

Review

Some remarks on carrot breeding (*Daucus carota sativus* Hoffm.)

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Abstract

Carrot breeding in the past 150 years has resulted in varieties with high yield, a short growing period, and excellent root colour. Recently, hybrid varieties have demonstrated good uniformity of roots, a quality accepted by most consumers. By contrast, only a few resistant varieties (mainly open-pollinated varieties) are offered by seed companies, most being resistant to *Alternaria*. Hybrid breeding offers a chance of combining good uniformity and different sources of resistance. Efforts in future breeding should concentrate on the improvement of health and the development of genotypes suitable for cultivation in suboptimal climates and regions, as well as for special applications.

**Key words:** *Daucus spec.* — synthetic varieties — hybrid varieties — male sterility — quality — resistance breeding

Carrot is an important vegetable and it is cultivated worldwide because of its high yield potential and use as a fresh or processing vegetable. This economic importance is reflected by its large production area: 297 000 ha in Europe, including the former USSR, 83 000 ha in America, 189 000 ha in Asia and 44 000 ha in Africa, representing a total world production of 14 million tonnes (FAO 1992). New varieties with a high carotene content (provitamin A) can increase vitamin A in human nutrition, especially in the third world. Vitamin A deficiency causes blindness in humans in some regions. Another fact that may further increase the importance of carrots is the anti-carcinogenic effect of carotene. This aspect was discussed by Halter (1989) and Ziegler (1989).

The cultivation of carrots has a long tradition in both Europe and the rest of the world. Today's orange-coloured carrot was first observed in the Netherlands in the 17th or the beginning of the 18th century. Prior to that, white and yellow carrots had been cultivated in Europe since the 16th century (Banga 1957a, b). Carrot was the first allogamous vegetable to undergo intensive selection breeding, begun by Vilmorin in France in the early 18th century (Fruwirth 1930). In later times, the centres of breeding were France and the Netherlands. During the 19th century, more than 100 ha of carrots were cultivated for seed production around Quedlinburg in Germany by using adapted lines of western European varieties. Today, carrot breeding exists in all developed countries and has changed in this century from mass selection to hybrid breeding. Despite these breeding activities, our genetic knowledge of the carrot is rather limited, as it is with most other vegetables. Only 20 genes have been described (review: Simon 1984a), as well as about 50 isozyme, RFLP, and RAPD loci (Westphal and Wricke 1991, Schulz

et al. 1994). Only the most patchy genetic knowledge exists concerning quality traits, e.g. root colour (Kust 1970, Buishand and Gabelman 1979), sugar and carotene content (Banga et al. 1958, Simon et al. 1979, 1985), cytoplasmic male sterility (Banga et al. 1964, Mehring-Lemper 1987), and root shape (Frimmel 1938). Carrot serves as a model plant for biotechnological techniques and is used in experiments analysing the physiology of plants. *In vitro* culture has been well developed and has been introduced into breeding programmes. The possibility of producing artificial seeds by somatic embryogenesis offers new ways of maintaining special lines (Kitto and Janick 1985, Kamada et al. 1989, Liu et al. 1992). In recent years, experiments have aimed to find molecular markers for different characters, especially genes responsible for male sterility (ms) (Scheike et al. 1992, Steinborn et al. 1992, Schulz et al. 1994). Increasing numbers of publications deal with experiments on gene manipulation and gene transfer (van Sluys et al. 1987, Wurtele and Bulka 1989, Thomas et al. 1989, Pawlicki et al. 1992). In this review, aspects of genetic resources, breeding methods, and breeding strategies for carrot, as well as for breeding on quality and resistance, are discussed.

Genetic resources

Intensive selection in the 18th and 19th century led to a great diversity of types in open-pollinated varieties as regards leaves and roots. The shape of the root can be circular, obovate, triangular, obtriangular, or narrowly oblong. A great variation also exists for harvesting time. In middle Europe, this time varies between 70 and 190 days depending on the varieties sown in spring. The gene pool in Europe has been divided into seven groups, named 'Amsterdamer', 'Berlicumer', 'Chantenay', 'Danvers', 'de Colmar', 'Nantaise' and 'Pariser Market', indicating the region where breeding of each particular variety in Europe began. The typical carrot in the USA and Canada, 'Imperator', is not included. For the classification of cultivars and the examination of their homogeneity 27 characters are used (UPOV 1976). The evaluation of this great diversity was performed, in general, by breeders, and, therefore, publication was rare. Exceptions are the reports of Strandberg et al. (1989) and Simon et al. (1991), who described more than 400 varieties, lines and undomesticated material from all over the world, based on some morphological and quality characters, as well as on some information on relative resistance to *Alternaria dauci* and *Meloidogyne hapla*. Large germplasm collections of cultivated carrots, including semicultivated and wild carrots,

do exist in the USA (CFREC, Sanford, Florida; USDA-ARS, Madison, Wisconsin), in Great Britain (HRI, Wellesbourne, England), the Netherlands (CPRO, Wageningen), France (INRA, Rennes), Russia (VIR, St. Petersburg) and Germany (IPK, Gatersleben). The carrot is classified by the International Board for Plant Genetic Resources (IBPGR 1981) in priority group 4, while onion is placed in group 2 and tomato in group 1.

