

Domestication, Historical Development, and Modern Breeding of Carrot

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Table 5.1 World carrot production and availability, 1965–1995.

Continent	Variable	1965	1975	1985	1995
Africa	Area (% world)	8	5	6	8
	Yield (t/ha)	11	12	12	12
	Availability (kg/capita)	0.5	0.7	0.7	1.1
Asia	Area (% world)	8	27	29	34
	Yield (t/ha)	28	17	21	22
	Availability (kg/capita)	0.2	0.9	1.2	1.7
Europe	Area (% world)	54	53	50	43
	Yield (t/ha)	24	24	28	20
	Availability (kg/capita)	4.6	5.0	6.4	9.1
North & Central America	Area (% world)	21	9	9	9
	Yield (t/ha)	24	30	28	33
	Availability (kg/capita)	3.1	3.6	3.7	4.7
Oceania	Area (% world)	2	1	1	1
	Yield (t/ha)	27	32	32	31
	Availability (kg/capita)	4.6	6.0	6.3	8.8
South America	Area (% world)	7	5	5	5
	Yield (t/ha)	13	15	18	19
	Availability (kg/capita)	1.0	1.5	2.0	2.2
World	Area (1000 ha)	196	459	558	756
	Yield (t/ha)	22	19	22	21
	Availability (kg/capita)	1.3	2.2	2.5	2.8

Source: FAO Yearbook Production Statistics; average of 3 years (i.e., 1975 = average of 1974–1976).

ing would, in fact, make this a vital carrot breeding goal in much more of the world.

Preferred carrot root shape varies in different world production areas (Fig. 5.1, Table 5.2). About two-thirds of the current world carrot production area utilizes 'Nantes' types, especially in Europe and Asia. A predominant type in parts of Asia, South America, and Africa is 'Kuroda'. As carrot production expands in warmer areas, demand for and the value of these two root classes can be expected to increase for both seed and crop production. The market for the 'Imperator' root class is already well-developed in North America and Australia. Cultivars will continue to be categorized and marketed in the currently utilized classes, but their genetic diversity will likely become broader as breeders introduce disease resistance and quality traits into diverse backgrounds.

Table 5.2. Value and area of use of the commercial carrot seed crop based on a survey of 26 major world vegetable seed companies, 1995-1996.

Root class	World			Seed value (% of Total)					
	Seed value (million \$)	Seed value (% of total)	Production area (% of total)	Africa	North & Central America	South America	Asia	Europe	Oceania & Australia
Nantes	46	53	68	—	1	2	16	33	1
Imperator	24	27	16	—	24	—	—	—	3
Kuroda	9	10	7	1	—	5	5	—	—
Berlicum + Flakkee + Amsterdam	6	7	7	—	—	—	—	7	—
Danvers + Chantenay	3	3	2	—	3	—	—	—	—
Total	88	100	100	1	28	7	21	40	4

Source: Survey of 26 major world vegetable seed companies.

The most recent increase in production area and yield since 1975 reflects the popularity of modern "baby" carrots, which are planted more densely. Small, whole "baby" carrots have been produced for several hundred years, but the modern "baby" carrots, also called "cut and peeled," are lightly processed three to seven cm segments of 'Imperator' roots. With the convenience and value of this product, per capita availability and total farm value have also increased steeply. It is interesting to note the dramatic shift in U.S. carrot production to California and away from New York since 1925. Concomitant with this geographic shift has been a move to production for fresh market sales, which is readily achieved year-round in California. Without regular input of raw product from other areas, single season production areas like New York can only meet year-round raw product needs with long-term refrigeration or importation from other areas.

III. CARROT GROWTH, REPRODUCTION, AND GENETICS

Carrot, celery, parsley, cilantro, fennel, dill, caraway, anise, cumin, and numerous other root, leaf, and seed crops belong to the Apiaceae. The growth and reproductive biology of carrot is similar to other root crops in this family including arracacha, Hamburg parsley, parsnip, and turnip-rooted chervil. Having recently been reviewed (Rubatzky et al. 1999), these aspects of carrot will be surveyed briefly.

A. Morphology and Growth

Carrot is a cool-season crop with optimal growth between 15° and 25°. Seed germination is often uneven (Salter et al. 1981; Gray 1984) and early seedling growth is slow. The hypocotyl and taproot of the carrot seedling develop into the storage root (Havis 1939; Esau 1940). Storage root enlargement is minimal until six to eight weeks after germination, but the genetic potential for root length is largely established in the first three weeks of growth (White and Strandberg 1978). The carrot of commerce is a storage root largely comprised of parenchymatous secondary xylem and phloem. Plant growth continues until harvest.

