10 Onion Breeding

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Onions are an important vegetable crop worldwide. There seems to be no limit to their use by any nationality. Even though their daily per capita consumption is small, the overall yearly per capita use was reported to be 10.1 lb in 1981 in the United States. This consumption was in the forms of fresh, frozen, and dehydrated bulbs and green bunching onions (*33*). Consumption in some countries is greater than in the United States, but accurate worldwide figures are not available. In addition, many closely related species are important food items such as garlic, leek, chives, and Welsh onions. Together, the onionlike plants are one of the most important horticultural crops in the world, considering the economic importance of the edible crop and its seed.

The 1981 U.S. acreage for dry onions was 111,630 with a production of over 35 million cwt and a farm value of approximately $472 million (*34*). The imports for the same period were reported to be 1.4 million cwt and the exports to be 2.6 million cwt (*33*).

World production in 1981 was reported to be 3.9 million acres with a production of 19.7 million MT. The leading countries in onion production are shown in Table 10.1 (*8*), and the major onion producing states in the United States are shown in Table 10.2 (*34*).

ORIGIN AND GENERAL BOTANY

Unlike most domesticated food crops, the origin of the onion *Allium cepa* L. is still somewhat a mystery. Linnaeus (*21*), Don (*5*), and Regel (*30*), men known for being

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TABLE 10.1. The Leading 20 Countries for Production of Dry Onions in 1981[a]

Country	Area (1000 acres)	Yield (cwt/acre)	Production (1000 tons)
China	534	111	2956
India	543	67	1815
United States	111	316	1759
USSR	420	76	1595
Japan	69	339	1174
Spain	79	291	1150
Turkey	178	124	1100
Brazil	183	94	855
Italy	54	219	583
Egypt	52	222	580
Pakistan	104	92	479
Poland	62	144	440
Romania	96	77	374
Yugoslavia	103	65	341
Iran	118	50	292
Indonesia	99	46	227
Bangladesh	79	39	154
Thailand	62	51	154
Viet Nam	106	27	147
Burma	49	46	116

[a]Adapted from FAO Production Yearbook (*8*).

monographers, could not pinpoint its origin. Vvedensky (*36*) listed *A. cepa* only as a cultivated plant, and in a review Hooker (*10*) said its origin was not known. Most botanists doubt that *A. cepa* exists today as a wild plant. Vavilov (*35*) suggested that the onion originated in the area of Pakistan. Others have suggested Pakistan, Iran, and the mountainous areas to the north (*15*).

One fact is certain: the onion has been around in its present edible form for thousands of years. Tackholm and Drar (*32*) listed the use of onions recorded in tombs as early as 3200 B.C. It was mentioned as a food in the Bible and in the Koran with reference thought

TABLE 10.2. Leading States for Commercial Dry Onion Production in 1981[a]

State	Area (acres)	Production (1000 cwt)
California	28,600	9,731
Texas	24,200	4,188
New York	14,300	3,933
Colorado	9,000	2,925
Michigan	7,300	2,446

[a]After U.S Department of Agriculture (*33*).

to be around 1500 B.C. In addition to being a food, the onion was considered by people during ancient times to be a medicinal plant having certain healing powers. Some early drawings indicate that onions were used in spiritual offerings.

Common Onion, Multipliers, and Shallots (*Allium cepa* L.)

This group includes the common bulb-type onion, potato or multiplier onions, ever-ready onions, and shallots. The common bulb-type onion is by far the most important in commercial trade. It generally can be described as a bulbing onion under long- or short-day conditions, depending on its adaptation. It produces a single bulb and has an umbel-type inflorescence, producing seed and no (or rarely a few) bulbils. It is reproduced typically from true seed. It may be of several bulb shapes and colors. Bulbing, controlled by a combination of day length and temperature, varies depending on where the specific cultivars were developed. It may also vary in pungency from mild to very pungent and vary in keeping quality with storage life ranging from a few weeks after harvest to almost 1 year. Soluble solids may vary from 4 to 25%. These characteristics are described in detail by Magruder *et al.* (*24*) and Jones and Mann (*15*).

The potato or multiplier onions are generally thought of as garden onions. They usually have smaller bulbs, may or may not flower, and generally do not produce seed. They continually produce new bulbs by dividing and are propagated by bulb division.

The ever-ready onion is similar to the multiplier onion, but usually has smaller bulbs. It was described by Stearn (*31*) as being a perennial home garden cultivar giving rise to numerous bulbs each year. Ever-ready onions rarely flower and are always reproduced by division.

The shallot is of commercial importance in Europe and in the United States. Shallots differ from multiplier onions and ever-ready onions in two ways: they form into single bulbs following division and their tops die down, indicating maturity. They go into a state of rest or dormancy similar to the common onion. Some cultivars flower freely and produce seed. However, due to their prolific bulb division, they are propagated asexually. This group has had some taxonomic description problems; but since the shallot crosses freely with the common onion and produces fertile progenies, it will be treated here as *A. cepa* L.

A. cepa L., generally know as a bulbing vegetable, has several closely related species: *Allium ampeloprasum* L. (great-headed garlic, leek, and kurrat), *Allium chinense* G. Don (rakkyo), *Allium fistulosum* L. (Japanese bunching or Welsh onion), *Allium sativum* L. (garlic), *Allium schoenoprasum* L. (chives), and *Allium tuberosum* Rottler ex Sprengel (chinese chives). A brief description of these closely related species follows. Detailed descriptions can be read in the text "Onions and Their Allies," by Jones and Mann (*15*).

Great-Headed Garlic, Leek, and Kurrat (*Allium ampeloprasum* L.)

This species is extremely variable, with many cultivars described in detail by Feinbrun (*9*). Generally the leaves are very flat, typical of leek. Bulbs range from well defined, such as produced in a type known as great-headed garlic, to non-bulb-forming types. The bulbs are actually bladeless storage leaves known as cloves. The clove is very similar to garlic. The scape (or seedstem) is round and solid. The umbels produce seed, but this species rarely produces bulbils, which are common in true garlic. Sterility is common. Leek produces almost no bulbing structure and so the elongated foliage base is eaten. It is propagated by seed. Kurrat is a leeklike form of small stature. It is raised for its edible tops and is also propagated by seed.

Rakkyo (*Allium chinense* G. Don)

This vegetable onion is native to China and eastern Asia and is grown by home gardeners mainly of Chinese and Japanese background. It is a plant similar to chives except that it bulbs and divides and looks similar to small dividing onions. When mature, the leaves die down. Seed stems are solid, but leaf blades are hollow as in common onions, which is unique among cultivated alliums. Flowers are purple in color but do not set seed, because they are tetraploids, as reported by Kurita (*19*).

Japanese Bunching or Welsh Onion (*Allium fistulosum* L.)

Japanese bunching or Welsh onions have been popular garden onions of China and Japan. It is not clearly understood where the name Welsh onion originated. The plants are vigorous and have hollow leaves and seedstems. Non-flowering plants look very similar to *A. cepa*. The plants never produce enlarged bulbs. One of the most distinguishing characteristics between *A. cepa* and *A. fistulosum* is the shape of the seedstem. *A. cepa* is characterized by a swelling in its scale midway in its length, whereas *A. fistulosum* has a straight uniform scape. *A. fistulosum* flowers tend to open fully at anthesis and are somewhat unique in that they open in regular order from central flowers outward to the umbel base. Hybrids have been successfully made with *A. cepa* resulting in bunching types such as Beltsville Bunching. The hybrids are generally sterile.

Garlic (*Allium sativum* L.)

The garlic plant has flat, longitudinally folded leaf blades very similar to *A. ampeloprasum,* but does not produce bulblets around the main bulb. In flowering plants, the inflorescences produce mainly small bulbs instead of flowers. Some flowers may partially develop but produce no seed. The cape is round, smooth, and solid for the entire length and may be somewhat coiled. The bulb is a composite of several cloves. Garlic is propagated by planting individual cloves. Large bulbs are always made up of several cloves, which also helps distinguish garlic from *A. ampeloprasm* (great-headed garlic) which has large single bulbs with smaller bulbs or cloves attached.

Chives (*Allium schoenoprasum*)

The chive is probably the most variable in type and range. It is known as a wild plant in North America, Europe, and Asia. Its great variation has created difficulty for classification. Domestication has brought few changes to the species. Despite its variability, the chive is easily separated from other alliums by its morphology. Its flowers, usually purple in color, open first at the top of the umbel then successively toward the base, which is opposite the flowering habit from all other alliums except the Japanese bunching onion (*A. fistulosum*). It is also free flowering, has slender leaves, and undergoes very rapid vegetative multiplication, thereby forming dense clumps.

Chinese Chives (*Allium tuberosum*)

This species is grown widely in China and Japan for its edible leaves and young flowers. The name chinese chive probably occurred since only the leaves are eaten, similar to the common chive. It does produce enlarged rhizomes but they are not used for food. It is propagated by division of the clumps of rhizomes. The foliage consists of grasslike leaves that are solid in cross section. The scape is solid and has two or more sharp angles running the entire length of the stem. The flowers are white and borne on flat-topped umbels, and generally there are few flowers per umbel.

FLORAL BIOLOGY

As described in the introduction, there are several important *Allium* species; but the floral biology, pollination control, and breeding aspects will be limited to *A. cepa* L.

Flowering of the onion is initiated by environmental factors. The primary inductive factor is cool temperature, with day length playing no role as with bulb development. Other environmental factors that slow growth of the plant seem to interact with cool temperatures to cause flowering, but data to support this are not available. Temperatures of 40°F or below for 1 week will generally induce flower formation in bulbs or growing plants with four or more leaves. However, temperature prior to and following the 40°F week can alter flower induction. Very small seedlings do not normally respond to cool temperatures. The larger the plant, generally the more easily it can be induced to initiate flower development. When the onion plant is induced to flower, the shoot apex ceases to produce leaf primordia and initiates the inflorescence. The inflorescence may consist of a few to more than 2000 flowers per umbel. The flower stalk (scape or seedstem), which bears the umbel consisting of the spathe and the flowers, is actually a one-internode extension of the stem. The stalk is initially a solid structure, but with growth it becomes hollow as it develops. The number of seedstems produced per plant depends on the number of lateral buds contained on the stem, which is the compact base plate on the bottom of the bulb (Fig. 10.1).

