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Advances in Genetics and Molecular Breeding for Nutritional Quality in Carrot: A Review

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Abstract

Carrot (*Daucus carota* L.) is an important biennial winter root vegetable crop. It is a repository of genetic resources for control of β-carotene, lycopene, lutein and anthocyanin contents in orange, red, yellow and black colored carrot, respectively. The research on carrot indicated the importance of marker technology for carrot genetic resources. However, the molecular marker technology, as well as reports in carrot, are lacking for targeting phenotypic traits. Development of robust microsatellite markers are utilized for identification of genes for marker intensity, high reproducibility, applicability and transferability, time and are labor saving. Recent carrot breeding focus is on enhancement of total anthocyanin and total carotenoid content because of bioactive compounds and antioxidants which affect health. There is little information available on genetic expression and markers linked to nutritional quality traits in carrot. The objective of this paper was to review the genetics of nutritional quality traits in carrot and to identify molecular markers linked to genes using established carrot genetic maps. Having information on genetic inheritance of carrot color would help to understand expression of nutritional compounds and would lead to development of high nutritional content carrots for the tropics.

Keywords: *Daucus carota; Anthocyanin; Lutein; Marker; Nutrition*

Introduction

Carrot (*Daucus carota* L., 2n = 2X = 18; 1C = 473 Mb) is a cool weather crop grown in temperate and subtropical regions for its edible storage tap roots for the fresh and processed market [1-3]. Among vegetables, carrot is one of the most nutritious root vegetable crops [4-7]. It is a potential source of carotenoids, anthocyanins and other flavonoids which scavenge free radicals, and reduce the risk of, and protect against and cardiovascular diseases [8,9]. Eastern carrots of yellow and purple color originated in Afghanistan during the mid-9th century [10]. These were grown in Europe in the middle ages which were replaced by Western carrots of white and orange colour due to selection and hybridization of yellow, purple and its wild relatives [11]. Orange, red, yellow and purple color of carrot are formed by α and β-carotene, lycopene, lutein and anthocyanins, respectively [12-19]. It led to increasing awareness to the consumer consumption and nutritional industry to make natural products rich in carotenoids and anthocyanins [20]. These information would help to understand the importance of various colored carrot with nutritional availability. A good understanding of genetic information of traits controlling nutrition improved carrots can be bred using molecular marker. The molecular marker technology can be effectively utilized to construct genetic linkage maps. The high saturated linkage maps provides information of identified markers which are intimately linked with gene(s) location on the chromosome region of interest. Polymorphic markers are identified between 2 different target trait parents which exhibit the recombination during gametogenesis on the same chromosome in the F2 and F2 derived F3 generations, backcross generations, recombinant inbred lines and double haploid lines for mapping markers [21]. Molecular marker technology is effective for introgression of targeted genes in a short period, possibility of effective genotypic selection and short breeding cycle which guides conventional breeding strategies [22-29]. Restriction fragment length polymorphisms (RFLP), random amplified polymorphic DNA (RAPD), microsatellite polymorphisms (SSRs and others), amplified fragment length polymorphisms (AFLP) or other molecular genetic markers can be successfully used for detection of DNA sequence that match specific chromosome region [30-34]. Microsatellites are unique for use in plant breeding due to their codominant inheritance and their detection is readily automated over RFLP, RAPD and AFLP markers. Marker assisted selection could be more efficient for phenotypic selection in larger populations [35-36]. Acceleration of effective breeding is done by construction of saturated molecular map with microsatellite markers in parental inbred lines of self- and cross-pollinated crops. Linkage drag effects of unwanted donor alleles in the targeted genomic regions can be overcome by the molecular marker technology.

Efforts have been made to improve carrot for production under tropical conditions through conventional breeding. However, supplementing with molecular breeding has a great potential in accelerating carrot nutritional quality. Efficient markers tightly linked with target traits is a prerequisite for effective marker assisted breeding. Use of molecular markers in carrot has been utilized for construction of linkage maps in wild relatives, putative ancestors and natural gene banks. These linkage maps are utilized for identification of simply inherited traits or quantitative traits linked to particular chromosome regions. Among molecular markers, microsatellite or simple sequence repeats (SSR) appear to be reliable and have the additional merits of high abundance, high percentage of polymorphism, random distribution, co-dominance, hyper variability, reproducibility, and are less cumbersome and time consuming [33]. Use of microsatellites has demonstrated linkage to genes of horticultural interest in many organisms [37]. Mapping is done due to availability of molecular markers with interval mapping methods. These identification and characterization of targeted genes by molecular markers help in precision phenotypic selection which leads to development of improved hybrids and varieties. A large set of microsatellite markers, derived from bacterial artificial chromosome end sequence (BSSRs), SSRs from expressed sequence tag (EST) libraries (ESSRs), and SSRs from genomic library enrichment (GSSRs) have been developed in carrot [33]. With availability of molecular markers, large numbers of molecular linkage maps have been developed in carrot [38-52]. Mapping in carrot has been reported for carotenoids [44,50], lycopene [53], anthocyanin [52,54] and lutein [55]. By utilizing these advances in genetics and molecular breeding we can develop multicolored, multivitamin with multimineral packed carrot varieties/hybrids. These varieties/hybrids would help to natural food color, nutritional food industry need supplements of naturally rich resources of black carrot for isolation of anthocyanins and carotenoids compounds. This review provides holistic carrot research approach in genetics, and molecular breeding that help researcher to identify research gap in carrot genetics and molecular breeding.

