9
Carrot Breeding

C. E. PETERSON
P. W. SIMON

The carrot is widely grown for use both fresh and processed. It provides an excellent source of vitamin A and fiber in the diet. Annual per capita consumption in the United States is estimated at about 7.5 lb; approximately 0.5 lb is frozen and 1.0 lb canned (69). These data for consumption probably are short of actual use because production is nearly 10 lb per capita. The estimates for processed consumption do not include a substantial tonnage of both processing and market types used in soups, mixed vegetables, and mixed juices. Probably the total production of 10 lb is divided more nearly 6 lb fresh and 4 lb processed.

Economically the carrot ranks among the ten most important vegetables, exceeded by potato, lettuce, tomato, onion, celery and sweet corn. The average annual farm value for the years 1978–1980, was approximately $162 million. California produced 44.1% of the U.S. carrot tonnage and 49.6% of the dollar value (Table 9.1). The three leading states, California, Texas, and Florida, produced approximately 65% by volume and 73% of farm value. In those states most of the production is for fresh market. In Washington, Wiscon-

TABLE 9.1. **Acreage, Production, and Farm Value of Carrots by State (1978–1980)**[a]

State	Acres	Tons	%	Value ($1000)	%
California	36,300	494,850	44.1	80,364	49.6
Texas	15,800	122,200	10.9	19,807	12.2
Florida	11,500	115,000	10.3	18,000	11.1
Michigan	6,100	78,000	7.0	14,910	9.2
Washington	4,600	100,000	8.9	8,227	5.1
Wisconsin	4,000	75,500	6.7	5,524	3.4
Minnesota	1,600	30,560	2.7	3,514	2.2
Oregon	1,400	29,400	2.6	2,524	1.6
Arizona	2,000	12,850	1.2	2,398	1.5
Colorado	1,000	12,650	1.1	2,357	1.5
New York	1,100	17,400	1.6	2,095	1.3
Illinois	300	4,300	0.4	698	0.4
Other states	1,460	28,333	2.5	1,582	1.0
Total	87,200	1,121,100		162,000	

[a]Data from USDA statistics for 1981, with added estimates of Florida production, which are not included in 1981 USDA figures.

sin, Minnesota, and Oregon, where the crop is produced mainly for processing, the higher yields from processing cultivars are offset by lower prices, with the result that the dollar return per acre is slightly lower for processing than for market carrots.

ORIGIN AND GENERAL BOTANY

The genus *Daucus,* which includes carrot, has many wild forms that grow mostly in the Mediterranean region and southwest Asia. Fewer representatives are found in Africa, Australia, and North America. For *Daucus carota* L. it is generally agreed that Afghanistan is the primary center of genetic diversity and therefore the primary source for dissemination. There are more than 400 plant introductions currently available in the United States.

In two comprehensive studies based on ancient writings and paintings Banga (8, 9) has provided evidence that the purple (anthocyanin) carrot together with a yellow variant spread from Afghanistan to the Mediterranean area as early as the tenth or eleventh century. It was known in western Europe in the fourteenth and fifteenth centuries, in China by the fourteenth century, and in Japan in the seventeenth century. The white and orange (carotene) carrots are probably mutations of the yellow form. Orange carrots were first cultivated in the Netherlands and probably in adjacent areas in the seventeenth century. The existence of orange and yellow–orange carrots is proved by the fact that they appear in seventeenth-century paintings exhibited in Netherlands museums (9).

The domestic carrot is closely related to and readily crosses with the highly diverse and widely adapted wild carrot known as Queen Anne's Lace. In nature the wild carrot has an annual or winter annual life cycle. Usually the seedling plants form a rosette in late fall, which undergoes cold induction during winter and completes its reproductive cycle the following summer. Wild accessions moved from semitropical to temperate zones will generally behave as annuals, with bolting following promptly after a brief exposure of seedling plants to low temperatures and to the longer photoperiod of northern latitudes.

Domestic cultivars have been selected for non-bolting and therefore behave as biennials or winter annuals. In practice they can be propagated on an annual basis by storing small roots (stecklings) for 6–8 weeks at 2°–5°C before replanting. In areas with relatively mild winters and an early snow cover, seed is produced from plants vernalized in the field during the winter. They will promptly bolt and mature a seed crop in a total of 12–13 months.

FLORAL BIOLOGY AND CONTROLLED POLLINATION

Floral Characteristics

The carrot umbel is a compound inflorescence (Fig. 9.1). The development of the umbel begins with a broadening of the floral axis and internode elongation (*18*). A primary umbel can contain over 1000 flowers at maturity, whereas secondary, tertiary, and quaternary umbels bear successively fewer flowers. Usually several floral stalks develop from a single plant.

In a given carrot flower, stamens, petals, and sepals develop simultaneously followed by carpel development. Flowers are arranged in umbellets and umbellets into an umbel. Within umbellets and umbels, floral development is centripetal and arrangement is spiral. Thus the first mature flowers are those on the outer edges of the outer umbellets.
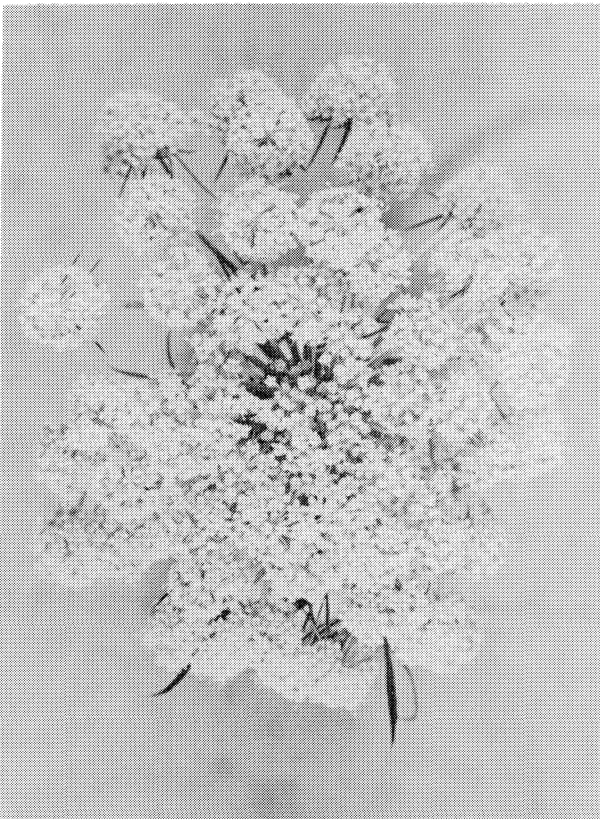

FIGURE 9.1. Carrot umbel consisting of umbellets.

The primary umbel consists mainly of bisexual flowers, but male flowers can occur frequently (between the edge and center of an umbellet) in subsequent umbels (*19*). The pollen from flowers at the center of an umbellet is larger and more frequently fertile than that from peripheral flowers (*50*).

Carrots are protandrous. The petals separate and the filaments begin unrolling to release the anthers at anthesis, although the anthers in one flower may not extrude simultaneously. After the filament is straightened, the pollen is shed and the stamen is quickly abscissed. The petals then open fully and the style elongates. The carrot has a split style, which separates when the flower is receptive to pollination. The petals of male-fertile plants fall soon after the split stigma is receptive. It is interesting that the petals of petaloid, but not brown anther, male-sterile plants are persistent until the seed ripens.

Carrot flowers are epigynous with five small sepals, five petals, five stamens, and two carpels (Fig. 9.2). The mature flower and consequent mature fruit are approximately 2 mm long. Early in development, each carpel bears two ovule primordia, but only the lower one continues to grow. The carrot embryo sac is monosporic (developing from the chalazal macrospore) and 8-nucleate (*17*). Nectaries on the ovary wall are important in insect attraction for pollination (*33*). Pollen longevity in storage has not been evaluated.

The carrot fruit is a bilocular schizocarp, which dries and splits upon maturity to yield two mericarps (achenes) with one seed each. The mericarps are covered with spines, which must be removed for ease of handling (Fig. 9.3).
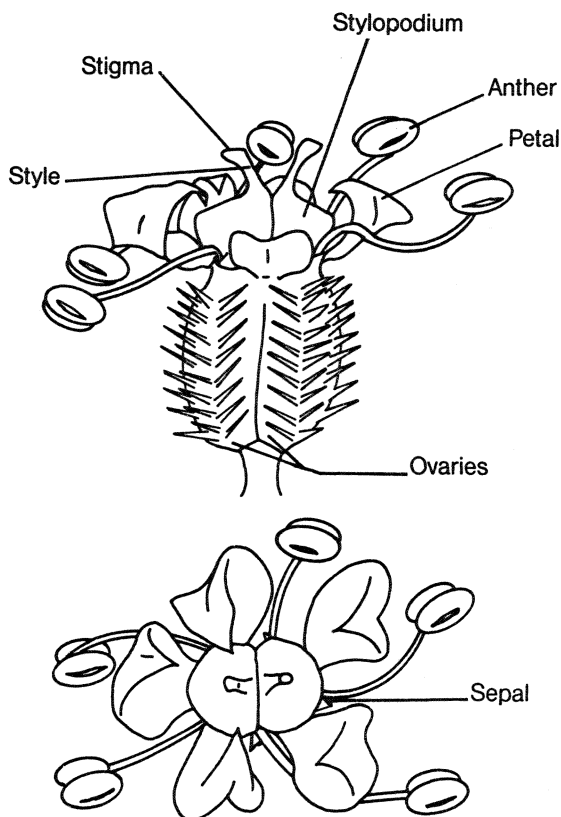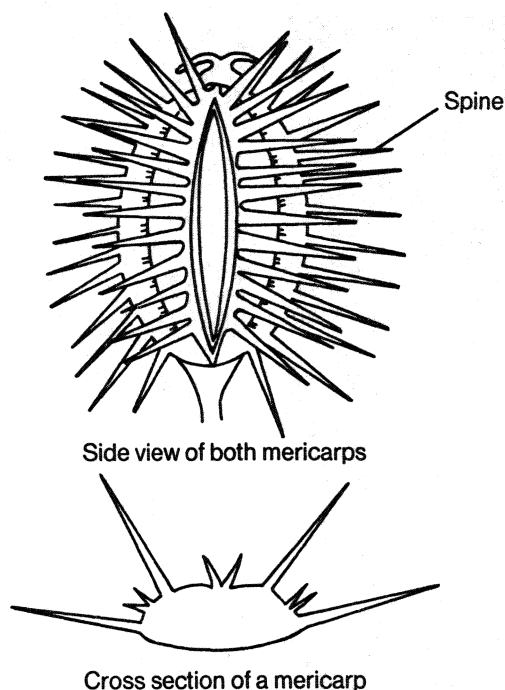

FIGURE 9.2. Carrot flower.

FIGURE 9.3. Carrot fruit.

Cytoplasmic Male Sterility (CMS)

There are two distinct types of male-sterile flowers, depending upon the source of sterility-inducing (S) cytoplasm. The brown anther type (Fig. 9.4), in which the anthers degenerate and shrivel before anthesis, is expressed in domestic cytoplasm from cv. Tendersweet, as reported by Welch and Grimball (72), and in cytoplasm from various commercial cultivars, as reported by Banga *et al.* (10). The other type of male-sterile flower is petaloid, in which the stamens are replaced by five petals (Fig. 9.5). Petaloid steriles exhibit a range of morphological structures, some of which have been described by Eisa and Wallace (30). In hybrid development petaloid steriles are more widely used than the brown anther type. If genetic and environmentally stable brown anther steriles were available, they would be preferred over petaloids because of their higher seed-yielding potential.

The 1947 report of Welch and Grimball (72) was followed in 1953 by the discovery of a sterile wild carrot (petaloid type) by H. M. Munger of Cornell University. From a detailed study of this wild carrot along with the brown anther material from Welch and three additional brown anther sources from Gabelman, Thompson developed a complex model for inheritance of pollen sterility (66). He concluded that there are at least two and probably three duplicate dominant maintainer genes and an epistatic restorer operating in the cytoplasm of both Tendersweet and the Cornell wild carrot. The useful maintainer line would therefore have to be free of the restorer and homozygous dominant at one of the *Ms* loci.