Plants grown from seed usually produce only one seedstem if induced to flower. Plants grown from bulbs may produce six or more seedstems since several lateral buds may be

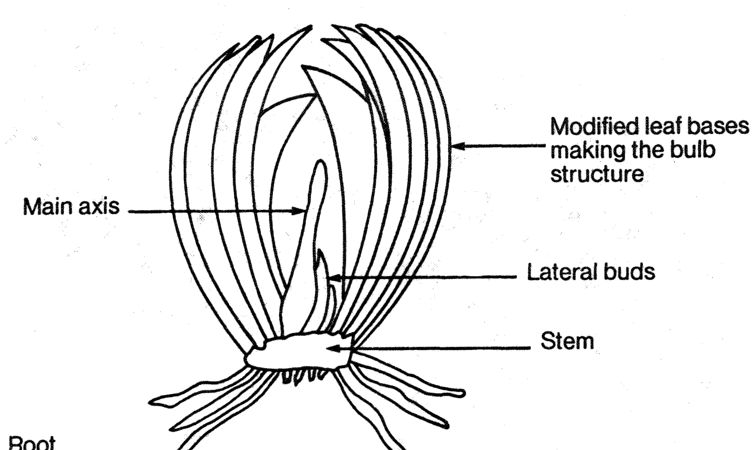

FIGURE 10.1. The stem of an onion is very compact and generally not seen by the casual observer. The leaf bases enlarge upon bulb initiation and form the bulb. Upon flower initiation, seedstems form in the apex of the leaf axis and elongate up through the bulb.

present that formed during development of the bulb. It should be noted that it is common for plants to produce bulbs and seedstems when grown during the winter and into the spring. This is due to the fact that one or more buds remain vegetative and produce leaves that form the bulb, while a lateral bud is initiated to form a seedstem. The plant then has both a bulb and a seedstem present at the same time.

The flowering structure is called an umbel (Fig. 10.2). It is an aggregate of many small inflorescences (cymes) of 5–10 flowers, each of which opens in a definite order, causing flowering to be irregular and to last for 2 or more weeks. If the plant produces two or more seedstems, the flowering sequence may actually occur for over a month (Fig. 10.3).

Each individual flower is made up of six stamens, three carpels united with one pistil, and six perianth segments (Fig. 10.4). The pistil contains three locules, each of which contains two ovules. The flowers also contain nectaries, which secrete nectar to attract insects. The anthers shed pollen over a period of 3 or 4 days prior to the time when the full length of the style is attained. The stigma becomes receptive at this time; and as a result of delayed female maturity (protandry), cross-pollination is favored. After pollination, the seeds develop; and as they mature, the capsules dry and split from the apex and down the center of each locule, which allows the seeds to fall free upon maturity.

The normal flower in onions is perfect, as previously described; but genetic and cytoplasmic sterility variations were discovered and reported by Jones and Emsweller (*14*) in a single-plant segregant of the cultivar Italian Red. Male-sterile plants developed from this original plant produced normal flowers except that the pollen did not develop into a viable stage. The inheritance was determined by Jones and Clarke (*12*) to be conditioned by a single recessive nuclear gene *ms*/*ms*, and a cytoplasmic factor, where one cytoplasm

FIGURE 10.2. A pair of healthy umbels showing good seed set. Note the difference in age of individual flowers. Some have seed development showing while others still show flower parts.

FIGURE 10.3. Typical seedstem and umbel formation in *A. cepa* L.

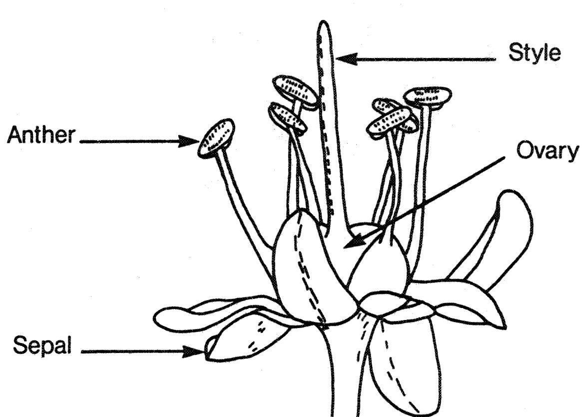

FIGURE 10.4. Each individual onion flower within the umbel is complete, having six stamens, three carpels united with one pistil, and six perianth segments. The pistil contains three locules each of which contains two ovules.

is considered normal (N) and the other sterile (S). To be made sterile, the onion plant must have the genetic and cytoplasmic condition S*ms*/*ms*.

The discovery, propagation, and techniques of maintaining male sterility in the onion have provided an excellent method for producing hybrid seed and will be discussed later in detail.

POLLINATION CONTROL

Pollination control in a cross-pollinating species such as onions is extremely difficult, considering each umbel has several hundred tiny individual perfect flowers. Therefore, it is important to understand onion flowering habits and the inheritance of as many characteristics as possible to be efficient in breeding the crop. Such information will help the student understand how to handle pollination so as to prevent many mistakes and the concomittant waste of time and money.

First, I shall discuss pollination control in a normal open-pollinated cultivar or breeding line. Selfing can be done only on a limited basis because inbreeding depression begins showing in the second (S_2) generation. To make the initial cross between two selections, the breeder has two choices. One is to hand emasculate stamens from one line, which is extremely difficult. The fact that flowers open on an umbel for 2 or more weeks adds to the problem of making the cross. The second choice is to make what is called a fertile × fertile cross, where two selections are caged together and then pollinated by hand or with

FIGURE 10.5. Small individual cages are used to obtain selfs on individual onion bulb selections. Flies are generally used to obtain pollination.

FIGURE 10.6. Small 2 × 2 ft nylon mesh cages used for making a three- to five-bulb mass following two generations of selection and selfing.

insects such as common house flies, blow flies, or bees. This method can efficiently be utilized if the two selections are different enough so that the F_1 can be differentiated from the two parents in the bulb stage. If they are different in that respect, seed should be saved separately from the two plants and planted in separate progeny rows. The hybrid bulbs can then be identified and distinguished from bulbs resulting from selfs of the two original parents that were caged together. The F_1 bulbs are harvested and then caged together to produce an F_2 progeny, or they can be used in a backcross program.

Once the selection process has begun in a segregating population, selfing is necessary for two generations to determine which progeny lines are desirable. To obtain the selfed populations, small individual cages are used to prevent outcrossing (Fig. 10.5). Flies are most commonly used to make these pollinations. Once desired progeny lines are selected, the breeder must begin making three to five bulb selections from the progeny rows and mass them in small cages. These are usually 2 × 2 ft, made of a nylon screen material, and fitted on a frame (Fig. 10.6). Flies are again the best choice to pollinate the small mass lots. Once a good line has been selected for commercial testing, a seed increase must be made in a large cage or small field isolation. Cages may be used up to 100 ft long by 12

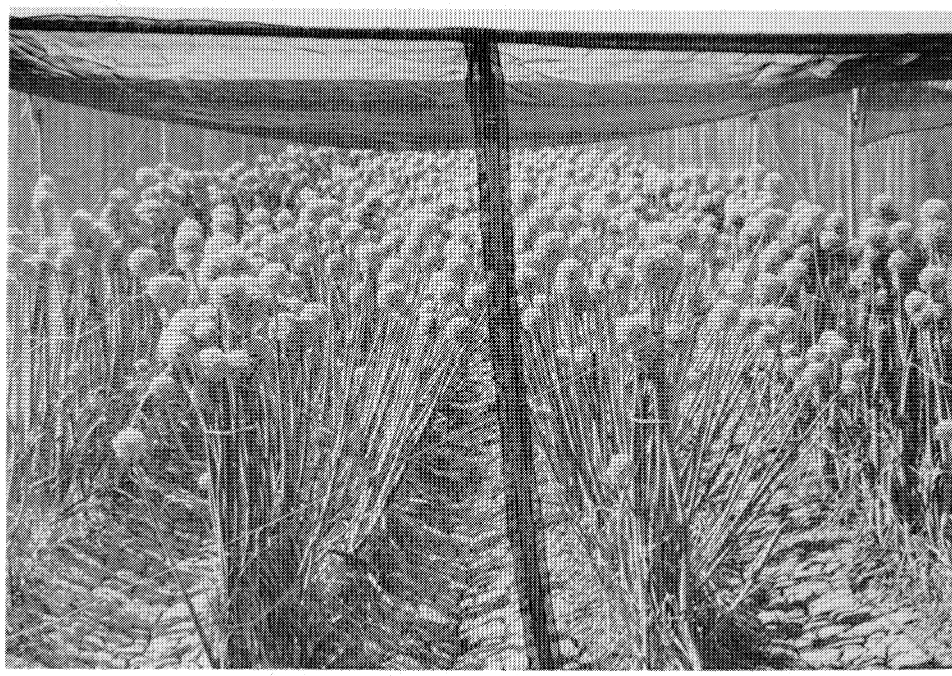

FIGURE 10.7. Large screen cages are used to increase seed for small commercial testing. Bees are used to obtain pollination.

ft wide (Figs. 10.7 and 10.8). Bees are used to pollinate the onions in large cage increases. Small field isolations and commercial seed production must be separated from other flowering onions by one or more miles to ensure production of noncontaminated seed. Greater distances should be used, if possible, for breeding lines being produced without screen cages.

Male sterility is another factor in pollination control for the onion, which is normally a highly outcrossing species. The male-sterile mechanism involves both genetic and cytoplasmic factors as mentioned earlier and will be discussed as a means of pollination control in the onion breeding section.

BREEDING ONIONS

After this general presentation of flowering and pollination control in onions, we can proceed into breeding of the crop. Onions fall into two major types, known as short-day and long-day onions. However, a third group should be recognized as intermediate day length types, which bulb somewhere between the two major groups.

My observations suggest that some cultivars may actually be day length insensitive, but at present no actual data have been produced. Considering the normal long-day and short-day onions, those that bulb when the day length exceeds approximately 11.5 hr fall into the short-day group, and onions that require 14 hr or more to bulb fall into the long-day group. These are general groups and may vary 1 hr either way since temperature also alters bulbing. Therefore, onion breeders must be aware of the requirements of a particular location to select the correct germplasm to begin their program.