The first true carrot leaf emerges one to two weeks after germination and internode elongation is greatly suppressed during the vegetative stage, i.e. during crop production. From two weeks to two months of exposure of carrots in the field or in storage to temperatures of 0° to 10° induces internode elongation and flowering in temperate-region carrots (Dickson and Peterson 1958). Photoperiods exceeding 12 h counteract the

Table 5.4. Continued

Gene symbol ²	Character description	Gene source	Reference
<i>Eh</i>	Downy mildew (<i>Erysiphe heraclei</i>) resistance	<i>D. carota</i> ssp. <i>dentatus</i>	Bonnet 1983
<i>g</i>	Green petiole	'Tendersweet'	Angell and Gabelman 1970
<i>gls</i>	Glabrous seedstalk	W-93 Wisconsin inbred	Morelock and Hosfield 1976
<i>lo</i>	Intense orange xylem	Miscellaneous	T. Kust, 1970 (cited in Buis-hand and Gabelman, 1979)
<i>L</i>	Lycopene synthesis	'Kintoki'	Umiel and Gabelman 1972
(<i>mh-1</i>), (<i>mh-2</i>)	<i>Meloidogyne hapla</i> resistance	'Rotin', Wisconsin inbreds	Wang and Goldman 1996
<i>Mj-1</i>	<i>Meloidogyne javanica</i> , resistance	'Brasilia'	Simon et al. 2000
<i>Ms-1</i> , <i>Ms-2</i> , <i>Ms-3</i>	Maintenance of male sterility	'Tendersweet'	Thompson 1962
<i>Ms-4</i> , <i>Ms-5</i>		'Tendersweet' 'Imperator 58', Pl 169486	Hansche and Gabelman 1963
<i>O</i>	Orange xylem	Miscellaneous	T. Kust, 1970 (cited in Buis-hand and Gabelman, 1979)
<i>P-1</i>	Purple root	Pl 173687	Simon 1996
<i>P-2</i>	Purple node	Pl 175719	Simon 1996
(<i>P-3</i>), (<i>P-4</i>)	Purple root	Miscellaneous	Laferriere and Gabelman 1968
<i>rp</i>	Reduced carotenoid pigmentation	W266 Wisconsin inbred	Goldman and Breitbach 1996
<i>rs</i>	Reducing sugar in root	Miscellaneous	Freeman and Simon 1983
(<i>sp-1</i>), (<i>sp-2</i>)	Seed spine formation	'Amkaza'	Nieuwhof and Garritsen 1984
<i>y</i>	Yellow xylem	Miscellaneous	T. Kust, 1970 (cited in Buis-hand and Gabelman 1979)
<i>Y-1</i>	Differential xylem/phloem carotene levels	Miscellaneous	T. Kust, 1970 (cited in Buis-hand and Gabelman 1979)
<i>Y-2</i>	Differential xylem/phloem carotene levels	Miscellaneous	T. Kust, 1970 (cited in Buis-hand and Gabelman 1979)

²Loci enclosed in parentheses were not named previously; suggested symbol. Isozyme and DNA markers not included.

that widespread introgression of wild carrot germplasm into domesticated forms has likely occurred.

After domestication and dissemination throughout Eurasia, the next known major change in carrots was the shift in storage root color from yellow and purple to orange in the late 16th and early 17th centuries (Banga 1963). The germplasm sources contributing to the color change in domestication of carrot are unknown. In particular, debate about the role of wild carrot germplasm in the history of carrot cultivar development remains unresolved. Vilmorin (1859) suggested an important role of wild carrot in its improvement in Europe. In particular, he suggested that orange root color came directly from wild carrots, based upon his studies involving pollination of wild carrot. It is likely that Vilmorin had not pollinated wild carrot, but rather wild \times domesticated hybrids, which are phenotypically similar to wild carrot (i.e. yellow or white storage root and tendency to early flowering). Yet Vilmorin's work does document his broad view of carrot to include its wild counterparts. It is interesting to speculate that Vilmorin's experiments brought an infusion of wild carrot into his early breeding program, which had a positive effect in broadening the allelic diversity of his subsequent selections. More recently, Small (1978), Brandenburg (1981), Heywood (1983), and Wijnheijmer et al. (1989) argued for a significant role of wild carrot in development of modern cultivars.

B. Modern Use of Carrot Germplasm

The broad germplasm base of carrot has been used regularly in modern carrot breeding. Important introduced traits include cytoplasmic male sterility; elevated carotene content; and resistance to several diseases and pests including aster yellows, carrot fly, nematodes, powdery mildew, and alternaria leaf blight (Table 5.5).