In contrast to the large number of varieties, the gene pool of the cultivated carrot is limited due to a unique mutation in the orange colour. In addition, use of inbred lines for hybrid breeding is still increasing (St Pierre et al. 1990, St. Pierre and Bayer 1991). An improvement in genetic variability is essential for the future. Wild germplasm forms are a potential source of greater variability. The genus *Daucus* contains 22 species, while, for the *Daucus carota* complex, which includes the cultivated carrot, more than 15 subspecies have already been described (Saenz Lain 1981, Heywood 1983). The main distribution is Europe and the Mediterranean region, although some species are found in southwest and central Asia and tropical Africa. Three species grow in America and only one species in Australia and New Zealand. The basic number of chromosomes is  $x = 9$  to  $x = 11$ . The cultivated carrot is diploid ( $2x = 18$  chromosomes with a size of 1.8–3.8  $\mu\text{m}$ ). Karyotype analysis has revealed five subterminal chromosomes, including one chromosome satellite and four median chromosomes (Essad 1985, Schrader et al. 1994). All subspecies of the *D. carota*-complex are also diploid. Most of the other species have a chromosome number of  $2n = 2x = 22$ . For *D. glochidiatus* Labill., a tetraploid state ( $2n = 4x = 44$ ), and, for *D. montanus* Humb. & Bonpl., a hexaploid state ( $2n = 6x = 66$ ) has been reported (Bell and Constance 1960, Moore 1971, Constance et al. 1976). Crossing barriers do not exist in the *Daucus carota* complex (McCollum 1975, Nothnagel 1992, Nothnagel and Straka 1994). Different species have been used for phytopathological studies and breeding of resistance to pathogens (McCollum 1977, Bonnet 1983, Kraus 1992, Ellis et al. 1993).

### Reproduction biology

The reproduction biology of carrot for the maintenance of samples in germplasm collections and breeding material is well known. The cultivated carrot has been selected as a biennial. Artificial vernalization of the developed roots for about 90 days at 2–5°C is necessary for the induction of flowering in the first year without risk of undesired selection. Seed production is realized in cool climates by production of cuttings from roots, cool storage over winter, and growth in the second year, as well as by vernalization in the field during the winter in regions with relatively mild winters and snow cover. The allogamy is influenced by protandry. The carrot is andromonoecious. Carrots possess a high reproduction potential: 50 000 seeds per plant can be obtained, but seed production is strongly dependent on environmental conditions and, for hybrid seed production, on the pollinator (Braak and Kho 1958, Bell 1971). The 1000-kernel weight varies between 1.0 and 1.5 g, and the germination rate is between 50 and about 100%. Investigations by Austin and Longden (1967) and Gray and Steckel (1983) demonstrated the possibility of increasing the germination rate by seed calibration.

Seeds of lines and special breeding lines are commonly produced in glasshouses. Honey bees and flies can be used for the pollination (Wilson et al. 1991). In some regions, the frequent

occurrence of wild carrots is dangerous for seed production in the field due to outcrossing. The wild form *D. carota* ssp. *carota* is regarded worldwide as a weed (Wijnheijmer et al. 1989).

### Breeding methods

#### Open-pollinated varieties and synthetics

Over the last two centuries, the most important breeding methods have been mass selection and pedigree selection within the different populations of orange-coloured carrots. This has resulted in a great number of open-pollinated carrot varieties, such as the more than 100 varieties of the type 'Nantaise' in the middle-season group that exist worldwide. Open-pollinated varieties (op) have been adapted for different markets as both fresh and industrial crops. High-yield and high-quality (colour and high level of carotene) varieties are available. Knowledge of tolerance to pathogens is often based purely on field observations. The yield of 'marketable carrots' is the most important economic factor. Several experiments, especially in the UK, have been undertaken to increase the percentage of marketable yield by optimizing the cultivation conditions and by increasing seed quality (Londgen 1968, Dowker and Jackson 1977, Gray and Steckel 1983). In combination with modern seed techniques, the current op-varieties permit the profitable production of carrots in many regions. Nevertheless, all efforts to breed varieties with high level of uniformity have been limited by genetic factors originating from breeding methods used for op-varieties. One reason for this is the heterozygosity of the op-varieties, while another is the inbreeding depression resulting from random selfing of plants within the population. The rate of selfing in populations is not well known. Thompson (1961) reported about 15% selfing in populations. Inbreeding depression is considerable and was investigated by Roth (1979, 1981). Some of his results, based on seven varieties, are given in Table 1. The most important factor is the strong inbreeding depression in seed yield. There is little variation between the varieties under middle European conditions, and so, as a result, selection of genotypes for low inbreeding depression has begun within the different op-varieties.

All op-varieties suffer from inbreeding depression and a limited degree of uniformity, and hybrid breeding of carrot has been started intensively to improve uniformity. In addition, hybrid breeding provides a rather high level of safety against uncontrolled reproduction.

