Vegetable Science (2023) Vol. 50 (Special Issue): 221-230
doi: 10.61180/vegsci.2023.v50.spl.08
ISSN- 0970-6585 (Print), ISSN- 2455-7552 (Online)
www.isvsvegsci.in

REVIEW ARTICLE

Carrot: Breeding and Genomics

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Abstract

The carrot (*Daucus carota*) is an important cool-season root vegetable grown and consumed globally. The storage root is a rich source of carotenoids, anthocyanins, dietary fiber and vitamins, besides imparting unique flavor and health benefits to consumers. Both classical and modern molecular breeding techniques have contributed to improving the productivity and quality of the crop across temperate, sub-tropical and tropical regions of the world. In this review, we briefly summarize the genetic resources available, progress in carrot breeding for yield, quality and major biotic and abiotic stresses, genomic resources and molecular breeding. The challenges and future perspectives in tropical carrot breeding for improving important traits, mainly beta-carotene, blunt root shape and scar-free smooth roots are also discussed.

Keywords: Carrot, *Daucus carota*, Root, Tropical, Breeding, Hybrid, Genomics.

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Citation: Kalia, P., Singh, B.K., Bhuvaneswari, S., Patel, V. and Selvakumar, R. (2023). Carrot: Breeding and Genomics. Vegetable Science 50(spl): 221-230.

Source of support: Nil

Conflict of interest: None.

Received: 10/08/2023 **Accepted:** 21/11/2023

Introduction

Carrot is a nutrient-rich root vegetable grown and consumed globally. During the last five decades (1967-2017), carrot production (combined with turnip) in the world has increased by 5.5 times from 7.3 to 40.3 mt. This can be attributed to an increase in area by 2.9 times from 0.39 to 1.15 mha and almost doubled productivity from 20.3 to 38.4 t/ha, respectively. Whereas in India, carrot production has increased by 5.81 times from 0.96 to 5.58 lakh tonnes owing to an area increase of 3.32 times from 0.11 to 0.36 lakh ha and a productivity increase of 1.75 times from 9.7 to 16.9 t/ha, respectively (FAOSTAT, 2023). The positive consumer impression of carrots as a nutritious, protective and functional food accounts for increasing their consumption, production and genetic improvement. Also, the sustainable improvement in carrot cultivars for the Indian subcontinent can be one of the strategic approaches for making the availability of natural sources of pro-vitamin A, a reported diet deficiency in young children, adolescent girls and pregnant women in the country.

The commercial produce of carrot is the storage root which is an enlarged swollen base of the tap root including the hypocotyls. It is composed of four distinct sections: peel (periderm), cortex or storage root (phloem, food-conducting tissue), cambium and central core (xylem, water-conducting tissue). Cultivated carrot (*Daucus carota* subsp. *sativus* Schubl. and Martens) are broadly classified into two groups based on (I) presence of root pigments i.e. Carotene group (*D. carota* ssp. *sativus* var. *sativus*) and anthocyanin group (*D. carota*

Figure 1: White, Red, Black, Orange, Yellow and Rainbow tropical carrot genotypes developed at ICAR-IIVR, Varanasi, India

ssp. *sativus* var. *altorubens*), and (II) need of vernalization (exposure to 1-5 °C for at least six weeks) i.e. Tropical/Eastern/Oriental carrot (does not require vernalization and annual in nature) and Temperate/Western/European carrot (requires vernalization and biennial in nature) (Heywood, 1983; Singh and Karmakar, 2021).

Carrots are distinguished by their distinct root shapes namely, Imperator, Danvers, Triangular, Chantenay, Kuroda, Nantes, Paris Market and Ox-heart. The carrot roots are rich sources of four pigments i.e. carotene (orange carrot), lycopene (red carrot), anthocyanins (black/purple carrot), and lutein/xanthophyll (yellow carrot); while rainbow carrot possesses a blend of all these pigments and white carrot lacks the pigment (Singh *et al*., 2018; Figure 1). Among these, orange, red and black carrots are popular and of economic importance cultivated in a varied climates from temperate to tropics (Singh *et al*., 2021). The red carrots are used for table, juice, halwa (sweet pudding), pickling; and orange carrots for table, canning, drying and frozen purposes. Furthermore, black carrot (solid purple) is suitable for salad, halwa, fresh and fermented juice, purple tea; and pharmaceutical and nutraceutical uses as a protective food supplement, healthy food colorants and cosmetics (Singh *et al*., 2022). Black carrots may be referred as 'functional food' as they are the richest source of anthocyanins (200–300 mg/100 g FW) and possesses very high anti-oxidative ability i.e. 18 to 23-folds higher than carotene carrots, five-fold higher than beetroot, ranks among top five food items and first among vegetables (Cavagnaro *et al*., 2019; Koley and Singh, 2019; Singh *et al*., 2022).