The most significant development in modern carrot breeding has been the incorporation and deployment of cytoplasmic male sterility for hybrid development. The "brown anther" cytoplasm, first described by Welch and Grimball in 1947, has been identified in several domesticated and wild carrot sources and is used widely in Europe (Bonnet 1985). The "petaloid" cytoplasm was discovered in 1953 by H. Munger in wild carrots, with a second source discovered in 1970 (Morelock et al. 1996). Both of these types of cytoplasmic male sterility were readily introgressed into adapted germplasm and became useful after several backcrosses with intensive selection for root color and shape. Virtually all new carrot cultivars developed today are hybrids utilizing genic-cytoplasmic

Alternaria leaf blight <i>Alternaria dauci</i>	1972	'Imperial Long Scarlet', 'Kokubu', 'Brasilia', 'Kuroda', wild carrot from Europe	Strandberg et al. 1972; Vieira et al. 1991; Boiteux et al. 1993	++
Cercospora leaf spot <i>Cercospora carotae</i>	1968	University of Wisconsin inbred WCR-1	Angell and Gabelman 1968	+
Powdery mildew <i>Erysiphe</i> sp.	1983	<i>D. carota</i> sp. <i>dentatus</i>	Bonnet 1983	++
Tropical root-knot nematode <i>Meloidogyne javanica</i>	1986	'Brasilia', 'Tropical', 'Kuronan'	Huang et al 1986; Simon et al. 2000	+
Northern root-knot nematode <i>Meloidogyne hapla</i>	1983	<i>D. carota</i> sp. <i>hispanicus</i> , 'Rotin', University of Wisconsin inbreds	Frese 1983; Wang and Goldman 1996	+
Aster yellows	1994	'Royal Chantenay', 'Scarlet Nantes', 'Gold King', 'Nanco', University of Wisconsin inbreds W33, W93, W263, W266; Oregon State University inbred OSU260	Gabelman et al. 1994	+

z+ = some use in cultivars, ++ = moderate use, +++ = extensive use.

pean cultivars and also in European by Asian crosses (Imam and Gabelman 1968; Laferriere and Gabelman 1968; Umiel and Gabelman 1972). The elevated carotene content in one European by Asian cross was especially interesting, since the high incidence of transgressive high-carotene segregants resulted in an F_2 mean carotene content greater than the higher parental stock (Simon et al. 1989). Derivatives of this population have been used as a source of high carotene content in the development of new breeding stocks and hybrids.

In summary, carrot germplasm diversity has contributed significantly to the development of modern cultivars. Improved seed production efficiency, crop uniformity, consumer and processing quality, and resistance to several diseases and pests, have resulted from the deployment of this genetic variation to much of the crop grown today. Recent germplasm evaluation projects supported by the U.S. Root and Bulb Crop Germplasm Committee have identified interesting new genetic variation for root carotene and anthocyanin content, as well as for resistance to alternaria leaf blight, root-knot nematodes (both *Meloidogyne hapla* and *M. incognita*), cavity spot (caused by *Pythium* spp.), and black crown (caused by *Alternaria radicina*) in carrot germplasm which may have application in future genetic improvement.

V. HISTORY OF CARROT CULTIVAR DEVELOPMENT

A. Carrots from 900 to 1600

Before the 10th century there is no clear evidence for the use of carrots as a root crop (Banga 1957a, 1963; Brandenburg 1981). The ancient Egyptians did use other members of the Apiaceae including celery, cilantro or coriander, dill, caraway, cumin, sweet fennel, and anise. The early Greeks and Romans also used all these umbelliferous vegetables and spices as well as parsnips, parsley, Florence fennel, chervil, and lovage. Some interpretations of the herbal of Dioscorides in the first century infer the use of carrot storage roots in early Greece, but based on more extensive descriptions from that era, it has usually been concluded that these reports were, in fact, referring to parsnips (Heywood 1983; Wijnheijmer et al. 1989). The confusion between parsnips and early carrots is understandable, since carrot storage roots before 1600 were not orange but rather yellow (sometimes referred to as white) or purple. When the first carrots were described in the 10th century in Persia and Arabia, it was long after the first description of other long-season vegetables in this region.

Root types of these early carrots were categorized as yellow or purple and a flavor difference coincided with the color. In Persia and Arabia, yellow carrots were generally regarded as more acrid in flavor and less succulent than purple carrots (Clement-Mullet 1866). In contrast to this, northern Europe shifted primarily to yellow carrots as they were regarded as having a more "refined" quality (Banga 1963). As purple root color is conditioned by a single dominant allele, (Simon 1996), it is not obvious how a single locus could have such a major effect on carrot culinary quality. The anthocyanins of purple carrots have no direct effect on flavor, but perhaps there are linked loci affecting flavor, ease of flower induction, rate of plant growth, or other important traits. Even so, the preference for purple carrots in Persia and Arabia, and for yellow carrots in northern Europe is a difference not readily explained.