Hansche and Gabelman (37) reported digenic control of male sterility with either of two genes, dominant (*Ms-4*) or a recessive (*ms-5*), producing sterility interacting with

FIGURE 9.4. Brown-anther male-sterile carrot flowers.

cytoplasm from the cv. Tendersweet. They suggested that the recessive (*ms-5*) might have been introduced into Tendersweet from a plant introduction (PI 169486) known to be segregating for male sterility. It has not been determined if their *Ms-4* is allelic to any of the dominant maintainer genes postulated by Thompson (*66*). The model proposed by Hansche and Gabelman was supported by the extensive genetic analysis of Banga *et al.* (*10*). They found evidence for two additional complementary dominant restorer genes, which produced fertility if each locus had one dominant. It was suggested that one or both of these restorers may have been absent from the material studied by Hansche and Gabelman and that their data were not inconsistent with the hypothesis presented by Thompson.

Both the S cytoplasm and interacting nuclear genes that maintain sterility are widely distributed in wild and domestic forms of *D. carota*. In addition to the Cornell source, two other wild sources have been reported. McCollum (*44*) described petaloid sterility in a wild carrot accession from Sweden, and Morelock (*48*) reported the discovery of a similar wild carrot petaloid in Wisconsin in 1970. Banga *et al.* (*10*) searched seed fields for new sources and promptly found male-sterile plants of the brown anther type in Amsterdam Forcing, Flakee, Nantes, Vertau, Grelot, Parisienne, and some high-carotene selections. Four of these were used in their studies of the genetics of cytoplasmic sterility. From this

experience it is expected that a systematic search would lead to discovery of cytoplasmic sterility in our domestic cultivars. No comparisons have been made to determine differences among sources of domestic cytoplasm, and so it is not known if any of those discovered in domestic cultivars in the Netherlands are superior to the Tendersweet source, which has been used to a limited extent for hybrid development in the United States.

A prolonged search in the wild carrot population around East Lansing, Michigan, failed to reveal any male-sterile plants. The petaloid sterile reported by Morelock (48) was found in a small isolated colony of wild carrot near Madison, Wisconsin. From populations segregating in this new cytoplasm, he concluded that the system of maintainer genes in the Wisconsin wild source was the same as that in Cornell wild cytoplasm and their morphological types were similar. He also demonstrated the decisive role of cytoplasm in determining the morphological type of sterility. By segregating identical genotypes from crosses between a petaloid maintainer (MSU 1558M) and a brown anther maintainer (W93M) it was found that only the brown anther type was expressed in domestic (Tendersweet) cytoplasm and only the petaloid type in the wild (Cornell) cytoplasm. His data supported the hypothesis that petaloid sterility in wild carrot cytoplasm is controlled by

FIGURE 9.5. Petaloid male-sterile carrot flowers. Note two whorls of petals.

two dominant nuclear genes (15 fertile : 1 sterile in F_2). The brown anther type in F_2 produced 15 sterile : 1 fertile in domestic cytoplasm to suggest control by two recessives.

The method used in these studies may have application in genetic studies involving other characteristics. First it is necessary to produce the F_1 from both sterile × fertile and fertile × fertile crosses, in this case W93S × 1558M and 1558S × W93M for sterile × fertile, and W93M × 1558M or 1558M × W93M for fertile × fertile. The segregating generations in the two types of cytoplasm were then produced as follows: [(W93S × 1558M) × (W93M × 1558M)], [(W93S × 1558M) × 1558M], [(W93S × 1558M) × W93M] to produce the appropriate segregation in domestic (W93S) cytoplasm, and similarly [(1558S × W93M) × (1558M × W93M)], [(1558S × W93M) × W93M], and [(1558S × W93M) × 1558M] to provide the same assortment of genotypes segregating in the Cornell wild (1558S) cytoplasm. If inbreeding is sufficient to establish homozygosity for characters in both the sterile and maintainer components of the inbred parents, then it is possible to produce the large populations needed for genetic studies without resort to laborious and often imprecise hand emasculation to produce backcross progenies.

TABLE 9.2. Simply Inherited Characters in Carrot and Their Gene Symbols

Gene symbol[a]	Character description	Gene source	Reference
A	α-*Carotene* synthesis (may be identical to *Io* or *O*)	Kintoki cv.	68
(Ce)*	*Cercospora* leaf spot resistance	WCR-1 Wisconsin inbred	3
(Cr)	*Cracking* roots (dominant to non-cracking)	Touchon cv.	27
Eh	Downy mildew (*Erysiphe heraclei*) resistance	*D. carota* ssp. *dentatus*	16
g	*Green* petiole	Tendersweet cv.	4
gls	*Glabrous* seedstalk	W-93 Wisconsin inbred	49
Io	*Intense orange* xylem	Miscellaneous	Kust (cited in *21*)
L	*Lycopene* synthesis	Kintoki cv.	68
Ms-1, Ms-2, Ms-3	Maintenance of *male sterility*	Tendersweet cv.	66
Ms-4, ms-5		Tendersweet cv., Imperator 58 cv., PI 169486	37
O	*Orange* xylem	Miscellaneous	Kust (cited in *21*)
(P-1), (P-2)	*Purple* root	Miscellaneous	42
Rs	*Reducing sugar* in root	Miscellaneous	36
y	*Yellow* xylem	Miscellaneous	Kust (cited in *21*)
Y-1	Differential xylem / phloem carotene levels	Miscellaneous	Kust (cited in *21*)
Y-2	Differential xylem / phloem carotene levels	Miscellaneous	Kust (cited in *21*)

[a]Loci enclosed in parentheses were not named previously; suggested symbol.

Genetics and Cytogenetics

Only 20 genetic loci have been described in carrots (Table 9.2) and no linkage groups have been defined. A wide range of amino acid and nucleic acid analog resistant cell lines have been isolated in carrot tissue culture, but definitive genetic analyses have not been performed on plants regenerated from these variants. The carrot has nine pairs of chromosomes, and little variation in length exists between chromosomes (12, 13, 47, 73). Four chromosome pairs are metacentric, four are submetacentric, and one is satellited. There are 22 recognized species of *Daucus,* most with 11 or 10 chromosome pairs and only two others with nine pairs. One interspecific hybrid between *Daucus carota* and *Daucus capillifolius* has been synthesized (45).

Controlled Pollination

Emasculation to accomplish controlled crosses between male-fertile plants is laborious and time consuming, particularly for genetic studies that require relatively large backcross populations. Anthers are removed from the early-opening outer flowers in the outer whorl of umbellets until enough have been emasculated to ensure the needed supply of seed. Emasculation is accomplished before any stigmas become receptive. Unopened central florets in the emasculated umbellets and all late-flowering umbellets are removed, leaving the female parent inflorescence with only emasculated flowers. This umbel is then isolated under a small cloth cage (Fig. 9.6) with a pollen-bearing umbel from the selected
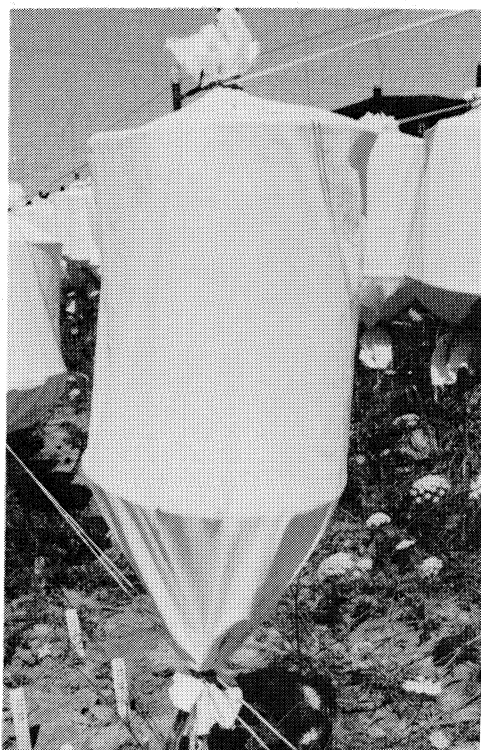

FIGURE 9.6. Small cloth cage for isolating one to five carrot plants.

male parent. Live house flies and pupae are introduced to ensure a continuing supply of active pollinators during the full period of stigma receptivity.

To produce fertile F_1 hybrids for breeding purposes it is more efficient and just as effective to make fertile × fertile crosses simply by putting under cloth cages one or two flowering umbels from each selected parent along with a supply of flies. Seed from each parent is then sown in adjacent field rows. In most cases each row will contain a mixture of hybrid and parent phenotypes that can be easily identified. If the cross involves inbred lines, hybrid plants are distinguished by their vigor, i.e., the selfs from the inbreds will produce much smaller roots. To ensure identification of hybrid plants, the stand should be uniform and relatively thin to permit expression of hybrid vigor.

BREEDING HISTORY

Until the early 1960s nearly all carrot cultivars in use were derived by selection in open-pollinated material. Because of the rapid loss of vigor, little effort had been made to achieve uniformity by inbreeding. With the discovery of cytoplasmic male sterility it became possible to follow the classic system of establishing pollen-sterile and -fertile inbreds for use as parents in F_1 hybrids that exhibit restored vigor and uniform horticultural quality. There was widespread interest in hybrid carrot development in the 1950s. Active projects were underway in several private seed and processing firms and at the Wisconsin, Idaho, California, New York, Oregon, and Michigan Agriculture Experiment Stations (AES) and the USDA at Beltsville, Maryland. As a result of this activity, hybrid cultivars began to appear in the early 1960s, and the frequency of new hybrid releases has continued to increase since then. By 1983, at least 50 hybrid cultivars had been introduced in the United States alone. The state breeding programs that provided parent inbreds for a substantial share of these hybrids were discontinued in the 1970s. Idaho, California, New York, Oregon, and Michigan AES had abandoned their carrot breeding projects by 1980. The increase in efforts by major vegetable seed firms has not replaced those of the terminated projects. The long-term effects of this decline in breeding activity and the concurrent shift of responsibility to a few private breeders cannot be estimated. A probable result will be to eliminate from competition the small seed firms that are unable to support independent breeding programs. High-risk, long-term objectives and development of unique types, for which there will be limited demand for seed, probably will be neglected.

CURRENT GOALS

Objectives have been to eliminate or minimize deficiencies in accepted open-pollinated cultivars and to exploit unique characteristics derived from introduced accessions. The main objectives of U.S. breeders are improvement of yield, visible characteristics such as color, shape, smoothness, and freedom from defects, resistance to a few common diseases, and non-bolting. During the past 5 years increasing attention has been given to the less obvious qualities of flavor, texture, and nutritional value.

Uniformity

Market carrots, which comprise nearly 80% of the U.S. production, are immature when harvested. For this reason, total yielding capacity is not as important as uniformity. A

field population of nearly identical genotypes will yield a high percentage of marketable product. Efforts made by growers to achieve what they term "high pack-out" include seed coating, precision planting, irrigation, and fertilization to provide a uniform growing environment. Genetic uniformity contributes substantially to the success of refined cultural practices.

Even for processing carrots, uniformity and quality are currently so important that maximum tonnage has not yet become a major objective. It is expected that when improved quality is available in a number of hybrids, yield will become the major goal.

Appearance

Root shape requirements are determined by the preferences of growers, consumers, and processors. The diverse shapes in breeding populations and open-pollinated cultivars provide breeders with all the genetic variability needed to meet established demands for popular shapes (Fig. 9.7). The smooth exterior demanded for both fresh-market and processing types is important for ease of cleaning and reduction of paring losses.

Exterior and interior color are important characteristics receiving attention in all breeding projects. It is possible to achieve a deep red–orange color in both xylem and phloem and to eliminate green color, both exterior and interior, from the crown area.

In addition to shape, smoothness, and color, genetic differences in certain root defects are evident and these defects are being minimized by appropriate breeding methods. By producing breeding material under conditions where defects develop it is possible to achieve effective selection.