Genetic Resources, Origin and Domestication

Carrot belongs to the family Apiaceae which also includes celery, parsnip, parsley, coriander, dill, fennel, anise and caraway. The family Apiaceae contains 466 genera and 3820 species and is one of the largest families of seed plants, and the genus *Daucus* contains ca. 40 species (Plunkett *et al*., 2018; Spooner, 2019). The cultivated carrot (2n=2x=18) is originated from domesticated forms of the wild carrot (Queen Anne's Lace), *D. carota* subsp. *carota*, native to Persian regions (Iran and Afghanistan). The wild carrots have small, spindle shaped, white, slender roots and are aromatic and acrid (Stolarczyk and Janick, 2011). The binomial nomenclature is derived from French, Greek and Latin words i.e. 'carotte', 'daukos' and 'carōta', respectively. The haploid chromosome number for the genus *Daucus* ranges from n=8 to 11. In addition to diploid species, a tetraploid (*D. glochidiatus*) and hexaploid (*D. montanus*) species have been reported (Spooner, 2019).

Cultivation of carrot roots for consumption dates back to 6th century when purple roots were grown in the area of Afghanistan. The black and yellow types were eventually developed and produced in Afghanistan, Turkey and Middle East areas during 10th century; white and orange types were evolved in the Europe and Middle East during 17th century; and red carrots are evolved in India, Japan and China during 18th century. Among different colored carrots the orange carrot, grown under temperate conditions probably developed from mutations of yellow forms followed by human selection which is thought to be originated in the Netherlands (Stolarczyk and Janick, 2011). Intensive selection in the 19th and 20th centuries led to a great diversity in open-pollinated varieties with respect to color, shape, size and quality of roots; maturity; and morphology of leaves and flowers. A great variation also exists for harvesting time from 70-120 days. More than 13000 accessions of carrot, including cultivated semi-cultivated and wild are conserved in the gene banks of various organizations across globe (Allender, 2019).

Breeding Objectives and Cultivars Developed in India

Yield, earliness, wider adaptability and tolerance to various stresses are the common breeding goals. In carrots, root size is an important yield factor as both undersized and oversized roots have less market value. Root shape, appearance and color also contribute significantly to marketable yield. In tropical carrots, the breeding programs need more emphasis on the development of roots with cylindrical shapes for better consumer preference; and smooth and scar-free root surfaces for better appearance, easy uprooting and post-harvest cleaning. Plants with premature bolting, wider/longer core, lower harvest index, and excessive root cracking/ forking/scars/hairs are undesirable. The important breeding objectives in carrots are:

- High storage root yield
- Higher carotenoid and anthocyanin content in roots.
- Uniformity in root color, shape and size.
- Self-colored, small and narrow core.
- Earliness and wider adaptability.
- Delayed bolting, smooth and shiny roots, flat/convex crown, and easy to uproot.
- Free from forking, cracking, root scars, and shoulder greening.

Table 1: Carrot cultivars developed in India

Variety/year of release	*Breeding procedure, specific features*	*Institution/ University*
Tropical Carrot		
Pusa Kesar (1963)	Selection from Local Red × Nantes Half Long	IARI, New Delhi
Hisar Gairic (1993)	Mass selection, light brick-red root	CCSHAU, Hisar
Pusa Meghali (1994)	Pusa Kesar × Nantes	IARI, New Delhi
Arka Suraj (2002)	Nantes × IIHR-253, orange colored	IIHR, New Delhi
Punjab Carrot-34 (2005)	Selection, Red colored root	PAU, Ludhiana
Pusa Rudhira (2008)	Red root	IARI, New Delhi
Pusa Asita (2008)	First black carrot variety	
Pusa Vasuda (2012)	First tropical hybrid using CMS system, red root	
Punjab Black Beauty (2013)	Black colored root	PAU, Ludhiana
Punjab Carrot Red (2014)	Selection, Red colored root	
Pusa Kulfi (2015)	Cream root	IARI, New Delhi
Durga 4 (2017)	Selection, dark red root	Jodhpur (Farmer)
Madhuban Gajar (2017)	Red root	Gujarat (Farmer)
Kashi Krishna (2019)	Black colored root	IIVR, Varanasi
Punjab Carrot 161 (2020)	Dark red colored root	PAU, Ludhiana
Kashi Arun (2022)	Selection, Red colored root	IIVR, Varanasi
Pusa Prateek (2022)	Selection, Red colored root	IARI, New Delhi
Pusa Vrishti	Heat tolerant tropical variety	
Solan Rachna	Introduction from Netherlands	YSPUHF, Solan
Temperate Carrot		
Early Nantes	Introduction from France, orange root	IARI, Katrain
Imperator	Introduction, orange root	
Chantenay	Introduction, orange root	
Nantes (1985)	Introduction, orange roots	
Pusa Nayanjyoti (2009)	CMS based temperate hybrid	
Pusa Yamadagini (1985)	Selection from EC 9981 × Nantes Half Long	IARI, New Delhi
Zeno	Introduction from Germany, orange root	HRS, TNAU, Ooty
Ooty 1	Selection from Half Sib Progeny, orange root	
Chaman	Tolerant to root cracking	SKUAST, Srinagar
Shalimar Carrot-1 (2006)	Selection from local population	