Carrot and its importance

Carrot originated in South Asia and is widely distributed in Afghanistan, Iran and Pakistan. Due to its nutritional value, it is cultivated throughout the world [56-58].

History of carrot color

Cultivation of carrot was started by the Persian Empire in the Iranian Plateau which encompasses Afghanistan, Pakistan and Iran approximately 1000 years ago (Brothwell and Brothwell, 1969). The two major domestications, described by Vavilov [59,60], were Eastern (var. *altorubens*) and Western (var. *sativus*). Eastern carrot with yellow and purple colors, which originated from Central Asia including northwest India, Afghanistan, Tajikistan, Uzbekistan, and western Tian-Shan, were first domesticated during the early to mid-8th century [61-63]. Western carrots with red and orange colors originated from the Anatolian region of Asia Minor (Turkey) and Iran [64-66]. Eastern carrots colored yellow, purple, and white have leaf characteristics of being slightly dissected, pubescent, and grey green; orange and red Western carrots have yellow-green leaves that are deeply dissected, and mostly glabrous [67]. Orange carrots originated in the Netherlands and were derived by natural mutation, natural hybridization and human artificial selection of Eastern wild carrots with yellow, purple, or white roots from Europe and the Mediterranean region during the 17th century [60,63]. Banga [52] concluded that orange carrots were derived by selection from yellow types of 'Late Horn' and 'Half Long Horn' during the 17th century. Orange, red, yellow and purple colors in carrot are formed by α- and β-carotene, lycopene and lutein and anthocyanins, respectively [12-15]. Xanthophylls of yellow roots (70 - 95%) had more total carotenoids than xanthophylls of orange and red roots (< 10%) [68]. Appreciable amounts of other pigments reported in carrot are phytoene, phytofluene, zeta-carotene, γ-carotene, and α-carotene [69-74].

Role of carrot pigments in human nutrition

Carotenoids

Carotenoids are important phytochemicals consisting of 700 compounds found in nature. The orange carrot contains 40 carotenes including the α- and β-carotenes [75]. Six carotenes of α-, β-, γ- and ζ-carotenes, β-zeacarotene, and lycopene are found in dark orange carrots [16,76]. The α- and β-carotenes are main source of provitamin A carotenes which are present at 13 - 40% and 45 - 80% in orange carrots, respectively [16,64,77]. Modern orange, yellow and red carrots have total carotenoid contents in the ranges of 64 - 600 $\mu g \bullet g^{-1}$, 15 - 71 $\mu g \bullet g^{-1}$, 0 - 1.5 $\mu g \bullet g^{-1}$ and 100 $\mu g \bullet g^{-1}$, respectively [78]. White roots are low in total carotenoids [72]. Total carotenoid content varies between carrot colors [16,79-81]. Awareness of natural functional foods, natural food colors and nutritional amendments, increased consumer interest of carotene rich carrot [82,83].

β-Carotene

β-Carotene is heterogeneously distributed across carrot roots, and in all yellow, orange, red, and purple color carrots is generally highest in the outer root, or phloem, and lower in the xylem (core) [84]. Carrot roots with high-carotene have high concentrations of β-carotene in the xylem [85].

Lutein

Yellow carrots are a rich source of lutein which has no provitamin activity but plays a role in eye health and protection from macular degeneration [86,87]. It contains low levels of total carotenoids, as well as β-carotene, than do dark orange, orange, purple yellow, red and purple carrots [88,89]. Orange carrots, with a yellow core, contain lutein and α- and β-carotene [90].

Lycopene

Red carrots are source of lycopene which has no provitamin A but protects against cancer [91,92]. Red carrots have higher lycopene concentrations than red tomato and contain appreciable amounts of α-carotene, β-carotene, and lutein [87,88].