Disease Resistance

Resistance to alternaria leaf blight, *Alternaria dauci,* present in all U.S. carrot-growing areas, is a major objective. Most currently popular open-pollinated market cultivars are

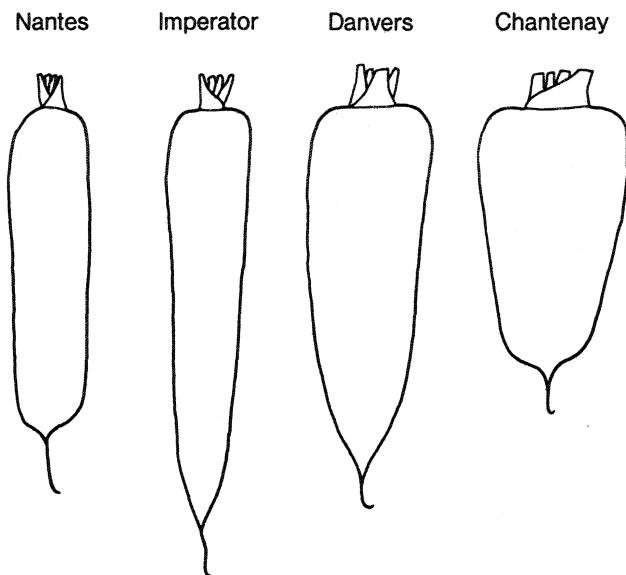Nantes   Imperator   Danvers   Chantenay

FIGURE 9.7. Typical shapes of popular U.S. carrot cultivar classes.

susceptible, and under severe conditions they require a regular fungicide program to avoid reduction in yield. The most serious damage is often the loss of so much foliage that roots cannot be lifted by mechanical harvesters. Processing types generally are more tolerant than market types. A high level of resistance has not yet been identified. With the available tolerance the size of petiole lesions is restricted and the plants generally retain enough foliage for mechanical harvest. In 1970, 241 plant introductions and 90 inbred lines were exposed to severe natural infestation at Belle Glade, Florida. Only nine retained enough foliage to be classified as resistant. The best were Japanese cvs. Kokubu (PI 261648), San Nai (PI 226043), and Imperial Long Scarlet (64). Resistance from these sources was incorporated in a breeding population released by the USDA and Florida AES in 1983.

Cercospora leaf blight *Cercospora carotae* is another common foliage disease with symptoms similar to those of alternaria leaf blight, but normally less severe. Resistance has been observed in certain lines. In areas where the disease is prevalent, selection for resistance under field conditions can be effective. Some use has been made of greenhouse screening for cercospora resistance (3).

One of the most devastating diseases in the northern United States is aster yellows, a mycoplasma transmitted to a wide range of hosts by the six-spotted leaf hopper *Macrosteles fascifrons*. Vector preference and probable plant tolerance in field exposure tests by the University of Wisconsin were reported in 1973 by Schultz (54). Since that time, continued field exposure and selection from many diverse cultivars and breeding materials by the University of Wisconsin have produced clear levels of plant resistance as well as vector preference. In recent replicated trials in which entries were planted with alternating rows of lettuce to ensure uniform exposure, the Wisconsin workers observed levels of infection low enough to suggest that eventually it might be possible for growers to produce resistant genotypes without pesticides. With these new sources of resistant germplasm, it is likely that carrot breeders will assume the major responsibility for long-term control of aster yellows.

Carrot motley dwarf, first described by Stubbs (65) is more common in the United Kingdom and Australia than it is in the United States. It is induced by two viruses, carrot mottle and carrot red leaf, transmitted by the willow aphid *Cavariella aegopodii*. The occasional outbreaks in California and the increasing prevalence of the disease in the Pacific Northwest justify including resistance as a minor breeding objective. Resistant germplasm is being developed in order to have useful material on hand in case the disease spreads to other producing areas.

Of many soilborne pathogens that affect carrots, only the *Pythium* species that have been implicated in a disease called brown root in the United States and rusty root in Canada have received attention. Selection has been for roots that do not develop forking in wet soils. Seedling resistance has been tested by Howard and Williams (40) using inoculated rooting media under controlled temperature. Field symptoms in muck-grown carrots are described by Mildenhall *et al.* (46).

Non-bolting

Premature development of seed stalks is a common cause of losses in yield and quality. In some genotypes there is good tolerance to low induction temperatures. To minimize losses from bolting, breeders are exposing segregating populations to induction environments and imposing continuing selection pressure for a high vernalization requirement.

Quality

Until recently, the opportunity to enhance eating quality has been neglected. This may be attributed to the fact that carrots have been included in diet recommendations as a source of provitamin A. Many consumers probably purchase carrots for their vitamins rather than taste. In open-pollinated cultivars the extremes of flavor, from harsh bitterness to sweet succulence, provide the opportunity for significant improvement; and increasing attention is being given to culinary quality and nutritive value. With improvements now becoming available, and the increasing interest in nutrition and food quality, these characteristics must be included as essential objectives.

Genetic variation has been reported for many quality attributes of carrot including carotenoids (22), fiber (52), texture (6, 41, 43), sugars (36), flavor (60), minerals (7) and toxicants (74). Reviews of genetic variation for eating quality have been prepared by Aubert and Bonnet (5) and by Simon *et al.* (62).

Inheritance of several of these quality attributes has been analyzed. Genetic variation for carotenoid type and amount in carrot roots, ranging from white to orange color, is controlled by at least three genes, with many more accounting for variation within the orange category (21, 42, 68). Consideration of carotenoid quantity is very important in carrots because they are the most important vegetable source of provitamin A in the U.S. diet, providing 14% of the total (56). An "average" carrot contains 90 ppm total carotenoids (71). Of this, approximately 20% is α-carotene, 50% is β-carotene, 0–20% is ζ-carotene, 0–2% is lycopene, and 0–10% γ-carotene (67, 68). Darker-orange carrots tend to contain a higher percentage of α-carotene, up to 50% of the total (42).

SELECTION TECHNIQUES

Color

Selection for color should be accomplished in uniform light. Under full daylight or incandescent light, roots may appear much darker and a more desirable deep orange than under fluorescent light. If light conditions are not uniform, it is easy to choose those exposed to full light and discard those illuminated by fluorescent light.

The desired bright-orange color should extend down to the tap root and up to the crown. The best color distribution can be achieved in populations segregating for interior color by selecting roots with the best exterior color and with color extending well down the tap root. The roots with color in the tap roots are referred to as "red tails." To observe interior color, a horizontal cut can be made approximately 1 in. from the bottom of the red tail selections. The color of interior tissues, cambium and the adjacent phloem and xylem, may differ greatly in a given root (Fig. 9.8). Roots with the best uniformity (match) between the color of xylem and phloem tissue and those with the least distinct cambium zone are then examined for color in the crown area. This selection is made by a transverse cut just into the xylem, one to two petioles deep, and extending outward and 1 or 2 in. down from the crown (Fig. 9.9). Interior color can then be selected easily by retaining those roots with little or no green in the cambium area or upper xylem, with the best color match between phloem and xylem, and with an indistinct cambium zone.

Improvements in the uniform dark-orange color that have been made by visual selection have been accompanied by increases in total carotene content. Some recently introduced hybrid cultivars with improved color have total carotene ranging from 120 to 150 ppm fresh weight, while the open-pollinated sources have 80–100 ppm.
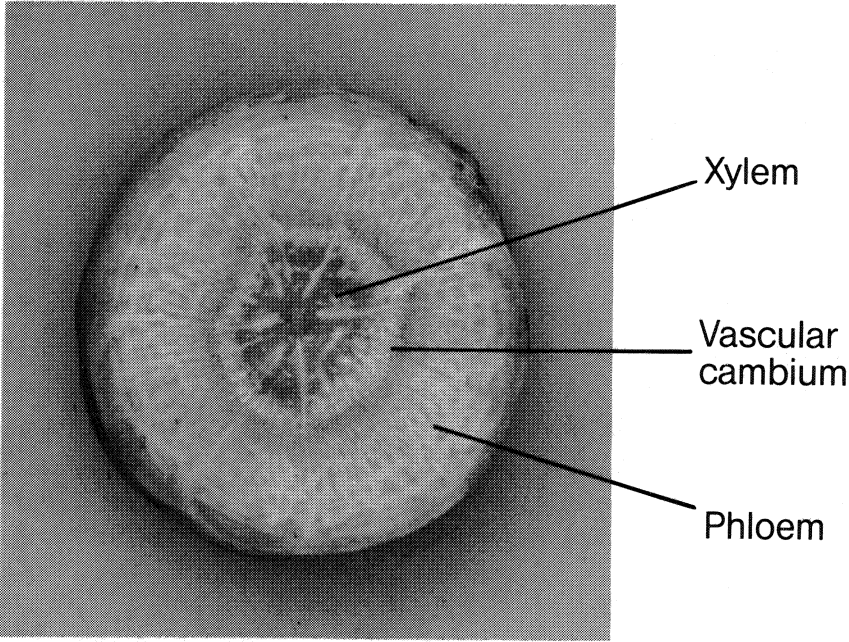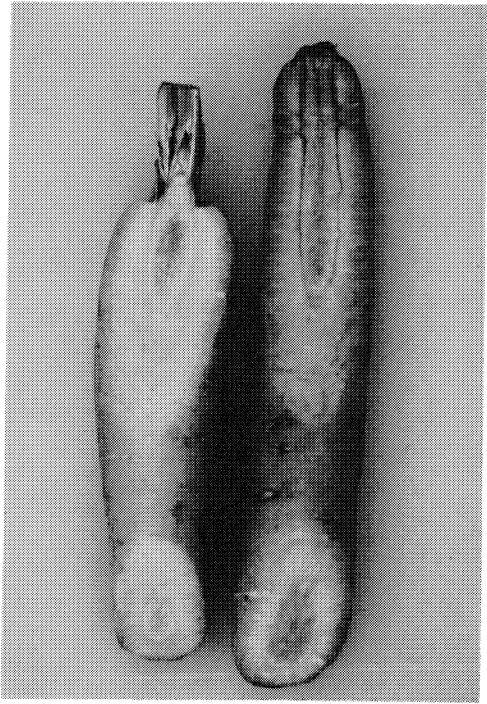
FIGURE 9.8. Cross section of carrot root.

FIGURE 9.9. Carrot roots cut to select for interior quality. Note undesirable pigmented cambium in the crown of root on the right.

Visual selection for differences in carotenoid content is feasible if alleles for pale-orange, yellow, or white color (less than 50 ppm carotenoids) occur in the population being considered (42). The presence of high lycopene in the root is visually detectable by characteristic red color even in dark-orange populations (100–140 ppm carotenoids), except in the presence of high α-carotene content. Visual selection is adequate for improving carotene content up to 120 ppm total carotenoids. Above this level it is more difficult to make visual assessments of carotenoid content even though roots classified as ''dark orange'' may range from 130 to over 200 ppm carotenoids. Consequently, selection for total carotenoid content must be based upon laboratory analyses to assure continued improvement.

Total carotenoids are determined analytically by comparing spectrophotometric transmission of 450-nm light through a hexane extract of root tissue to the percentage transmission through a pure β-carotene standard solution. The hexane extract can be obtained by either of two methods: (a) blending frozen raw carrot slices in a mixture of hexane and acetone, followed by removal of the more polar acetone (along with water from the carrot) in a separatory funnel (67) or b) lyophilizing raw carrot slices and blending directly in hexane (60). The latter method is somewhat more rapid. Individual carotenes can be quantified by thin-layer chromatography but the procedure is time consuming (21, 22). High-performance liquid chromatography may be well suited for rapid analysis.

Interior Quality

Interior qualities other than color can be observed for selection purposes with the same cuts that expose interior root tissues for color selection. Among the interior defects that may be exposed are cottony xylem, hollow heart, and spongy phloem. These defects are most likely to appear under stress and in mature roots; therefore, it is prudent to provide an environment that will induce interior defects so that alleles conditioning their expression can be eliminated. To select against hollow heart and cottony xylem, the plants should be allowed to mature and remain in the soil for at least as long as the crop is held in the field under commercial practices. Of course, this applies only to processing carrots, which often are held (unharvested) for 4 or more weeks after they have attained nearly maximum size.

The spongy-phloem defect develops in winter carrots subjected to low temperatures in moist soils. It is a common defect in winter areas like the Imperial Valley of California, where the crop may be planted in September or October and harvested in February or March, a schedule that entails exposure to 1 or 2 months at relatively low soil temperatures. Selection must span several seasons to increase the probability of exposure to the environment that will induce spongy phloem. The defect has not been observed in our plots in midwest organic soils, and genetic susceptibility cannot be detected in such environments. Some otherwise good lines, carefully selected in Michigan, Wisconsin, and New York, were unacceptable because the spongy-phloem defect appeared upon exposure to the winter environments of California and Arizona. This experience illustrates the importance of early-generation selection of inbred lines and the testing of their hybrids in the environment where they are likely to be produced.

Growth cracks may occur under many growing environments, but appear to be most severe in processing cultivars when harvest is delayed after roots are mature. This field storage during wet autumn months results in longitudinal splitting, which is followed by healing and slow, prolonged growth. Such roots are unacceptable to the trade. This defect occurs to varying degrees in all U.S. growing areas. It is particularly severe in the Pacific

Northwest, where mild fall weather permits prolonged field storage. There are genetic differences in the incidence of growth cracks (*14*). Some of our lines that have undergone crack selection in the Puget Sound area of Washington have shown a significant reduction in the incidence of growth cracks compared with unselected populations.