The life cycles of short- and long-day onions differ considerably and must be understood by the breeder. Short-day types are planted in the United States as seed in the fall, generally between October 15 and November 15, and are grown to maturity during April and May. This may vary by as much as 1 month either way depending on location. Bulbing requires approximately 180 days when grown as a seed-to-bulb crop. Bulbs are harvested and stored until September 15 to October 1, then reselected and planted to produce seed. Therefore, storage time is approximately 150 days. The planted bulbs begin growing immediately and will flower during May of the following spring with seed maturing in July.

Long-day onion seed is planted generally during late March and April to produce bulbs that mature in early September. Maturity requires approximately 150 days. Bulbs are harvested and stored until April, and then planted to produce seed. Flowering occurs in late June with seed maturing in August. Should the breeder decide to utilize seed-to-seed practices, seed must be planted in mid-August to produce a large plant to overwinter so that it will flower the following spring. Seed-to-seed production is a method of forcing an immature plant into flowering without producing bulbs. Plants must have produced four or more leaves and attained a diameter of approximately ⅓ in. before being subjected to temperatures below 45°F for flowering to be initiated. No definite size of plant or number of hours below 45°F can be presented as cultivars respond so differently. Most onions that are large enough to be initiated for flowering will flower if subjected to 7–10 consecutive

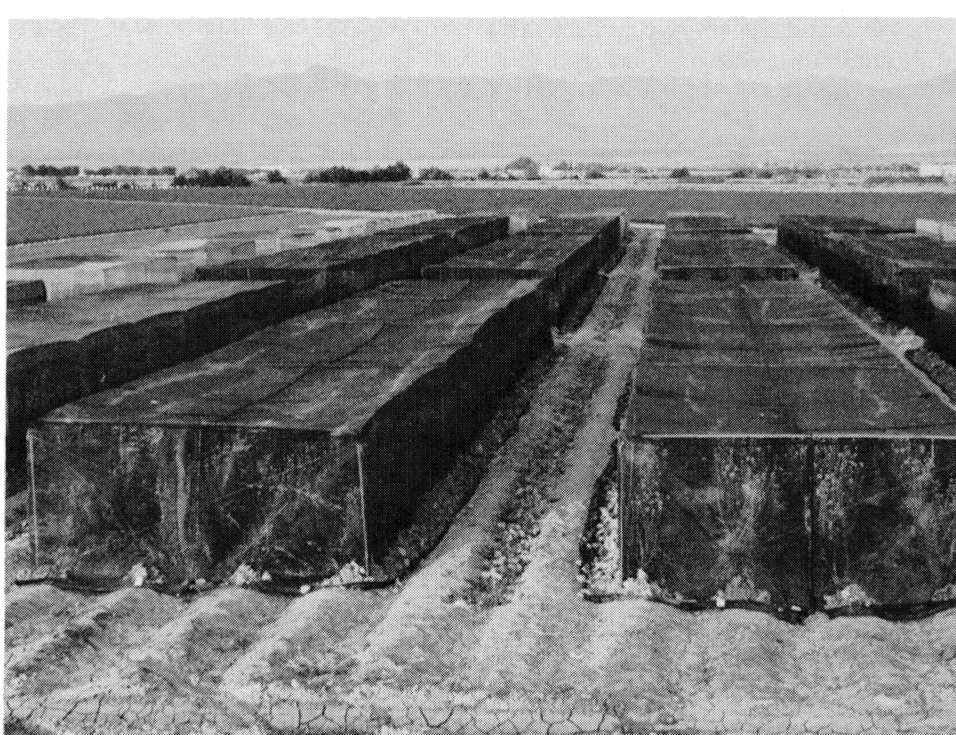

FIGURE 10.8. Large screen cages allow for isolation of several breeding lines of onions in close proximity of each other rather than providing one or more miles of separation for small field increases.

days of temperatures below 45°F or for longer periods of 50°F. Some cultivars are much more resistant to bolting and require more cold induction to cause flowering. It seems that several factors influence flowering. For example, if warm temperatures follow cold weather, bolting will be less than if followed by cool weather. Plant age and certainly plant size are important. The older and larger the plant, the easier it can be induced to flower. Therefore, when using seed-to-seed practices, it is extremely important to provide conditions that will cause all plants to flower, thus preventing selection pressure favoring easy bolters.

In addition to long- and short-day bulbing types, there are onions for different uses within those two categories. The three main types include fresh market, storage, and dehydration. In general, long-day types are primarily storage onions and short-day types are primarily fresh-market onions. Dehydrators may be either short- or long-day types. However, I recently developed two short-day onion cultivars that store for long periods of time, which shows that it is possible to develop short-day storage types (*29*), a development contrary to the conventional wisdom. Most long-day onions are much more pungent than short-day types. Again however, some long-day types are fairly mild and may be used for fresh market.

Major Breeding Achievements

The onion has been greatly improved in characteristics such as quality, yield, uniformity, and breeding practices. Breeders developed the crop during the years 1925–1940 to the point that it might be considered a classic example of crop improvement. The work done during that period, primarily by Henry Jones and co-workers, provided an enormous amount of information on the crop dealing with genetics and breeding methods. Jones worked on onions for over 50 years. Unfortunately, little new information has been published on the genetics and breeding of onions during recent years, mainly because Jones did such an excellent job of research and also because of the long-term efforts needed to study the crop. However, excellent cultivar improvement has been achieved by present-day onion breeders in relation to yield and quality.

The common onion, *A. cepa,* has a basic chromosome number of $n = 8$ and is known only as a diploid ($2n=16$). Extensive studies on meiosis and mitosis of the crop and related species have been done by Cochran (*3*), Emsweller and Jones (*7*), Levan (*20*), and Maeda (*23*). The reader is referred to these papers for detailed description.

Cytoplasmic Male Sterility

The most notable achievement with onion breeding began in 1925 when Jones and Emsweller (*14*) discovered a male-sterile plant in the cv. Italian Red growing in their breeding nursery at the University of California at Davis. The breeding entry was identified as 13–53 and is considered the historical pedigree number of male sterility. The plant produced no seed but did produce several bulbils among the florets, which saved it from extinction. The bulbils were saved and replanted to produce new plants. They were crossed with other onions, and the resulting progenies were studied to determine the inheritance of the male-sterile character. The results proved that the character was conditioned by an interaction between a recessive nuclear gene and a cytoplasmic factor. The cytoplasmic factor was designated N for normal fertile cytoplasm and S for the sterile condition. The nuclear genetic condition was designated as *Ms/–* for the normal fertile condition and *ms/ms* for the sterile condition. There are various combinations of genetic

TABLE 10.3. Progenies Resulting from Various Genetic and Cytoplasmic Combinations Crossed onto a Male-Sterile Onion Line[a]

Male-sterile line (A)		Male-fertile line (B)	Progenies
S*ms*/*ms*	×	N*ms*/*ms*	S*ms*/*ms*
		N*Ms*/*ms*	S*Ms*/*ms*
			S*ms*/*ms*
		N*Ms*/*Ms*	S*Ms*/*ms*
		S*Ms*/*Ms*	S*Ms*/*ms*
		S*Ms*/*ms*	S*Ms*/*ms*
			S*ms*/*ms*

[a]Only the S*ms*/*ms* condition is male sterile.

and cytoplasmic factors that provide male sterility and fertility. Table 10.3 illustrates why male sterility can only be maintained by having two lines with the following condition. The female line must be homozygous for S*ms*/*ms* and the male line must be homozygous for N*ms*/*ms*. Keep in mind that the fertile cytoplasmic factor does not transfer to the female during the cross. Therefore, the N cytoplasm provides for normal fertility in the male line (known as the maintainer or B line), yet does not restore fertility in the progeny when crossed onto the female line (known as the A line). Any other combination of genetic and cytoplasmic factors in the male line will give either fertile or segregating progenies.

It is important for the breeder to understand fully the information presented in Table 10.3 so the system can be handled in the breeding program. By using any known male-sterile line and any breeding selection that proves to a B line (identified by making testcrosses), the breeder can easily develop new A line–B line pairs in which the genotype of the A line will, through backcrossing, become identical to that of the B line.

The system shown in Table 10.4 shows that within six or more backcrosses, the A line

TABLE 10.4. The Method of Developing New A Lines in Onions Using the Backcross Method with Identified B Line Selections

Male-sterile line (101A)		Identified B line (101B)	
S*ms*/*ms*	×	N*ms*/*ms*	
S*ms*/*ms*	×	N*ms*/*ms*	(BC_1)
(50% 101A, 50% 101B)			
S*ms*/*ms*	×	N*ms*/*ms*	(BC_2)
(25% 101A, 75% 101B)			
S*ms*/*ms*	×	N*ms*/*ms*	(BC_3)
(12.5% 101A, 87.5% 101B)			
S*ms*/*ms*	×	N*ms*/*ms*	(BC_4)
(06.25% 101A, 93.75% 101B)			
S*ms*/*ms*	×	N*ms*/*ms*	(BC_5)
(03.12% 101A, 96.87% 101B)			
S*ms*/*ms*	×	N*ms*/*ms*	(BC_6)
(01.56% 101A, 98.44% 101B)			

originally used has become essentially identical to the recurrent parent B line for all other genetic traits except fertility.

Genetics of Bulb Color

In addition to male sterility, studies on the inheritance of onion bulb color have been major contributions. The inheritance of color is very complex and creates major problems in both breeding the crop and producing commercial seed. A study by Clarke, Jones, and Little (*2*) provided the major work. Jones and Peterson (*17*) reported on the inheritance of a condition where yellow crossed by yellow gave all pink bulbs. El-Shafie and Davis (*6*) reported data suggesting that two additional genes, *G* and *L*, were responsible for variations in color of onion bulbs. More research is needed to explain more completely the many total color patterns that continually present themselves but do not fit the simple explanations as reported.

