recessive and from the homozygous dominant I_1 genotype will breed true. Each I_2 family from each such I_1 plant will have the same *S*-allele specificity. Each such I_2 population will be reciprocally cross incompatible with all the plants of other populations of its own homozygous *S*-allele genotype, and will be reciprocally cross compatible with all plants of the other true-breeding homozygous *S*-allele genotype. In the I_2 generation any populations from an I_1 plant of heterozygous *S*-allele genotype will segregate and behave like the I_1 generation. The true-breeding dominant homozygous I_2 plants will be identified by their incompatibility with about three-fourths (the heterozygous $S_a < S_b$ plus homozygous dominant S_bS_b genotypes) of the plants of any I_2 populations that are segregating, and by simultaneous compatibility with the remaining smaller fraction (about 25%) of the plants of the segregating I_2 (the S_aS_a recessive genotypes). Simultaneously, the *recessive* homozygous true-breeding I_2 populations will be indicated by compatibility with the same larger part of the I_2 populations that are segregating and by incompatibility with the same smaller fraction of the plants.

In the procedures above for types II and III, no immediate use was possible for expression of reciprocal incompatibility between two I_1 plants. After one plant with each of the three I_1 genotypes has been identified, knowledge about incompatibility between a plant of known *S*-allele identity and other I_1 plants of unknown *S*-allele genotype will either identify, help to identify the unknown genotype, or will verify an already determined genotype. Therefore, all information about incompatibility between the I_1 sibs should be saved. These same relationships apply fully for type I and partially for type IV. Therefore, for all four types, it is expressed compatibility for one or both of the pair of reciprocal crosses between two I_1 plants that is the first information required in order to identify the *S*-allele genotype of any and then all I_1 plants.

The procedure described above assumed a reciprocal difference was observed for at least one of the first pairs of reciprocal crosses made between the I_1 sibling plants. That is,

it accepted that compatibility (or incompatibility) was observed when a first I_1 plant was crossed as female parent to a second as male, but that the reverse (incompatibility or compatibility) resulted from the reciprocal cross for which the second plant was female while the first was male.

The reciprocal difference between two I_1 plants was the first of two compatibility relationships that each by itself indicated the same thing, as follows: One of the two reciprocally crossed I_1 plants must be the homozygous recessive genotype, while the second plant must have the dominant *S*-allele phenotype. Expression of dominant phenotype indicates the genotype to be either heterozygous $S_a < S_b$ or homozygous S_bS_b, but does not differentiate. The reciprocal difference simultaneously indicated the type to be II or III (Table 11.5), which only occurs for the crosses between the homozygous recessive genotype and a heterozygous genotype with the dominant S_b phenotype expressed by either male (type II) or female (type III), while simultaneously expressing both S_a and S_b (codominance) in the other sexual organ. Therefore, simultaneously, a reciprocal difference indicates three facts: (1) one of the I_1 plants is S_aS_a; (2) the second I_1 plant with its dominant *S*-allele phenotype is genotype $S_a < S_b$; (3) the second plant is not S_bS_b.

Reciprocal compatibility is the second and only other possible compatible relationship between two I_1 plants. By itself reciprocal compatibility also demonstrates, like reciprocal difference, that one of the two reciprocally crossed I_1 plants must be the recessive genotype S_aS_a, but cannot indicate which plant carries which of the two genotypes, and also leaves unresolved the alternative of heterozygote vs. homozygote for the plant with the dominant phenotype. The second I_1 plant, however, must have the phenotype of the dominant allele, but may be either the heterozygote $S_a < S_b$ (for type I) or the homozygote S_bS_b (for any of types I, II, III, or IV).

Neither a reciprocal difference nor reciprocal compatibility can by itself specify which of the two I_1 plants is the homozygous recessive genotype, and which is the I_1 plant with the dominant *S* allele(s) and consequent dominant phenotype. This differentiation is achieved as both of these two compatibility results have identified the same I_1 plant as being either the recessive S_aS_a or one of the two genotypes with dominant phenotype. By expressing reciprocal compatibility with one or more of its I_1 sibs and reciprocal difference with one or more other I_1 sibs, a plant is identified as the homozygous recessive genotype, since only the recessive S_aS_a can express both and only for types II and III. Since the reciprocal difference identifies the second involved I_1 plant as the $S_a < S_b$ genotype, and the reciprocal compatibility identifies the third involved I_1 plant as the homozygous S_bS_b genotype, differentiation is simultaneously achieved between all three genotypes: S_aS_a, S_aS_b, and S_bS_b.

The procedure described above for types II and III assumed that a reciprocal difference was observed prior to observing reciprocal compatibility. Purposely, thereafter, to efficiently identify that one of the two I_1 plants that was truly the recessive genotype, both of these two plants were reciprocally crossed to a third, fourth, etc., I_1 plant until reciprocal compatibility was found. If reciprocal compatibility is observed prior to finding a reciprocal difference, which must always occur for types I and IV because they cannot have a reciprocal difference, then the efficient second step toward identifying the genotypes of all I_1 plants is to cross the two reciprocally compatible plants with a third, fourth, etc., I_1 plant in search of a reciprocal difference (for types II and III), or to find a third I_1 plant that is reciprocally incompatible with both of the two reciprocally compatible I_1 plants (for type IV). The order in which reciprocal compatibility and then reciprocal difference is

found is of no consequence; the essential ordering is to find expression of both by the same I_1 plant. Type I presents an additional problem because dominance of allele S_b over S_a in both stigma and pollen makes it impossible to differentiate between S_aS_b and S_bS_b except by a test to detect either segregation or homozygosity of progeny.

A reciprocal difference will occur for ⅛ of the pairs of reciprocal crosses among the sibling I_1 plants if, but only if, the type is II or III (Table 11.5). The ⅛ probability arises from the I_1 generation ratios of ¼ S_aS_a × ½ genotype S_aS_b = ⅛ probability from each pair of reciprocal crosses for a reciprocal difference. For each of types I, II, III and IV a reciprocally compatible result will occur for 1/16 of the crosses between two I_1 plants, from the ratios ¼ S_aS_a × ¼ S_bS_b. For type I, reciprocal crosses will occur with an additional frequency of ⅛, to give a total probability of 3/16, because the homozygous recessive ¼ of the plants of genotype S_aS_a will also be reciprocally compatible with the ½ of the I_1 plants that are the heterozygous genotype $S_a < S_b$. Another factor that influences the proportion of crosses between the I_1 plants that will give a reciprocal difference is that about half of the sexual organ × S-allele interactions are usually type II or III, leaving about ¼ for each of types I and IV.

Type IV has codominance in both pollen and stigma of the heterozygous S-allele genotype (from Table 11.5). Thus, the heterozygote has strong activity by both alleles in both its pollen and its stigma. Type IV is therefore indicated when an I_1 plant is reciprocally incompatible with both of two I_1 plants that are reciprocally compatible with each other. The I_1 plant that is reciprocally incompatible with both reciprocally compatible plants is the heterozygous genotype. The two reciprocally compatible I_1 plants must be one plant of each of the two homozygous genotypes. These two plants can be arbitrarily assigned tentative S_aS_a and S_bS_b identities, because the alleles are codominant and there is no recessive versus dominance S-allele interaction. That is, both alleles are simultaneously expressed with nearly equal intensity in the heterozygote. With the same criteria, the genotypes of all of the other I_1 plants can now be designated after each plant of unknown genotype has been reciprocally pollinated to two of the three known I_1 genotypes.

Permanent S-Allele Identities

Most permanent S-allele identities (S_1, S_2, . . . , S_{50}) are assigned by the breeder, but the National Vegetable Research Station at Wellesbourne, England, has a collection of all known S alleleles, which constitutes the internationally accepted nomenclature.