A related defect, of some importance in both processing and market carrots, has been termed longitudinal cracking (*27*) and is generally called "harvest cracks" or "shatter cracks" by growers and shippers. It occurs when turgid roots are subjected to mechanical abuse at harvest. Genotypes differ in their tolerance to this type of cracking. Selection can be accomplished and inbred lines evaluated by pricking freshly dug roots with a pen knife. There is little experimental evidence to support the general belief that roots with the best eating quality are most subject to harvest cracking. The cv. Nantes, one of the best for eating quality, is vulnerable to longitudinal cracking when handled mechanically. If this relationship holds true generally, breeders may need to compromise quality in order to achieve the durability demanded for mechanical harvest and packing. It is possible that machinery will be designed and practices modified to minimize mechanical damage. This will permit breeders to develop genotypes with the highest possible table quality without the risk of rejection because of excessive damage in mechanized handling.

Sugar and Flavor

A simple taste test can be used to identify good flavor and texture. A thin cross-sectional slice is cut from the color-selected roots for tasting; those with harsh flavors are eliminated (*62*). The ability to detect some volatile components that contribute to bitter or harsh flavors varies among individual tasters. Therefore, if eliminating roots with undesirable flavor is to be effective, the selector must be able to detect flavor differences.

The concentration of stored sugars contributes to sweetness and is an important component of overall preference (*60*). Total sugars can be selected by refractometer estimates of total dissolved solids (TDS) (*24*). This can be accomplished by using a drop of juice from a freshly cut or frozen root sample for refractometer reading to estimate concentration. The small (5 g) frozen sample, sealed in a polyethylene bag and held at $-10°C$, is thawed and macerated within the sealed bag. A needle puncture will release the drops of juice needed for refractometer reading. This simple selection procedure is effective for increasing total sugars and total dry matter. Selection for high soluble solids and dry matter can be accomplished by specific gravity (*11*). High dry matter is important to processors of whole carrot products to meet drained-weight specifications.

Sugar quantity, TDS, and percentage dry weight exhibit quantitative inheritance patterns (*53*). Total sugar quantity and either TDS or percentage dry weight have correlation coefficients (r) of .75–.95, whereas TDS and percentage dry weight are more highly correlated ($r = .85$–.95). The latter correlation may be higher because soluble solids often account for over 90% of the dry weight, whereas total sugars account for only 60–75% of the soluble solids and 40–60% of the dry weight (*24*). As a point of reference, the "average" raw carrot is 88% water, 6–8% sugar, 1–2% fiber, 0.7–1.2% protein, 1% ash, 0–0.3% fat, and is starch free (*51, 71*).

Percentage dry weight, a standard variable in much biological research, can be determined quickly by simply weighing a fresh sample, drying, and reweighing. The measurement of total sugar quantity is more time consuming. Free sugars have been measured colorimetrically, but the advent of high-performance liquid chromatography has allowed for more rapid sugar analysis (*36*). With this technique three to five samples can be analyzed per hour by one worker, including all operations involved. Total dissolved solids or dry weight analysis can be determined in ⅓ to ⅒ the time.

The main goal in breeding for altered sugar quantity, TDS, and percentage dry weight has been to increase sugar content and thereby improve carrot flavor. The correlation between rapidly measurable TDS or dry weight and total sugars suggests that the use of either rapid technique effectively alters sugar levels.

Volatile terpenoids and other potent compounds, other than sugars, have important effects on carrot flavor. Carrot roots must be taste tested to achieve the correct balance between volatile terpenoids and sugar levels. The lack of consistent flavor improvement by selecting for increased TDS (*53*) and the failure to improve the flavor of high-volatile terpenoid carrots significantly by dipping slices in 30% fructose lead to the conclusion that volatiles play a decisive role in overall flavor. Genetic differences for sweetness found in raw carrots are also reflected in the processed carrots (*59*).

Total sugar is the sum of glucose, fructose, and sucrose since these sugars account for 98–100% of the free sugars in carrots. Even though complete sugar analysis is a time-consuming procedure for selection purposes, it has elucidated an interesting, simply inherited trait. The reducing sugar (*Rs*) locus controls the ratio of reducing sugars (glucose and fructose) to sucrose, independent of total sugar (*36*). Dominance is for high reducing sugars and low sucrose. The quality of deep-fried carrot chips may be damaged by the presence of high reducing sugars (*Rs/−*). Conversely, high reducing sugar may be desirable for improving flavor of raw carrots since the average sweetness of glucose plus fructose is 20% greater than that of sucrose (*57*). The potential for improvement with high reducing sugars remains to be tested since the sweetness levels cited are for weak, aqueous solutions of sugars, not solid matrices like carrot roots.

Selection for reduced levels of volatile terpenoids must be the prime concern in the improvement of raw carrot flavor. Carrots low in volatile terpenoids are bland but edible, whereas those high in volatile terpenoids are inedible. Terpenoid quantity and associated harsh flavor exhibit great genetic variation. An approximate range is from 5 to 200 ppm with surprisingly little environment (soil, climate) or maturity effect (*39, 63*). Volatile terpenoid levels of 20–50 ppm are desirable. Carrots with higher levels have a harsh flavor, while those with lower levels lack a desirable, typical carrot flavor.

Harsh flavor is common in available carrot cultivars (*61*), but rapid improvement of flavor is made feasible by the dominance for mild flavor in hybrids that have one mild parent (*63*). Since the inheritance of harshness is multigenic, selection for mildness should be initiated early in inbred development and applied in every generation. Laboratory assessment of terpenoid types and amount is useful in selecting for extreme individual roots to be used in establishing elite, experimental populations, but the use of a trained tester to ascertain flavor is more practical for routine selection. Volatile terpenoids and harshness are quite stable in cold-stored carrots, but processing reduces volatile terpenoid level, harshness, and overall raw carrot flavor (*59*).

Isocoumarin, which may contribute to bitter flavor, also demonstrates quantitative genetic variation. Hybrids tend to be comparable to the more bitter parent (*23*). Since isocoumarin bitterness is the consequence of extended cold storage, particularly in the presence of ethylene, it is not a primary concern in present carrot breeding programs. The role of isocoumarin in bitter flavor is not fully known (*58*).

Non-bolting

In northern latitudes, cold weather often occurs during early growth of seedlings and results in premature seeding (bolting) of a significant percentage of the population. Bolting can cause serious losses in yield and quality. It is important to impose continuing selection pressure for non-bolting in order to avoid a genetic shift toward easy bolting.

The first precaution is to provide a cold-induction treatment of stecklings adequate to bolt 100% of the breeding population. This procedure avoids selection against bolting-resistant genotypes. It has been established that 8–10 weeks at a temperature below 40 °F (5°C) are required for complete vernalization of stecklings harvested in Michigan in late August and intended for seed production in the greenhouse (28). The second recommended procedure in northern latitudes is planting as early as possible in the spring so that seedling plants are exposed to as much natural cold as possible. A cold-unit system for determining exposure needed for vernalization of seedling plants was worked out by Dickson et al. (29). They found that a good screening system required 650 hr below the base temperature of 50°F (10°C) during the first 2 months after planting, followed by 3 months of growth to allow all potential bolters to develop. Seasonal differences that do not provide the necessary cold may make it impossible to select non-bolters every year in spring-planted carrots. Relying on early planting and natural cold treatment further imposes a tight schedule on the breeder who must produce stecklings in time to provide for 2-month induction and 4–5 months to mature and process seed for the next early spring planting. In a breeding program based on an annual cycle, the best schedule is 8–10 weeks of root storage below 40°F (5°C), followed by planting in the greenhouse using a night temperature of 55°F (13°C) until seed stalk development begins. Then 70°F (21°C) nights and 80°F (27°C) days are used to hasten anthesis and seed maturity (29).

Another practical procedure for selection is to utilize winter cold induction in areas where winters normally do not produce 100% vernalization of fall-planted carrots and to select non-bolting or slow-bolting plants. Cultivars or breeding lines with known bolting tendency must be included as standards in such plantings. These locations may be used to index bolting tendency in established cultivars and breeding lines.

Disease Resistance

Selection for resistance to alternaria leaf blight has been accomplished by exposing breeding materials to natural infestation in areas where the disease is generally severe. Susceptible cultivars, planted between rows of breeding material, are inoculated to ensure the presence and uniform spread of the disease. Most years in central Florida these procedures have been effective in producing severe defoliation of susceptible cultivars. Resistance is not complete. The presence of vigorous tops is due in part to the ability of certain genotypes to produce new leaves rapidly to replace those lost to the disease. In addition to inherent top vigor, the resistant genotypes show a restriction in area or depth of lesions on leaf blades and petioles that reduces defoliation. Roots selected on the basis of top vigor and lesion type are used in developing inbred parent lines or breeding populations.

For resistance to cercospora leaf blight the same procedures can be used. Since both diseases may develop in the same season it is possible to make selections by using field exposure. With *Cercospora* a method for greenhouse inoculation and incubation was described by Angell and Gabelman (3). However, laboratory screening procedures for resistance to leaf blight diseases have had only limited use. Precisely controlled, repeatable screening methods are needed for more rapid and efficient development of resistant genotypes.

Field exposure has been used in the University of Wisconsin program to classify and select plants for resistance to aster yellows. The incidence and severity of the disease in northern carrot areas varies from year to year, depending upon the number and levels of

pathogen infestation in migrating leaf hoppers and upon the timing of their movement from southern areas. Lettuce may be planted in alternate rows with carrot breeding material to encourage increase of the vector population and ensure uniform spread of the disease. Greenhouse screening techniques that might eliminate the effects of weather and vector preference have not been applied.

A similar field method has been adopted in our preliminary efforts to select for resistance to the virus complex that causes motley dwarf. At Corvallis, Oregon, motley dwarf is almost an annual occurrence, especially in carrots planted early enough to be exposed to the first generations of the aphid vector. It is difficult to grow virus-infected plants through the seed cycle even when foliar symptoms are not severe. It has been noted that plants with symptoms of carrot mottle may be quite vigorous with little loss in yields. Some genotypes, apparently tolerant to mottle, either escape or resist the red leaf component. It appears that there is resistance to one or the other of the viruses implicated in motely dwarf as well as resistance to both. The best procedure available at this time is early planting to ensure infection, then production of seed on surviving plants. Because of the uncertainty of seed production on surviving plants, it is necessary to produce the same populations in a virus-free area and make selections for self-pollination on the basis of data from the motley dwarf plots. This index system is slow and costly if the disease plots are remote from other breeding operations. It is more efficient to breed for resistance in an area where the disease is prevalent.

Inbred Vigor

Selection for tolerance to inbreeding has been accomplished without much effort to evaluate inbreeding depression. The loss of vigor associated with inbreeding is dramatic and especially noticeable in early-generation carrot lines extracted from open-pollinated cultivars. In early hybrid development, many inbreds simply failed to survive or were discarded when they appeared to be too weak to reproduce. Lines that survived to S_3 or S_4 and possessed improved horticultural qualities were tested in experimental single-cross (sterile × fertile) hybrids that frequently were substantial improvements over their source cultivars. The serious lack of vigor in inbred parents was partially solved by resort to three-way hybrids for female parents in order to secure acceptable yields of seed.

As surviving lines accumulated, systematic recycling of inbreds was initiated by making crosses between individual fertile plants selected from maintainer inbreds. Progenies from these crosses were inbred in turn to S_3 or S_4 before they were selected for an additional cycle of fertile × fertile crosses, followed by inbreeding and selection. The level of inbreeding has been dictated by survival of lines and the degree of uniformity demanded by the market. Some of our most promising inbreds trace back through four generations of such matings to the original open-pollinated source. The net result has been elimination of many recessive genes that contribute to inbreeding depression and the accumulation of those that contribute to color and other qualities for which selection pressure has been imposed. This strategy has enabled us to achieve intense inbreeding (as high as S_{10}) to establish the homozygosity required for genetic studies.

As this process continues, it is expected that increasing tolerance to inbreeding will be achieved and that inbred lines with enough vigor for direct use in single-cross hybrids will be developed. A similar long process in the development of inbred parents for hybrid corn (*Zea mays*) has resulted in gradual improvement of inbred vigor to a level that has permitted increasing use of inbred lines as parents in single-cross hybrids. Achievement of

a comparable level of inbred vigor in carrot will take longer because of its long life cycle and because there are fewer breeding programs in which inbreds are being selected for vigor.