When the *I/I* condition exists, the bulbs will be white regardless of the other color genes (Table 10.5). The *I/I* factor is known as a color inhibitor gene and acts as a dominant gene in the homozygous condition. In the heterozygous condition *I/i* this gene gives an off-white or buff-colored bulb. When the genotype is *i/i*, the other color genes *C/–* and *R/–* are expressed and condition the color of the onion bulb. It should be noted that a recessive white condition occurs when the *c/c* genotype exists regardless of the genotype at the *R/–* locus. In addition, the fact that pink color occurs when crossing two

TABLE 10.5. The Genetics of Several Traits in the Onion Summarized[a]

Onion traits	Genetic condition
Albino seedling	*a/a*
Yellow seedling linked with glossy	*y1/y1*
Yellow seedling not linked with glossy	*y2/y2*
Pale green seedling	*pg/pg*
Virescent seedling	*v/v*
Glossy foliage	*gl/gl*
Exposed anther	*ea/ea*
Yellow anther	*ya/ya*
Pink root resistance	*pr/pr*
Male sterility[b]	*ms/ms*
Bulb color	
Homozygous red	*i/i,C/C,R/R*
Heterozygous red	*i/i,C/c,R/R*
Heterozygous red	*i/i,C/C,R/r*
Heterozygous red	*i/i,C/c,R/r*
Homozygous yellow	*i/i,C/C,r/r*
Heterozygous yellow	*i/i,C/c,r/r*
Homozygous recessive white	*i/i,c/c,R/R*
Homozygous recessive white	*i/i,c/c,R/r*
Homozygous recessive white	*i/i,c/c,r/r*
Homozygous dominant white	*I/I,–,–*
Heterozygous dominant white (buff)	*I/i,–,–*

[a]The studies were conducted by Clarke, Jones, and Little (*2*) and Stevenson (*13*).

[b]Male sterility is expressed as a recessive when in the presence of sterile cytoplasmic factor S.

homozygous yellow bulbs creates a complex problem. This indicates the existence of complementary genes that modify bulb color. I have also observed variation of color intensity within most colors such as were reported by El-Shafie and Davis *(6)*. For example, color may vary from deep purple to pink, dark yellow to very pale yellow, and even differences in brightness in the white bulbs. There are possibly many complementary and additive genes involved in onion bulb color. Selection in my program has led to development of bright-yellow cultivars and very deep red breeding lines, which have pigment going to the center of the bulbs.

Inheritance of Morphological and Other Characters

In addition to male sterility and color, most other characteristics seem to be conditioned by multiple genes or additive action. McCollum *(26)* reported heritability to be low for bulb weight and diameter, intermediate for height, and high for solids. Bulb shape is an important selection criterion, and the desired shape depends on the market preference. Genetic variability for shape ranges from extremely flat to oblong. Crosses between extreme shapes tend to produce F_1 bulbs intermediate between the two, but more toward the flat parent. Unless constant selection pressure is applied, the drift in shape moves toward flat. Single-center onions are important for producing nice, round-shaped onions with complete rings for onion ring processing and better storage. This trait is probably conditioned by additive gene effects and tends to drift to types with multiple centers unless constant selection pressure for single centers is applied. Ease of bolting is another important trait that acts the same way. Bolt resistance is important to prevent loss of yield to seedstem formation in bulb production. Unless constant selection pressure is applied for bolt resistance in a breeding program, the drift is toward easy bolting. Long storage and high percentage dry matter fall into the same categories. The trend of drift is toward poor storage quality and lower soluble solids. Foliage color, foliage morphology, disease resistance, and insect resistance are generally controlled by multiple genes. Jones and Perry *(16)* reported the inheritance of pink root disease resistance under field conditions to be controlled by a single recessive gene, which was later confirmed by Nichols *et al.* *(26a)* using a laboratory screening test. However, this resistant gene does not hold up to all strains of the fungus. My observations suggest a more complex inheritance because various levels of resistance have been observed. Several plant type characters under simple single-recessive gene control have been studied and are shown in Table 10.5. Thrip resistance was shown to be linked with the glossy-foliage character by Jones, Bailey, and Emsweller *(11)* and Peterson *(27)*.

I have made several crosses between long-day and short-day types in my breeding program and observed that bulbing response is somewhat intermediate between the two parents but tends to be closer to the short-day parent. I have also observed that date of flowering correlates closely to bulb maturity. In other words, earlier maturing breeding lines or cultivars tend to flower earlier. This is important to know when planning to make hybrids, as flowering dates must be close enough to achieve making the cross in commercial hybrid seed production.

Goals and Objectives

Plant breeders must have established objectives within their programs before they begin breeding onions. They must know if they need to be working with long- or short-day types and whether the industry they intend to serve has a storage market, fresh market, or dehydration market. They must also be familiar with the disease and insect problems of the intended production areas and the onion bulb color preference of the intended market. In most instances, the size and shape of the bulbs are important. Pungency, lack of pungency, and percentage dry matter are important depending on the intended use of the onion. Examples include sweet mild onions for fresh-market use, firm long-storage types for processing and exporting, and a high-percentage dry matter with white color for dehydration. Onions used in salad bars should be mild, sweet, and red for good flavor and have an attractive appearance in the fresh salad. The various combinations of requirements are too many to list, but knowing the needs of the industry is very important in establishing the breeding objectives. These facts are mentioned because breeding onions is a long-term, complex, and expensive project.

In general, however, the resulting cultivar or hybrid should be of the type desired by the particular industry, including shape and color. It should be uniform for all characteristics including maturity. It should be high yielding, resistant to as many diseases and insects as possible, free of other defects such as short storage life, and easy bolting. It must be adapted to the area where it is to be grown, taking into consideration its sensitivity to day length, temperature, and other climatic conditions. Therefore, the breeding program should be in the location where the crop is to be grown; or at least the progeny selections must be made in that area because onions are not widely adapted to different growing conditions.

Selection Techniques

Selection techniques used in improvement of onion cultivars differ depending on whether the breeder is developing open-pollinated cultivars or hybrids. It will also differ between onion breeders. Some breeders practice more selfing than others; some believe only in developing hybrids. I shall discuss breeding techniques that have proven productive in my program for development of open-pollinated cultivars and shall present techniques used by the majority of onion breeders for improvement of hybrids.

The trend has been toward development of hybrids by commercial seed companies for two reasons: (1) hybrids are generally more uniform, and (2) this system prevents production of that hybrid by other seed companies. However, after passage of the Plant Variety Protection Act in 1970, some work is being done on development of improved open-pollinated cultivars. I feel that open-pollinated cultivars continue to have a place because they do not have such a narrow genetic base as hybrids and may prove to be better adapted to the environmental stresses that occur in many areas of production.

Several important qualities in onions are not visible to the eye, and so they need specialized selection methods. These will be briefly discussed here.

Selection for Dry Matter

The dehydration industry requires a much higher solids onion ($\geq$20%) than found in fresh-market or other processing types. The breeder cannot visually distinguish between low and high solids, and so instruments must be relied upon to assist in the selecting process. Most breeders use a refractometer to determine soluble solids, which provides a good estimate of dry matter. A good-quality hand-held refractometer is adequate for this selection process. Only one drop of juice is required from each bulb for determining its soluble solids. This can be obtained by taking a small plug of bulb tissue with a cork hole cutter or knife, and then squeezing the juice onto the glass plate of the refractometer.

Bulbs with high solids are saved for replanting. This method of selection has proved to be highly successful by breeders who put strong continual selection on dehydrator types.

Selection for Storage Quality

Storage quality is extremely important in onions as they are held for the most part in noncontrolled storage conditions. Many unknown factors seem to determine shelf life, and so the only method of screening is with storage trials. Long-day types should be stored under similar conditions (cool and dry) as the commercial crop. Short-day types should be stored under warm, humid conditions similar to those which occur during harvest of the crop. Good ventilation should be provided in storage for both short- and long-day types. The reason for suggesting storage of short-day onions under warm, humid conditions is that a high percentage of the short-day production is in hot, humid areas of the world. Therefore, they must be adapted to those poor natural handling and storage conditions. Selection is made in each generation for bulbs that do not sprout or rot in storage. Excellent progress can be made for better storage quality in three generations. There seem to be two major contributing factors involved in storage quality: in my observations, dormancy seems to be the primary factor and disease resistance a major secondary factor. If either one is weak, sprouting and or rotting occurs soon after harvest.

Selection for Flavor

Onion flavor is a factor that has no real guidelines. To one group of consumers, pungency is desired, while to another a lack of pungency is preferred. Generally, pungency is important for cooking onions while mildness is favored in fresh-market types. Pungency, lack of pungency, and sweetness are difficult to measure and actually vary within a cultivar depending on what time of year and where the onions are grown. Extreme differences also occur between cultivars and can be incorporated into new cultivars or hybrids through selection. The method for selection is difficult for two reasons: (1) variability as a result of growing conditions, and (2) the lack of a good measuring technique. At present, taste tests are the best selection method, with most of the effort going into the short-day fresh-market types, where sweetness and mildness are extremely important.

Development of Open-Pollinated Cultivars

It must be understood that open-pollinated cultivars are extremely heterozygous for many genetic traits. They may look uniform when observed in a production field; however, after selfing, the resulting progenies will look very different.