A homozygous plant of tentative S_aS_a or S_bS_b genotype will be known to represent the breeder's S_3S_3 genotype when S_aS_a or S_bS_b is demonstrated to be reciprocally incompatible with the breeder's inbred of S_3 genotype. Similarly, it will be $S_{26}S_{26}$ of the international allele nomenclature when it is reciprocally incompatible with plants of known international S-allele genotype S_{26}. The S_aS_a and S_bS_b will be compatible with all plants having other S-allele genotypes.

Unknown alleles in plants of heterozygous S-allele genotype can usually be specifically identified by partial incompatibility with reciprocal crosses with the corresponding homozygous S-allele genotype. Thus, with dominance the S-allele activity will be strongly expressed only in the stigma (type IV from Table 11.5) or only in the pollen (type II) or strongly expressed in both (type I). Both alleles will be strongly expressed in both the stigma and pollen for type IV. Alternatively, with recessiveness the allele will be weakly expressed in the pollen but strongly in the stigma (type III), or weakly in the stigma but

strongly in the pollen (type II), or weakly expressed in both stigma and pollen (type I). Because of these complexities, assignment of permanent *S*-allele designations is most easily done using plants known to be homozygous S_aS_a or homozygous S_bS_b.

Production of Hybrid Cultivars

The self-incompatibility character is used to enforce the cross-fertilization required in producing hybrid seed of cabbage, cauliflower, broccoli, Brussels sprouts, and kale. Sibling plants of inbred lines that have been selected for homozygosity of an *S* allele followed by selection for strong expression by this *S* allele of self-incompatibility will not cross-fertilize each other. As a result there will be little selfed (inbred) seed. On the other hand, such an inbred S_1S_1 when planted in rows alternating with another inbred S_2S_2 in every other or every second or third row, or with both inbreds in alternating blocks of three or four rows, will be readily cross-fertilized. The fertilization will be by pollen carried from one inbred to the other by pollinating insects (mostly bees). These insects must readily visit the flowers of both entries if high seed production is to be obtained. The cross-compatibility between inbreds S_1S_1 and S_2S_2 assures the production of F_1 hybrid seed. If both inbreds are incompatible, the seed produced on the S_1S_1 and S_2S_2 inbreds will be identical except for possible maternally conditioned and/or inherited characteristics. Thus, commercial seed of the same F_1 hybrid can be harvested from both inbreds. The inbred A (S_1S_1) × inbred B (S_2S_2) cross and its reciprocal will constitute a standard A × B single-cross F_1 cultivar.

To date, most of the cabbage hybrids produced in the United States are topcrosses. United States breeders have not fully advanced to single crosses. For topcrosses an open-pollinated cultivar with good horticultural characteristics is used as the pollen parent. It is used to pollinate a single self-incompatible inbred line that is the female parent. Topcross hybrids are numerous because U.S. seedsmen have not until recently had full understanding of efficient procedures for identifying *S*-allele genotypes (*47*). Japanese *Brassica* breeders, and a few U.S. and European seedsmen, have advanced beyond single-cross F_1s to three- and four-way crosses. For three- and four-way hybrid cultivars, a single-cross F_1 such as A × B derived above is used as the seed parent. The heterosis of this F_1 as seed parent compared to the vigor of an inbred used as the female parent gives increased seed yield. A three-way cross may use an inbred line as a pollen parent only; or if it is self-incompatible, the inbred may simultaneously be used as a seed parent. Also, an open-pollinated line may be used as the pollen parent, thus giving a three-way topcross hybrid cultivar.

When the third line is an incompatible inbred, seed can be harvested from all the plants. When a highly self-incompatible single-cross C × D is used in conjunction with A × B, the resultant four-way hybrid seed can also be harvested from every plant in the field. This plus the larger seed production per plant due to the hybrid vigor of both single-cross seed parents (which are both also pollen parents) will give the lowest production cost for the hybrid seed.

Successful seed production of hybrids requires much effort to select not only for horticultural characteristics but also for horticultural combining ability and for simultaneous flowering of the parents. Many excellent potential hybrids have not been successfully produced because the intended parents did not nick with respect to flowering time. Two inbreds developed from the same I_1 population, but selected for homozygosity for the opposite *S* alleles present, are often used as the two inbred parents of a single-cross F_1.

Their common origin combined with the selection for common horticultural characteristics (except for different *S* alleles) minimizes the genetic variability that the single-cross F_1 will introduce into the three- or four-way F_1 hybrid cultivar. Uniformity in all respects, and especially for time of harvest, is the major advantage of hybrid cultivars. Much selection and effort is required to achieve this and attendant goals.

Because uniformity is highly important, it may be beneficial to select and self the *S*-allele heterozygotes through the I_1 and then identify the *S*-allele genotypes in the I_2 generation. If the S_aS_a and S_bS_b counterparts are selected after two generations of selfing, they should give an S_aS_b single cross that will produce three- and four-way hybrids that are more uniform for desired horticultural characteristics. A disadvantage of two and especially more generations of selfing prior to selecting the S_aS_a and S_bS_b counterparts is that hybrid vigor of the S_aS_b single cross may be reduced.

The use of male sterility in hybrid seed production is expected to increase rapidly. The same requirements for successful seed production expected of inbreds using incompatibility will be required of the male-sterile inbred. Likewise, a three-way cross can be made using male sterility just as with incompatibility. In addition, the three-way cross using male sterility may be easier and more seed productive, since the F_1 hybrid is likely to be heterozygous for incompatibility factors, resulting in less problems from incompatibility when the third parent line is crossed with the F_1 hybrid.

Pollination by Hand

Self-Pollination

Self-pollination of cabbage can be obtained by brushing or shaking the open flowers if the plant is self-compatible. If the plant is self-incompatible, the buds can be opened 1–4 days before they will open naturally and be bud pollinated. As illustrated in Fig. 11.9, the largest unopen bud is probably too old for successful bud pollination as the incompatibility factor will be biosynthesized by that stage. A younger bud 3–4 days prior to natural flower opening will have the least self-incompatibility and still be large enough for bud pollination. Thus six to eight buds can be opened at one time with a pointed object such as a toothpick or forceps, and pollen from an older open flower can be transferred to the stigma and seed obtained. Pollen can be transferred with a brush or onto a thumbnail. Also, a fertile flower in full bloom is often used by brushing the anthers across the stigmatic surface to transfer the pollen. Williams (*49*) has suggested the use of bee sticks, using the hairy abdomen of bees mounted on a toothpick as pollen carrier.

Cross-Pollination

When the pollination is for a breeding objective such that self-incompatibility is not being considered, the bud should be emasculated using buds expected to open in 1 or 2 days if elimination of selfing is essential. The desire pollen is then transferred to the stigma in the same manner as for bud pollination. If a male-sterile or self-incompatible plant is used as a female parent, then an open flower with protruding pistil can be used to avoid the time and effort required to open the flower bud. However, only certain lines have these protruding pistils. When the cross-incompatibility between two plants is being assayed, the open flowers need not be emasculated. Cross-pollinating without emasculation also saves considerable time and labor and permits estimations of the porportion of cross-fertilization (hybrid) and selfed (inbred) seeds of the F_1 plants of that inbred.