GROWING THE SEED CROP

Various types of cages are used to accomplish the isolation necessary for advancing selected plants (roots) through their reproductive cycle. A root selected for producing the next generation represents a substantial investment, not just in growing it to the root stage, but in the years of breeding involved in bringing it to a state of genetic improvement. Therefore, every precaution must be taken to ensure its successful propagation. The following procedures, evolved in our program, will not have universal application. They represent the type of measures that must be adapted and modified to ensure successful seed production wherever the project is carried on.

Storage and Vernalization

Stored carrot roots are vulnerable to a number of rotting organisms that are favored by a film of water on the root surface. An effective means of maintaining the high humidity necessary to prevent desiccation and still avoiding condensation of free water on root surfaces involves the use of polyethylene bags, paper bags, and dry wood shavings. The tops are cut to about 1 in. Roots are then dipped in a fungicide mix appropriate for the organisms to be controlled. Concentration is not critical because drying will leave a full-strength deposit of the chemicals on the root surface. After dipping, the roots must be dried thoroughly before packing. It is important that no water remains on the root surface. The dry roots are then placed in paper bags with a volume of dry wood-shavings approximately equal to that of the carrots. The paper packages are then placed in polyethylene bags, tied, and placed in a refrigerated storage at 38°F (3°C). After about 1–2 weeks, droplets of water will condense on the inner surface of the polyethylene bags and will be blotted up by the paper bags. At that time the polyethylene bags should be punctured to allow excess moisture to escape. By this method the roots remain dry while their microenvironment is maintained near the desired 100% relative humidity. Storage for 8 weeks will accomplish the vernalization necessary for prompt bolting in the field or greenhouse. Roots harvested in the fall can be stored for spring planting without losses from decay.

Planting

Care must be taken in planting to protect against a variety of hazards that will vary with location. Cuts made in the process of color selection leave the roots especially vulnerable to drought. They must be planted with crowns about 1 in. below the soil surface. Enough water is poured around each root to ensure good contact with the soil. They then receive a local soil application of a systemic insecticide to control the leafhopper vector of aster yellows. After the insecticide treatment, some adjacent soil is used to cover the crown to the desired depth and to provide a mulch that will delay drying.

Pest Control

In addition to the systemic pesticide applied at planting, a regular schedule of spray treatment, mainly for leafhopper control, is necessary until cages are installed. Effective

control before flowering is important because of the difficulty of controlling pests after pollinating insects are introduced. To control aphids, lady bird beetles are introduced into isolation cages after insecticide applications are discontinued. In areas where rabbits and other carrot-loving animals are common, it is necessary to provide protection. In our Wisconsin plots where rabbits are the common pest, a fine (1 in.) mesh chicken wire fence, approximately 2 ft high, is placed around the area devoted to breeding plots and cage isolations. After 2–3 weeks of growth, the plants are no longer attractive and the fence can be removed.

Since breeding areas are small, appropriate herbicide treatments can be applied with hand-propelled or knapsack sprayers. The same cages are often used for one or two other insect-pollinated species along with carrots, and so care must be taken to use compatible herbicides or to direct applications only to the target species. Much hand weeding can be avoided by following a timely herbicide schedule.

Disease Control

Alternaria leaf blight, aster yellows, and bacterial blight (*Xanthomonas carotae*) are the most common diseases encountered in outdoor breeding plots and cages. Alternaria can be controlled by a weekly spray schedule with an effective fungicide. It is important to select a fungicide that is not toxic to pollinating insects. Spraying must be continued during pollination in order to prevent alternaria damage to the flowers.

In addition to the systemic insecticide applied at planting for control of the aster yellows vector, it is necessary to begin an insecticide schedule as soon as top growth begins and to continue until pollinators are introduced. A motorized backpack sprayer is effective in projecting a fine spray mist through the screens after the cages are installed.

Control of bacterial blight must be accomplished by hot-water treatment of the seed from which roots are produced. If the disease is introduced with systemically infected roots, some spread can be expected and no effective control is available. The disease is especially damaging in the environment provided under screen isolators where plants are shaded and air movement is restricted.

Isolation and Pollination

The cages used in controlling pollination vary from small cylindrical cloth cages to 6-ft-high screen enclosures that range from 3.5 × 6 ft to 12 × 80 ft (Fig. 9.10). The large cages, 12 × 24 ft and larger, are used to increase finished lines and to produce experimental hybrid combinations for trial. Under one screen, several female parents may be isolated with a single pollinator. For line increases it is preferable to isolate only the male-sterile and its companion maintainer in order to minimize chances for contamination. Small screen cages (6 × 6 ft and 3.5 × 6 ft) are used for advancing, on a mass basis, the early-generation inbred pairs, which usually are at the BC_2 or BC_3 generation in S cytoplasm.

Design of the large isolation cages will vary widely and can be made to conform to the breeder's preference. For our program, we use 6 × 6 ft panels constructed of heavy-duty electrical conduit as basic units. These panels are secured to supporting steel fence posts by means of heavy-grade filament tape. Screen covers, constructed with heavy-duty zippers for access, are installed before plants begin to flower. Multiples of the basic 6 × 6 ft panel can be used to fit the full range of screen cover sizes.

The small cloth-covered, cylindrical cages used to isolate umbels from one to five
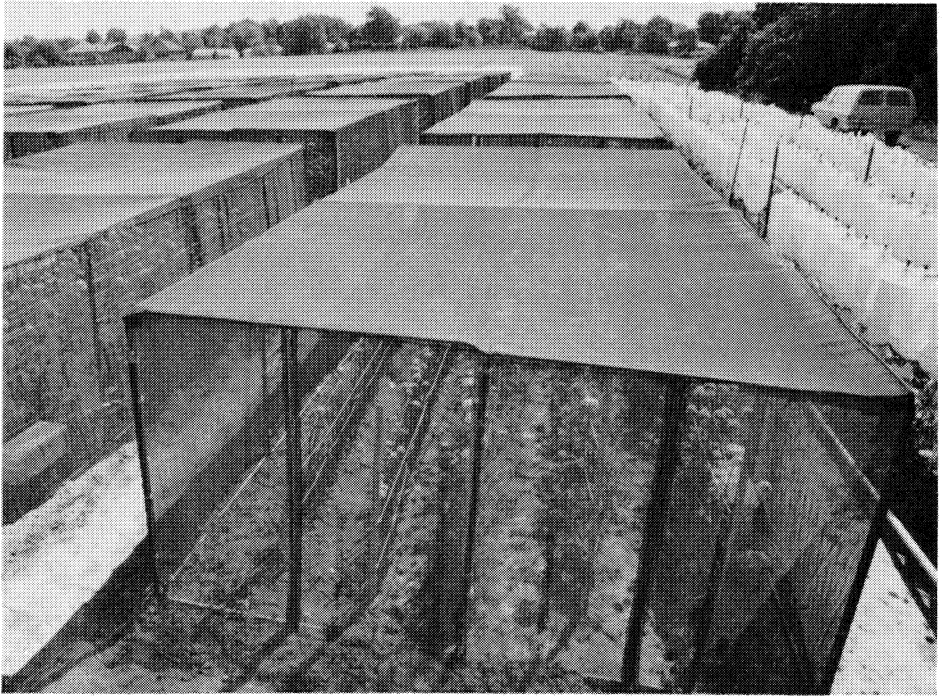
FIGURE 9.10. Large screen cages for increasing parent inbreds and producing experimental carrot hybrids.

plants are constructed in a way that will permit easy introduction of house fly pupae (Fig. 9.6). At the top, the cloth cages are fastened around a short section of garden hose. These small isolators are used for selfing, making testcrosses, and for single-plant backcrosses in the early stages of inbred development. They are used for isolating two selected fertile plants to make fertile × fertile crosses from which new inbred lines are extracted. Umbels for isolation in these small cages should represent two or three stages of maturity. The late-flowering umbels will provide pollen during the time that stigmas on early-flowering umbels are receptive.

House flies (*Musca domestica*) are reared following a standard procedure with batches of pupae being produced at 3- or 4-day intervals to ensure a continuing supply. The pupae are dropped into the cages through the tube at the top and closed with a cork (Fig. 9.6). In hot weather the adult house fly is short lived. Mature pupae must be introduced two or three times per week to avoid interruption of the pollinating process. They should not be introduced until nearly mature. If immature pupae are used, they are likely to desiccate and succumb to high temperatures before they can emerge. Unlike honey bees, flies do not discriminate between lines on the basis of nectar quality and do not display preference for certain sources. Therefore, we introduce flies into the large cages to supplement bee activity and to ensure the necessary transfer of pollen from male-fertile to male-sterile plants. Nucleus hives of bees, placed in the large isolation cages at the beginning of bloom, are complete with queens and brood. The normal social organization needs to be complete to make sure that nectar-foraging bees will be available and that they will

function. It must be remembered that nectar foragers are the ones that accomplish most of the necessary transfer of pollen from fertile to male-sterile parents. Pollen foragers generally collect only pollen and will not visit male-sterile plants. While nucleus hives are confined in screen cages, they must be provided with water and food; and their activity must be closely monitored so that replacements can be provided if the necessary activity does not occur.

Processing and Storing Seed

To ensure maximum yields, seed from parent lines in the screen cages should be harvested two or three times as it matures. Risk of mixture can be minimized if harvest is accomplished before umbels begin to shatter. After thorough drying the seed may be separated and despined by hand rubbing or with a motorized scarifier, a device used only to despine and not to scarify. A small blower designed for experimental samples is used to separate seed from chaff.

To accomplish the prescribed hot water treatment for control of bacterial blight (*X. carotae*), all seed lots (even down to a few grams) from single-plant isolations are placed, with an identifying number, in fine-mesh bags and submerged in a water bath. The range of acceptable combinations of time and temperature is narrow and must be controlled precisely. Too little heat will result in some survival of the pathogen and too much will cause injury to the seed. A temperature of 51°C for 12½ min is effective for carrots. After heat treatment the seed lots are removed from the water bath and plunged into cool water, then drained, and spread out to dry. When thoroughly dried they are packaged in new seed envelopes and transferred to a refrigerated seed storage. Because carrot seed is short-lived, it should be stored in a cool, dry room. The maximum should not exceed 50°F (10°C) and 50% RH. Longevity will be improved with lower humidity and temperature.

Commercial Seed Production

Inbred parent lines and hybrids will not serve their intended purpose unless profitable seed crops can be produced. The breeder should be familiar with essential production practices and with seed problems that relate to characteristics of inbred parents. In addition to acceptable yielding capacity of the female parent, there must be an adequate and timely supply of pollen, effective insect pollinator activity, and appropriate cultural procedures.

Seed is grown either from roots (stecklings) harvested in the fall and held in cold storage for spring planting or, in areas with relatively mild winters, from roots harvested in early winter and replanted immediately. Both schedules are defined as ''root-to-seed'' production. In the first case, cold induction (vernalization) occurs in storage; in the second it occurs in the field after stecklings are transplanted from root beds to production fields. The alternative to a root-to-seed system is a seed-to-seed schedule in which plants from seed sown in late summer remain in the field through the winter. Having received more than adequate natural cold induction, the plants promptly bolt and mature a seed crop the following summer.

Root-to-seed allows for inspection of harvested roots and elimination (roguing) of off-types that result from outcrosses or mixtures. Another obvious advantage is that less stock seed is required, approximately ¼ lb per acre compared with 1–2 lb for seed-to-seed. The disadvantage is the high cost of root harvest, storage, and replanting. Carrot roots are not easy to store and excessive losses frequently occur. Some lines are susceptible to storage

diseases. If root storage is to be involved, attention must be given to the inherent storage quality of inbred parents.

The characteristically low seed yields from many cytosterile inbreds used as female parents in single-cross hybrids have encouraged breeders and seedmen to adopt three-way hybrids, in which male-sterile F_1 hybrids are used for seed parents. In the breeding program, it is necessary to produce and evaluate single-cross, male-sterile F_1 hybrids for use as seed parents. This must be done on a continuing basis as new sterile and maintainer lines become available. An obvious but essential requirement for hybrid seed parents is that roots of the inbred components must be as nearly identical as possible in visible characteristics such as shape, length, and color in order to minimize segregation in the three-way hybrid.

As a result of the high cost of root harvest, storage (including losses in storage), and replanting, most commercial production of hybrid seed is on a seed-to-seed schedule. In order to maintain genetic uniformity, increases of parent stocks should be made on a root-to-seed schedule. Elite stock seed must be increased from carefully selected roots under screen isolation. This cage-grown seed is adequate for outdoor root-to-seed production of the stock seed for commercial seed fields. One hundred plants grown under screen from carefully selected roots will produce about 1 lb of seed, enough for at least 4 acres of root-to-seed increase. Only one outdoor root-to-seed cycle should be used for increasing the components of a hybrid cultivar. To ensure uniformity, the roots for this one cycle should be rogued for off-types that result from mixtures or outcrosses.