First Year

Breeders should begin by growing out several open-pollinated cultivars or plant introductions that they feel will contribute to achieving their objectives. Selection of 200 bulbs from each line should be made during the growing season in the area of commercial production, and then stored until planting time to produce the seed crop. For long-day types, the selection is in the fall and bulbs are stored at above-freezing temperatures until early spring. They are induced to bolt in storage and will flower following growth when planted in the field the next spring. Short-day types are selected in the spring, as they are grown during the winter months and bulb in early spring. They are stored during the summer at ambient temperatures in covered buildings and then replanted in the fall after

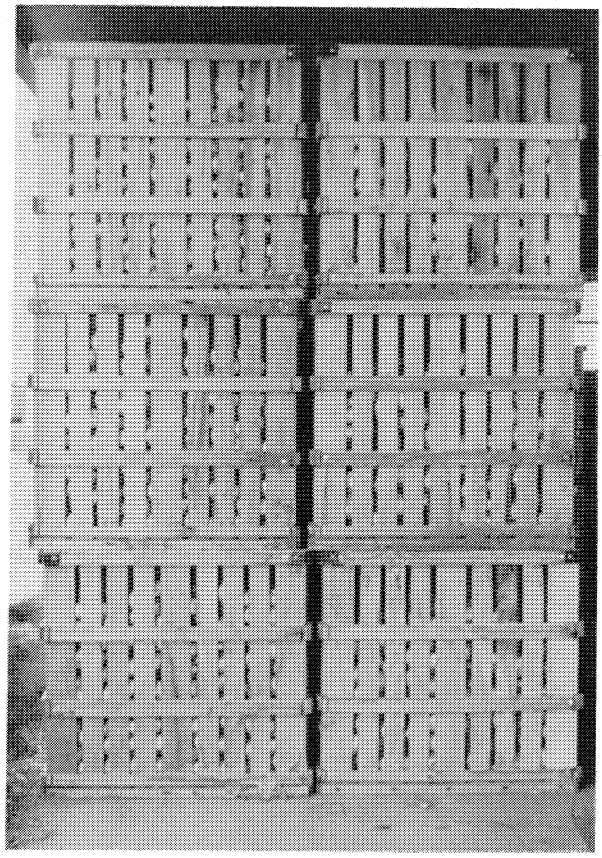

FIGURE 10.9. Onion bulbs stored in ventilated wood pallet boxes. Good ventilation is essential for long storage.

their dormancy is broken (Fig. 10.9). They sprout and grow during the winter and flower the following spring. These are the main differences in handling mother bulbs of the two types. Selection pressure should be applied for storage and possibly single centers, but little else, because much segregation will result from the first selfing.There should be at least 100 bulbs left for planting from each cultivar or as many as can be handled in cages and progeny rows the following year.

Second Year

A minimum of 100 bulb selections from each cultivar should be planted for selfing. At the same time I suggest making several fertile × fertile crosses to bring in additional germplasm that might not be achieved by selfing within a single cultivar. If breeders intend also to work simultaneously on hybrids, they should pair a known sterile bulb with the selection they intend to self. This immediately provides a testcross progeny to determine if that particular selection is a maintainer (B line). This will be discussed more fully in the section on hybrid development. The selected bulbs must be planted in a manner so they can be caged when flowering occurs (Figs. 10.10 and 10.11). Several types of selfing cages are used, ranging from paper bags covering the umbels to special designs of

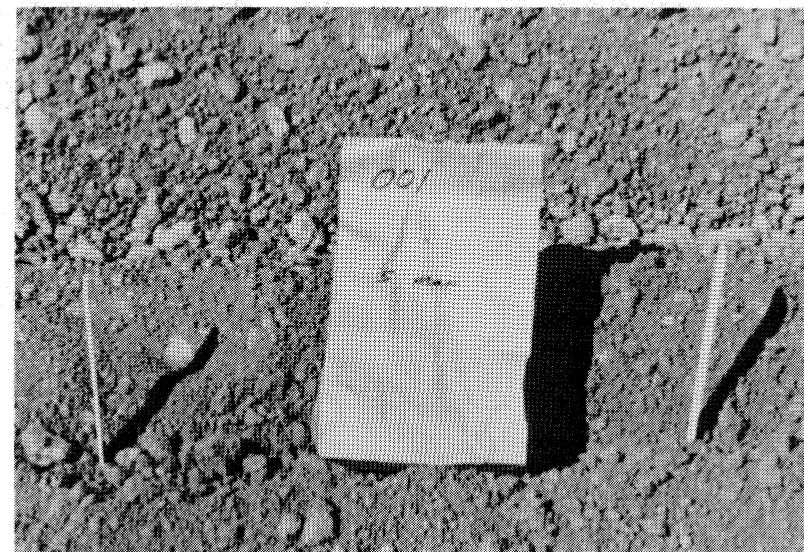

FIGURE 10.10. Bag showing field number and instructions to plant as a five-bulb mass. Bulbs and numbered field stake are in bag ready to plant before going to the field plot. The two stakes limit the area to be planted so that a cage can be placed over the flowering onions in the spring.

FIGURE 10.11. Laying out small-lot selections of onions in a breeding-seed increase plot.

aluminum screen mesh or nylon cage covers. Once the cages are placed over the plants, pollination must be achieved. I use common house flies placed inside the cage as pupae, which hatch and pollinate the flowers as they feed on nectar. Other breeders use house flies or blow flies, and some even use honey bees or small brushes. Handling of bees is difficult as is using brushes, and obtaining blow flies in large quantities has been a problem. Whatever method of pollination works best for the breeder is undoubtedly the one that should be used. After selfing or the making of fertile × fertile crosses, seed should be allowed to mature. When black seed can be seen in a few capsules, harvest and dry the seed being careful not to mix lots. The seed should be quickly threshed and placed in a good seed storage room because onion seed loses viability within a few weeks if exposed to hot, humid conditions. Keep in mind that it takes 2 years to complete one generation of breeding onions: it takes 1 year to grow, make, and store bulb selections, and a second growing season to produce the seed. Many breeders, including myself, have attempted to obtain early flowering from selected bulbs but have not been successful. Seed to seed is possible in 1 year, but no selection for bulb characteristics is possible using that technique. However, seed to seed is practical in developing new A lines and will be discussed later.

Third Year

Plant S_1 seed from selfs or F_1 seed from crosses in the breeding plots during the same season, as commercial growers might be expected to do in their fields. I prefer to use a lower seeding rate than commercial rates, however, so that bulb evaluation will be easier to accomplish. For example, many growers plant four rows per bed or at high rates to obtain stands under poor weather conditions or to achieve maximum yields. I prefer two rows per bed so that bulbs will have the potential to develop size and express their true shape. Different cultural practices in different onion-growing areas will dictate breeder production practices. It is important that selection be practiced in the same area and under similar conditions as on commercial farms. Ten feet of progeny row should be sufficient for producing F_1 bulbs and 40 ft for S_1 lines. If seed is available, two separate plantings should be made to ensure against loss due to uncontrollable conditions. Thirty bulbs of F_1 and 100 bulbs of S_1 progenies should give the breeder sufficient observations for making selection decisions and providing material for advancement. Each progeny line should be kept separate to evaluate progeny lines at this time. Strong selection pressure for all traits in the objectives for each generation should be applied. For example, if resistance to pink root disease (*Pyrenochaeta terrestris*) is an objective, grow the plots on pink-root-infected land (Fig. 10.12). There is no reason to select bulbs that do not have the necessary genetic potential to make a new cultivar. The only exception is if the F_1 bulbs are being grown from a cross. In that case, the only interest in obtaining the F_1 bulbs to replant is to get the F_2 seed.

First, select progeny lines that show resistance to disease and the desired shape, color, etc. Discard poor progeny rows completely. Then make selections within the best progeny rows. I prefer to keep all the acceptable bulbs from the selected progeny rows, up to 100, because this is only the initial selection process. Many of these bulbs may be lost in storage, which is fine, as storage quality should be a major goal in all breeding programs. Also, extra bulbs allow for further selection such as for single centers, good interior color, and high dry matter. Then only the best 10 bulbs within each selection will be used for replanting to obtain the second selfing. I should note that occasionally, if a large number

FIGURE 10.12. A progeny resistant to the pink-root organism, *P. terrestris.* Note the healthy root system even at bulb maturity.

of selfs are made, progeny rows may be found that are extremely uniform and may be massed for immediate increase to release as an improvement of its parent cultivar. I have seen it occur only once out of several thousand selfs, but the possibility does exist.

In most instances, the new onion breeder will be surprised to see that most selfs will give very different progenies from what would be expected from the cultivar chosen as the parent source. For example, 100 selfs out of a given cultivar might provide 100 different phenotypes. Some will seem very poor as breeding lines, while others may show good uniformity, and occasionally one will appear outstanding. This is due to the fact that the onion is an outcrossing species and is in a heterozygous condition at many loci.

Fourth Year

Store the selected S_1 and F_1 bulbs until time for replanting, when further selection is made for other quality traits just prior to planting. Most breeders cut off the top one-third of the bulbs to check for color, single centers, ring thickness, etc., before planting. Selection pressures should be severe at this time to prevent ending up with thousands of progeny rows the next generation. The final selection for selfing should include 5–10 of the best bulbs from each of the selected progeny rows. The breeder should make a few three- to five-bulb masses from rows that were uniformly good, as the possibility exists for quick improvement of a cultivar in onions. Jones and Mann (*15*) reported success with this method also. If segregation occurs in the next generation, those progenies can be discarded or new selections can be made. Obtain seed from the second selfing as described for the first selection.

Fifth Year

Plant the S_2 and F_2 seed to produce bulbs. The progenies this year represent bulbs that have resulted from two selfings or F_2 progenies from original crosses, depending on which choice was made in the beginning of the program. Progeny lines resulting from selfing will generally be surprisingly uniform for most characteristics, depending on the selection criteria in the previous generation. Therefore, in this third selection process only very uniform progeny rows should be saved. The main exception is color if two different-colored onions were crossed in the beginning. If that was the case, study the inheritance of bulb color in order to make the right decisions regarding color selections. If not, the work to obtain the desired true-breeding color will take many years longer than necessary. Store bulbs as described earlier.

Sixth Year

Since onions suffer from inbreeding depression, it is not advisable to plan on a third selfing for development of open-pollinated cultivars.

Following the final selection process, and just prior to planting, select several 12- to 15-bulb groups that look identical for the traits desired. These are then planted to be massed in small cages. I use Saran screen cages on pipe frames 2 × 4 ft. The reason for several small masses selected from each progeny line is that these bulbs are still heterozygous at several loci, and the probability of getting a uniform cultivar is greater by using several cage masses rather than one. This procedure has worked very well for me, especially where bulb color, shape, and maturity are also objectives.

It should be mentioned that breeding procedures are the same in handling bulbs resulting from an original cross beginning with the F_3 progeny. In other words, F_3 bulbs should also be handled as small masses. In most instances, seed obtained from the small three- to five-bulb mass will produce uniform progenies.

Seventh Year

I prefer to plant seed obtained from the small masses of the S_2 or F_3 bulbs in observational trials, which are grown in the same manner as commercial onions. Select only from the best progenies. Harvest 200 or more bulbs and store for use in seed production.