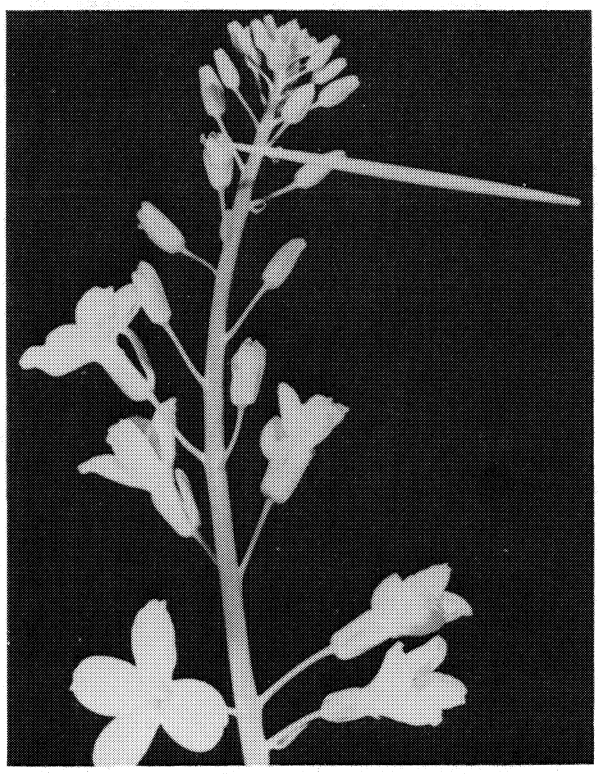

FIGURE 11.9. Raceme showing flower buds at stage for bud pollination and toothpick used to open bud and transfer pollen.

Seed Increases

Hand pollination can best be performed in the greenhouse or in a large screened cage to eliminate insects. If crosses or self-pollination are desired in the field, cheesecloth bags can be used to enclose the blossom of one or two plants. More preferable is enclosure of several plants in a screen cage 6 ft high for a small increase. Bees are the best pollinators and are supplied to facilitate cross-pollination in a cage. If large-scale, outdoor increases are to be made, the minimum isolation distance between lots should be 400 yards. More isolation is needed if one lot is downwind from another. Asexual plant propagation can be obtained by cutting off the head and allowing the lateral buds to develop. The buds can be excised, rooted on a moist medium, vernalized, and allowed to flower in small 2- to 4-in. pots (Figs. 11.10 and 11.11). Buds from stored cabbage heads that have been previously cut from their supporting stems can be similarly excised, rooted, vernalized, and allowed to grow, bloom, and be pollinated.

MAJOR BREEDING ACHIEVEMENTS OF THE RECENT PAST

Two achievements stand out above all others in terms of the genetic improvement of cabbage cultivars. All important U.S. cultivars now have fusarium yellows resistance and most are hybrids. Many imported hybrids do not have yellows resistance but otherwise

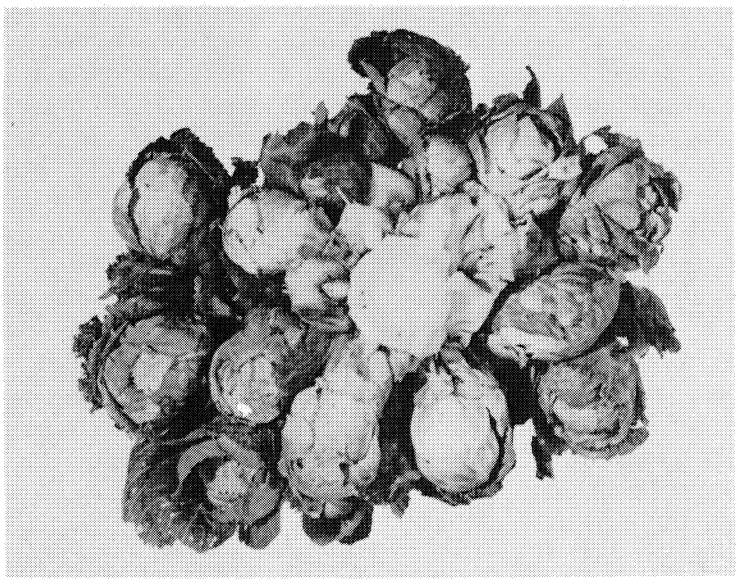

FIGURE 11.10. Cabbage stump with large buds ready for removal and rooting.

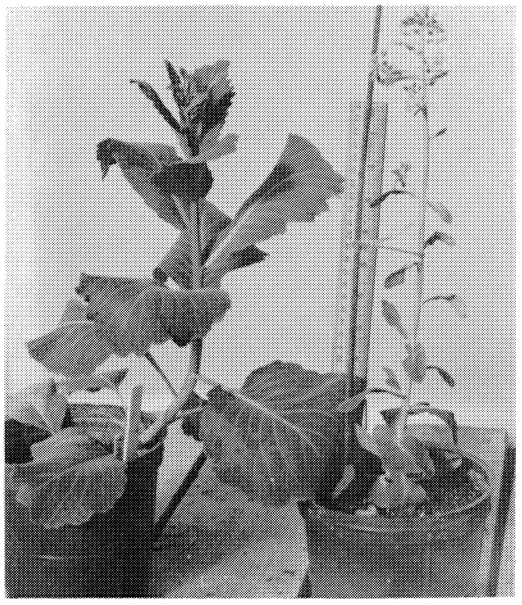

FIGURE 11.11. Small plants from rooted and vernalized buds.

may be well adapted. The second achievement that has required major efforts at the basic and applied levels is the development of hybrids utilizing self-incompatibility. In 1960 essentially all cabbage cultivars were open-pollinated. By 1980 most were hybrid except for some old cultivars that still perform well in special locations.

Old cultivars were of varied shapes from pointed to flat and many had large frames. New cultivars are all essentially round and have small compact frames, allowing more plants per acre. The heads have become more solid and in some cases more resistant to splitting.

Thirty years ago bolting was a problem, but it is rarely so now. Twenty years ago the cultivars used for processing had large heads, but the heads were loose, the frames very large, and the dry matter low. The new cultivars have compact frames and solid heads, and are adapted to machine harvest. The heads can withstand being rolled or can be dropped without shattering. Tolerance to virus, mildew, and clubroot has been incorporated in some hybrids.

Twenty years ago cabbage was harvested by hand. Now almost all cabbage for processing as kraut or for immediate use in coleslaw is machine harvested. The harvester loads the crop directly into a truck. (At present all harvesters are made by Castle Harvester of Seneca Castle, New York.)

Recent advances in storage techniques, using refrigerated or even controlled-atmosphere (CA) storage, and improvement in cultivars have resulted in the ability to store cabbage for up to 6 months. This contrasts with a previous maximum of 2 to 3 months common storage. Common storage functions by inserting cool air into the storage during nights and colder days and by preventing entry of the warmer daytime air. The stored product, principally from New York, is excellent for coleslaw and is shipped around the United States for this purpose.

CURRENT GOALS OF BREEDING PROGRAMS

The incorporation of multiple-disease resistance [especially black rot and turnip mosaic virus (TuMV) resistance], insect resistance (especially lepidopterous worm and root maggot), and tipburn resistance is a major current breeding objective. To combine these characters in hybrid cultivars suitable for production of fresh-market, processing, and storage cabbage is the broad aim of almost all breeding programs. Selecting for incompatibility or incorporating male sterility is an additional major concern of broad programs because one of the two systems is essential for the now required hybrid seed production for new cultivars. The commercial cabbage seed market demands that all new cultivars be hybrids.

Black-rot-resistant hybrids and hybrids using cytoplasmic male sterility are just starting to appear on the market or for extensive trial. Some researchers and commercial breeders anticipate a rapid increase in the use of male sterility in new hybrids because the system is simpler to develop and less influenced by the environment than the incompatibility system. Whether or not this occurs depends to a large extent upon the ease with which compatibility can be incorporated in the most desirable parental lines.