B. Carrots from 1600 to 1950

1. Carrots in Europe. After 1600, two significant developments occurred in carrots in Europe: orange carrots were first noted, and carrots were first described and categorized by attributes other than storage root color including earliness of harvest, root shape, and/or root size. These developments were well-documented by Banga (1957b, 1963) in an extensive series of studies, including close examination of both written records and paintings, i.e., still life depicting carrots. Banga noted 'Yellow Belgian' as a carrot type recorded as early as 1553, while the first orange carrots he noted in paintings were the shorter 'Horn' in 1618 and 'Long Orange' in 1621. These names were not actually found in use until 1721, but their coincidence with longer and shorter orange-rooted types found in paintings reinforces the idea that written records were referring to distinct materials in the market. Banga further noted three orange-rooted carrots in 1763, 'Early Short Horn', 'Early Half Long Horn', and 'Late Half Long Horn', which he surmised were descended from 'Horn' and 'Long Orange'. Eight more orange-rooted types of carrot were noted in the 1800s with a broader range of root shape, earliness, and intensity of color. It should be noted that Banga catalogued over 45 cultivar or type names for carrots in his studies and lumped most of them into the nine diagrammed in Fig. 5.2 based upon either descriptions in seed catalogues or, to a lesser extent, field evaluations. Furthermore, many of the genetic origins he indicated were conjectured. But this is not to take anything away from his efforts. On the contrary, his efforts are to be applauded since he used the scant written records and his best judgment on a large mass of information to make a plausible simplified structure of European carrot origins and relationships. It has not been possible to

an evaluation of wild carrot germplasm from Turkey demonstrated orange segregants (Simon 1996), so it may be possible that orange carrots had an earlier and/or separate origin. Or it may be that introgression occurs not only in the direction of wild carrot to domestic but also from domestic to wild, and the 1996 study represents an example of broadening the genetic diversity of a wild form with domesticated germplasm (Banga 1963).

2. Carrots outside of Europe. Relatively little is recorded about carrot cultivar development from 1600 to 1950 outside of Europe. Domesticated carrots arrived in the Americas with European settlers in the 1500s (Sparke 1878). Although orange, yellow and purple cultivars were still used in Europe at that time and were grown in the U.S. through the mid-1800s (Burr 1865), records indicate orange-rooted types became popular rapidly once introduced in the U.S. (Babb et al. 1950). The first reports of carrot in Japan in the 1600s refer to first purple and yellow and then orange types in the 1700s (Banga 1963).

One interesting new carrot root type, which arose in North America, is 'Imperator', which is the result of a cross between 'Nantes' and 'Chantenay' in 1928 by the Asgrow Seed Company to develop a bunching carrot (i.e. carrots harvested with haulms left attached, tied together, and sold in bunches). The 'Imperator' type is notable for its continuing predominance in North America. It also demonstrates the plasticity in selecting diverse carrot root types. In this case, a cross between two relatively short-rooted, blunt types yielded a much longer, more conical root shape.

In considering carrots outside of Europe, cultivar development for western temperate regions has taken a subset of European 'Danvers', 'Chantenay', 'Nantes', 'Oxheart', and 'Flakkee' types, as well as 'Imperator' types, and selected for local adaptation and production requirements. This collection of temperate carrot germplasm was adapted for both summer production in cooler areas of North America as well for winter production in warmer areas of North and South America, and Australia. With the relative insensitivity to photoperiod of carrots some cultivars have been used in both summer and winter production in North America.

Carrot cultivar development was ongoing in sub-tropical regions of the world such as India and southern China from 1600 to 1950, but has not been well described. Sub-tropical carrots are a very important and expanding category of the crop, which is likely to become more important in the future. As for temperate carrots, it may be presumed that a main breeding focus was on earliness of harvest, low bolting tendency,

first public sector carrot inbred (brown anther) in 1963 and C. E. Peterson, then at Michigan State University, released the first public sector petaloid male sterile inbred in 1964. Seed company carrot breeders in that era usually had the responsibility for developing cultivars of at least two, and up to eight or more other vegetable crops. Therefore their task focussed primarily on evaluating a few carrot hybrids derived directly from public sector releases with little effort for developing inbreds of their own. By the late 1990s only one of the European national programs was left, that of the Agricultural University in Krakow, Poland, and the only four North American public sector programs remaining were those of Texas A&M University, the University of Guelph, the University of Wisconsin, and the USDA, ARS. Concomitant with this change, 10–15 vegetable seed company breeders usually with multinational corporations located in North and South America, Europe, and Japan have come to develop most of the new carrot open-pollinated cultivars, inbreds and hybrids today, as each of them has a primary or sometimes an exclusive focus on carrots. Thus, the hybrid era brought an expansion of the number of traits improved by carrot breeders and a more focussed, in-depth consideration of the crop by a smaller number of specialists, in Europe and North America.