- Good eating quality (TSS, flavor, dry matter).
- Resistance to Alternaria blight (*Alternaria dauci*), Cercospora leaf blight (*Cercospora carotae*) and root-knot nematode (*Meloidogyne*).

In India many varieties/hybrids, especially tropical types have been released for cultivation by various institutions (Table 1).

Classical Breeding in Carrot Improvement

Carrot is a cross-pollinated crop (up to 95%), suffering with high inbreeding depression (18–35% for root length, 40-55% for root weight and 62–82% for root yield). The main breeding methods for carrot are population improvement (mass selection, stratified mass selection, gamete selection, family selection, line breeding, recurrent selection and mass-pedigree); backcross breeding; hybrid breeding; and marker-assisted breeding approaches. During the 19–20th centuries, population improvement were applied to accomplish higher productivity, better quality and greater uniformity. This has resulted in a great number of open-pollinated (OP) varieties of orange, red and black carrots which have been adapted for fresh market as well as processing industries. But, the OP varieties suffer with less uniformity in the population. Nonetheless, hybrid breeding began in the fourth quarter of the 20th century to harness the potential of heterosis for yield, quality and uniformity. In the 21st century, the progress made in biochemical, molecular, genomic and biotechnological tools facilitated and diversified breeding approaches towards precise and faster breeding.

Population improvement

Mass selection has been widely used for the genetic improvement of carrots in India. Based on progeny evaluation, modifications including mass-pedigree and family selection are found better and more effective than simple mass selection. Recurrent selection is used for the improvement of quantitative characters under control of additive gene action. Further, the pedigree method of breeding has also been followed by the breeders to combine the traits of economic importance such as root size, color, etc.

Cytoplasmic male sterility (CMS) in carrot

Male sterility is the dysfunction of stamens resulting in the lack of development of functional pollens. The discovery of CMS paved the way for the development of hybrid cultivars in a commercial scale in many crops. The CMS system is based on a complex interplay between maternally inherited mitochondrial and nuclear genetic information. There are various phenotypic forms of male sterility in carrot namely brown anther, petaloid, GUM type, MAR type (petaloid-like) and GAD type (Linke *et al*., 2019). The 'brown anther' type with Sa-cytoplasm of male sterility is characterized by the formation of normal stamens followed by disruption in microsporogenesis, browning of anthers and inability of anthers to produce pollen grains. (Thompson, 1961) described that dominant allele(s) at any of three duplicated genes (*Ms1*, *Ms2*, *Ms3*) are necessary to maintain sterility for brown anther and petaloid type. Moreover, (Banga *et al*., 1964) suggested that two duplicate genes, one recessive (*aa*) and one dominant (*B*), led to the expression of male sterility, while dominant alleles of either of two complementary genes (*D*, *E*) can restore the fertility. However, many researchers reported that male sterility for brown anther is conditioned by a recessive gene.