In special areas such as New York, there is interest in developing better quality in cultivars that are adapted to long-term storage in refrigerated or CA storage. Selected late-maturing lines are harvested in late October or early November and placed in storage. They are evaluated two or three times during the winter for keeping ability. Heads will exhibit storage breakdown due to TuMV or bacterial speck if they are susceptible and

infected with these diseases. This is a major problem in commercial storages. The heads will also be assayed for color and leaf retention.

For sauerkraut production, the following selection criteria are important: high yield, good solidity, small ribs, white internal head color, high-percentage dry matter, ease of removal of outer wrapper leaves, short core length (25% or less of head diameter), core not excessively tough and woody, and cracking resistance both in the field and following mechanical harvest. All selections are evaluated for these characteristics and final selections are made on the basis of recorded data.

For the Texas winter fresh market, plants that are resistant to bolting are essential because the long, cool growing season with widely fluctuating temperatures can result in premature bolting. Cultivars adapted to summer production in the North are usually not suitable. For fresh market, heads with dark-green, well-developed wrapper leaves are essential.

SELECTION TECHNIQUES FOR SPECIFIC CHARACTERS

Cabbage Head Shape

Cabbage head shape has changed from pointed, flat, or round to almost exclusively round heads within the past 20 years. Pointed head is dominant to round. However, it is generally agreed that many genetic factors determine head shape. Selection is made by cutting the head vertically through the core, allowing selection for head shape, internal solidity, leaf configuration, and core size and length. The cut core will heal and flower stalks will arise from leaf axials of the upper stem just below the head.

Heading vs. Non-heading

The distinguishing character of cabbage is the development of several wrapper leaves surrounding the terminal bud. These are tight enough to form a head or heart. It is generally agreed that heading is recessive to non-heading. The F_1 between a non-heading type and a heading cabbage will be intermediate. Depending how wide the cross, two genes (*n*1 and *n*2) or more are involved in heading (*29*). Likewise the loose head of a savoy cabbage is recessive to the hard head of a smooth-leaf cabbage.

Head Maturity and Annual vs. Biennial Habit

There have been several papers (*10,46*) on *B. oleracea* reporting that annual habit is dominant over biennial and that early maturity is dominant over late. There must be a dominance series of genes and/or alleles to account for the range of genetic variability in vernalization requirements and earliness. The genetics of variation of extremes has not been studied. However, there is a continuous range from Chinese kale and very early summer cauliflowers, such as Pusa Katki, which need no vernalization even when grown at 27°C, to late-maturing cabbage and winter hardy kales and Brussels sprouts, which require 12 weeks of vernalization below 10°C. Summer cabbages mature early and, if left in the field, will often produce seed stalks soon after splitting. Except for the strongly annual *B. oleracea* cultivars, all cultivars require some cold for veneralization and can only be vernalized after reaching a minimum size. In broccoli and summer cauliflower the maximum temperature for effecting vernalization may be as high as 20°–25°C, while for true biennials it is generally considered to be 10°C.

Head Leaves

In a cross between lines with few and those with many wrapper leaves, few is dominant. There are modifying factors. Evaluation and selection is made following vertical splitting of mature heads with a knife.

Size of Head

Head size is inherited quantitatively with hybrid vigor sometimes expressed. Cabbage is quite responsive to photoperiod. Large heads develop under the long summer days of the north and extremely large heads develop in Alaska, whereas much smaller heads develop in Texas and Florida under the short days of winter.

Plant Height

There is a major gene *T* for height (*30*). Most cultivars are recessive in this respect. In addition there are modifiers of this character (*31*). A tall, long stem is undesirable as it will fall from the weight of the cabbage head.

Core Width

Core width inheritance has not been studied, but wide core appears to be dominant to narrow core. A narrow core is desirable, but is less important than a short core.

Core Length

Core length is controlled by two incompletely dominant genes for short core (Fig. 11.12). A short core less than 25% of head diameter would be desirable (*13*).

Core Solidity

The solidity or toughness likewise has not been studied. A soft core is desirable over a tough core, especially for processing cabbage where the core is cut up and processed. Some hybrids, such as Roundup, have very tough cores that result in woodiness in the processed product.

Frame Size

Older cultivars generally had large frames and large basal leaves. In adapting cabbage to mechanical harvesting and in the effort to develop high-yielding cultivars, the trend has been toward smaller frames. Fresh-market cultivars generally have had smaller frames than processing types. However, an adequate frame is needed for photosynthesis, depending on the size of the head desired.

Head Splitting

Head splitting is controlled by three genes acting additively with partial dominance for early splitting. According to Chiang (*6*), narrow sense heritability for splitting was 47%. To evaluate cultivars for splitting, they all must be allowed to go to full maturity to assess the splitting tendency. Long-cored cultivars usually split at the top of the head, while short-cored cultivars tend to split at the base.

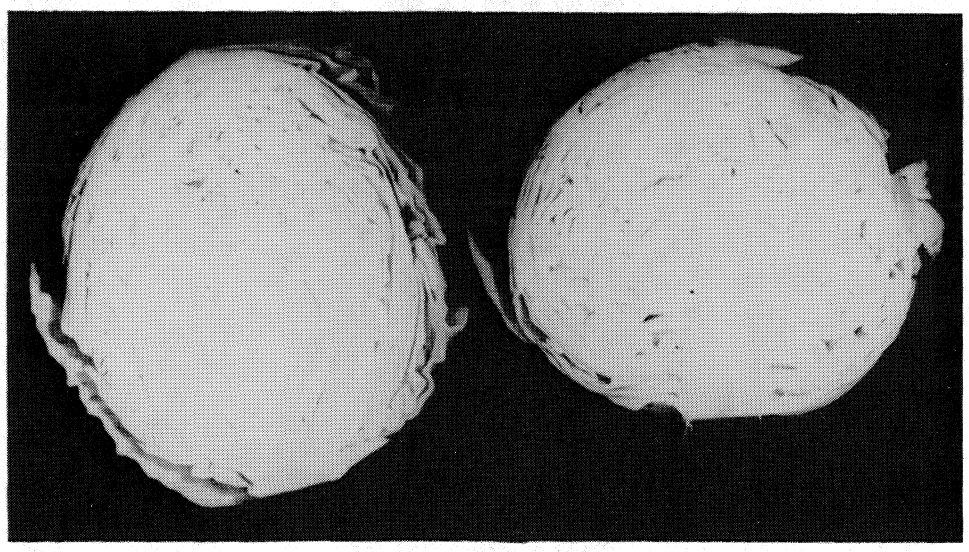

FIGURE 11.12. Cross section of cabbage heads with short and long cores.

Axillary Heading

Axillary heading occurs as buds or large sprouts below the head and as buds in the head. Both factors are undesirable since they make for a loose head and cause difficulty in harvesting the crop. Precocious axillary heading is recessive and controlled by one major gene plus modifiers (*1*). Heritability is low, making selection a difficult and slow process. Axillary heading is best assessed by splitting the head vertically through the core.

Red Coloration

The anthocyanin color of red cabbage is due to several factors and is quantitatively inherited (*18,36*). An F_1 plant of green × dark red will be pink. The gene *M* produces magenta (*20*) and with *S* gives purple on the upper side of the leaf. There have been a number of studies on anthocyanin inheritance without good agreement on the inheritance pattern.

Dry Matter

Dry matter or percentage soluble solids is inherited quantitatively (*15*) with low dry matter (6%) being recessive and present in early cultivars, whereas the highest dry matter (9–10%) occurs in late-winter storage types and savoy cabbage. Dry matter reaches a plateau when the cabbage is mature. Thus, if dry matter is to be measured, the head must be mature. If dry-matter readings are in agreement for two successive readings taken 2 weeks apart, then the cultivar is mature. Density can also be used in the same way as a criterion of maturity. Density is measured by placing a weighed head in water and measuring the water displaced. The denser the head, the closer to unity will be the ratio of head weight to weight of water displaced. Dry matter is measured by sampling a portion of the head (200 g), not including core tissue, and measuring the wet and dry weights of the samples to obtain percentage dry matter. Dry matter is correlated ($r = .78$) with soluble solids, but

soluble-solid readings on cabbage juice are difficult to read on a hand refractometer. Usually analysis of dry matter of five individual heads will give a good assessment of the dry-matter potential of the cultivar. If the samples of a mature cultivar are not ±0.5% of the mean, the cultivar is either not uniform or not mature.