Another aspect of carrot cultivar development since 1950 has been a significant series of advances in sub-tropical carrots brought about by public sector programs, and more recently by seed companies, especially in Brazil, India, and China. Several uniform, higher-yielding open-pollinated cultivars have been released in India and Brazil. Indian germplasm was derived from a broad base of eastern sub-tropical cultivars (Kalloo et al. 1993), whereas the Brazilian cultivars combined eastern and western germplasm in 'Kuronan' (Ikuta et al. 1983) and 'Brasilia' (Vieira et al. 1983). Recently sub-tropical carrot hybrids have been developed. These materials have significantly increased summer carrot production capacity in South America and merit broader evaluation in other sub-tropical regions of Africa and Asia.

VI. CARROT BREEDING METHODS

A. The Open-Pollinated Era

Phenotypic recurrent selection has been the primary approach to population improvement of carrot. As an outcrossing diploid with significant inbreeding depression, adequate population size is vital to maintain population vigor in development of open-pollinated cultivars. In the

ability become very important attributes during inbred development, since several generations of self-pollination are incurred to achieve the uniformity necessary for modern hybrids. The first carrot hybrids were single crosses, but as a wider array of inbreds became available, three-way crosses have become the predominant format for the constitution of most carrot hybrids. The details of carrot inbred development and hybrid testing have been described (Peterson and Simon 1986).

Since that review, the primary change in carrot hybrid development is some movement back toward single-cross hybrids, although three-way crosses still predominate. This movement depends on the "recycling" of old carrot inbreds, whereby new inbreds are derived from inbred \times inbred or inbred \times open pollinated (O.P.) cultivar crosses, rather than the earlier practice of starting with a single root selected from an open-pollinated cultivar or an O.P. \times O.P. cross. With inbred "recycling," new inbreds tend to be more vigorous, thus allowing adequate seed production of single crosses. Another change is the trend toward inclusion of more generations of self-pollination or small-population (2-3 plants) sib-mating before large population increase and testing of new inbreds. The demand for more uniformity in higher-value, precision-planted hybrids drives this trend.

As carrot breeding has progressed from an era with many small seed companies field testing cultivars in relatively small regions, to fewer, larger seed companies field testing on, in some cases, a global basis, it has become possible for a carrot breeder to evaluate the same materials in a large number of environments. This has allowed the evaluation of genotype by environment interactions more extensively than has ever been possible before. With the lack of photoperiod sensitivity in carrot, this will eventually provide a better understanding of those attributes that are known to be influenced by both genotype and environment, such as tendency toward early flowering, top (haulm) size, root color, flavor, and growth rate.

Reliable development of open-pollinated carrot cultivars does not require selection during cultivar development beyond that performed in the field. However, before the development of an effective seed-to-seed method, it was necessary to remove outcrosses during large-scale production of foundation or even commercial seed. Although the seed-to-seed method eliminated the need for selection in large-scale seed production, modern carrot inbred development utilizes extensive selection beyond the field. For example, effective selection for root-knot nematode and *Alternaria* leaf blight resistance has been initiated in greenhouse-grown plants at the F_3 or even the F_2 generation. Seedling and steckling selection are being evaluated for other diseases as well.

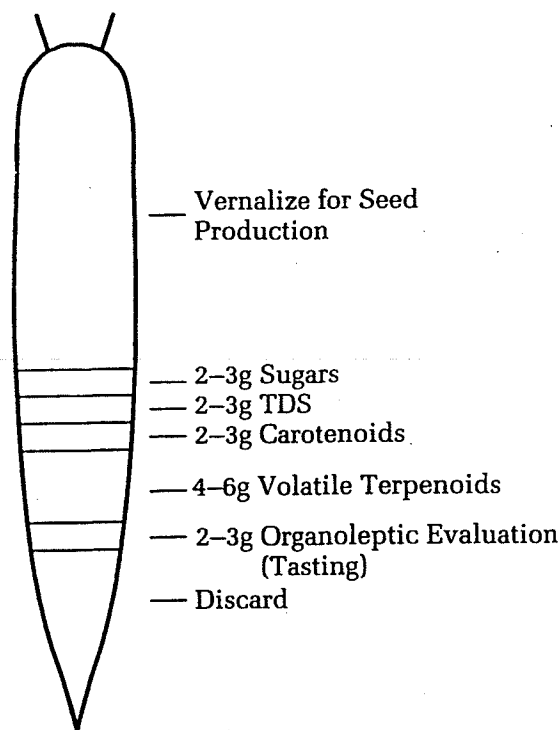


Fig. 5.3. A scheme for sampling a carrot storage root for quality components while retaining an adequate portion of the root for seed production.

Table 5.6. Typical range and standard error of quality constituents in carrot roots.