The petaloid male sterility is characterized by a replacement of the either stamen with petals or both stamens and petals with bract-like structures (filamentous to spoon-like to three-lobed protrusions). Furthermore, the coloring of the petaloid florets can range from white, yellowish, white-green, green, to purple flowers (Linke *et al*., 2019). Petaloid sterility was first discovered by Munger (1953) in a North American wild carrot (*D. carota* subsp. *carota*) and was later termed 'Cornell-CMS' (Thompson, 1961; Peterson and Simon, 1986). Petaloidy CMS has also been reported as Wisconsin-CMS (Morelock *et al*., 1996) and Guelph-CMS from Canadian wild carrots (Wolyn and Chahal,1998). (Tan *et al*., 2018) found a wild petaloid male sterile line (Wuye-BY) which was related to a shorter length of ATP synthase subunit 6 (atp6 gene). (Thompson, 1961) described that dominant allele(s) at any of three duplicated genes (*Ms1*, *Ms2*, *Ms3*) are necessary to maintain sterility for brown anther and petaloid type. Three independent genes, one dominant M, two recessive genes ll and tt responsible for petaloid sterility, and heterozygous Mm plants can be restored at high temperatures (Mehring-Lemper, 1987). Petaloid-CMS system is most stable across varied environmental conditions and is being commercially used for heterosis breeding of tropical carrots, including India.

In the last decade of the 20th century, few new CMS forms were identified, namely GUM CMS, MAR CMS and GAD CMS, respectively in the following wild relatives *D. carota* subsp. *gummifer*, *D. carota* subsp. *maritimus*, and *D. carota* subsp. *gadecaei*. The GUM type is characterized by a nearly complete loss of petals and stamens in an early stage of organ development. The CMS-MAR type is comparable to the common petaloid CMS flower types. Flowers of the CMS-GAD type have only short filament-like stamen rudiments. One or two homozygous recessive alleles (gum1, gum2) seem to be responsible for the male sterility for GUM; and one or two dominant alleles lead to the male sterility in MAR type (*Mar1*, *Mar2*) and GAD type (*Gad1*, *Gad2*). In some cases, petals were revealed as sepal-like characters and stamens were completely replaced by carpel-like structures indicating multiple stigmata termed as carpeloid CMS (Linke *et al*., 2003; Dyki *et al*., 2010). Further, (Kalia *et al*., 2019) verified that the appropriate sequence for producing the trait-specific markers is located between both the 3' end of the *atp9-1/atp9-3* gene and the 5' end of the region of homologous to *Arabidopsis thaliana* mtDNA.

Backcross breeding and isogenic line development

Backcrossing is used to transfer one or a few favorable genes of an economic trait into a desirable cultivar. In carrot, this approach has been used extensively for the transfer of CMS in elite backgrounds. ICAR-IIVR, Varanasi has developed many robust petaloid-CMS lines in various backgrounds of tropical carrot such as red root (VRCAR-211, VRCAR-212 and VRCAR-214); orange root (VRCAR-231, VRCAR-234 and VRCAR-241); yellow root (VRCAR-271 and VRCAR-272); black root (VRCAR-251 and VRCAR-252); and rainbow root (VRCAR-291 and VRCAR-292) (Singh and Karmakar, 2021). Among these, two petaloid CMS lines i.e. VRCAR-214 (INGR22160) and VRCAR-252 (INGR22088) have been registered as unique germplasm. Further, ICAR-IARI, New Delhi also developed many CMS lines for red, orange and purple roots, and heat tolerance (Kalia *et al*., 2019), and four of them registered as unique germplasm (INGR20115, INGR20116, INGR21056 and INGR21090).

Progress in hybrid breeding

Heterosis breeding provides an opportunity to harness hybrid vigor and uniformity for various economic traits. The development of CMS lines is a prerequisite to enable hybrid breeding in carrots hybrid breeding in carrot is reported to increase root yield and uniformity by different workers

(Simon and Strandberg, 1998; Verma *et al*., 2002; Jagosz, 2012; Singh, 2017; Turner *et al*., 2018), carotenoid content (Santos and Simon, 2006) and resistance to *Alternaria* leaf blight (Simon and Strandberg, 1998). Carrot hybrid development programme is based on a line system (A, B and C line). In India, the ICAR-IARI, New Delhi has developed two CMS-based hybrids Pusa Nayanjyoti and Pusa Vasuda; and promising hybrids developed by ICAR-IIVR, Varanasi (VRCAR-211×VRCAR-86, VRCAR-211×Kashi Arun, VRCAR-214×VRCAR-85 and VRCAR-214× VRCAR-201) and ICAR-IARI, New Delhi are in the evaluation stage.

Inheritance and breeding for biotic stresses

Fungal leaf blights in carrots are caused by pathogens *Alternaria dauci* and *Cercospora carotae and* bacteria *Xanthomonas campestris pv.carotae*. The lesions of *Alternaria* blight occur on older leaves, while the lessions of *Cercospora* blight form on new leaves. Blight tolerant genotypes and cultivars have been reported which delay the spread rate. (Angel and Gabelman, 1968) and (Lebeda *et al*., 1988) reported a single dominant gene responsible for resistance to *C. carotae*. Whereas resistance to *A. dauci* was found to be under polygenic nature and 11 QTLs were identified (Le Clerc *et al*., 2015). Further, (Koutouan *et al*., 2019) observed a positive correlation between content of terpenoids and flavonoids and resistance to *Alternaria* leaf blight.