Dry matter is positively correlated with later maturity, and it will always be difficult to develop early, high-yielding, high-dry-matter cabbage cultivars. In effect, high dry matter is a concentration of the product of photosynthesis.

Individual heads are sampled for dry matter in a segregating population at the time when the head is split for internal character assessment. Plant stumps of heads having high dry matter can then be saved for seed production.

Storageability

Late, slow-growing cultivars are best suited for storing. Dry matter of the better storage types, such as the new Dutch hybrids, is higher than standard and early cultivars. The heads are firm and have think finely veined leaves. Intermediate-storing cultivars, such as Green Winter, are coarser. Eating quality of the very late storage cultivars is inferior because they have leaves that are very hard and tough. Also, in some of the very late cultivars the leaves wrap together very tightly. Heads of desirable types are placed in storage for extended periods, and then selected heads, which have maintained their color and quality, can be rooted and seed produced. The head will form roots at the base of its core, or alternatively the axillary buds at the base of each leaf can be excised and rooted (Figs. 11.10 and 11.11). The desired color depends on potential use. Cabbage to be used for coleslaw should be white, while if it is to be sold for fresh market, it should be green.

Winter Cultivars

Some cultivars, such as Round Dutch, Greenback, Rio Verde, and Superette, are adapted to overwintering and growth during midwinter in the South. These cultivars are bolting resistant, requiring a long cold period to induce flowering. They are often slightly savoyed or have blistered leaves.

Selection for bolting resistance can best be done in the South. Planting is done earlier than for the main crop, resulting in larger plants when cold weather occurs and greater susceptibility to vernalization. Plants not bolting rapidly under such conditions must be bolting resistant. Alternatively, in the North, seed can be planted in late February or early March and large seedlings transplanted to the field in early April. Plants that bolt instead of producing heads are eliminated.

Savoy

The savoy leaf texture is controlled by three or more genes. The yellow savoy cultivars are high yielding and considered by many to be better flavored and less gas producting than the smooth-leaved cultivars. The savoy cultivars are the highest in solids or dry matter of all cabbages.

SELECTION FOR PEST RESISTANCE

Procedures for screening for single- or multiple-disease resistance are described in detail by Williams (*49*).

Cabbage Yellows

Cabbage yellows is a soilborne fungus disease [*Fusarium oxysporum* f. sp. *conglutinens* (Wr) Snyder & Hansen]. Fusarium yellows is a soilborne vascular wilt favored by warm soil temperatures with the optimum at 28°C; the symptoms are progressive yellowing followed by brown necrosis of the plant starting with the lower leaves; frequently unilateral vascular browning occurs. The plant is stunted and premature leaf drop may occur.

There are two types of cabbage yellows resistance, designated type A and type B by Walker (*43*). Type A is determined by one dominant factor and is carried by most resistant cultivars. This resistance is not influenced by the temperature. Type B resistance is conditioned by several genes and breaks down at temperature above 22°C. Testing for type A resistance is done by dipping young seedlings in an inoculation suspension (*49*) and then growing them at 27°C. In 2 or 3 weeks susceptible plants will be dead. Recently, a pathotype of the fungus capable of breaking type A resistance in cabbage has been found. Fusarium yellows is a classic example of stable resistance controlled by a single gene.

Downy Mildew

Downy mildew is a fungus disease [*Peronospora parasitica* (Pers. ex Fr.)]. Downy mildew is soilborne and spreads when soil is transferred by wind and rain. It attacks the lower leaves first, beginning as a sparse to densely packed white mat on chlorotic to partially chlorotic lesions. Resistance has been found in cabbage and broccoli, but the genetics of resistance is complicated by the existence of numerous pathogenic races (*21*). Cabbage PI 245015 has dominant genes for resistance to races 1 and 2, each inherited independently (*21*).

Testing for resistance is done by spraying the cotyledons of young plants with a spore suspension and placing the treated plants in a saturated atmosphere at 16°C for 12–18 hr and 5 days later returning them to the chamber for 24 hr. Susceptible plants will have a heavy sporulation on the lower leaf surface.

Black Rot

Resistance to black rot bacteria [*Xanthomonas campestris* (Pam. Dows.)] was found in the cv. Early Fuji (*52*). The disease is seedborne and is also spread by wind and splashing water. The symptoms are vascular bacteriosis causing yellowing of the leaves and brown to black discoloration of the veins. Resistance is controlled by a major gene *f*, plus two modifier genes, one dominant and the other recessive.

For artificial inoculation a bacterial spore suspension is sprayed on well-developed plants early in the morning. This introduces bacteria into the guttation droplets. As the day warms, the bacteria will be drawn back into the leaves through the hydathodes. In 2–3 weeks susceptible plants will develop large lesions on the leaf margins and blackening through the veins of the leaf and stem. Resistant cultivars will only show slight necrotic infections at the leaf margins (Fig. 11.13).

Powdery Mildew

Resistance to powdery mildew fungus (*Erysiphe polygoni D.C.*) was found in Globelle, and the resistance in this cultivar is controlled by a single dominant gene, although modifying genes may influence its expression (*44*). Powdery mildew shows up in late fall,

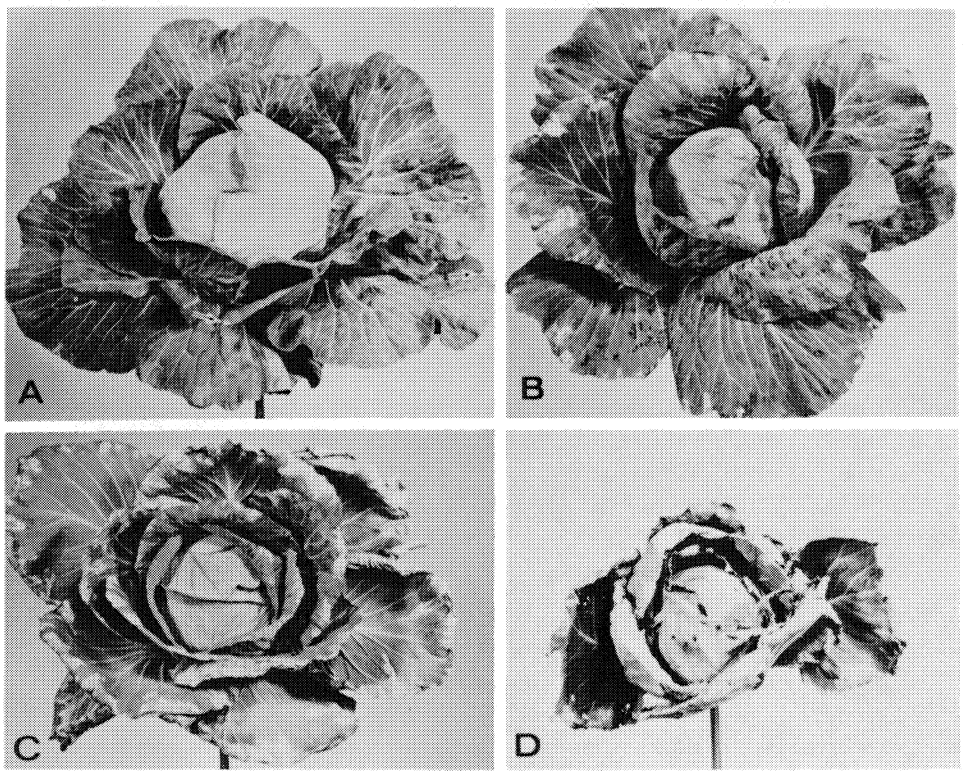

FIGURE 11.13. Black rot in cabbage (note V-shaped lesions). (A) Resistant plant: arrows indicate hypersensitive reaction at hydathodes. (B) Moderate resistance. (C) Susceptible. (D) Highly susceptible.
Courtesy of P. W. Williams.

especially if it has been a dry season. The common symptom is a fine necrotic flecking on the exposed head and lower leaves, near the base of the large ribs. Natural field infection (if heavy) is the easiest method to use for selection for resistance.