Eighth Year

Selection should be made for storage quality, uniformity, single centers, solids, or other qualities, depending on program objectives as before. Approximately 100 of the best bulbs should be planted in a 9 × 10 ft cage to produce enough seed to begin replicated trial testing. Seed yields should be observed and recorded along with other plant characteristics that might be useful in obtaining plant variety protection or use as a future pollinator in hybrid seed production.

Ninth Year

Seed should be planted in replicated yield trials and, if possible, in small plantings on commercial onion farms. Several locations will help in deciding which lines are best. If lines prove to be superior, select enough bulbs to plant a 12 × 24 ft cage to obtain seed for several small grower evaluations.

Tenth Year

Plant the 12 × 24 ft cage to make the seed increase. If the line is not sufficiently uniform, cut the bulbs to observe for single centers, solids, and other quality characteristics. I prefer to continue to make such selections until the final release. Again, observe and record plant flowering habit, seed yields, and other plant characteristics.

Eleventh Year

Seed produced is entered into the yield trial and if possible put out with a few selected growers. The decision is made during that season to increase the line further. Shipping quality is observed and the final decision is made for release as a new cultivar. Note that onion breeding is certainly a long-term program, requiring 11–13 years to develop the new cultivar (Table 10.6). I stress using strong selection pressures and large numbers of progeny lines to ensure success.

Development of New A and B Lines

To utilize the male-sterile condition in hybrid development, the breeder must develop pairs of breeding lines known as A and B lines. These lines are developed as was shown in Table 10.4 by continual backcrossing of the B line (fertile) to the A line (male sterile). After five or more backcrosses, the A line has essentially the same nuclear genotype as its B line. The B line is used to maintain the seed supply of the male-sterile A line. Since the fertile cytoplasm factor is not transferred to the female, the A line remains male sterile when crossed with the B line, which differs only by its sterile cytoplasmic factor. Both factors, genetic sterility and cytoplasmic sterility, must be present for the plant to be male sterile.

TABLE 10.6. A Schematic System for Breeding Improved Open-Pollinated Cultivars.

Year	Procedure
1	Grow source lines and select 100 bulbs; store bulbs
2	Plant selected bulbs and self
3	Plant S_1 seed in progeny rows, select best bulbs from best progeny rows, discard poor progenies completely; store bulbs
4	Plant S_1 bulbs and self 5–10 selected bulbs from each progeny; also make a few 3–5 plant masses from same progeny rows
5	Plant S_2 seed and three-bulb mass seed obtained in fourth year; select lines that look best; if any 3- to 5-plant masses look good and are uniform, select those lines also; store bulbs
6	Plant S_2 bulbs, i.e., mass 12–15 S_2 bulbs from selected progeny rows
7	Plant seed to begin observation trial testing and early evaluation of bulbs; select superior progenies and discard others
8	Mass 100 bulbs and plant in a 9 × 10 ft cage for small seed increases of selected lines
9	Plant seed for yield trials, and in small plantings on commercial farms; several locations will help in deciding which lines are best; select stock bulbs for seed increase
10	Plant bulbs to make a 12 × 24 ft cage for seed increase; observe seed yields
11	Plant several commercial plantings to evaluate for all requirements such as shipping, storage, and processing, which was not possible during earlier testing
12	Release superior line as a new cultivar

The best way to develop new A lines is to make testcrosses of plants from open-pollinated cultivars with known A lines to identify any *ms/ms* genotypes within those populations (Table 10.7). From my experience and that of other onion breeders, one can expect to find approximately 5% B lines in any population of most cultivars (Fig. 10.13). It has been reported by Little *et al.* (*22*) and Davis (*4*) to be as high as 50% for the *Ms/ms* condition. Therefore, by pairing up single bulb selections from cultivars or breeding lines with known A-line bulbs, one can determine which pollinators were B lines by growing out the F_1 progenies. The F_1 progenies with 100% male-sterile plants indicate which selections were B lines. Seed of the selfed selection from each testcross must be saved so that once the B lines are identified, they can be used in a backcross program to develop the A line to the point where it is identical in genotype to the B line selection. The above procedure usually involves many pairs in the onion-breeding program because the development of a new A line does not ensure that it will make a good hybrid. Once several A lines are developed, they must be tested with other inbred B lines or C lines in hybrid combinations to determine if they will make superior hybrids.

Development of new A lines and their maintenance requires the same repetitive procedure. It is a continual backcrossing process, the only difference being cage size or field isolation. The A lines must continually be rogued for any fertile plants and the B lines should continually be rogued for the type desired. Extreme care must be taken to prevent mixing seeds or bulbs in the program. In all phases of bulb or seed storage, growing, and handling, the A and B lines should be kept separate. For example, A-line bulbs should be grown as a group separate from B- or C-line bulbs. Seed should also be cleaned separately, as either A- or B-line groups to prevent accidental mixing.

The procedure described is the easiest way to develop new A lines and the only way to maintain or increase A-line seed. However, it is possible to make crosses between known B and C lines to make new B lines, and then go into a backcrossing program with a known

TABLE 10.7. A Procedure to Develop New Male-Sterile Onion Breeding Lines (A Lines) Using the Testcross and Backcross Method

Year	Known A-line bulb	Fertile selection bulb
1	Plant bulb	Plant bulb; self and cross to A line
2	Plant F_1 seed	Plant S_1 seed
3	Plant F_1 bulbs following storage at 40°F or plant and overwinter; read at flowering and pair with B-line selection under a screen cage if all are sterile to make first backcross; if not 100% sterile, discard	Plant S_1 bulbs along side F_1 bulbs, using 5–10 bulbs to prevent severe inbreeding; pair with sterile F_1 plants; if F_1 was segregating or fertile, discard at this time; cage with the sterile F_1 to make 1st backcross; mass 3–5 bulbs of the S_1 (B line)
4	Plant BC_1 seed to produce BC_1 bulbs	Plant seed from small mass of B-line selections to produce S_2 B-line bulbs; make selections for type desired
5	Store at 40°F or plant and overwinter; observe flowers for male sterility; all should be sterile; cage with B line	Same induction procedure as A line; plant beside BC_1 A line; cage with new A line to make second backcross
	Continue until fifth backcross	Continue until fifth backcross
	New A line	B line, maintainer for A line

FIGURE 10.13. Small cages are used for making testcrosses where a known A line is paired with a selected bulb. Several hundred pairs are usually made, as about 5% of the selections are expected to be B lines from any given population.

A line. A third method of obtaining new A lines is possible if the breeder has the opportunity to observe flowering in large fields where seed is being produced. In several cultivars, a very low percentage of male-sterile plants has been observed. Peterson and Foskett (*28*), Kobabe (*18*), Banga and Petiet (*1*), Makarov (*25*), and Yen (*37*) all reported observing such male-sterile segregants in seed production fields. I have observed occasional steriles in breeding lines as well as cultivars. When male-sterile lines are found within a cultivar, they can be paired with a fertile in a testcross. If by chance the seed saved from the male sterile is 100% sterile, the breeder knows that the selection used in the testcross was a B line. There is thus, an immediate new A line with a maintainer B line without the necessity of going through all the backcrossing described above.

Development of Hybrids

The development of hybrids in the onion follows a completely different approach from development of open-pollinated cultivars. In cultivars, uniformity of certain desired characteristics is sought while at the same time maintain heterozygosity in order to keep plant vigor. In hybrids, it is possible to develop inbred lines having much more homozygosity and less vigor, because that vigor will be restored when the inbreds are crossed. In many ways, the development of hybrids is the easier of the two methods of cultivar improvement as it allows the breeder to work with more homozygosity. Better evaluations of the true genotypic value of desired selections can be made. The time required to develop improved hybrids and the effort needed to maintain inbred lines are much greater. Hybrids require development of A lines, their B-line maintainers, and C lines that are inbreds used as pollen parents in hybrids. If the breeder decides to make three- or four-way hybrids, then the time of development and testing is greater and the procedure more complex.

When planning a new hybrid onion-breeding program, one should not anticipate new hybrids before 15–20 years. If good A lines are available, new improved hybrid combinations can be expected in approximately the same length of time to develop new open-pollinated cultivars. As mentioned earlier, it is possible to work both programs simultaneously if when selfing, a sterile is included in the cage to make a testcross. However, I shall approach development of hybrids as a separate method and readers can decide which system to use in their programs.

First Year

Grow and select 50–100 desirable bulbs from each of the cultivars adapted to the area that show potential for use as a parent. At the same time, save an ample supply of A-line bulbs that have been grown from seed obtained from some other program. Sources include breeders within state Agricultural Experiment Stations, USDA, and commercial seed companies. Some hybrids are made up from A-line × B-line crosses and are therefore sterile. If necessary, use F_1 hybrids that were determined to be sterile. Store selected bulbs to allow them to go through dormancy as described earlier.

Second Year

Plant in two-bulb pairs: one will be a known A line and the second will be a selection. Cage the plants prior to flowering and leave a seedstem out on the sterile bulb if it has more than three. This allows for easier observation when checking for sterility. If it is sterile, simply break it off. If fertile, remove the entire plant and transplant another sterile in its place. Onions transplant fairly easily even when they are flowering. Be sure to pick off all open flowers on the fertile side of the pair if this is necessary, because some crossing may have occurred in the cage with the first plant, which was thought to be sterile. Begin placing fly pupae inside the cage and continue to do so twice a week for 3 weeks. Note that the plants must be free of insects such as thrips and spider mites prior to adding pollinators, because further spraying will also kill the flies.

After pollination is complete and seed set is observed, gently separate the umbels between the A line and its pair so that upon maturity, no possible mixing of seed can occur. The cage is removed at this time and it is advisable to stake the seedstems to prevent them from falling or getting broken by wind. Harvest the seed heads separately into small paper bags and number them as pairs so they can be maintained together throughout the remainder of the program. Also clean all seed from sterile parents separately from selfs. What is accomplished during the making of a testcross is identification of a possible B line from a chosen cultivar and selfing the fertile selection to start the inbreeding process. I prefer to number the pairs such as 40001 and 40002. The smaller odd number will always be the sterile pair for the next higher even number. The paper bags would read 40001 for the seed collected from the sterile and 40002 for the selfed fertile plant. Of course, other breeders use different systems and each breeder should use the system preferred. My numbering system always uses the year as the first digit and provides for 10,000 entries each year. This system provides numbers that do not show up again for 11 years. Note that entry numbers only need to be changed each generation, or every 2 years, because the bulbs grown and replanted are still the same generation as the seed planted to produce those bulbs. In other words, the new number assigned to the seed at planting will also be the same number assigned the bulbs when they are planted the following season.