Powdery mildew (*Erysiphe heraclei*) has been documented across carrots growing regions but tends to be severe in warm, semiarid regions, especially with drip or furrow irrigation. The fungus produces white mycelium and sporulation on any above ground part of carrot plants, including leaves, petioles, flower stalks, bracts, and umbels. The resistance to powdery mildew is controlled by single dominant gene (*Eh*) was identified by Bonnet (1983) in *D. carota* subsp. *dentatus*. However, (Lebeda and Coufal, 1987) interpreted incomplete dominance and quantitative resistance to powdery mildew.

The root-knot nematodes (RKNs) *Meloidogyne hapla*, *M. javanica* and *M. incognita* are of economic importance in carrot globally. Losses may occur up to 100% with yield reduction and shape deformation (taproot forking and gall formation) that make carrots unmarketable. *M. hapla* is a predominant species in in cooler production areas, while the incidence of *M. javanica* and *M. incognita* are common in warmer areas. The gall formation and nematode tolerance appeared to be associated with root type e.g., Nantes and Long Chantenay root types exhibited tolerance generally, while Danvers root type was mostly susceptible. (Simon *et al*., 2000; and Ali *et al*., 2014) identified simply inherited single dominant genes *Mj-1* (Brasilia) and *Mj-2* (PI652188), respectively for resistance to *M. javanica*. Further, (Yunhee *et al*., 2014) reported that resistance to *M. incognita* is governed by one or a few dominant genes. (Singh *et al*., 2019) established an *in vitro* approach for determining related DNA markers and screening carrot for RKN. During RKN resistance breeding, the *STS-SQ1* marker and *in vitro* screening would be helpful for screening segregating population.

Understanding genetics of abiotic stress tolerance

In order to develop carrot cultivars for warmer climates, the impact of high temperatures on crop growth and development has been studied by different workers. According to research by Bolton and Simon (2019), the majority of carrot seeds germinated 50% less frequently at 35°C than at 24°C. "Brasilia" was the only cultivar to germinate at 37.5°C, although only at a rate of less than 10%. Enzymes called laccases, which contain copper, may help plants withstand environmental stress. These might be crucial as their expression changes when carrots are exposed to heat, salt, and metals (Ma *et al*., 2015). The mechanism and main component of cold tolerance have been discovered (Smallwood *et al*., 1999). It uses polygalacturonase inhibitor protein (PGIP) gene family member, antifreeze protein (AFP) secreted PGIP proteins include AFP. AFP may be able to generate cold particles and impede apoplast ice recrystallization due to a unique function (Meyer *et al*., 1999). Carrot AFP has been demonstrated to boost cold resistance when introduced to plants by genetic engineering. Hypoxia is an abiotic stress that may inhibit carrot root growth and development. (Que *et al*., 2018) showed that at low oxygen, carrot roots were more lignified. Three alcohol dehydrogenases (ADH1–3) were up-regulated in hypoxic roots compared to aerated roots.

Breeding for root quality traits

Carotenoids and anthocyanins are natural pigments abundantly found in various colored roots of carrots and are known to be beneficial for human health. The accumulation of various pigments is varied in the carrot root with different root colors and root tissues. The difference in the accumulation is due to differential expression patterns of pigment biosynthesis genes in specific tissues. Santos and Simon (2002) identified putative QTLs that are associated with the accumulation of ξ-carotene, α-carotene, β-carotene, lycopene and phytoene in carrots. Two phytoene synthase (PSY) genes were found in carrots by Just *et al*. (2007). Moreover, (Ma *et al*., 2017) suggested that carotene hydroxylase genes are involved in α-carotene accumulation and xanthophyll formation.