Constituent/ compound	Units (fresh wt)	Range	SE	Reference
Free sugars (total)	mg/g	25-140	3	Freeman & Simon 1983;
Glucose	mg/g	0-25	2	Stommel & Simon 1989
Sucrose	mg/g	5-100	3	
Total dissolved solids	%	5-15	0.2	Stommel & Simon 1989
Carotenoids (total)	ppm	0-500	20	Buishand and Gabelman
β -carotene	ppm	0-250	10	1979; Simon & Wolff
α -carotene	ppm	0-300	10	1987
Volatile terpenoids (total)	ppm	10-500	20	Senalik & Simon 1987
Terpinolene	ppm	1-300	8	
E- γ -bisabolene	ppm	0-30	4	
Harsh flavor (index)	arbitrary	1-5	1	Simon et al. 1980
Sweet flavor (index)	arbitrary	1-5	1	Simon et al. 1980

VII. APPLICATIONS OF BIOTECHNOLOGY

Genome size is relatively small (1.0pg/2C; Bennett and Leitch 1995), variation in molecular genetic markers is quite extensive, and both genetic transformation and regeneration of carrot are readily achieved. Therefore, carrot is a good candidate for biotechnological application, but relatively little has been done to date.

The carrot genetic linkage map includes around 1000 isozymes, RFLPs, AFLPs, RAPDs, and other molecular markers (Westphal and Wricke 1989a,b; Schultz et al. 1994; Vivek and Simon 1999). From 10–25% of genomic clones tested were estimated to be in high copy numbers, while 20–30% of the RFLP probes and RAPD primers, and 40% of AFLP bands were polymorphic. The incidence of molecular marker polymorphism and map size to date makes marker-assisted selection a viable option. Reports of success have not yet been published but markers linked to nematode resistance, CMS restorers, carotene content, and sugar content are being sought. One significant limitation to the application of molecular markers to carrot improvement is the need for radioactive labels, which cannot to be used in many laboratories. Because of this, efforts are underway to convert AFLPs to PCR-based codominant markers (Bradeen and Simon 1998), and to develop microsatellite markers (Niemann et al. 1997).

One of the most intensively studied traits of carrots today continues to be CMS with a particular emphasis on molecular evaluation. Mitochondrial restriction fragment pattern and protein product differences between fertile, petaloid, and brown anther cytoplasms have been compared and analyses of variation for a few specific genes, such as *atpA* have been reported (Ichikawa et al. 1989; Pingitore et al. 1989; Scheike et al. 1992; Steinborn et al. 1992). Furthermore, several interspecific and sub-specific crosses have yielded interesting new CMS systems, which are under study (Nothnagel 1992).

With the pioneering work of F. C. Steward and co-workers, totipotency of plant cells was first demonstrated using carrot (Steward et al. 1964). Carrot has, in fact, proven to be a model organism for plant tissue culture, transformation, and regeneration (Hardegger and Sturm 1998). Taking advantage of carrot's facile manipulation in cell culture, carrot-*Daucus capillifolius* and carrot-bishop's weed (*Aegopodium podagraria*) protoplast fusions were among the first examples of successfully regenerated somatic hybrids (Dudits et al. 1977, 1979). Maize transposable elements have been successfully introduced into carrot cell cultures and found to be mobile (Van Sluys and Tempe 1989). Two

rot germplasm has been elusive. Success in this area would have a significant positive impact. Attempts to move the carrot nucleus to new cytoplasms in tissue culture ("cybridization") have also been made as an alternative to backcrossing into male sterile cytoplasm (Tanno-Suenaga et al. 1988). So far, stable lines of this sort have not been developed.

There have been several suggestions and attempts to develop other uses of carrots. These include carrots for carotene extraction, carrot chips (like potato chips), and carrot for sugar or biomass production, since its energy production per unit time and space is among the highest for any plant (O'Hare et al. 1983; Munger 1987). These specialty uses of carrot would require specially bred genetic stocks and/or processing facilities to be successful. A more realistic and, in fact, likely development is further adaptation of carrot for more successful production in lowland tropical regions. Since carrot is relatively easy to grow and store, and is an excellent source of vitamin A and energy, an expanded production to these climates would be desirable. With greater adaptation to warmer climates, better disease and pest resistance, and broader distribution of information to help small growers, sustainable production could be achieved.

IX. CONCLUSIONS

Carrot has had a relatively brief history in agriculture with relatively little attention given to its improvement. By a poorly documented set of circumstances, orange carrot root color was selected and became popular, resulting in its status today as one of the best sources of dietary vitamin A. Due to its ease of manipulation in somatic embryogenesis, carrot also was used in pioneering research as a model organism to demonstrate and understand totipotency of individual plant cells. More attention has been given to carrot improvement in the last 50 years, resulting in more efficient production of a more widely consumed, nutritious, appealing crop. Expansion of carrot production into warmer climates has begun and is likely to result in an even greater availability of this crop in the future.