In cases where extreme uniformity seems to be unnecessary for some industry purposes, e.g. for juice or pulp production or for regions with weakly developed agriculture, breeding of synthetics would also be possible, but no such varieties exist as yet. Experimental synthetics have been developed with different varieties of the late carrot types 'Berlicumer' and 'Danvers', using results of tests on general combining ability. These synthetics have been tested in comparison to op-varieties and

Table 1: Mean inbreeding depression of seven varieties in carrots after one generation of selfing (Roth 1981)

Character	Level (%)	Range (%)
Weight of root	50.5	39.1–55.3
Weight of leaves	45.3	37.3–56.8
Length of roots	23.5	17.7–35.2
Yield of seeds	72.8	62.2–81.9

Table 2: Comparison of the yield of different synthetics (*Syn* 1) and  $F_1$  hybrids relative to their primary op-varieties (M. Stein unpubl. data)

'Berlicumer' group		'Danvers' group	
<i>Syn</i> a	107	<i>Syn</i> a	106
<i>Syn</i> b	111	<i>Syn</i> b	120
<i>Syn</i> c	100	<i>Syn</i> c	120
<i>Syn</i> d	120		
$F_1$ hybrids	130	$F_1$ hybrids	112
op-varieties	100	op-varieties	100

adapted hybrid varieties (Table 2). For improving yield, the development of synthetics seems to be a successful approach, connected with rather low breeding costs.

### Hybrid varieties

In Europe, Frimmel and Lauche (1938) were the first to recommend the breeding of  $F_1$  carrot varieties, however, the lack of a system of producing hybrid seed in large quantities prevented the introduction of this method. When male sterility in carrot was detected and analysed by Thompson (1961) and Hanschke and Gabelman (1963), this situation changed. The first hybrids were sold in the early 1960s in the USA (Peterson and Simon 1985). Today, more than 100 hybrid varieties exist worldwide. The percentage of hybrids is 60–90% in Europe for early and late varieties. In the USA, the cultivation of hybrids for special purposes has reached approximately 100% (Rubatzky pers. comm.).

Hybrid breeding is generally based on two systems of cytoplasmic male sterility (CMS) with different genetic backgrounds and origin: 'brown anther' type and the 'petaloid' type. Several genetic models of the inheritance of CMS have been published (Frese 1982, Mehring-Lemper 1987, Kaul 1988). The 'brown anther' type (ba) is present in all cultivated orange-coloured op-varieties but at differing levels (Banga et al. 1964). More than 40% of ms plants were found in the variety 'Marktgärtner', a special German type of 'Nantes' (Weit 1979). The phenotype is characterized by deformed, brown-coloured anthers without functional pollen, caused by a genetic block in meiosis (Struckmeyer and Simon 1986). According to Banga et al. (1964) the type 'ba' results from an interaction of the 'Sa'-cytoplasm with two independent nuclear genes (homozygous recessive *aa* or dominant *B*). The two complementary genes *E* and *D* operate with their dominant alleles as restorer genes. Due to this complicated genetic system, many test crosses are necessary for the development of a suitable maintainer. The probability of finding good combinations of ms lines and maintainers is between 5 and 15% (Weit 1979). While experimental results by Frese (1982) and Mehring-Lemper (1987) were in agreement with Banga's hypothesis (1957a, b), Thompson (1961), Hanschke and Gabelman (1963), as well as Timin and Dobrutska (1981), reported a more simple mechanism of inheritance. Those results reflected the genetic variability among the basic material used.

The cytoplasm of the 'petaloid' type (pt) is derived from a wild form of *Daucus carota* L. (McCollum 1966) and has been introduced into many op-varieties of cultivated carrot. The 'pt' type is characterized by a transformation of the anthers into petals or petal-like structures which do not produce functional pollen. The deformation of the androecium varies in degree and the phenotype has been classified into several groups, e.g.

Table 3: Stability of male sterility in ms lines of 'ba' type in Quedlinburg, Germany (Dame et al. 1988)

ms lines	First-year stability		Second-year stability		Third-year stability	
	n	(%)	n	(%)	n	(%)
001	28	93	39	100	77	99
003	43	100	26	96	31	100
06	114	100	122	100	120	100
03	51	100	55	94	68	100
074	50	84	30	87	31	87
075	57	90	39	80	35	89
11	170	98	137	67	33	100
13	181	91	45	67	46	91

'spoon' type, 'strap' type or 'carpeloid' type (Eisa and Wallace 1969, Chada and Frese 1981, Struckmeyer and Simon 1986, Mehring-Lemper 1987). For the inheritance of this type, an interaction between Sp-cytoplasm and two independent dominant genes (*M1*, *M2*) was postulated by Morelock (1974). A maintainer for this type cannot be detected in the  $F_1$  because of the dominant state of the *M* genes. Backcrosses should be performed by use of the male-fertile genotype (Sp) *m1m1, m2m2* as a tester in order to find dominant alleles. Investigations by Mehring-Lemper (1987) led to a contradictory hypothesis. He postulated a model of an interaction between the Sp cytoplasm and three independent genes, one dominant gene (*M*) and two recessive genes (*ll* and *tt*). The heterozygous state (*Mm*) is temperature-sensitive and leads to partial fertility under specific conditions. Nevertheless, this hypothesis cannot explain all segregation results.