Black carrot is one of the richest sources of anthocyanins which vary from 13-283 mg/100 g FW among carrot genotypes (Singh *et al*., 2022). The main anthocyanins in purple carrot roots are cyanidin glycosides; and the percentage of acylated anthocyanins to the total anthocyanin content found across different studies varied from 49.6 to 99% (Algarra *et al*., 2014). Genes in phenylpropanoid and anthocyanin biosynthesis for phenylalanine ammonialyase (PAL), flavanone 3-hydroxylase (F_3H), chalcone synthase (CHS), dihydroflavonol 4-reductase

(DFR), and leucoanthocyanidin dioxygenase (LDOX) biosynthesis pathway have been identified in carrots (Hirner *et al*., 2001). Three monogenic dominant genes namely *P1*, *P2* and *P3* have been reported for controlling purple pigmentation in the roots, nodes, and roots and petioles, respectively (Simon, 1996; Cavagnaro *et al*., 2014). Further, a simply inherited gene *Raa1* responsible for root anthocyanin acylation was discovered and mapped in chromosome 3 at 17.9 cM (Cavagnaro *et al*., 2014). Moreover, (Iorizzo *et al*., 2011) produced first large-scale transcriptome of carrot and confirmed the potential of short read platforms for de novo EST assembly and identification of genetic polymorphism in carrot. Flavonoids profiling of different F_2 carrot populations revealed the presence of three acylated and two non-acylated compounds (Selvakumar, 2016). Moreover, Kalia (2004) investigated the quality and root attributes of 100 tropical carrot selections and identified superior lines for quality traits. Further, line IPC53 had the greatest positive significant GCA impact for four characteristics (reducing sugar, total carotene, ascorbic acid, and Cu) and had the second highest significant GCA effect for five characters (K, P, Mn, Zn and Fe). Six hybrids IPC53 × IPC122, IPC126 × IPC116, IPC98 × IPC16, IPC55 × IPC16, IPC98 × IPC13 Red, and IPC126 × IPC76 were found to have significant SCA effects for total carotene, β carotene and lutein (Selvakumar *et al*., 2021a, 2021b, 2022a, 2022b).

The carbohydrates in carrot root are composed mainly of reducing and non-reducing free sugars (mainly glucose, fructose and sucrose) and influence flavor, total dissolved solids (TSS) dry mater content, and quality traits for fresh-market and processing. Generally, total sugar content in carrots varied from 5-15 g/ 100 g FW. Single dominant gene *Rs* was reported to be associated with the content of reducing sugar in the storage root of carrot (Freeman and Simon, 1983). In another study, three sucrose synthase genes, namely *DcSus1*, *DcSus2* and *DcSus3* reported for biosynthesis of the sucrose in carrots (Liu *et al*., 2018).

The beta-carotene-rich orange carrot is typically temperate in nature and doesn't flower in tropical and sub-tropical climates. Hybridization (orange temperate and red tropical genotype) and selection from flowering plant population for higher beta-carotene (>7 mg/100 g FW) in orange genotypes is being carried out at ICAR-IIVR, Varanasi. Also crosses made for developing important economic root traits like blunt root shape and scar-free smooth roots which are easy to uproot and clean in red, orange and black colored tropical carrots.

Biotechnological Applications in Carrot Improvement

In-vitro regeneration and micro-propagation

The carrot is regarded as a model species for tissue culture of plants where (Steward *et al*., 1958) published the first findings of proliferation and growth in any organism. Carrot has been used to examine the viability of in vitro screening, particularly for resistance to disease (Baranski *et al*., 1997; Grzebelus *et al*., 2013), tolerance to antibiotics and sugar analogs Stommel and Simon (1989). With reports of regeneration (Grambow *et al*., 1972) and improved methods (Grzebelus *et al*., 2012) for maintaining the development of carrot protoplasts in the environment of fungal disease filtrates, carrot has also served as a model organism for protoplast culture (Grzebelus *et al*., 2013). In order to create genetically distinct carrot plants, somatic hybridization of carrot protoplasts was performed (Dudits *et al*., 1977a). Additionally, the cultivated carrot and its wild relative, *Daucus carota* L. ssp. *capillifolius* (Gilli) Arbizu, were fused (Dudits *et al*., 1977b). The cultivation of unfertilized ovules (Kielkowska and Adamus, 2010) and the production of haploids from anther cultures have been reported (Andersen *et al*., 1990; Li *et al*., 2013; Kiszczak *et al*., 2017). Using somatic embryos produced in suspension cultures and encapsulated with alginic acid, artificial carrot seeds have been successfully developed (Liu *et al*., 1992; Latif *et al*., 2007).