LITERATURE CITED

- Andersen, S. B., I. Christiansen, and B. Farestveit. 1990. Carrot (*Daucus carota* L.): In vitro production of haploids and field trials. p. 393-402. In: Y. P. S. Bajaj (ed.), *Biotechnology in agriculture and forestry*, vol. 12. *Haploids in crop improvement I*. Springer-Verlag, Berlin.

- hybridization of *Daucus carota* and *D. capillifolius* by protoplast fusion. *Theor. Appl. Genet.* 51:127-132.
- Ellis, P. R., P. L. Saw, and T. C. Crowther. 1991. Development of carrot inbreds with resistance to carrot fly using a single seed descent programme. *Ann. Appl. Biol.* 119:349-357.
- Emsweller, S. L., P. C. Burrell, and H. A. Borthwick. 1935. Studies on the inheritance of color in carrots. *Proc. Am. Soc. Hort. Sci.* 33:508-511.
- Esau, K. 1940. Developmental anatomy of the fleshy storage organ of *Daucus carota*. *Hilgardia* 13:175-226.
- FAO, Yearbook Prod. Stats. 1964-1996. Rome.
- Freeman, R. E., and P. W. Simon. 1983. Evidence for simple genetic control of sugar type in carrot (*Daucus carota* L.). *J. Am. Soc. Hort. Sci.* 108:50-54.
- Frese, L. 1983. Resistance of the wild carrot *Daucus carota* ssp. *hispanicus* to the root-knot nematode, *Meloidogyne hapla*. *J. Plant Dis. Prot.* 81:396-403.
- Gabelman, W. H., I. L. Goldman, and D. W. Breitbach. 1994. Evaluation and selection for resistance to aster yellows in carrot (*Daucus carota* L.). *J. Am. Soc. Hort. Sci.* 119:1293-1297.
- Goldman, I. L., and D. N. Breitbach. 1996. Inheritance of a recessive character controlling reduced carotenoid pigmentation in carrot (*Daucus carota* L.). *J. Hered.* 87:380-382.
- Gray, D. 1984. The performance of carrot seeds in relation to their viability. *Ann. Appl. Biol.* 104:559-565.
- Hamerschmidt, I. 1993. Producao de horticolas e assistencia tecnica no Brasil. *Hort. Bras.* 11:156-157.
- Hansche, P. E., and W. H. Gabelman. 1963. Digenic control of male sterility in carrots, *Daucus carota* L. *Crop Sci.* 3:383-386.
- Hardegger, M., and A. Sturm. 1998. Transformation and regeneration of carrot (*Daucus carota* L.). *Molec. Breed.* 4:119-129.
- Havis, L. 1939. Anatomy of the hypocotyl and roots of *Daucus carota*. *J. Agr. Res.* 58:557-564.
- Heywood, V. H. 1983. Relationship and evolution in the *Daucus carota* complex. *Israel J. Bot.* 32:51-65.
- Huang, S. P., P. T. Della Vecchia, and P. E. Ferreira. 1986. Varietal response and estimates of heritability of resistance to *Meloidogyne javanica* in carrots. *J. Nematol.* 18:496-501.
- Ichikawa, H., L. Tanno-Suenaga, and J. Imawura. 1989. Mitochondrial diversity among cultivars of *Daucus carota* L. and their wild relatives. *Theor. Appl. Genet.* 77:39-43.
- Ikuta, H., J. V. Vieira, and P. T. DellaVecchia. 1983. Cenoura 'Kuronan'. *Hort. Bras.* 1:41.
- Imam, M. K., and W. H. Gabelman. 1968. Inheritance of carotenoids in carrots, *Daucus carota* L. *Proc. Am. Soc. Hort. Sci.* 93:419-428.
- Kalloor, G., A. Singh, D. S. Balyan, K. S. Baswana, and P. S. Partap. 1993. 'Hisar Gairic': carrot bred for nutrition. *Indian Hort.* 37:21.
- Laferriere, L., and W. H. Gabelman. 1968. Inheritance of color, total carotenoids, alpha-carotene, and beta-carotene in carrots, *Daucus carota* L. *Proc. Am. Soc. Hort. Sci.* 93:408-418.
- Laufer, B. 1919. Sino-Iranica. Chicago, Field Museum of Natural Hist. Pub. 201; *Anthropol. Ser. Vol.* 15:451-454.
- Mackevic, V. I. 1929. The carrot of Afghanistan. *Bull. Appl. Bot. Genet. Plant Breed.* 20:517-562.
- Morelock, T. E., and G. L. Hosfield. 1976. Glabrous seedstalk in carrot: Inheritance and use as a genetic marker. *HortScience* 11:144.