Turnip and Cauliflower Mosaic Virus

These viruses are spread by infected aphids feeding on the plants. Wild plant hosts are the overwintering disease reservoir. The symptoms are mottling and nerotic spots or ringspots. There is no known resistance to cauliflower mosiac virus, but some cultivars, such as Globelle, exhibit quantitative resistance to races 1 and 2 of turnip mosaic virus (TuMV). Provvidenti (*32*) has shown that TuMV has at least four or more races, and there is complete resistance to all four races in Chinese cabbage. Resistance to each race is inherited independently. Screening for resistance can best be done in the greenhouse. Seedlings are inoculated, held for 7 days at 25°C to allow development of the virus, and then grown at 15°C to encourage expression of susceptibility. If plants are inoculated and planted in the field, the virus will express itself best when cool weather develops (Fig. 11.14).

Clubroot

Clubroot (*Plasmodiophora brassicae* Woron.) is a soilborne fungus disease. The symptoms are fusiform or spherical enlargements and malformations (galls) on the roots. Severely infected plants wilt in direct sunlight, and the plants will be more or less stunted. There are many races of clubroot that infect various species. Resistance in *B. oleracea* usually involves several genes for control of each race. Resistance has come primarily from kale and rutabaga. Interspecific hybridization has been extensively used by crucifer breeders, primarily for the purpose of transferring resistance to specific races (*7,8*). Screening is best performed by growing seedlings in heavily infested soil at temperatures of 20°–25°C and pH about 5–6. Alternatively, seedlings can be dipped in a suspension of spores for a few hours and then planted. Severe infection may be obtained after 5–6 weeks. Races 2, 3, 5, 6, and 7 are known in North America, and over 24 races have been identified around the world. Jersey Queen and Badger Shipper cabbage and Laurentian and Wilhelmburger rutabaga are used as international differential hosts (*48*). Badger Shipper, which has resistance derived from kale, is resistant to races 1, 3, 5, and 6. Chiang (*7*) found in *B. napus* resistance to races 1 and 3 controlled by a single dominant gene and resistance to race 5 controlled by two recessive genes. Strandberg (*37*) found a dominant gene for resistance to races 6 and 7 in Chinese cabbage.

Rhizoctonia or Bottom Rot

The bottom rot pathogen *Rhizoctonia solani* Kuhn. is soilborne. Early infection produces seed decay and pre- and postemergence damping-off. Later infection on the stem produces cankers and wire stem, and older plants develop a bottom rot of the lower leaves and head

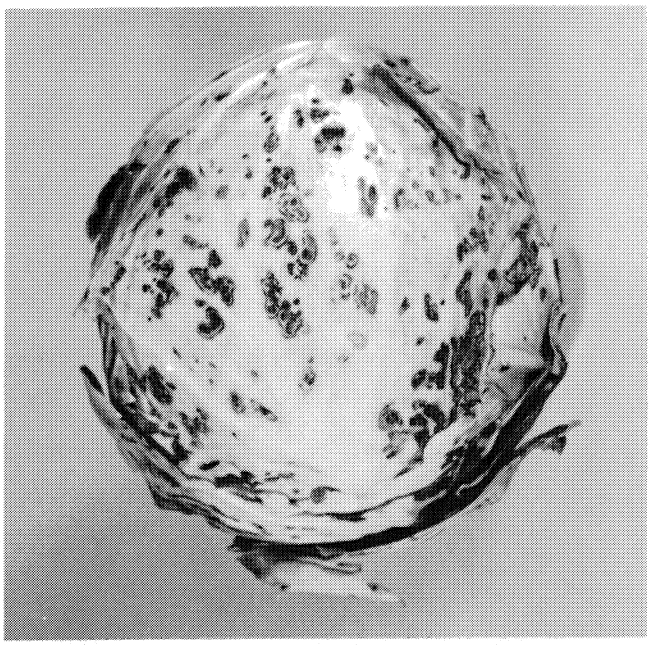

FIGURE 11.14. Cabbage head showing TuMV lesions.

rots. Williams and Walker (*53*) have shown that resistance is controlled by a single dominant gene that is present in the cv. Globelle.

Tipburn

Tipburn is a physiological disease of major importance worldwide (Fig. 11.15). It is associated with lack of calcium translocation to the tips of rapidly growing leaves, resulting in death of the cells and consequent browning and blackening of leaf tissue in the head. High nitrogen and rapid growth are associated with the disease. Palskill *et al.* (*27*) reported that factors that produced or increased root pressure deficits were associated with increased tipburn. Thus, for effective selection against tipburn, conditions that stress the plant are required in order to identify resistant plants. Selection efficiency can be meaningful by creating conditions for rapid vigorous growth and then stressing the plant by withholding water, root pruning, or reducing translocation by holding the plants in a mist chamber for several days. Walker *et al.* (*45*) reported that resistance was controlled by two or three recessive genes, whereas Dickson (*12*)—studying other selections—presented evidence for dominant resistance controlled by two or three genes. Many factors influence tipburn, making selection difficult. Repeated selection over several generations is necessary to be reasonably sure the breeder has developed a resistant line. Cultivars differ widely in susceptibility; for example, Green Boy and Rio Verde are very susceptible while Titanic, Roundup, and Superboy are much less so.

Lepidopterous Worm Resistance

There is a variability in susceptibility of cabbage cultivars to worms. Red cabbages are generally much more resistant than the green cabbages. This in part is due to vector preference for the green cabbage. Dickson and Eckenrode (*14*) found that PI 234599 cauliflower, which has glossy leaves, was immune in the field to the cabbage looper (*Trichoplusia ni* Hubner), imported cabbage worm (*Pieris rapae* L.), and to diamondback moth (*Plutella xylostella* L.). Resistance is recessive and quantitative, and it is partially linked to the glossy character. Cauliflowers with leaves having normal bloom

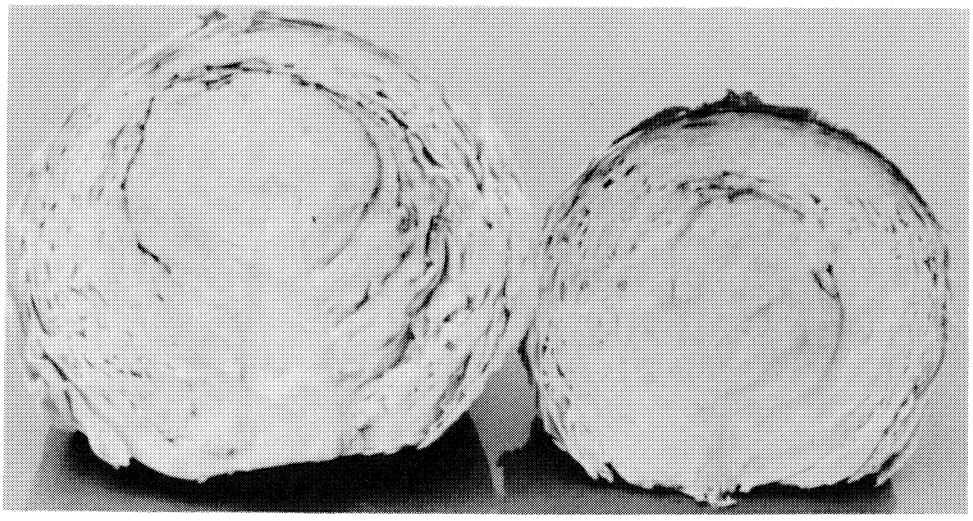

FIGURE 11.15. Cabbage heads showing internal tipburn.

and moderate resistance have been developed. Screening in the field, using natural pest populations developed by growing a susceptible genotype every third row, was preferable to screening in cages or greenhouses. Both high nitrogen and low light reduce resistance. Resistance is due to antibiosis, i.e., the larvae do not grow as healthily on the resistant lines. Chemical identity of the antibiotic substance is unknown, but resistant plants in feeding studies imparted no deleterious effects on rats.