Anthocyanin and its importance

Purple carrots, also called black carrots, have purple phloem and white, yellow or orange xylem. Purple carrots are a potential source of dietary anthocyanins which have been reported to protect against cardiovascular diseases [93,94] and cancer [95,96]. Anthocyanin plays a role in protecting against cell death by acting as monosaccharide transporters and osmotic adjusters [9]. Purple carrots have higher amounts of anthocyanin than purple orange, purple with white core, and orange carrots [97-101]. The structural profile of anthocyanin is comprised of cyanidin-3-(2-xylose-6-glucose-galactoside) (Cy3XGG), cyanidin-3-(2-xylose-galactoside) (Cy3XG), cyanidin-3-(2-xylose-6-sinapoyl-glucose-galactoside) (Cy3XSGG), cyanidin-3-(2-xylose-6-feruloyl-glucose-galactoside) (Cy3XFGG), and cyanidin-3-(2-xylose-6(4-coumaroyl)glucose-galactoside) (Cy3XCGG) [52,102-105]. Organoleptic studies determined that purple carrots were preferred more than orange carrots, although the sweetness of purple carrot was less than orange carrot which has high total sugars. Purple carrots are substitutes for orange carrot in terms of total soluble sugars [5]. Surles*., et al.* [18] reported that white and orange colored carrot roots were more acceptable than purple, red, yellow carrots and concluded that color group were independently different for flavor and taste. Purple carrots can be commercially exploited for anthocyanin through breeding [52,76,106].

Genetic inheritance studies for colour and its nutrition

Carrot has a wide genetic diversity due its single locus mutations, hybridization of its wild relatives and ancestors, and human selection [107,108]. The allele collection of carrot include dominant alleles such as *A* (α-carotene accumulation), *Io* (intense orange xylem, which may be an allelic form of A), L_1 and L_2 (lycopene accumulation), O (orange xylem, which may also be an allelic form of A) as well as the recessives alleles y (yellow xylem) and *rp* (reduced pigmentation) (Table 1). The three dominant loci *Y*, Y_1, and Y_2 control differential distribution of α- and β-carotene in the xylem and phloem. The Y2 mutant controls low carotene content of storage root xylem (core) in high carotene orange backgrounds [108]. Laferriere and Gabelman [12] demonstrated that in a yellow × white cross, white color was dominant over yellow and controlled by a single dominant gene. They reported that three dominant genes were responsible for absence of pigmentation in white × orange crosses. Light orange color is dominant over orange [68]. Kust [72] postulated three dominant alleles *Y*, Y_1 and Y_2 which prevented formation of orange color in root xylem tissue. Buishand and Gabelman [14] characterized effects of series of *Y* alleles on carotenoid content in phloem and xylem. The *Y* and Y_2 allele governed white pigmentation of roots which was dominant to orange (yy).

Laferriere and Gabelman [12] hypothesized that a single major gene governed white color of roots of yellow × white crosses and three major genes determined white and orange colors. Further, research studies showed that two major genes were responsible for white and orange colors in yellow ×white cross whereas 4 major genes were involving in an orange × yellow cross for the yellow and orange colors. Imam and Gabelman [69] reported that lemon (light yellow) was dominant over light orange in a lemon × light orange cross whereas light orange was dominant over orange in a light orange × orange cross.

Symbol	Type of marker	References
A	α-carotene synthesis ('Kintoki')	Umiel and Gabelman [13]
L	Lycopene synthesis ('Kintoki')	Umiel and Gabelman [13]
P-l	Purple root (PI 173687)	Simon [45]
P-2	Purple node (PI 175719)	Simon [45]
(P-3), (P-4)	Purple root	Laferriere and Gabelman [12]
Y-l	Xylem/phloem Carotene	Kust [72]
Y-2	Xylem/phloem Carotene	Kust [72]
rp	Reduced carotenoid pigmentation (W266 Wisconsin inbred)	Goldman and Breitbach [110]
Io	Intense orange xylem	Kust [72]
O	Orange xylem	Kust [72]
rs	Reducing sugar in root	Freeman and Simon [113]

Table 1: *Genetics for nutritional traits in carrot.*

Kust [72] described the dominant alleles of the genes *Y*, Y_1 and Y_2 control orange color in the xylem which was epistatic to the pigment enhancing genes *IO* and *O*. The orange color of phloem was governed by the pigment enhancing genes *IO* and *O* in equal, or higher, number without dominant alleles (*Y*-) and combinations of these color enhancing genes with the dominant alleles *Y*, Y_1 and Y_2; he suggested that the genetic constitution of white was recessive (*y1y1y2y2ioiooo*).

β-carotene and anthocyanins imparts orange/yellow and purple color to carrot, respectively. Genetic control of carotene synthesis is complex including several enhancer and inhibitor genes. Kust [72] postulated the dominant (Y_2) locus control can lead to carotene accumulation in carrot xylem core; the recessive (y_2/y_2) locus conditioned the β- and γ-carotene rich orange xylem core. The dominant heterozygous (Y_2-) locus determining the xanthophyll-rich yellow and white color in core (xylem) region of temperate carrot [14]. The Y, *y* and Y_2 loci had more influence on amount and distribution of α- and β-carotene in which *Y* locus blocks synthesis of α- and β-carotene as well as xanthophylls; *y*, and Y_2 block synthesis of carotenes but not xanthophylls [14].