Seed is produced in the arid west, mainly in Idaho, Oregon, Washington, and central California, where winters are cold enough to accomplish vernalization, yet mild enough for survival of overwintering plants. Areas like southern California occasionally have mild winters in which only part of the plants are vernalized. This kind of natural selection for easy induction will result in an increase of bolters in the hybrid crop. The risk is greater if stock seed is subjected to this unintended selection. Stecklings from cold storage can be planted for seed production in any of the seed-to-seed areas, a practice that is often followed to ensure some production in the event of winter-killing of the direct seeded crop. The late stages of hybrid development must include pilot production of candidate hybrids to permit evaluation of parents in their reproductive cycle and to provide enough seed for commercial trials.

In hybrid seed production fields, a common ♀ : ♂ ratio is 4 : 1, usually in an 8 : 2 arrangement with four, two-row beds of female alternating with single two-row beds of the pollen parent (Fig. 9.11). Some lines selected as good male parents by performance of their prototype hybrids produced under screen will be unsatisfactory seed producers under field conditions. For good field production an abundant supply of pollen is needed during peak flowering of the female. Some evaluation for pollen production can be accomplished in cage isolations. For conclusive evaluation of performance, they must be observed under field conditions. The female parents with their specific male parents also need to be evaluated for seed production potential in field isolations. Petaloid steriles generally set a lower percentage of their potential than do brown anther types. Brown anther steriles have been disappointing mainly because of their environmental instability (*38*). Lines that survived inbreeding and selection for brown anther CMS through many generations have later developed unacceptably high percentages of pollen-bearing plants in production fields. This experience, together with the fact that brown anther steriles are difficult to distinguish from fertiles in the roguing process, has resulted in a diminished interest and

FIGURE 9.11. Hybrid carrot seed production field.
Courtesy of Alf. Christiansen Seed Company, © 1982.

very little use of brown anther steriles in hybrid seed production. However, their superior seed set justifies continued efforts to establish stable lines.

Pollen transfer from a specific male to a specific female must be accomplished for successful production in hybrid seed fields. Whether or not this will occur can be determined only by experience with the parent lines and insect pollinators involved. Therefore, pilot seed production is an essential step in identifying hybrid combinations that can be reproduced economically. The domestic honey bee will discriminate between nectar sources, temporarily develop fidelity to a specific nectar, and return for frequent visits, while other lines are neglected. Differences in seed yield have been correlated with foraging preferences (34). Field testing is the only means now available for determining if a specific pair of parents will satisfy all requirements for nectar quality and pollen supply, to ensure adequate pollen transfer. Some of the many wild insects that visit carrot flowers are effective pollinators (15). By selecting sites where wild pollinators are prevalent, the domestic honey bee can be supplemented or replaced.

During the process of growing breeding lines through their reproductive cycle, some selection for seed-producing capacity can be accomplished. Inbreeding depression and the resulting low seed yields produced on inbred steriles have dictated the almost exclusive

use of F_1 seed parents. Another means of ensuring reasonable yields is to use BC_1 females. In hybrid trials, single-cross F_1s are the most uniform and generally receive the highest marks for appearance. When an outstanding single-cross hybrid is identified, a near duplicate can be reproduced by using the BC_1 generation for the seed parent rather than the more intensely inbred seed parent, which usually is at BC_4 or more. In many cases, the small reduction in seed yield compared with an F_1 parent is offset by greater uniformity. This strategy can approximate the uniformity of inbred $\times$ inbred without the low seed yields generally produced on inbred parents. The BC_1 system has been used successfully in the recently introduced hybrid Orlando Gold. Its prototype was first observed as the single-cross B3640 $\times$ F524. The nonrecurrent component of the BC_1 parent B4367S was selected for its similarity to the recurrent line B3640M. To produce a near duplicate of the single cross we used [(B4367S $\times$ B3640M) $\times$ B3640M] $\times$ F524. The use of this BC_1 plan may not find favor with seedsmen who are reluctant to complicate their production program with the extra cycle necessary to produce the BC_1 parent. An obvious advantage is high yields of seed from F_1 plants that bear the BC_1 seed for field production.

BREEDING PLAN

At northern latitudes carrot breeding can be accomplished by growing roots of source material (open-pollinated cultivars, breeding populations, or segregating generations from fertile $\times$ fertile crosses) in the field and then producing seed from selected plants in the greenhouse. To produce seed in the greenhouse in time for spring planting it is necessary to replant roots from field selection before mid-November. To provide time for adequate vernalization, the crop must be harvested in early September. This inflexible schedule means that seed maturing in the greenhouse often must be rushed to the field for planting in order to complete the life cycle in 1 year. An additional disadvantage is the cost of greenhouse production and the limited quantities of seed of established parent lines and experimental hybrids that can be produced under glass. The obvious advantages of greenhouse production are the environmental controls and protection from weather. The relatively immature roots used in the greenhouse schedule permit more precise color discrimination. Xanthomonas blight does not damage greenhouse plants, making the hot water treatment unnecessary unless field seed production is anticipated.

If production sites are available at both southern and northern locations, it is possible to produce and select breeding material in typical carrot production areas during the winter months and then to grow seed from selected roots in the north. Under this schedule, seed is sown in central Florida, southern California or Texas in early October and roots are harvested in February or early March. Adequate cold induction can be accomplished by late April when the roots are planted for seed production in breeding plots and cages. Seed from these summer isolations is mature early in September in time for processing and planting at the southern sites in October, completing the life cycle in one year. Because summer seed production is difficult in areas most useful for winter root production, the breeder needs a site for seed production adapted to the root production schedule. Whether the seed cycle is produced in the greenhouse or field, it is possible to complete the life cycle of this normally biennial crop on an annual basis and thus hasten the achievement of breeding goals. The following annual operations are typical and represent the sequence and time required to complete development of a hybrid cultivar.

Year	Period	Step	Cycle[a]	Operation
1	Oct.–Mar.	a	V	In areas for which the eventual cultivar is intended, grow and select roots from a diverse collection of open-pollinated cultivars and breeding populations
2	May–Sept.	a	R	Self-pollinate and cross to a cytosterile tester as many as possible of the plants grown from these roots, taking care to include selections from a range of acceptable sources to maintain diversity
	Oct.–Mar.	b	V	Select in the production areas 5–10 roots of the best S_1 lines with their companion F_1 testcrosses
3	May–Sept.	a	R	Pair the 5–10 individual roots from each selected line with its F_1 under small cage isolators to produce S_2 and BC_1 seed
	Oct.–Mar.	b	V	From the best families of 5–10 sister S_1 lines, select 10 or more roots from only one of these sister lines in order to avoid narrowing the genetic base; the BC_1 roots should be selected to resemble their companion S_2 as nearly as possible; store and vernalize 40–50 BC_1 roots to use in progeny tests for maintainer genotypes
4	May–Sept.	a	R	Pair 5–10 single S_2 plants under small isolators, each with a plant from its BC_1 (making sure that the BC_1 plant is pollen sterile before caging) to produce S_3 and BC_2 seed
		b	R	Classify the 40–50 BC_1 plants (as male fertile or sterile) in the progeny tests in order to identify maintainer lines
	Oct.–Mar.	c	V	Follow the same procedure for the vegetative cycle as in 3b, again selecting roots from only one of the 5–10 sister S_3 lines; 40 or more roots are needed for isolation under increase and crossing cages.
5	May–Sept.	a	R	Mass under a large isolation cage 15 or more plants grown from S_3 roots of the maintainer (M) line and 5–10 phenotypically similar selections from the companion BC_2 (S) line
		b	R	For a preliminary test of combining ability, isolate an additional 10–20 S_3 plants with one or more established pollen-sterile (S) lines or F_1 hybrid seed parents to produce experimental hybrid combinations
	Oct.–Mar.	c	V	At as many locations as possible evaluate the prototype hybrids from step 5b to identify the lines that show promise as parents

Year	Period	Step	Cycle	Operation
		d	V	At the same locations produce roots from the BC_3 and S_3 mass$_1$ seed produced under screen in step 5a; select for re-production 20–40 roots of the candidate lines identified in the hybrid trials (5c)
6	May–Sept.	a	R	Isolate under large cages the roots from 5d to produce BC_4 sterile (S) and S_3M_2 maintainer companion lines of the best inbreds
		b	R	Plant samples of 5–10 BC_3 roots from 5d under screen with selected pollen parents to test new lines as potential seed parents
		c	R	Isolate maintainer with selected female parents to reproduce the best hybrids in preceding trials 5c and to produce additional experimental combinations; selected single-cross steriles may be included to produce experimental three-way hybrids
	Oct.–Mar.	d	V	Test new hybrid combinations in observation plots; advance the best from preliminary trials 5c to replicated trials and expand to additional locations
		e	V	Produce and select roots of candidate lines for maintenance and increase
7	May–Sept.	a	R	Increase (BC_5 of the S and S_3M_3 of the maintainer) lines identified in replicated trials as potential hybrid parents
	Oct.–Mar.	b	V	Repeat in replicated trials the most promising entries of those tested in 6d
		c	V	Produce roots from 7a in numbers large enough for pilot seed production of candidate hybrids on a root-to-seed schedule
8	May–Sept.	a	R	Establish outdoor root-to-seed isolation in seed-producing area to produce hybrid seed for commercial trials; determine if seed yield is acceptable
		b	R	Make additional cage increases of parent inbreds from 7c roots to provide for seed-to-seed pilot production
	Oct.–Mar.	c	V	Distribute seed produced in 8a for commercial trials (strip plantings) in production areas using all standard production, harvesting, processing, packing, and distribution procedures
9	Sept.–Aug.	a	R	Plant the parent lines from cage increases (8b) on seed-to-seed schedule in a seed-producing area to provide hybrid seed for commercial trials and to evaluate seed-yielding potential
10		a		Distribute seed from 8a and 9a for second year and more extensive commercial trials in all producing areas where the

Year	Period	Step	Cycle	Operation
				candidate hybrid is likely to be produced
11		a		Release a hybrid cultivar and its inbred parent components if warranted by performance in trials for yield of roots, quality, and seed yield

[a] V, vegetative cycle (roots); R, reproductive cycle (seeds).

Notes on the Breeding Plan

At year 4 step (b) the progeny test may not be necessary if lines have been extracted from sources with a high incidence of maintainer genotypes. If pollen-fertile plants are observed, all of the BC_1 progeny should be discarded and the companion S_2 plants isolated to produce S_3 lines that may then be evaluated as pollen parents. Pollen-fertile plants in the BC_1 progeny indicate the presence of restorer genes in the recurrent line. Rarely is such a line worth the effort necessary to establish it as a maintainer. Hybrids in which it is the pollen parent will be fertile or will segregate fertile plants. This precludes its use in F_1 seed parents, but it may serve as a pollen parent for production of commercial hybrid seed. There is no disadvantage in having male-fertile individuals in the commercial root crop, unless the originator wishes to prevent the extraction of parent lines from the proprietary hybrid.

Also, at year 4 the most uniform S_2 lines may be massed rather than selfed in order to minimize inbreeding depression. This decision must be made on a line-by-line basis. Some lines may be massed while a few selected plants are selfed as well. The criterion in this case is to arrest the inbreeding process as soon as the level of uniformity dictated by the market is achieved. Massing at this stage can avoid the unacceptably low seed yields that result from inbreeding depression.

At year 5, step (a), a few S_3 lines that show good tolerance to inbreeding should be selected for additional generations of selfing. Homozygosity for selected horticultural qualities may thus be established. The inbred lines advanced to S_4 and beyond will provide parents for fertile × fertile crosses between lines of diverse origin. This type of recycling is a most productive source of improved inbred lines.

At year 5, step (c), some single-cross hybrids with similar but unrelated parents should be selected for testing as F_1 (sterile-hybrid) seed parents to be used in three-way crosses.

At year 6, step (b), there may be an assortment of BC_3 lines originating about the same time, but from roots of diverse origin. One or more of these male-sterile inbreds (BC_3) may be isolated with a proven pollinator to produce experimental F_1 hybrids. This provides an early test of combining ability of new sterile inbred lines.

At year 6, step (d), sufficient seed should be available for distribution to testers in all important producing areas. This schedule includes observation and replicated trials only at southern locations where the breeding lines are grown in the winter for selection and increase. If possible, these same hybrids should be tested in summer areas where the root production season corresponds to that used for the reproductive cycle in the above schedule.