Genetic transformation and gene editing

Carrots have been utilized widely in gene transfer investigations due to efficient cell and tissue proliferation under *in-vitro* conditions (Baranski, 2008). The first report of an *A. tumefaciens*-mediated modification in carrots was provided by Scott and Draper (1987). Carrot has also been effectively altered using protoplast uptake, electroporation, and microprojectile bombardment (Deroles *et al*., 2002). Baranski and Lukasiewicz, (2019) reported putative resistance genes evaluation for effectiveness in resistance to 13 different carrot diseases. Additionally, recombinant proteins and recombinant enzymes have been produced in transgenic carrots as biopharmaceuticals to treat a number of human diseases, such as diabetes, cholera, TB, HIV, measles, and rabies. One of the successful recombinant proteins taliglucerase alfa (Elelyso® Protalix Biotherapeutics) has been approved for enzyme replacement therapy to treat Gaucher's disease (Baranski and Lukasiewicz, 2019). Recently, optimization of CRISPR/Cas9 with Atecas9 for F3H mutation was demonstrated in carrot for successful site-directed mutagenesis (Klimek-Chodacka *et al*., 2018). DcPDS and DcMYB113 genes were edited in orange and purple carrots respectively for knocking out pigmentation using four sgRNA cassettes demonstrating stable gene-edited carrot plants (Xu *et al*., 2019)

Molecular breeding

In carrot, important economic traits including growth, root morphology, root quality, nuclear restorers of CMS, male sterility, disease and pest resistance traits have been mapped by linkage studies. Identification of genomic regions corresponding to a trait of economic importance with help of molecular markers aids selection in crops. Marker-assisted selection (MAS) has been successfully employed in the introgression of dominant resistance gene *Mj-1* against

root-knot nematode, *Meloidogyne javanica* using linked sequence tagged site markers (Boiteux *et al*., 2004). High sucrose *rs/rs* plants were found to have a 2.5 kb insert in the acid-soluble invertase isozyme II gene (Yau and Simon, 2003; 2005). Another gene *rs* controlling relative content of reducing sugar (glucose, fructose) to sucrose in the storage root is selected using three linked markers (Yau *et al*., 2005). Genetic diversity studies using molecular markers have been reported by Jhang *et al.* (2010) and Kushlaf (2011). Different QTL distributed across carrot genome for polygenic traits namely carotene content, anthocyanin content, and volatile terpenoid content have been identified (Simon, 2019). Selvakumar *et al*., (2022) reported genomic simple sequence repeats (GSSRs) and BAC end sequence-based SSR (BSSR) markers for the identification and precise selection for anthocyanin-rich carrot in F_2 population.

Advances in carrot functional genomics

Availability of high-quality chromosome level genome sequence of orange carrot Iorizzo *et al.* (2016) provided insights into the molecular basis of carotene accumulation in roots and opened opportunities for single nucleotide polymorphism (SNP) level genotyping for crop improvement. Carrot genome size (473 Mb) containing about 32,113 genes is relatively smaller and comparable to rice genome size (480 Mb). Many important trait QTLs mapped before genome sequencing were also confirmed their genomic positions like carotenoid accumulation on chromosomes 5 and 7. The functional polymorphic region in gene DCAR_032551 on chromosome 5 with 212-nt insertion (variant 1) and single nucleotide insertion (variant 2) in second exon was identified as responsible for high carotenoid pigment accumulation in orange carrots. Resequencing of diverse carrot subspecies identified a very large diverse SNPs (13.9 million) depicting genome divergence in the species. Also, close resemblance of eastern cultivated carrot lines with wild carrots through phylogenetic studies strengthened the evidence for the centre of origin of carrots from Central Asia and Middle East. The large allelic divergence in cultivated carrots in Middle East and Asian countries including unpigmented, black lines provides clues for scope in breeding efforts for improving root morphology and pigmentation. The genome sequence of orange carrot variety 'Kurodagosun' belonging to Kuroda type popular in China and Japan adds to genomic resources from Eastern region (Wang *et al*., 2018).

The availability of carrot genome sequence has enabled genome-wide association studies (GWAS) for mapping complex loci possible. A total of 30 QTLs were identified for 15 terpenoid volatiles influencing taste and flavor by metabolite profiling, genotyping-by-sequencing and identified four genomic regions on three different carrot chromosomes corresponding to distinct monoterpenes and terpene synthase candidate genes (Keilwagen *et al*., 2017). Multiple QTLs for highly polygenic and previously uncharacterized root traits influencing shape and size defined in four phenotypes namely length, aspect ratio, maximum width and root fill were identified by GWAS combined with digital image analysis, genomic-estimated breeding values GEBVs (Brainard *et al*., 2022). Analysis for orange pigmentation in diverse carrot germplasm through GWAS identified a genomic region on chromosome 3 containing *Or* gene responsible for carotenoid presence and a nonsynonymous mutation in exon 5 co-segregating with carotenoid content (Ellison *et al*., 2018). The study also identified twelve putative genomic regions subjected to selection during domestication.