- Simon, P. W., and J. O. Strandberg. 1998. Diallel analysis of resistance in carrot to *Alternaria* leaf blight. *J. Am. Soc. Hort. Sci.* 123:412-415.
- Simon, P. W., and X. Y. Wolff. 1987. Carotenes in typical and dark orange carrots. *J. Agr. Food Chem.* 35:1017-1022.
- Simon, P. W., X. Y. Wolff, C. E. Peterson, D. S. Kammerlohr, V. E. Rubatzky, J. O. Strandberg, M. J. Bassett, and J. M. White. 1989. High carotene mass carrot population. *HortScience* 24:174.
- Small, E. 1978. A numerical taxonomic analysis of the *Daucus carota* complex. *Can. J. Bot.* 56:248-276.
- Sparke, J. 1878. The second voyage of Sir John Hawkins. p. 8-64. In: C. R. Markham (ed.), *The Hawkins' voyages*. 57th work of the Hakluyt Society. London.
- Steinborn, R., A. Weihe, and T. Borner. 1992. Mitochondrial genome diversity within a cultivar of *Daucus carota* (ssp. *sativus*) revealed by restriction fragment analysis of single plants. *Plant Breed.* 109:75-77.
- Steward, F. C., M. O. Mapes, A. E. Kent, and R. D. Holsten. 1964. Growth and development of cultured plant cells. *Science* 143:20-27.
- Stommel, J. R., and P. W. Simon. 1989. Phenotypic recurrent selection and heritability estimates for total dissolved solids and sugar type in carrot. *J. Am. Soc. Hort. Sci.* 114:695-699.
- Strandberg, J. O., M. J. Bassett, C. E. Peterson, and R. D. Berger. 1972. Sources of resistance to *Alternaria dauci*. *HortScience* 7:345.
- Tanno-Suenaga, L., H. Ichikawa, and J. Imamura. 1988. Transfer of the CMS trait in *Daucus carota* L. by donor-recipient protoplast fusion. *Theor. Appl. Genet.* 76: 855-858.
- Thompson, D. J. 1962. Studies on the inheritance of male-sterility in the carrot, *Daucus carota* L. *Proc. Am. Soc. Hort. Sci.* 78:332-338.
- Umiel, N., and W. H. Gabelman. 1972. Inheritance of root color and carotenoid synthesis in carrot, *Daucus carota*, L.: Orange vs. red. *J. Am. Soc. Hort. Sci.* 97:453-460.
- USDA, Agr. Stats. 1924-1996, Washington, DC.
- Van Sluys, M. A., and J. Tempe. 1989. Behavior of the maize transposable element *Activator* in *Daucus carota*. *Molec. Gen. Genet.* 219:313-319.
- Vavilov, N. I. 1951. The origin, variation, immunity and breeding of cultivated plants. *Chron. Bot.* 13:1-366 (Translated from Russian by Starr Chester).
- Vieira, J. V., V. W. D. Casali, J. C. Milagres, A. A. Cardoso, and A. J. Regazzi. 1991. Heritability and genetic gain for resistance to leaf blight in carrot (*Daucus carota* L.) populations evaluated at different times after sowing. *Rev. Brasil. Genet.* 14:501-508.
- Vieira, J. V., P. T. Della Vecchia, and H. Ikuta. 1983. Cenoura 'Brasilia'. *Hort. Bras.* 1:42.
- Vilmorin, M. 1859. Notice sur l'amelioration de la carotte sauvage. p. 5-29. In: L. Vilmorin (ed.), *Notice sur l'amelioration des plantes par le semis*. Librairie Agricole, Paris.
- Vivek, B. S., and P. W. Simon. 1998. Genetic relationships and diversity in carrot and other *Daucus* taxa based on nuclear restriction fragment length polymorphism (nRFLPs). *J. Am. Soc. Hort. Sci.* 123:1053-1057.
- Vivek, B. S., and P. W. Simon. 1999. Linkage relationships among molecular markers and storage root traits of carrot (*Daucus carota* L. *sativus*). *Theor. Appl. Genet.* 99:58-64.
- Wang, M., and I. Goldman. 1996. Resistance to root knot nematode (*Meloidogyne hapla* Chitwood) in carrot is controlled by two recessive genes. *J. Hered.* 87:119-123.
- Welch, J. E., and E. L. Grimbail. 1947. Male sterility in carrot. *Science* 106:594.
- Westphal, L., and G. Wricke. 1989a. Genetic analysis of DIA, GOT, and PGI isozyme loci in *Daucus carota* L. ssp. *sativus*. *Plant Breed.* 102:51-57.
- Westphal, L., and G. Wricke. 1989b. The inheritance of PGM, 6-PGD, and SKD isoenzymes in carrot. *Vortrage Pflanzenzucht.* 15:28-32.