A third CMS system has been detected in an alloplasmic form of orange-coloured carrot originating from a cross between the wild carrot *D. carota gummifer* Hook. fl. and the cultivated carrot *D. c. sativus* Hoffm. (Nothnagel 1992). This type of male sterility, called 'gum' type, is characterized by a total reduction of anthers and petals. Recent results on the genetic mechanisms suggest that an interaction of the 'gummifer' cytoplasm with a recessive allele (*gugu*) in the nucleus is responsible for the expression of this type of male sterility. The 'gum' type can potentially be used as a new source of CMS for carrot breeding. The simple mode of selection and phenotypic stability are especially advantageous (Linke et al. 1994).

The two CMS systems 'ba' and 'pt' generally suffer from instability of male sterility under specific conditions. The instability is mainly influenced by high temperature (review: Kaul 1988). Nevertheless, observations over many years have revealed that other factors such as dry conditions, growing time or long day conditions operate provocatively (Hanschke and Gabelman 1963, Nieuwhof 1968, Michalik 1979). A strict selection scheme is therefore necessary because carrot is partially andromonoecial, i.e. in umbels of higher order, male flowers can be produced. Umbels of the 5–7th order must be examined carefully. Variation regarding instability exists between the different CMS lines. CMS lines of the 'ba' type developed in Quedlinburg, Germany, can be divided into different groups (Table 3). The line 06 has also shown a high degree of stability under different conditions in Russia (Shidkova and Stein 1986). Other lines have shown different degrees of instability. Selection including new cycles of crossings and tests within the usable ms and maintainer lines has only been of limited success. Those

results suggest a strong influence of the cytoplasm, or an interaction between genes in the cytoplasm and the nucleus. The reason for instability is not yet clear; possibilities may include the different origins or changes of cytoplasm and the oligogenic system of restoration.

The inheritance of the organelle genomes and the stability of the mitochondrial genome — the general opinion is that CMS is encoded by mitochondria — has recently been investigated. Investigations by means of RFLP and Southern blot techniques have shown a highly conserved chloroplast genome (cpDNA). Polymorphisms have only been found between *Daucus* species (de Bonte et al. 1984, Boblenz 1991). By contrast, a great variation in the mitochondrial genome (mtDNA) has been found between species, subspecies, and varieties (de Bonte et al. 1984, Ichikawa et al. 1989), as well as within op-varieties of cultivated carrot (Steinborn et al. 1992). Some results suggest, in very rare cases, the possibility of biparental inheritance of the organelle genomes (Boblenz et al. 1990, Hause 1991, Linke 1992, Steinborn 1993). Extensive investigations support the view that both organelle genomes are exclusively inherited by the maternal parent in most, if not all, interspecific and intraspecific crosses (Linke et al. 1994). The frequent spontaneous restoration of fertility is unlikely to be caused by a paternal or biparental inheritance of mitochondria. Research is under way to analyse the molecular basis of the CMS in *Daucus*. This includes investigations of arrangements which might affect genomic regions surrounding specific mitochondrial genes, including both the transcript patterns and the mitochondrial protein patterns (Scheike et al. 1992, Linke et al. 1994).

Mapping of genes for the restoration of the pollen fertility is of special interest for hybrid breeding. By means of tightly linked molecular markers, it would be possible to study the nuclear-cytoplasm interaction. At present, a genetic map of carrot is available which contains, in total, 58 isozyme, RFLP, and RAPD loci in eight of the nine possible linkage groups (Schulz et al. 1994). Linkage analysis indicates that one of the restorer genes which was postulated by Mehring-Lemper (1987) is located in linkage group six. Molecular markers for the specific alleles of the restorer/maintainer genes for the different types of male sterility could be used as an effective tool for selection of ms and maintainer lines.

The development of the ms and maintainer lines is a very laborious process due to the dominant state of male sterility. Crossing, backcrossing, selfing and testing of the progenies in

the following two generations, including isolation of the positive progenies, are characteristic steps in breeding processes (Niewhof 1968). Due to the biennial character of carrot, 7–8 years are necessary. However, the time can be reduced to half by winter annual culture in glasshouses, including artificial vernalization (Dame et al. 1988). The breeder is forced to eliminate male fertile plants or phenotypes with partial male fertility within the ms lines developed, and to develop new lines with low inbreeding depression. Such lines can be found but they rarely have good combining ability. The first results that predicted the performance of phenotypes using small plantlets were described by Stein (1986).