Radcliffe and Chapman (*33*) have reported the differences in cultivar response by various cruciferous crops to attack by various insects in the field.

GENE LIST

The gene list (Table 11.6) was prepared in part from the lists published by Yarnell (*55*) and by Wills (*54*) in the *Eucarpia Cruciferae Newsletter*. People interested in crucifer genes should contact either A. B. Wills, Scottish Horticultural Institute, Mylnefield, Dundee, Scotland or Paul Williams, University of Wisconsin, Madison, for an up-to-date gene list.

DESIGN OF A COMPLETE BREEDING PROGRAM

Let us assume that a poor-quality plant introduction line (A) of cabbage carries downy mildew resistance, having a single dominant gene for resistance to two races. We want to incorporate the downy mildew resistance into a desirable inbred cabbage cultivar (B). Let us assume also that the A line has no resistance to fusarium yellows, but cultivar B does carries the A-type dominant resistance to fusarium yellows.

Generation 1

May 1. Plant 10 or more plants each of parents A and B.
June 5. Transplant A and B to the field.
September 1. Dig and pot several plants of both the A and B lines, removing the outer leaves. Place the plants in cold storage at 5°C or in a cold greenhouse. During storage remove any rotting leaf bases or tissue. If cabbage maggots were observed in the stem when the plants were dug, treat the plants with insecticides after potting.
November 15. Remove the plants from cold storage and move to a greenhouse at 15° ± 5°C. Water plants and fertilize as needed. Trim the outer part (leaves) of the heads of both A and B plants without damaging the core.
December 1. Remove dehisced leaves from plants. These will begin to rot and may cause the whole plant to rot if they are not removed.
January 1. Make crosses using B (the yellows-resistant parent of desirable horticultural phenotype) as the pistillate parent. Emasculate the buds before they are fully open to guarantee that no self-pollination occurs.
March 1. Harvest seed as pods turn pale or become dry. Do not let pods dry to the point that they dehisce.

Generation 2

About May 1, plant 20–30 F_1 seed in a row of a flat or in a single pot. When the seedlings are 2 weeks old and the cotyledons fully developed, screen them for mildew resistance to both races. All should be heterozygous at both loci and therefore resistant. The B parent should be susceptible and the A parent resistant. Transplant the F_1 survivors plus 10 plants

TABLE 11.6. Simply Inherited Characters of Cabbage and Their Gene Symbols[a]

Symbol	Character description	Reference
Foliage color		
c	Anthocyanin-less: recessive, epistatic to *A*; anthocyanin suppressed in all parts	*18,36*
A	Basic *anthocyanin* color factor: allelic series; intensifiers	*18*
A^{rc}	Colored lamina: color intensifier in red cabbage	*18,36*
B	Light red midrib alone: with *A* gives a dark-red violet	*18*
G, H	Complementary factors for deep purple: *Gh*, sun color; *gH, gh*, green	*19*
M	*Magenta* plant color	*20*
R-1, R-2	Duplicate factors for sun color: need reconciling with *G* and *H*, and also with *S*	*19*
S	*Sun* color: see *G, H, R-1* and *R-2*	*20*
Leaf morphology and heading		
As	*Asparagoides*: bizarre protuberances from leaf midrib and veins; originally designated *A*	*30*
En	*Entire* vs. hyrate leaf: originally *E*	*30*
fc	*Fused* cotyledon: outer edges of cotyledon fused to form funnel	*53*
gl	*Glossy* foliage: both recessive and dominant; series of non-allelic genes with similar phenotype; wax inhibited; dominant types produce wax on stems	*3*
Hr-1	*Hairy* first leaf: hairs on margin; sometimes poor expression in heterozygote	*35*
sm	*Smooth* leaves: with *wr*; originally *S*	*19*
Pet	*Petiolate* sessile vs. leaf: originally *P*	*30*
W-1, W-2, W-3, W-4	Series of factors for frilled leaves	*2*
K	Dominant factor for heading	*2*

of cultivar B to the field. In September dig three F_1 plants and three of parent B. For transfer of the mildew resistance only one is needed, but three allow for possible loss to rots, genetic variability, or other contingencies. More than three should be used if the breeder is interested in breeding hybrids or open-pollinated cultivars. The larger number of *S* alleles will enhance the potential for the cross-pollination required. Pot and place these plants in cold storage for vernalization. Repeat the procedures for vernalization and transfer to the greenhouse for pollination.

Backcross one or more of the F_1 plants to parent B as female. Emasculation and pollination of about 50 parent B flowers should provide plenty of seed. The emasculation guarantees that there are no selfed plants in the backcross pollinations. Emasculation is not essential, since any selfs of parent B will be mildew susceptible. They should not remain after selection for this resistance, except when the disease incidence is low and escapes occur. Crossing without emasculation saves time during the crossing procedure. The use of all three F_1 and more than one B parent plant will maximize the number of *S* alleles occurring in the ultimately developed disease resistant population. Harvest the seed when ripe.

TABLE 11.6. (*cont.*)

Symbol	Character description	Reference
n-1, n-2	Recessive factors for heading; it is suggested that these might be substituted for *k-1, k-2, k-3*	*29*
W	*Wide* leaf	*29*
Plant habit		
Ax	*Axil* sprouts: originally *A*	*1*
dw	*Dwarf*: short internodes, round leaves	*56*
T	*Tall* vs. short plant	*29*
Flower color		
An	*Anther* spot: tip of anther purple spotted; suppressed by *C*	*54*
Wh	*White* petal	*28*
Flower morphology		
cp	*Crinkly petal*: allelic series	*53*
Genic male sterility		
ap	*Aborted pollen*: anthers appear normal, but pollen does not germinate	*54*
ms-1	Broccoli, Anstey's *M*2, linkage group 5	*9*
ms-2	Brussels sprouts	*34*
ms-4	Purple cauliflower	*5*
ms-5	Cauliflower	*24*
ms-6	Broccoli	*11*
Cytoplasmic male sterility		
ms	Cytoplasmic factor with R, radish cytoplasm	*4,26*
ms	Cytoplasmic factor with N, *nigra* cytoplasm	*28*
Self-incompatibility		
S	*Self-incompatibility*: multiallelic	*25*
Miscellaneous		
f	Major gene for resistance to black rot	*52*

[a]Adapted from Yarnell (*55*).

Generation 3

Plant 500–600 BC_1 seed, plus cultivar B. Screen for resistance to mildew; one-fourth should have resistance to both races. Transplant survivors and parent B in the field.