In the crossing cages where sterile inbreds and single-cross hybrids are isolated with selected pollen parents to produce early-stage experimental hybrids, it is useful to record

seed yields per plant. Such data provide some indication of seed production potential for candidate hybrids. Further data on seed yield are secured from the first root-to-seed and seed-to-seed pilot production.

All of the stages listed above probably will be proceeding at the same time. New and diverse material should be used each year in fertile × fertile crosses and for inbreeding to establish new lines. The number will be limited by resources available. Early-stage inbreds should be generated at a rate sufficient to replace those that are discarded.

Beginning at about year 5, step (a), when S_3 roots are in hand, serious consideration should be given to establishing breeding populations from which new breeding lines may be extracted. The method we have used involves isolating, under large screen cages, a single F_1 root from each of several crosses between plants selected from maintainer lines. The parent lines at S_3 or more are selected from diverse origins and possess at least one superior characteristic. Seed is harvested separately from each F_1 and grown in separate rows. To ensure an approximately equal contribution from each of the original parents the best four or five roots from each single-plant progeny are then planted for seed production under screen. The resulting population can be subjected to selection for several characteristics and recycled through mass selection as long as substantial genetic gains are achieved. One population has been selected through four generations for color and flavor and resistance to alternaria leaf blight. From the diversity of its original components it may be assumed that the population will yield a wide range of sugar and pigment levels when laboratory selection is applied.

TRIALS OF ADVANCED LINES

Because market carrots are harvested at a premature size that best meets market-grade specification, it is impossible to secure precise quantitative data in terms of total yields. The important performance characteristic of market carrots is marketable yield, which is likely to be influenced by stand density and time of harvest. The uniformity in size and shape and lack of serious grade defects, which depend to a large degree on genotype, become the important cultivar differences that need to be defined and evaluated in market carrot performance trials. In the case of processing carrots, one of the most important variables is total yielding capacity. Yields determined at maturity for processing carrots are more reliable and easier to secure than are those for market types.

The relatively wide range of maturity (root growth rates) represented by an array of entries in market carrot trials makes it impossible to select a harvest date optimum for all entries. Early-maturing entries may have a high percentage of oversized, low-value roots, while late entries may have undersized roots that do not make minimum marketable grade.

In our observation trials we have relied on subjective evaluation of new or early-stage experimental hybrids to identify specific combinations for advancement to replicated or commerical trial. These "beauty contests" have been judged by breeders, seedsmen, processors, growers, and shippers. The entries have been displayed and quality rated at several locations in carrot-growing areas. The numerical values for quality (1, unacceptable, to 5, excellent) have been reliable in identifying the entires preferred by a diverse group of judges. The scores have been useful for interpreting changes or trends in preference. During 10 years of such trials, it was apparent that exterior and interior color became increasingly important and that the long taper of cv. Imperator became less acceptable than those with slight taper and intermediate blunt tips. Recent trials have revealed an increasing preference for the nearly cylindrical blunt-rooted type. These

subjective evaluations are important in providing data upon which selection of inbred lines and cultivars can be based, and they define future market trends that permit timely adjustment in selection criteria.

From the preliminary observation trials, entries with consistently high scores are selected for replicated and commercial trials. In most cases, remnant seed from cage production is sufficient to provide for replicated trials. Whenever possible, additional production under screen isolation is undertaken immediately to provide seed for the expanded testing program.

Replicated trials vary according to the type of information desired and the preference of the operator. Because of the difficulty experienced in establishing uniform stands it is usually necessary to overplant and thin to achieve the uniform stands needed to secure reliable yield data. For market carrots we have successfully used miniplots of single rows 1 m in length with nine replications. An estimated 60 seeds/plot are hand planted. After the stand is established, these plots are thinned to 30 plants/plot. At harvest we record the total number and weight of roots and the number and weight of marketable roots. The major types of culls are classified and weighed. In addition to these quantitative data, the roots are described from the standpoint of physical type and their quality factors are recorded (length, shape, smoothness, interior and exterior color). Recently, attempts have been made to conduct a taste panel evaluation of the best entries or those considered as candidates for release.

From small-plot data it is impossible to predict the performance of a carrot cultivar under commercial cultural and marketing practices. Therefore it has proved necessary to provide enough seed for planting and harvesting with the equipment used for the commercial crop and enough product to follow a candidate hybrid through harvesting, packing, and distribution. It is in commercial production and handling of the crop that potential deficiencies become evident. Among the defects that may emerge under commercial culture are (1) insufficient top length or strength for mechanical harvesters, (2) fragile roots that suffer mechanical damage in harvesting and packing, and (3) in processing carrots, an unacceptable canned or frozen product. In the latter case preliminary processing trials may avoid advancing an unacceptable candidate hybrid to commercial processing trials.

FUTURE GOALS

Hybrid carrot development through the 1970s was concerned with the most urgently needed and easily attained improvements. Until recently almost any combination of selected inbreds resulted in hybrids that were superior to open-pollinated cultivars. The apparent ease with which breeders were able to produce acceptable hybrids resulted in a proliferation of named releases. In many cases serious seed production problems emerged that made it difficult or impossible for seedsmen to provide a reliable, continuing supply of high-quality seed. As the number of available hybrids is narrowed by greater discrimination on the part of growers and by improved seed production of a few successful hybrids, priority will be given to objectives that have been receiving little attention.

One high-priority goal for future work is to improve seed-yielding capacity. This might involve the following: (1) establishing reliable brown anther lines, (2) early-generation evaluation of seed production potential of female lines under simulated commercial production, and (3) developing parent lines attractive to pollinating insects.

Other opportunities for future improvement lie in adapting to unusual uses. These

include high-yielding, high-sugar lines for producing alcohol or sugar. Without the stringent quality requirements imposed on edible carrots, it should be possible to combine 10% or more fermentable carbohydrates with yields of more than 40 tons/acre. Such genotypes should be established so that material is on hand for prompt development in the event of a critical need for fuel alcohol. A winter carrot crop in the southwest sugar beet areas might provide a biomass or sugar source at a season of the year when sugar beet processing plants are idle. A non-bolting, high-sugar, white carrot would be suitable.

Breeding efforts probably will be directed toward other minor but potentially important uses. In some cases future product development will depend upon the imagination and initiative of breeders in creating raw products designed for special uses. Carrots can be fermented and processed like cucumbers to produce a pickled product of excellent eating quality. The carrot designed for this purpose will need to be low in fermentable carbohydrates, low in volatile terpenoids, high in carotene, and of a uniform interior color. These characteristics are also needed for juice or for blending with other vegetable or fruit juices. The special genetic characteristics required for producing quality deep-fried carrot chips are available. The most important requirement is for a low level of the reducing sugars, which char at high temperatures and result in an unattractive brown product. High-sucrose carrots produce attractive light-colored chips. The appearance and nutritive value of carrot chips can be improved by using high-carotene roots with uniform color distribution for chipping. Low-volatile compounds may not be a priority goal in products subjected to high temperatures in processing. The needs for an improved raw product for various kinds of dehydration should receive attention.

Resistance to additional serious or potentially serious diseases, insects, and nematodes will become high-priority objectives as the more urgent problems are solved and as improved germplasm becomes available. More comprehensive plant exploration and refinement of screening techniques are needed to identify sources of resistance and provide for efficient selection.

Powdery mildew, *Erysiphe polygoni,* first reported in California in 1976 (*1*), has been observed with increasing frequency since that time. The fact that in California resistance has been observed in some advanced breeding lines and hybrids suggests that progress can be achieved promptly. In France, Bonnet (*16*) found dominant resistance to a powdery mildew incited by a different species (*E. heraclei*) in *D. carota* ssp. *dentatus.* He suggested backcrossing and using his early inoculation method to transfer resistance to selected inbreds.

Work on resistance to root-damaging soilborne pathogens and pests has been limited to observations of levels of resistance in collections of introduced accessions and domestic cultivars or breeding material.

Apparent genetic differences in response to a type of root defect described as cavity spot have been observed. The cause or causes of cavity spot are not well established. Anderson *et al.* (*2*) proposed the names cavity spot for the disease caused by *Clostridium* spp. and rhizoctonia canker for that caused by *Rhizoctonia solani.* They classified as tolerant or resistant only 10 out of 125 cultivars and breeding lines tested against *R. solani.* In 1981 DeKock (*26*) reported that cavity spot was a typical calcium deficiency symptom that may be induced by overfertilization with potassium. Typical cavity spot symptoms described by Fawzi and Kelly (*35*) in 1982 resulted from feeding of the fungus gnat *Bradysia impatiens* (Joh.). They achieved complete control with a systemic insecticide and were unable to produce cavity spot symptoms under calcium deficient culture. Whatever its cause, cavity spot often results in serious losses; and there is enough evidence of genetic resistance to justify including it in future long-term goals.

One of the most serious soilborne pests on carrots is root-knot nematode *Meloidogyne hapla,* controlled by costly soil fumigation. Reports of genetic tolerance (*20, 25, 70*) give rise to hopes that eventually a level of resistance can be achieved that will minimize damage or contribute to reducing populations and to improving effectiveness of control measures. There are no active breeding programs now using controlled screening for nematode resistance.

In a 1977 report, Scott (*55*) suggested that differences in mortality of lygus bugs *Lygus hesperus* Knight and *Lygus elisus* van Duzee on inbred lines from the open-pollinated cv. Imperida were great enough to make breeding for resistance feasible. Lygus bugs on the seed crop cause serious reduction in seed quality. Immature seeds attacked by lygus bugs do not develop embryos and they cannot be separated from normal seeds in the milling process. Eventually, the possibility of exploiting genetic resistance will need to be explored.

Another potential pest is the carrot fly *Psila rosae,* reported as a common root feeder in Europe and Canada, but not yet a serious problem in U.S. carrot-producing areas. Ellis *et al.* (*31, 32*) recently found that strains of the cv. Nantes were damaged less than some processing types. Whether or not the observed level of resistance will provide adequate protection is not known.

Some widely publicized techniques for rapidly modifying the genetic constitution of higher plants have been neglected by carrot breeders, who generally have been inclined to concentrate on conventional breeding methods. New techniques classified as biotechnology or genetic engineering probably will not soon become major sources of genetic variability needed for carrot improvement. Most urgently needed genetic characteristics are available in domestic cultivars, breeding populations, and exotic accessions. Genes controlling needed characteristics are easily transferred by classical techniques of hybridization and selection. It is likely that conventional approaches will continue to occupy the attention of carrot breeders. However, the carrot is a good organism for exploring the potential application of advances in biotechnology. In cell culture it readily produces callus and protoplasts and provides a model for plant regeneration. Improvements that may be incorporated through biotechnology and that are not attainable by conventional means have not been identified. When they are identified and incorporated, conventional procedures probably will be necessary to establish stable genotypes that can be produced on the farm. Despite the general reluctance of breeders to adopt new techniques, biotechnology offers promise for future advances and should be exploited. One possible application is rapid development of inbreds by means of anther or pollen culture to obtain haploids. Another is selection for resistance in cell cultures exposed to disease toxins or herbicides.

It is impossible to predict future goals accurately, but we can be confident that unexpected problems will be encountered. New needs certainly will emerge and novel uses for carrots probably will be developed. Fortunately, most of the genetic diversity necessary to meet new demands is available. The breeder must be alert to develop germplasm and apply procedures for solving future as well as present problems.

REFERENCES

1. Abercrombie, K., and Finch, H. C. 1976. Powdery mildew of carrot in California. Plant Dis. Rep. *60,* 780–781.
2. Anderson, N. A., Davis, D. W., and Shehata, M. A. 1982. Screening carrots for resistance to cankers caused by *Rhizoctonia solani.* HortScience *17,* 254–256.

3. Angell, F. F., and Gabelman, W. H. 1968. Inheritance of resistance in carrot, *Daucus carota* var. *sativa,* to the leaf spot fungus, *Cercospora carotae.* Proc. Am. Soc. Hortic. Sci. *93,* 434–437.

4. Angell, F. F., and Gabelman, W. H. 1970. Inheritance of purple petiole in carrot, *Daucus carota* var. *sativa.* HortScience *5,* 175.

5. Aubert, S., and Bonnet, A. 1978. Nutritional value of the Umbelliferae with the example of the carrot (*Daucus carota*). Ombelliferes: Contrib. Pluridiscip. Syst., Actes Symp. Int. 2nd, 1977 pp. 809–822 (in French).