An excellent uniformity of the hybrid varieties demands a high degree of homozygosity in the ms and maintainer line, but selection of lines with low inbreeding depression reduces the probability of finding good parents for hybrid varieties. To overcome this problem, the development of three-way hybrids has been recommended (Bonnet 1982, 1990). In this way, the production of hybrid seed is realized on ms F<sub>1</sub> lines (Fig. 1). For this method, an original maintainer and a second line (exchange maintainer) are necessary. The universal maintainer which can maintain all ms lines due to their complete homozygous state of the maintainer genes is desirable for such a system (Elen et al. 1970). A universal maintainer must also possess the specific characters of the ms line and a good combining ability. Exchange maintainers have therefore been propagated which were selected following a diallel with all lines of one type (Dame et al. 1988). These lines must have the same genetic state as the specific ms line, a state which can be found relatively frequently (Fig. 1). Thus, the best line for performance and uniformity can be selected. Recently, exchange maintainer lines for the most important ms lines have become available and can be used for seed production. They also provide an excellent pool for production of new lines. Pollinator lines which are necessary for hybrid seed production are derived from op-varieties or special breeding lines by using a top-cross system for the testing of general combining ability (Stein et al. 1985). The pollinator lines can be included in cycles of recurrent selection to improve yield and quality when the pollinator provides a sufficiently high variability (Weit 1979). Biotechniques become more and more important in some steps of the development of hybrid systems. A new way is to develop CMS-basic lines by somatic hybridization. Tanno-Suenaga et al. (1988) described the transfer of the 'ba' ms cytoplasm into an x-ray-

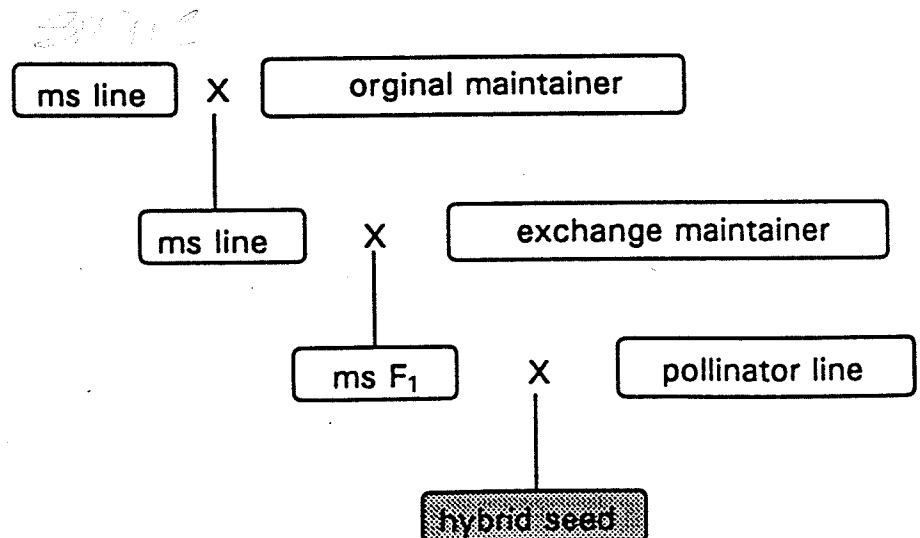


Fig. 1. Maintenance of lines and hybrid seed production of three-way hybrids

irradiated *Daucus carota* L. recipient, the development of cybrid plants, and the different expression of male sterility. This technology offers a chance of combining any genotype with a CMS cytoplasm, providing a good stability in the expression of male sterility or with cytoplasm from wild carrots (Dudits et al. 1977, Ichikawa et al. 1987). Nevertheless, the problem of the cytoplasm-nucleus interactions, as well as the development of maintainer lines, still exists. Anther culture with a large percentage of homodiploids may provide an opportunity of finding homozygous genotypes without inbreeding depression and with a good combining ability (Anderson 1984, Hägnfelt 1988, Hu et al. 1993). By means of somatic embryogenesis and the production of artificial seeds, the development of maintainer lines could, potentially, be substituted (Kitto and Janick 1985, Kamada et al. 1989, Dereuddre et al. 1992, Liu et al. 1992, Wake et al. 1992).

### Quality

Consumers today demand a uniformly orange-coloured root without differences between phloem and xylem. The origin of the orange colour is the carotenoid, carotene. More-or-less red-coloured genotypes from Asian sources contain carotenoids but in the form of lycopene, the main carotenoid in tomato. Nevertheless, only  $\beta$ -carotene is important as provitamin A for quality. Orange-coloured carrot and tomato are the main vegetables containing vitamin A.

In Germany, Schuphan (1942) was the first to recommend breeding carrots with a high level of  $\beta$ -carotene. A great variation in colour intensity and level of carotene exists within the op-varieties. Therefore, uniformly coloured op-varieties were initially selected that possessed a reduced yield. A problem is the variable colour expression in the phloem and the xylem (heart). Two genes seem to be important for the different carotene content in both parts of roots (Simon 1984). A systematic breeding programme for carotene content has been started in some regions only. In developed countries, the main attention has been directed towards uniform root colour because the minimum level of vitamin A for humans is already provided by fruits and vegetables throughout the year. Recently this situation has changed, since  $\beta$ -carotene is important for its anti-carcinogenic and other health-promoting effects. Breeding of carrots with high a content of carotene is always necessary in regions where the food supply or the import of fruit are strongly limited. A typical region in this respect is Russia (the former Soviet Union). Some varieties with a high level of carotene and a remarkable yield have been produced, e.g. the op-variety 'Vitaminaja 6'. Furthermore, hybrids, ms lines, and maintainer lines with a high carotene level are available. For a long time, the genetics of root colour were available only without specific information concerning the chemical background. Recently, many genetic investigations have been performed to study the genes involved in the biosynthesis of carotenoids (especially  $\beta$ -carotene), as well as in root colour (Kust 1970, Buishand and Gabelman 1979, Krivsky and Sverepora 1985, Iman and Gabelman 1968, Simon 1984b, Buishand and Gabelman 1980, Laferrier and Gabelman 1968).