I also begin another series of bulb selections the second year. By doing so, one does not have all bulb selections in the first year and all seed production in the second. The result is to have essentially twice as large a program with only half the required cages.

Third Year

The seed from the testcrosses and selfed bulbs are now ready to be planted. The seed should be assigned new numbers. It is important to separate all pairs into sterile and fertile groups and also to plant in that order. This prevents accidental mixing of sterile and fertile lines during planting and later during harvesting. At bulb maturity, select for desirable progeny rows within fertile lines obtained from the selfs. Discard all fertile lines not up to the standard of selection and also discard the corresponding sterile testcross progenies, because they serve no further purpose. Make selections within the selected fertile lines, a procedure similar to that described for improvement of open-pollinated cultivars. From the sterile testcross lines corresponding to the selected rows, select 25 bulbs that look healthy. No strong selection pressure is necessary at this time for the potential sterile line. Store selected paired progenies separately to ensure against accidental mixing.

Fourth Year

Plant 10 selected bulbs from the fertile S_1 progeny and the 25 taken from the testcross F_1 in paired rows (Table 10.8). Take extreme care not to mix bulbs during planting.

At flowering, carefully observe each F_1 plant for the presence of fertile umbels. If the total 25 plants are sterile, the probability is good that the paired self is a maintainer line having the cytoplasmic–genetic condition N*ms*/*ms* and can be classified as a B line. All open flowers on the 10 fertile plants and 10 of the sterile plants must be picked off to make the first backcross. The remaining 15 F_1 plants can be discarded. They should be caged as pairs to obtain the second selfing on the potential new B line and to make its backcross. Seed should be saved separately from each pair (self and cross) and handled as described earlier.

F_1 progeny lines that produced fertile umbels should be discarded along with their fertile pairs as they serve no purpose in the hybrid program. However, if you are also breeding open-pollinated cultivars, move the fertile line over into that program.

Fifth Year

Plant seed from both plants (S_2 and BC_1) as previously described in the nursery plots and again select the best progeny lines of the fertile side of the pair. Since this is now the second generation of selfing, the B lines will show considerable uniformity and the A-line pairs will begin to look similar to their maintainer. However, at this time much will

TABLE 10.8. A Schematic System for Breeding Improved Onion Hybrids

Year	Procedure
1	Grow and select 100 bulbs, store, and plant; also grow supply of male-sterile bulbs for use in testcrosses
2	Self selected bulbs and at the same time, testcross with known sterile
3	Grow out bulbs from self and F_1 testcrosses, select, discard poor progeny rows and their F_1 pair, store
4	Plant bulbs for seed production; observe sterility characteristics in F_1 lines; if 100% sterile, self selection and make backcross to F_1; discard pairs with fertile F_1 lines
5	Grow out A and B lines as pairs, continue to select in B line side, save best bulbs from A line for next backcross
6	Self B line of selected progenies and make backcross to sterile side of pair
7	Grow bulbs and make final selection on basis of B line side
8	Mass B line using 10–20 bulbs in cage while making the second backcross to the sterile side of the pair
9–12	At this point, begin going seed to seed and continue through the fifth backcross using the same procedure as in the eighth year; several A and B lines should have been developed; begin making hybrid combinations for testing

depend on how closely the original sterile resembled the fertile used in the cross. Select uniform bulbs from the most uniform progeny lines on the fertile side and, where possible, select A line bulbs that look the most like their maintainer. Although the A line will eventually become identical to its maintainer, some speeding up of the process can be made with selection. Harvest the selections and store until planting time.

Sixth Year

Plant bulbs (S_2 and BC_1) as for last cycle to obtain the third selfing and to make the second backcross. Not more than 10 sterile plants are needed, but one must always check for sterility when making the backcross. Harvest seed and handle as before.

Seventh Year

Plant the seed in progeny rows as before. We now have fertile lines that have been selfed three times and that should be very uniform and have much reduced vigor. The second backcross to the sterile side of the pair now has 87% of the genes of the maintainer and should be looking quite similar. At this time select only the one or two best progeny lines from the 10 under observation. From this time on, the next two generations are handled as masses of 20 bulbs for the B-line backcrosses. Further selfing would only lead to such loss of vigor that the B line could not be maintained in most cases and certainly would not contribute to any improvement of a new hybrid. The next two backcrosses will carry through the eleventh year.

The procedure for making new A and B lines to use in hybrid combinations has been explained, and now the procedure for making and testing hybrids will be discussed. With the A- and B-line genetic and cytoplasmic factors in onion, F_1 hybrids, three-way hybrids, and even four-way hybrids can be made. However, I feel that F_1 or three-way hybrids are superior and will limit the discussion to them.

F_1 hybrids are made by crossing A lines with unrelated B or C lines. Three-way hybrids are made by crossing A lines with unrelated B lines to produce the sterile F_1 and then by crossing that F_1 with either another B or C line. The main reason to use a three-way hybrid is to improve seed production, which is generally low when using inbred A lines. The F_1 seed parent will exhibit hybrid vigor and will produce greater seed yields.

The making of hybrids is essentially the same procedure as maintaining the A- and B-line pairs except that unrelated parents are used. The decision to make hybrids must be based on the objectives desired by the plant breeder. The most obvious reason for making hybrid onions is to obtain uniformity of the onions produced and to control the date of maturity. In some instances, seedling vigor and even yields may be improved. Other reasons might include adding disease, insect, or environmental stress resistance to the crop or producing a hybrid that will mature somewhere between that of the two parents.

Once the breeding objective is determined, the breeder must make testcrosses between various inbred A, B, or C lines using knowledge of these inbreds. Only small amounts of seed are needed for onion yield trials, and so the normal procedure to produce experimental hybrids is to place several A lines and one B or C line in a screen cage. Using a hive of bees for pollination, several hybrids can be produced in each cage. The same group of A lines is therefore placed in several cages, with each cage containing a different fertile inbred line.

After the pilot production of these experimental F_1 hybrids, seed is planted in yield trials in the various areas of onion production so they can be evaluated as potential new hybrids. It is extremely important that they be tested in the actual areas of production since onions are sensitive to day length and temperature. Yield trials should be replicated with each test row being 10 ft or longer. Rows of 10 ft seem to be sufficient if the soil is uniform in the field. I plant six replications, using one for field day observation and five for collecting data. It is advisable to repeat this planting in at least three locations.

The experimental hybrids must be critically evaluated for all characteristics important to onions in the particular growing area. Yield alone means little in today's market. Size, shape, color, date of maturity, storage or shipping quality, and disease resistance must all be observed in determining the value of the hybrid. Seed production is also just as critical in the value of a cultivar as bulb production, since good seed yields are necessary for the seed industry to be able to grow and sell the crop.

This evaluation procedure must be made for at least 3 years in each location to ensure the adaptation of the crop. One good year in one location has little value, since growing seasons vary so much from year to year. Three good years, and especially in several locations, give the breeder a good idea of the value of the new hybrid.

In my opinion, hybrids need more testing than open-pollinated cultivars since they have a narrow genetic base and have been observed to vary more in performance due to environmental stress. Once these hybrid combinations are tested and proven in trials, small commercial tests are the next step as with any crop. The remainder of testing would be the same as described in development of open-pollinated cultivars.

MANAGEMENT OF ONION SEED PRODUCTION

Management of onion breeding lines to obtain seed from selections is possibly the most important and critical part of a breeding program. Many good bulb selections are made by the breeder and lost for various reasons, thereby leaving the development of improved lines or cultivars incomplete. These include loss in storage, bulb mixtures, seed mixtures, or outcrossing occurring during seed increase. The handling and increasing of seed on A and B lines further complicates the management of the breeding program.

Assuming bulbs are at the stage for selection in the field, we shall proceed with steps to manage the physical operation of a program. Bulbs will be selected, based on objectives, from the progeny rows and laid in a group next to the field stake. Nonselected bulbs or progeny rows are discarded. In dealing with short-day onions, the bulbs are topped (foliage clipped leaving at least 1 in. of neck on the bulbs) and put into mesh onion sacks. The roots do not need clipping. The stake from the plot is placed inside the sack and a wire-strung shipping tag is labeled and attached to the sack. A knot should not be tied in the sack string because it may be necessary to open the sack several times during the selection process. The sacks of onions are left in the field for 2 or 3 days if the weather is dry so that the necks can dry down. If that is not possible, they must be placed in a dry place where fans force air through the sacks to dry them quickly. In the case of long-day storage onions, less drying is needed because they are generally allowed to become dry in the field before harvest.

Extreme care must be exercised at all times during handling and storage to keep progenies separate. It is even more important when working with A and B lines. Remember that they should always be planted separately from each other to prevent seed mixtures and bulb mixtures. The bulbs must then be stored until dormancy is broken. Short-day onions are harvested in the spring and long-day onions are harvested in the fall. In both cases, the bulbs must be kept dry and well ventilated.

Short-Day Onion Storage Procedures

Short-day onions are usually stored in open-air structures with only shade provided for temperature control. Small lots can be kept in any kind of container that is ventilated. I use wire milk carton crates, which each hold approximately 25 lb of bulbs and stack easily. They can usually be purchased from milk companies, which are currently switching to lighter, plastic crates. There are also several sources of ventilated plastic containers. Some commercial seed companies use wooden crates, and I have seen bulbs stored simply in mesh or burlap bags. However, ventilated crates are best (Fig. 10.14).

The bulbs are harvested in April, May, or June and stored until the latter part of August. At this time, they should be taken out and selections made for planting. Sprouts, rots, and bulbs showing doubling should be discarded. The decision based upon objectives should be made at this time. Bulbs should be labeled for selfing, making testcrosses, masses, and increases; then placed in paper or mesh bags with field numbers and instructions attached. For example, all selfs should be together for planting in small cages, three- to five-bulb masses next, 9 × 10 ft cages next, etc., so that cage plantings will end up in an organized manner (Fig. 10.15). Careful notes must be taken as selections are made and bagged for planting. If single centers are part of the objectives, cut off the top one-third of the bulb to be sure they are single centered. Other selection pressures are applied at this time. At the completion of this selecting period, which in a large program may last 2–3 weeks, plant the bulbs in the field in a way so that cages can be placed over them at flowering the next spring (Fig. 10.16). The bulbs should be pressed into loose soil or into a shallow furrow so that only the bottom half of the bulb is in the soil. Do not cover the entire bulb as wet weather can cause considerable loss due to rotting.