6. Aubert, S., Bonnet, A., and Szot, B. 1979. Rheological indices of texture in relation to biochemical characteristics of carrot (*Daucus carota* L.). Ann. Technol. Agric. *28,* 397–422 (in French).

7. Bajaj, K. L., Kaur, G., and Sukhija, B. S. 1980. Chemical composition and some plant characteristics in relation to quality to some promising cultivars of carrot (*Daucus carota* L.). Qual. Plant.—Plant Foods Hum. Nutr. *30,* 97–107.

8. Banga, O. 1957. Origin of the European cultivated carrot. Euphytica *6,* 54–63.

9. Banga, O. 1963. Origin and distribution of the western cultivated carrot Genet. Agrar. *17,* 357–370.

10. Banga, O., Petiet, J., and van Bennekom, J. L. 1964. Genetical analysis of male sterility in carrots. Euphytica *13,* 75–93.

11. Bassett, M. J. 1974. Screening carrot roots for high soluble solids by specific gravity. Hort-Science *93,* 232–233.

12. Bayliss, M. W. 1975. The effects of growth *in vitro* on the chromosome complement of *Daucus carota* (L.) suspension cultures. Chromosoma *51,* 401–411.

13. Bell, C. R., and Constance, L. 1960. Chromosome numbers in Umbelliferae. II. Am. J. Bot. *47,* 24–32.

14. Bienz, D. R. 1968. Evidence for carrot splitting as an inherited tendency. Proc. Am. Soc. Hortic. Sci. *93,* 429–433.

15. Bohart, G. E., and Nye, W. P. 1960. Insect pollination of carrots in Utah. Bull.—Utah Agric. Exp. Stn. *419,* 1–16.

16. Bonnet, A. 1983. Source of resistance to powdery mildew for breeding cultivated carrots. Agronomie *3,* 33–37.

17. Borthwick, H. A. 1931. Development of the macrogametophyte and embryo of *Daucus carota.* Bot. Gaz. (Chicago) *92,* 23–44.

18. Borthwick, H. A., Phillips, M., and Robbins, W. W. 1931. Floral development in *Daucus carota.* Am. J. Bot. *18,* 784–797.

19. Braak, J. P., and Kho, Y. O. 1958. Some observations on the floral biology of the carrot (*Daucus carota* L.). Euphytica *7,* 131–139.

20. Brzeski, M. W. 1974. The reaction of carrot cultivars to *Meloidogyne hapla* Chitw. infestation. Zesz. Probl. Postepow Nauk Roln. *154,* 173–181.

21. Buishand, J. G., and Gabelman, W. H. 1979. Investigations of color and carotenoid content in phloem and xylem of carrot roots (*Daucus carota* L.). Euphytica *28,* 611–632.

22. Buishand, J. G., and Gabelman, W. H. 1980. Studies on the inheritance of root color and carotenoid content in red × yellow and red × white crosses of the carrot, *Daucus carota* L. Euphytica *29,* 241–260.

23. Carlton, B. C. 1960. Breeding and physiological studies of a bitter compound in carrots. Ph.D. Thesis. Michigan State University, East Lansing.

24. Carlton, B. C., and Peterson, C. E. 1963. Breeding carrots for sugar and dry matter content. Proc. Am. Soc. Hortic. Sci. *82,* 332–340.

25. Clark, R. L. 1969. Resistance to northern root-knot nematode (*Meloidogyne hapla*) in plant introductions. FAO Plant Prot. Bull. *17,* 136–137.

26. De Kock, P. C., Hall, A., and Inkson, R. H. E. 1981. Cavity spot of carrots. An. Edafol. Agrobiol. *40,* 307–316.

27. Dickson, M. H. 1966. The inheritance of longitudinal cracking in carrots. Euphytica *15*, 99–101.

28. Dickson, M. H., and Peterson, C. E. 1958. Hastening greenhouse seed production for carrot breeding. Proc. Am. Soc. Hortic. Sci. *71*, 412–415.

29. Dickson, M. H., Rieger, B., and Peterson, C. E. 1961. A cold unit system to evaluate bolting resistance in carrots. Proc. Am. Soc. Hortic. Sci. *77*, 401–405.

30. Eisa, H. M., and Wallace, D. H. 1969. Morphological and anatomical aspects of petaloidy in the carrot, *Daucus carota* L. J. Am. Soc. Hortic. Sci. *94*, 545–548.

31. Ellis, P. R., Hardman, J. A., Jackson, J. C., and Dowker, B. D. 1980. Screening of carrots for their susceptibility to carrot fly attack. J. Natl. Inst. Agric. Bot. (G.B.), *15*, 294–302.

32. Ellis, P. R., and Hardman, J. A. 1981. The consistency of the resistance to carrot fly attack at several centers in Europe. Ann. Appl. Biol. *98*, 491–497.

33. Erickson, E. H., Garment, M. B., and Peterson, C. E. 1982. Structure of cytoplasmic male-sterile and fertile carrot flowers. J. Am. Soc. Hortic. Sci. *107*, 698–706.

34. Erickson, E. H., Peterson, C. E., and Werner, P. 1979. Honeybee foraging and resultant seed set among male-fertile and cytoplasmic male-sterile carrot inbreds and hybrid seed parents. J. Am. Soc. Hortic. Sci. *104*, 635–638.

35. Fawzi, T. H., and Kelly, W. C. 1982. Cavity spot of carrots caused by feeding of fungus gnat larvae. J. Am. Soc. Hortic. Sci. *107*, 1177–1181.

36. Freeman, R. E., and Simon, P. W. 1983. Evidence for simple genetic control of sugar type in carrot (*Daucus carota* L.). J. Am. Soc. Hortic. Sci. *108*, 50–54.

37. Hansche, P. E., and Gabelman, W. H. 1963. Digenic control of male sterility in carrots, *Daucus carota* L. Crop Sci. *3*, 383–386.

38. Hansche, P. E., and Gabelman, W. H. 1963. Phenotypic stability of pollen sterile carrots, *Daucus carota* L. Proc. Am. Soc. Hortic. Sci. *82*, 341–350.

39. Heatherbell, D. A., and Wrolstad, R. E. 1971. Carrot volatiles. 2. Influence of variety, maturity and storage. J. Food Sci. *36*, 225–227.

40. Howard, R. J., and Williams, P. H. 1976. Methods for detecting resistance to Pythium and Rhizoctonia root diseases in seedling carrots. Plant Dis. Rep. *60*, 151–156.

41. Kirtschev, N. A., and Kratchanov, C. G. 1980. On the pectins of certain varieties of *Daucus carota*. Z. Lebensm.-Unters. -Forsch. *170*, 31–33.

42. Laferriere, L., and Gabelman, W. H. 1968. Inheritance of color, total carotenoids, alpha-carotene, and beta-carotene in carrots, *Daucus carota* L. Proc. Am. Soc. Hortic. Sci. *93*, 408–418.

43. Martens, M., Fjeldsenden, B., and Russwurm, H., Jr. 1979. Evaluation of sensory and chemical quality criteria of carrots and swedes. Acta Hortic. *93*, 21–27.

44. McCollum, G. D. 1966. Occurrence of petaloid stamens in wild carrot (*Daucus carota*) from Sweden. Econ. Bot. *20*, 361–367.

45. McCollum, G. D. 1975. Interspecific hybrid of *Daucus carota* × *D. capillifolius*. Bot. Gaz. (Chicago) *136*, 201–206.

46. Mildenhall, J. P., Pratt, R. G., Williams, P. W., and Mitchell, J. E. 1971. Pythium brown root and forking of muck-grown carrots. Plant Dis. Rep. *55*, 536–540.

47. Moore, D. M. 1971. Chromosome studies in the Umbelliferae. *In* The Biology and Chemistry of the Umbelliferae. V. H. Heywood (Editor), pp. 233–256. Academic Press, New York.

48. Morelock, T. E. 1974. Influence of cytoplasmic source on expression of male sterility in carrot, *Daucus carota* L. Ph.D. Thesis. University of Wisconsin, Madison.

49. Morelock, T. E., and Hosfield, G. L. 1976. Glabrous seedstalk in carrot: Inheritance and use as a genetic marker. HortScience *11*, 144.

50. Nair, P. K. K., and Kapoor, S. K. 1973. Pollen morphology production of *Daucus carota* L. J. Palynol. *9*, 152–159.

51. Paul, A. A., and Southgate, D. A. T. 1978. The Composition of Foods. American Elsevier Publishing Co., New York.

52. Robertson, J. A., Eastwood, M. A., and Yeoman, M. M. 1979. An investigation into the dietary fibre content of named varieties of carrot at different developmental ages. J. Sci. Food Agric. *30*, 388–394.

53. Scheerens, J. S., and Hosfield, G. L. 1976. The feasibility of improving eating quality of table carrots by selecting for total soluble solids. J. Am. Soc. Hortic. Sci. *101*, 705–709.

54. Schultz, G. A. 1973. Plant resistance to aster yellows. Proc. North Cent. Branch Entomol. Soc. Am. *28*, 93–99.

55. Scott, D. R. 1977. Selection for Lygus bug resistance in carrot. HortScience *12*, 452.

56. Senti, F. R., and Rizek, R. L. 1975. Nutrient levels in horticultural crops. HortScience *10*, 243–246.

57. Shallenberger, R. S., and Birch, G. G. 1975. Sugar Chemistry. AVI Publishing Co., Westport, CT.

58. Simon, P. W. 1985. Effect of genotype, growing conditions, storage, and processing on carrot (*Daucus carota* L.) flavor. *In* Evaluation of Quality of Fruits and Vegetables. H. E. Pattee (Editor), Chapter 9. AVI Publishing Co., Westport, CT.

59. Simon, P. W., and Lindsay, R. C. 1983. Effects of processing upon objective and sensory variables of carrots. J. Am. Soc. Hortic. Sci. *108*, 928–931.

60. Simon, P. W., Peterson, C. E., and Lindsay, R. C. 1980A. Correlations between sensory and objective parameters of carrot flavor. J. Agric. Food Chem. *28*, 559–562.

61. Simon, P. W., Peterson, C. E., and Lindsay, R. C. 1980B. Genetic and environmental influences on carrot flavor. J. Am. Soc. Hortic. Sci. *105*, 416–420.

62. Simon, P. W., Peterson, C. E., and Lindsay, R. C. 1981. The improving of flavor in a program of carrot genetics and breeding. ACS Symp. Ser. *170*, 109–118.

63. Simon, P. W., Peterson, C. E., and Lindsay, R. C. 1982. Genotype, soil, and climate effects on sensory and objective components of carrot flavor. J. Am. Soc. Hortic. Sci. *107*, 644–648.

64. Strandberg, J. O., Bassett, M. J., Peterson, C. E., and Berger, R. D. 1972. Sources of resistance to *Alternaria dauci*. HortScience *7*, 345.

65. Stubbs, L. L. 1948. A new virus disease of carrots: Its transmission, host range and control. Aust. J. Sci. Res., Ser. B *1*, 303–332.

66. Thompson, D. J. 1962. Studies on the inheritance of male-sterility in the carrot, *Daucus carota* L. Proc. Am. Soc. Hortic. Sci. *78*, 332–338.

67. Umiel, N., and Gabelman, W. H. 1971. Analytical procedures for detecting carotenoids in carrot (*Daucus carota* L.) roots and tomato (*Lycopersicum esculentum*) fruits. J. Am. Soc. Hortic. Sci. *96*, 702–704.

68. Umiel, N., and Gabelman, W. H. 1972. Inheritance of root color and carotenoid synthesis in carrot, *Daucus carota* L.: Orange vs. red. J. Am. Soc. Hortic. Sci. *97*, 453–460.

69. U.S. Department of Agriculture 1981. Agricultural Statistics. U.S. Government Printing Office, Washington, DC.

70. Vrain, T. C., and Baker, L. R. 1980. Reaction of hybrid carrot cultivars to *Meloidogyne hapla*. Can. J. Plant Pathol. *2*, 163–168.

71. Watt, B. K., and Merrill, A. C. 1963. Composition of foods—raw, processed, prepared. U.S. Dep. Agric., Agric. Handb. *8*.

72. Welch, J. E., and Grimball, E. L. 1947. Male sterility in carrot. Science *106*, 594.

73. Whitaker, T. W. 1949. A note on the cytology and systematic relationships of the carrot. J. Am. Soc. Hortic. Sci. *53*, 305–308.

74. Yates, S. G., and England, R. E. 1982. Isolation and analysis of carrot constitutents: Myristicin, falcarinol, and falcarindiol. J. Agric. Food Chem. *30*, 317–320.