Peterson et al. (1988) and Simon et al. (1989) reported that genotypes had been selected with an extremely high level of carotene (>500ppm) in a crossing programme using Asian genotypes; a fivefold higher level than in common varieties. The high carotene carrots 'HCM' and 'Beta III' are present in the 'Imperator'-type, which is only important in the USA. Simon

Table 4:  $\beta$ -carotene as percentage of the total content of carotene in op-varieties, lines and hybrids of carrot (Schäfer and Stein 1973)

Genotype		% $\beta$ -carotene	% $\beta$ -carotene
'Juwarat' (op)	J	65.1a	
'Primantes' (op)	P		64.1a
Line	9	74.2d	
Line	16	74.6d	72.1b
Line	1		74.1b
Line	2		73.0b
Hybrid	9 $\times$ J	67.6b	
Hybrid	16 $\times$ J	71.2c	
Hybrid	1 $\times$ P		78.7c
Hybrid	2 $\times$ P		70.0d
Hybrid	16 $\times$ P		71.0b

a-d Different letters indicate significant differences based on Newmann-Keuls-test at  $P = 0.05$

(1990) started experiments growing carrots in the developing world and under tropical conditions. By backcrossing, the high level of carotene can be transferred into other genetic backgrounds which are adapted to conditions in regions where vitamin A deficiency is prevalent. In hybridization experiments,  $F_1$  progenies could be found which contain the same level of  $\beta$ -carotene as the best parent but more detailed analysis is necessary. Since hybrid vigour has not been observed, at least one parent must have a high  $\beta$ -carotene content (Stein 1979). In general,  $\beta$ -carotene is the main component of carotene in European varieties. Other components such as  $\alpha$ -,  $\gamma$ - and  $\zeta$ -carotene are only present in small amounts. For breeding of high-carotene carrots, attention must be given to the composition of carotene when foreign material is introduced. The 'HCM' line described by Simon and Wolff (1987) contains 45–65%  $\beta$ -carotene out of the total carotene, whereas, in other varieties, including hybrids, the level is about 70% (Table 4). So far, the genetics of the different components is unknown. Generally, only a weak correlation is observed between the orange colour and the carotene content (Laferriere and Gabelman 1968). The application of HPLC analysis for selection of high-carotene varieties was reported by Simon and Wolff (1987). Biophysical methods for colour selection, based on the measurement of spectral transmission, have also been applied (e.g. the CIELAB-System, Quilitzsch 1994). Some quality measures are given in Table 5 for four varieties using this system.

In Europe, an increasing number of carrots are used as fresh or prepared dressing carrots (bunching carrots). Therefore, special requirements for taste and consistency exist. A typical sweet-carrot taste based on two major components of content — free sugars and volatile terpenoids — is demanded for all varieties for fresh market. Glucose, fructose and sucrose form up to 95% of the free sugars. A great variation between the genotypes can be observed. Extensive investigations by Simon et al. (1980a, 1982) and Freeman and Simon (1983) have demonstrated a monogenic dominant inheritance for the high sugar content. The level of total dissolved solids and reducing sugar can be increased by some cycles of recurrent selection (Stommel and Simon 1989). A pleasant carrot taste is the effect of many components, especially of terpenoids (Simon et al. 1980b, 1982), which can mask the sweetening effects. In breeding, the taste has generally been analysed organoleptically. The introduction of HPLC-analysis (Freeman and Simon 1983) or HPTLC-analysis (Höfer and Gennari 1994) enables an exact

Table 5: Colour, carotene, and sugar components in four varieties of different origin grown in Quedlinburg, Germany (Höfer and Gennari 1994, Quilitzsch 1994)

Variety	Source	Colour CIELAB-System	Carotene (mg/100g fresh matter)	Sugar (% in dry matter)			Σ
				Sucrose	Glucose	Fructose	
HCM	USA	52.64	25.82	13.08	3.43	3.58	20.09
Beta III	USA	56.21	17.46	10.47	5.74	5.24	21.45
Vitaminaja	Russia	57.11	11.39	14.30	14.82	12.37	41.49
Lange Rote Stumpfe	Germany	59.74	10.37	13.39	10.83	9.92	34.14

analysis of the related sugars and other taste-influencing components. To prevent an unsatisfying carrots taste in hybrid varieties, an analysis of basic lines with regard to specific components is necessary (Stein 1992).