In September select for vigorous plants with moderate-sized basal leaves, no lateral buds sprouts, and round solid heads. Cut off the heads, and split them vertically through the core. Observe heads for internal tipburn, short core, head solidity, and lack of open spaces in the head, especially at its base. Select the 5–15 best plants and place them in cold storage. During storage, check the plants for rot of the cut surface. Remove any rot and dust the infected area with fungicide.

Generation 4

Backcross the selections (BC_1) onto cultivar B. Plant 500–600 BC_2 seed in the greenhouse. At 2 weeks of age test seedlings with fusarium yellows inoculum. Include some seedlings of A or other known susceptible such as Copenhagen Market or Pennstate Ballhead as a susceptible check. All seedlings should be resistant to yellows. Test 4-week-

old seedlings in a mist chamber for resistance to both races of downy mildew (one-fourth should be resistant to both). Transplant the 100–150 survivors to the field. Repeat the selection procedures for type in September. If recovery for the type of cultivar B has been achieved, self-pollinate selections. Make a further backcross and repeat the cycle if the type of cultivar B has not been achieved.

If the type of cultivar B was achieved, select 5–10 or more plants; pot and vernalize them as described above. The larger the number of plants, the larger the number of *S* alleles that will be represented. At bloom, self-pollinate each plant separately. Bud selfing will probably give the maximum seed set, and open flower selfing will provide an assay of the plant's self-incompatibility. Make test crosses to adapted male sterile or self-incompatible inbreds (6–12 flowers). This will test each new selection for combining ability.

Generation 5

The objective is to verify the disease resistances and to identify the homozygous resistant plants of generation 4. Screen seedling progeny of each selfed BC_2–F_2 selection separately for yellows resistance and resistance to both races of mildew. Seven out of eight selections should be homozygous resistant to yellows, and one-fourth of the seedlings from each selection should be resistant to both races of mildew. Transplant the survivors, keeping all the progeny plants from each F_2 selection separate. Repeat the selection and self-pollination procedure. Repeat and make further testcrosses onto adapted male-sterile or self-incompatible inbreds to test for combining ability in terms of seed production and primarily for field performance.

If incompatibility is desired, it must be recognized that the F_2 generation is also the I_1 generation, which is the most effective population for use in identifying *S*-allele genotypes. Also, the observed number of seeds per pod from pollination of open flowers of the F_1 plants (generation 4 here) provides an assay of self-incompatibility/self-compatibility of the line.

Generation 6

For further verification of disease resistance and homozygosity, repeat the screening procedure as in generation 5. This will identify BC_2–F_3 lines that are homozygous resistant to fusarium yellows and mildew. For the development of self-incompatible inbreds with the yellows and mildew resistances, the BC_2–F_3 lines represent the I_2 generation. During this generation, homozygosity of the *S*-allele homozygous genotypes identified during the previous (BC–F_2, i.e., I_1) generation can be verified. Selection for or against strong self-incompatibility can be applied to this (generation 6) and subsequent generations. To obtain uniform inbred lines, selection and selfing through the F_3 and F_4 (I_2 and I_3) generations is usually required.

At this stage the lines will be ready for release as new inbreds that will give experimental hybrids with mildew resistance. Resistance in this one parent of the hybrid is adequate since resistance is dominant for both diseases.

TRIALS OF ADVANCED LINES

Testing of open-pollinated cultivars or potential hybrid cultivars can be done as follows. A satisfactory procedure is to have two concurrent trials. One should be an observational trial of new hybrids with only one replicate. The second is a replicated trial using three or

four replications with 30–40 plants per replication, testing only those hybrids previously selected in the observational trial. Complete data will be taken on the replicated trial. The best and worst hybrids are noted in the observation trial. The most promising of these are advanced into the replicated trials of the next planting season. Following the advanced trials the best lines will be recommended to the grower for trial, at which time commercial small-scale evaluation of their potential for shipping, storage, or processing may be initiated.

Plant spacing within trials should be adjusted to 24-in. rows and in row spacing of 12 in. for fresh market. For processing and storage cabbage, use 30- to 36-in. rows and in row spacing of 15–18 in. The trials can be direct seeded and thinned or can be transplanted. Transplanting is usually simpler for a trial and also conserves scarce seed. Cabbage growth rates change with seasonal variations in moisture and temperature. Therefore, duration from seeding to harvest will fluctuate ±2–3 weeks from year to year. There is no precise way of knowing when a cabbage is mature, and so a sequential harvest at weekly or biweekly intervals provides the best evaluation. The first harvest should be made when the line is first considered mature or when the first head splits. If the cabbage is for processing or storage, constant week-to-week dry-matter or head density determinations will indicate if maturity is reached. Both density and dry matter will increase from week to week prior to maturity. Once maturity is reached, both values will remain constant until the head splits.

Heads should be evaluated for splitting, and for protective formation of wrapper leaves about the head. Heads must be cut open and evaluated for tipburn, head solidity or lack of open spaces, core length and width, internal head color, rib size, and leaf thickness. If thrips are a problem, this is also the time to record their presence or absence.

Cabbages for storage are harvested at early maturity and placed in storage for 3–6 months to evaluate their storage potential. Fully mature heads will not store as well. Enough heads must be placed in storage to allow sampling two or three times during the storage period.

Currently, two types of breeding lines are released to seed companies by public-sector breeding programs. One type is fully developed inbred lines for use in specific hybrid combinations, which the seedsmen may produce and market. They may also use the inbred line in combination with their own lines to produce private hybrids. Partially developed lines with special attributes are another common type of germplasm release. Seedsmen will further inbreed and refine these lines prior to using them in hybrid combination. Some public breeders do not select for *S*-allele homozygosity and self-incompatibility. In this case the seedsmen may find that additional selection for incompatibility is necessary before the inbred can be used as the female parent of a hybrid. They may also find it impossible to obtain adequately strong incompatibility if the breeder has not endeavored to maintain a relatively large frequency of *S* alleles. This is more likely to be true if the line was developed with some specific attribute in mind, such as disease or insect resistance.

Commercial Hybrid Seed Industry

Commercial cabbage seed is produced in Washington, Oregon, and California. The seed bed is planted in early September and transplanted to the field, with every fifth row being left for the male row if hybrid seed is to be produced. When both inbreds are self-incompatible so that seed can be harvested from both, then two rows of each parent

usually are planted alternately. The plants will grow and develop until cool weather stops growth, and vernalization occurs during the cold months. When warm weather comes in the spring, the plants produce seed stalks, and bloom in May and June. The seed is harvested in July and August. Yields of hybrid seed will vary from 200 to 600 lb/acre.

Breeding programs for *Brassica* crops occur all over the world. In Europe, Japan, or various parts of the United States, the seed companies breeding cabbage have their own research facilities. Seed production in Washington is rather concentrated and the location of each field or plot is carefully planned to avoid contamination with foreign pollen.

In Washington, a very cold winter may sometimes kill many of the plants. Excess rain in the summer can also ruin the seed crop. Another serious concern is to prevent seed from being contaminated with disease, such as blackrot or phoma. Great care is taken to ensure that seed planted in the seed production area is free of disease.

Male sterility is just starting to be used in the commercial production of hybrid cabbage. However, it is expected that its use will increase quite rapidly as new hybrids are developed, since it is simpler to manipulate than the self-incompatibility system and less subject to environmental effects. Also it is impossible to have inbreds as contaminants in commercial seed if male sterility is used, whereas when using incompatibility in some crosses and some years a considerable percentage of inbreds can occur. The inbreds are smaller than the hybrids and are considered undesirable. A seed lot will be discarded if the inbred contamination is in excess of about 5%. However, along with development of male-sterile inbreds and their maintainers will be the need to select for self-compatibility.

Useful additional references are Niewhof (*23*), Eucarpia-Cruciferae Newsletter (*16*), and Williams (*50*).

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