FIGURE 10.14. Short-day onion storage boxes should be placed under a covered shed in a dry area. Long-day varieties must be placed in an enclosed building to prevent freezing.

FIGURE 10.15. A view of an organized group of onion-breeding cages. The 2 × 2 ft cages begin in the foreground, and larger cages follow until the field is completed with 12 × 80 ft cages. Such an arrangement helps in physical handling and erecting, management of cultural practices, introduction of flies and handling bees, and seed harvesting.

Grow the onions as any other winter crop using good cultural practices. Insect, disease, and weed control is necessary to ensure good seed production. The bulbs will rapidly sprout and grow when irrigated. Lateral buds will grow and the resulting plant will usually have three to five growing points. The foliage will continue to grow, and flowering will be initiated during the winter months. Begin caging the plants as soon as bolting begins in the spring, because flowering will generally occur within 30–45 days once seedstems appear.

FIGURE 10.16. Bulbs being set with root plates down after being scattered in the breeding-cage areas. Soil should be pulled up to the bulbs but bulbs should not be covered.

Long-Day Onion Storage Procedures

Long-day bulb selection and harvest occurs in the fall. Following selection, the bulbs are stored in similar containers as for short-day bulbs. The bulbs are stored inside a building and kept dry and above freezing temperature. Air circulation is important as with short-day types. Sometime during midwinter, the bulbs are observed for sprouting and rotting. Generally, data are collected and weights are recorded again to determine storage quality. In most programs, bulb evaluations are made at this time to determine superior storage lines. Decisions are made in early spring as to what breeding steps need to be taken as with the short-day program. The bulbs are planted in a similar manner as discussed earlier, when the danger of hard freezes is past. The bulbs are ready to flower since they were stored under cool temperatures. Thus they produce fewer new leaves than short-day types and quickly send up seedstems.

Caging of Onions for Seed Production

When seedstems begin to show, cages should be taken out of storage and carried to the field. Frame parts and cages should be arranged by size and laid out in an organized manner to correspond to planted onions in the field. This organization is very important since up to several hundred cages must be erected in a 1-week period (Fig. 10.17). Cage frame legs, cross braces, length braces, etc., should be stacked separately as different-sized cages use pieces of different lengths. I color-code all pieces and keep them stored in separate bundles to simplify organization. Cages must be erected and covered prior to any flowering to prevent outcrossing (Fig. 10.18). It is advisable to use cross wiring on the frames tp provide additional bracing, as the screen covers catch wind and may be blown over (Fig. 10.19). Such precautions are well worth the cost and effort, since many years of work lie under the cages. It is very important to stake and tie up the seedstems on the

FIGURE 10.17. It is very important that frame parts and cages be arranged in an organized manner because several hundred cages will be erected during a one-week period.

FIGURE 10.18. Cages should be erected over the planted bulbs when seedstems begin to develop and prior to flowering. This allows for normal cultivation practices during plant growth, yet still gives enough time to put up cages before actual flowering occurs.

FIGURE 10.19. Additional bracing against wind damage is provided by cross wiring the cage frames.

outside rows of the cages to prevent them from touching the screen. If allowed to touch, the flowers may be pollinated through the screen with foreign pollen (Fig. 10.20). The same is true for the ends of all the rows. When flowering begins, flies or fly pupae need to be placed in the small cages and bees in the larger cages. Water must be provided for the bees at all times and the life of flies will also be extended if they are also provided with water (Fig. 10.21). Flies generally need to be added to the small cages twice each week for 3 to 4 weeks.

When the seed is set, the bees need to be removed, as excessive death loss occurs in the confinement of cages. Cage covers should be left on, however, until umbels are ready to harvest so as to provide protection from winds or hail. The umbels are ready to harvest when a few black seed coats can be seen as capsules begin to split. Remove the cages carefully and cut off any umbels that might have touched the screen.

When harvesting the seed, be sure that the bags or containers are correctly labeled and placed in the cage grouping. Small cages are harvested into paper bags and stapled closed. Larger cages are harvested into tightly woven burlap or cotton bags or pallet boxes. If the cage contains A and B lines, extreme care must be taken to prevent mixing of seed.

The cage frames are then taken down and organized by cage pieces in bundles. The cage covers are folded and everything is loaded on a trailer to be put into storage. Wire that was used to brace the frames should be picked up and disposed of to prevent future problems with equipment in the field. Seed should be dried quickly to prevent heating or molding. If the area is humid, artificial drying is needed to get the seed dry so that it can

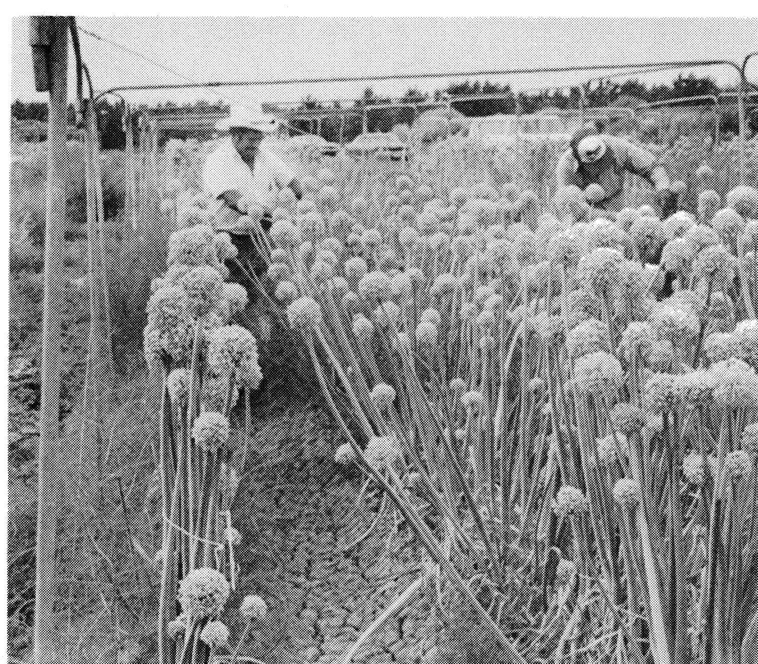

FIGURE 10.20. The rows next to the side of the cage and plants on the row ends must be staked and tied to prevent umbels from touching the screen. Insects can pollinate flowers touching the screen and can cause contamination of the isolation.

FIGURE 10.21. A good seed set in a small massing cage. String is used to tie umbels to prevent them from touching the screen during flowering. String is also tied around the perimeter of the cage to keep the wind from pressing the screen into the umbels. Water is provided for flies in small containers.

be threshed (Fig. 10.22). Seed can be dried at temperatures of 100°–110°F. When the umbels are dry enough to feel brittle, they should be rubbed through ⅛-in. mesh hardware cloth, which breaks the seed free from the capsules and causes little damage. The old method was rubbing with a corrugated rubber mat in a box. However, some seed was usually damaged and the procedure was slow.

For larger field isolations, I have a custom-built belt thresher, which consists of two rubber belts moving in the same direction. The top belt moves 1.5 times as fast as the bottom belt, which creates a gentle rubbing action as the seed moves through the machine. The threshed seed is cleaned with an air column blower or an aspirator-type cleaner for small lots. Larger lots are cleaned in a small, two screen seed cleaner, which has a blower to remove light seed and trash.

If the seed lots are poor, washing may be necessary to remove light seed and trash. Float off the unwanted material, collect the good seed, which sinks, and dry quickly by using screens and forced dry air. Once seed is cleaned, it must be packaged, labeled, and

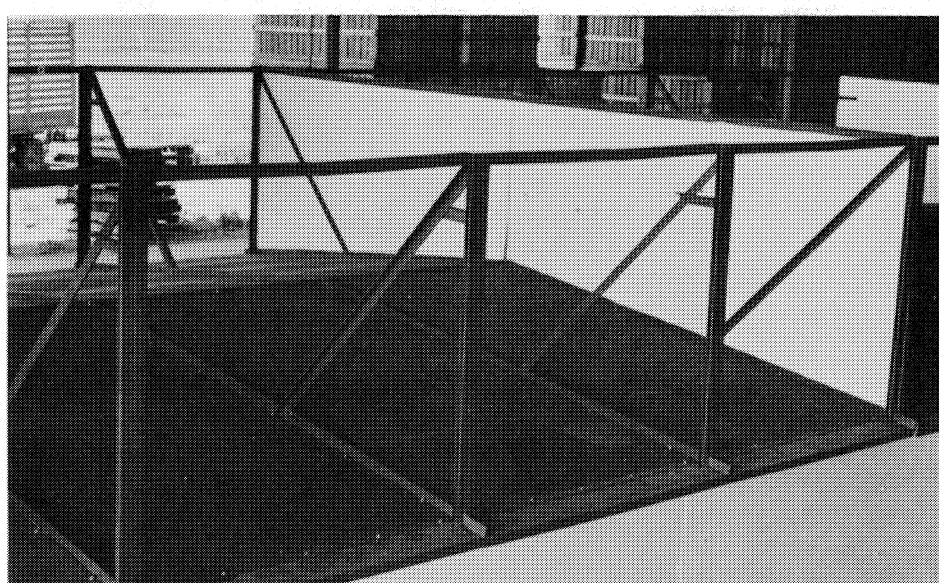

FIGURE 10.22. An onion seed drying bin. Seed is placed on the perforated sheet metal, which has holes too small for onion seed to fall through. Air is forced up through the seed, which may be stacked 4–5 ft high.

stored in a good seed storage room. An excellent storage condition consists of a temperature of approximately 40°F and a relative humidity of 40% or less.

Once breeders have the cleaned seed in the seed storage room, they can finally relax and feel good that they have been successful in moving one generation closer to the development of a new cultivar of onions.

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