The 'cracking' of roots before or after harvest, especially in varieties of the early and midseason group, can decrease yield. The reasons for cracking are both genetic and environmental, particularly with regard to irrigation (Bienz 1968). Nevertheless, the influence of growth technology has been described. Investigations into inheritance have revealed that cracking susceptibility may be governed by a single dominant major gene, but with a low heritability (Dickson 1966). Dowker and Jackson (1977) reported the effects of the drilling date, plant density, and growing season. They suggested a selection programme under different environments. New technical methods have been developed to select against cracking (Cantwell et al. 1991). 'Bolting' of plants in the first year in most varieties also has a genetic origin. Nevertheless, spontaneous crosses between cultivated and wild carrots during breeding and seed production are the main reason (Wijnheijmer et al. 1989). The tendency to bolt in a population of cultivated carrots can be increased by speeding up plant growth, thus reducing the generation time, using glasshouses. 'Forking', another negative factor for quality, can also decrease the yield. The cause of this may be soil conditions and pathogens such as *Meloidogyne hapla*. Genotypes react differently to these conditions and offer the possibility of selection by use of provocation tests. The 'greening of shoulders' — external and internal (heart) — leads to a decrease in marketable yield. McCollum (1971) reported a low heritability ( $h^2 = 0.23$ ) for this character. Greening of roots is influenced by environmental conditions, and especially by high sun intensity. For selection, a vertical cutting of roots is possible. Both halves of cut roots can be used for reproduction after selection and wound healing. The content of nitrate in roots is dependent on the genotypes, as observed by several authors (Zuchenko and Andruschenko 1980, Granges and Quincho 1982). However, the level of nitrate in roots is very low in comparison to other vegetables. The improvement of 'storage capability' of special varieties or lines is part of some breeding programmes, especially in regions where storage of carrots has great economic importance. In general, the adapted varieties of the late types possess good storage capability but differences exist between varieties. Conventional tests of storage capability require much work and are time-consuming (Hofftun 1985). Therefore, a simple and cheap test system has to be developed. In this context, a method proposed by Meini et al. (1986) for cabbage breeding could be useful. The physiological background of this method is based on different degrees of senescence in plant organs from different genotypes, which result in differences in loss of biomass and degree of infection by various pathogens. Some parallel experiments were performed

with carrots but the first results did not provide enough data to introduce the method successfully into carrot breeding (Volkmann 1988). Perhaps material differences (cabbage leaves, carrot roots) underlie the unsatisfactory results; the heterogeneity of the samples may also have an effect. The whole area of root health must also be kept in mind.

#### Resistance and tolerance

The cultivated carrot is attacked by different pathogens and pests which decrease yield and quality. There are at least three viruses, two bacteria, more than 15 fungi, and at least 15 pests (Bedlan 1984, Spaar et al. 1985, Hardman et al. 1990). The expansion of carrot cultivation into suboptimal regions and the increased genetic homogeneity of the varieties favour disease attacks. Breeding has to increase plant resistance or tolerance, especially because of restrictions in the application of chemical plant protectives. Many methods are available for analysing the general degree of resistance or tolerance in populations, but a further development of methods for single-plant selection in populations is required. Although breeding research has provided a lot of information about carrot varieties that is of value to breeders, only a few resistant varieties have been developed in recent years. The high costs of breeding resistant genotypes in relation to the low number of seeds per ha, resulting in relatively small profits for seed companies, limit research.

Recently, most efforts have been concentrated upon the animal pathogen carrot fly (*Psila rosae* L.) and northern root-knot nematode (*Meloidogyne hapla* Chitwood). In experiments at 12 locations in Europe, Ellis and Hardman (1981) found differences between varieties in the damage caused by carrot fly. The op-variety 'Sytan' is least susceptible whereas 'Danvers' is highly susceptible. Breeding efforts based on selection within populations and in progenies of crosses using 'Sytan', have had limited success. De Ponti (1978, 1980) reported only small differences between the varieties, but he also found 'Sytan', and furthermore 'Vertou', to be least damaged. For selection, a method developed by Cole (1985) and Cole et al. (1988), relying on a good correlation between the concentration of chlorogenic acid in roots of plantlets and the resistance to carrot fly, has been used. In Germany, 'Sytan' also shows a low incidence of carrot fly damage, followed by 'Marktgärtner', an old adapted op-variety (Stein and Lehmann 1984). The resistance of the wild species *D. capillifolius*, which has been evaluated in Wellesbourne (England), is also of high value for carrot breeding (Cole 1985, Ellis et al. 1993). After selection and production of the  $F_6$  progenies, the best lines were not as resistant as the wild parent but significantly better than the partially resistant selected lines of 'Sytan'. The genetic background is mostly unknown, so additive effects are probable. As yet, no resistant or tolerant varieties can be found in the catalogues of seed companies.

Northern root-knot nematode can lead to extreme decreases in yield and quality. The risk is high in regions where carrots and potatoes are cultivated side by side, with short rotation periods. In rotation with maize, barley and *Brassica campestris*, the pathogen level can be minimized. Clark (1969) and Brzeski (1974) were the first to provide data on sources of resistance from different regions. Hoser-Krauze and Brzeski (1978), Yarger and Bauer (1981), Stein (1982), Nieuwhof (1968) and Santo et al. (1988) claimed new sources of resistance within the cultivated carrot. Frese (1982, 1983) and Frese and Weber (1984) found relative resistance in the wild form *D. c. hispanicus*, and Kraus (1992) reported good tolerance in *D. c. azoricus*. Extensive genetic analysis suggested complicated polygenic inheritance. Recent efforts in Hannover (Germany) have aimed to map the resistance genes from *D. c. azoricus*. Varieties with a high degree of resistance have not yet been submitted.