Table 2: Genomic tools for carrot

Database	*Database link*	*References*
RoBuST	http://robust.genome.com	(Bhasi *et al*., 2010)
CarrotDB	http://apiaceae.njau.edu.cn/carrotdb	(Xu *et al*., 2014)
Carrot genome	https://phytozome.jgi.doe.gov/pz/portal.html#!info?alias=Org_Dcarota	(Iorizzo *et al*., 2016)
CarrotOmics	https://carrotomics.org/	(Rolling *et al*., 2022)

Carrot bioinformatics tools

The genomic and transcriptome database of *D. carota* sp. *sativus* was used as the foundation for Carrot Database (CarrotDB) (http://apiaceae.njau.edu.cn/carrotdb) in Table 2. It offers the Basic Local Alignment Search Tool (BLAST) and Genome Map tools for finding sequences of scaffolds, target genes, assembled transcriptomic sequences, expressed gene in the transcriptome, *de novo* assembled whole-genome sequences, putative gene sequences or gene fragments, and putative protein sequences of carrot (DC-27), as well as gene annotation, and submitting information to the genome map group (Xu *et al*., 2014). Whole genome sequencing was used to carry out the *de novo* assembly and analysis of DC-27. Transcriptomic sequences of DC-27 are available from the National Center for Biotechnology Information (NCBI) using the Sequence Read Archive (SRA) database (http://www.ncbi.nlm.nih.gov/sra/). The RoBuST database (http://robust.genome.com) allows users to quickly start exploring and analyse the sequence annotations of 3663 genes, 5959 RNAs, 22,723 ESTs, and 11,438 regulatory sequence elements from the Apiaceae and Alliaceae plant families. Additionally, the RoBuST database facilitates comparative genomic investigation of the splicing patterns of 6015 plant species' 659,369 splice signals (Bhasi *et al*., 2010). A comprehensive, well-curated, open-access database of carrot genomic resources called CarrotOmics (https://carrotomics.org/) is recently developed by MainLab bioinformatics, Washington State University (Rolling *et al*., 2022) and is timely for exploiting genomic information by

carrot geneticists and breeders across globe for trait-based breeding in climate-changing scenario and newer niches.

Conclusion and Future Perspectives

Carrot breeding progress has resulted in enhanced productivity, better quality and wider adaptation to varied climate conditions. Many studies on the domestication, germplasm resource, trait inheritance, breeding, and molecular insight of various types of carrots have been reported. For sustenance of carrot production in the tropical region, future breeding work may focus on the development of cultivars with smooth root surfaces and cylindrical root shape in red, black and yellow carrots; enhancing the tolerance to biotic and abiotic stresses mainly heat tolerance, water stress and salinity; and improving cultivars with medicinal, pharmaceutical and cosmetic values. Accumulation of knowledge on genetic inheritance and molecular basis of important market class traits is envisaged to propel the improvement for sustainable production in warmer climates and desired consumer quality in the future.

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सारांश

गाजर ठंडे मौसम की जड़वाली एक महत्वपूर्ण सलाद सब्जी हैए जिसे वैष्विक स्तर पर उगाया और खाया जाता है। उपभोक्ताओं को अद्वितीय स्वाद और स्वास्थ्य लाभ प्रदान करने के अलावा, गाजर की जड़ कैरोटीनॉयड, एंथोसायनिन, आहार फाइबर और विटामिन का समृद्ध स्रोत है। पारंपरिक और आधुनिक दोनों तकनीकों ने दुनिया के समषीतोष्ण, उपोष्णकटिबंधीय और उष्णकटिबंधीय क्षेत्रों में गाजर की उत्पादकता और गुणवत्ता में सुधार करने में महत्वपूर्ण भूमिका निभायी है। इस समीक्षा में, उपलब्ध आनुवंषिक संसाधनों, उपज, गुणवत्ता एवं प्रमुख जैविक और अजैविक कारकों, जीनोमिक संसाधनों तथा आणविक प्रजनन के लिए गाजर की आनुवांषिक उन्नयन में प्रगति का विवरण दिया गया है। इसके साथ ही उष्णकटिबंधीय गाजर में बीटा-कैरोटीन की मात्रा, विषिष्ट स्वाद, बेलनाकार जड़, चिकना एवं चिन्हमुक्त जड़ सतह, इत्यादि महत्वपूर्ण आर्थिक गुणों में सुधार से सम्बन्धित चुनौतियों और भविष्य के दृष्टिकोण पर भी चर्चा की गई है।