In subtropical and tropical regions, *Meloidogyne javanica* is a dangerous pathogen. Huang et al. (1986) reported varietal screening and studies on the heritability of resistance. Estimated  $h^2$  values indicate that the resistance level of varieties to *M. javanica* can be improved by recurrent mass selection.

*Alternaria dauci* [Kühn] Grov. et Skolko is the most important fungus causing black spot or late blight on leaves (Levandovskaja and Timoshenko 1981). Fedorenko (1983) and Strandberg et al. (1989) analysed a large collection of genotypes for the attack of *Alternaria* and detected variability within both cultivated carrots and wild forms. The phytotoxic effect of infection by *Alternaria* is due to an increased content of zinniol (Barash et al. 1981). Genetic investigations in Brasilia have shown a medium heritability ( $h^2 = 0.40$ ) for *Alternaria* tolerance in the op-variety 'Brasilia'. These results suggest that the level of resistance could be increased by recurrent selection (Boiteux et al. 1993). New prospects are offered by optimized methods for resistance selection in either the laboratory or the field (Bruno and Smolka 1994). Today, seed companies do offer some op-varieties, as well as hybrids, with a high field tolerance to *Alternaria*.

Other important pathogens causing leaf diseases are *Cercospora carotae* (Pass.) Kazn. et Siem, *Stemphylium radicum* (M., Dr. et E.) Neerg., and *Erysiphe umbelliferarum* de Bary (Anderson et al. 1982, Bedlan 1984). Angel and Gabelman (1968) detected a dominant gene for resistance to *Cercospora* in an inbreeding line from Wisconsin, and resistant varieties have been introduced by breeders from the Netherlands. Janyaska (1971) reported that, out of 120 varieties, five showed relative tolerance to *Stemphylium*. The pathogen *Erysiphe umbelliferarum* de Bary is becoming more and more important in Europe. The powdery mildew destroys the leaves, especially in moist and warm summers, causing yield losses, and it leads to difficulties in harvesting using modern techniques. Great differences exist between op-varieties: the variety 'Berlanda' is very sensitive and can be used as a control in tests, and, in some varieties, a good level of resistance has been detected (Vintsunas 1980, Lebeda and Coufal 1985, 1987, Bonnet 1990). After artificial infection, 30 healthy plants were selected from 10 out of 95 varieties. 7% symptomless genotypes have been selected from 'Karsa' which generally serves as a tolerant variety (Kiessling pers. comm.). Recently, some varieties with tolerance to powdery mildew have become available in seed catalogues. In four subspecies of *Daucus*, good resistance has been found (Umiel et al. 1975, Bonnet 1977) and breeding was started. Bonnet (1983) described *D. carota dentatus* Bertol. as a source of resistance which is inherited by a dominant single gene *Eh*.

Different pathogens can cause great losses during storage, especially when storage conditions are suboptimal. The fungi *Alternaria dauci*, *Stemphylium radicum*, *Sclerotinia sclerotiorum* (Lib.) de Bary; and *Botrytis cinerea* Pers., and the bacterial pathogen *Erwinia carotovora* (Jones) are the most dangerous under certain conditions (Hofftun 1985, Bedlan 1984). Some data on the background of potential resistance are available for *Botrytis cinerea* (Heale and Sharman 1977, Goodlife and Heale 1978, Harding and Heale 1981). Experiments to select genotypes resistant to *E. carotovora*, including the development of infection and test methods, have been reported by Skadow (1978), Lebeda (1985), and Michalik et al. (1992). Pronounced differences between lines,  $F_1$  hybrids and op-varieties have also been found in Germany.

Losses of seed yield originate from different pathogenic organisms. A screening method for attack on the umbels by *Lygus hespeus* Knight and *L. elisus* v. Duza has been developed and variation between varieties could be detected (Scott 1970). Virus diseases can lead to a decrease in root yield by 50% or even total loss when a severe infection occurs (Lebeda and Coufal 1985). The symptoms caused by the most important persistent viruses, the carrot motley virus and red-leaf virus, cannot easily be analysed in the field because of multiple infection (Waterhouse 1985). Another virus, named yellow-carrot virus (Cadman 1964), was identified first via varietal differences in symptoms on the leaf. Varieties possessing resistance to virus attack or vectors (all viruses are transferred by aphid vectors, e.g. *Cavariella aegopodii*) are not available (Elnagar and Murrant 1978, Dijk and Bos 1985). Investigations have been reported on induced resistance or tolerance of carrot to *Erysiphe heraclei* (Schönbeck and Dehne 1983) and *Meloidogyne hapla* (Janas 1977). To increase the resistance level further, species and subspecies of *Daucus* need to be included. Some wild carrots have been described as potential sources (Strandberg et al. 1989, Hardman et al. 1990, Ellis et al. 1993). The absence of crossing barriers offers a possibility for introducing resistance genes into the cultivated carrot genome and, in this context, marker-assisted selection could be a valuable tool.

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