Umiel and Gabelman [13] studied F_2 populations of orange × red crosses and determined that inheritance of orange color was governed by a single dominant gene which is epistatic to the red color gene. They proposed, based on biochemical analyses, that '*A*' gene for accumulation of α-carotene originated from the orange parent and '*L*' gene for lycopene formation originated from the red parent. Rhodes [109] observed in F_2 populations of a red × light yellow cross the segregation ratio was 15:1 of yellow-orange to red color. He suggested that two dominant genes condition conversion of lycopene to α- and β-carotene.

The white, or un-pigmented, roots were conditioned by the recessive gene (rp) which controls β-carotene synthesis. The mutant gene '*rp*' causes a 93% reduction of total carotenoids [110]. Koch and Goldman [111] postulated that the '*rp*' mutant produces more α-tocopherol which is provitamin-E. Because this provitamin-E highly available in animal sources than plants. So this '*rp*' mutant plant produces high vitamin-E along with β-carotene content.

The dominant gene of P_1 confers purple color to roots which is only partially responsible for variation in roots and is hypostatic to the P_2 gene influencing pigmentation in aerial parts of petioles, leaves and floral corolla [108]. Anthocyanin accumulation in carrot phloem is controlled by the P_1 locus, with purple (P_1) dominant to non-purple (p_1). The P_1 and Y_2 loci are unlinked in F_2 and BC populations to Eastern carrot germplasm [108]. The purple petiole of 'Tender Sweet' was conditioned by a single dominant gene '*G*', dominant to green '*g*' [112]. Purple color of roots was governed by two complimentary loci in F1 progeny of two non-purple inbreds [12].

The sugar content of carrot is governed by a single dominant gene (*Rs*). These genes express more reducing sugars of glucose and fructose in *Rs*/- plants in contrast to *rs/rs* plants which produce more sucrose [113]. Broad sense heritability estimates have been determined for total dissolved solids (40 - 45%) [114]. The *rs/rs* mutant plants have carrot invertase enzyme which block the function enzyme [115]. This play an important role to understand reducing sugar phenotype plant, thus, helps to bred total soluble solids rich carrot cultivars.

Molecular markers

Molecular marker tools are essential for genetic analyses and manipulation of horticultural traits and have been used to improve traits by fingerprinting of elite genetic stock, genetic diversity analyses, and selection for difficult traits with neutral environment. Use of molecular marker technology, and their greatest potential application, appears to accelerate the rating of selection for suitable genetic phenotypes and mapping for simply inherited traits, as well as quantitatively inherited complex traits which perfectly place interacting genes that govern complex traits. Genetic mapping is the first step in manipulation of targeted genes. Potential and effective marker assisted introgression and/or selection would be helpful for identifying better recombinants over traditional breeding. Morphological, biochemical, and molecular marker systems are used across families, and it would be helpful to have more genetic information applicable in high through-put technology, and comparative and structural genome biology. Functional molecular markers have identified new vistas in genomics assisted crop improvement.

A powerful DNA marker is easy to detect, highly polymorphic, and distributed across the genome at random. There exist the DNA markers Restriction Fragment Length Polymorphism (RFLP), Random Amplified Polymorphic DNA (RAPD), Amplified Fragment Length Polymorphism (AFLP), Cleaved Amplified Polymorphic Sequences (CAPS), Sequence Tagged Sites (STS), Simple Sequence Repeats (SSRs), Expressed Sequence Tags (ESTs), Diversity Arrays Technology (DArT), and Single Nucleotide Polymorphism (SNPs). The earliest DNA marker system, the RFLP proved to be useful, but its development and utilization is laborious, time-consuming, expensive and not suitable for high throughput automation. For these reasons, PCR-based markers such as RAPD, AFLP, ISSRs, SSRs, CAPs, SNPs and their derivatives have become popular for molecular genetic studies [21]. Of the PCR based markers, SSR markers quickly became the one chosen for plant and animal genomes because of the small sample size (genomic DNA) requirement for analysis and their suitability for automation and high-throughput [116,117].

Molecular markers and their importance

The high amount of DNA diversity in plants is identical in their DNA sequences. The DNA sequence variation between 2 organisms have been detected in restricted genomic DNA of plants and RFLP paved the way for development of various molecular markers [118]. Advanced molecular marker systems changed genetic analyses and led to construction of whole genome linkage maps in plants [119]. These maps were applied in downstream applications such as gene cloning, genome analyses and marker assisted selections in crops [119,120]. With potential use of molecular marker systems, it is possible to transfer targeted genes and introduce novel genes from related species into cultivated varieties with desirable traits in a short period of time [121]. Molecular markers detect unambiguous, single-site genetic differences that can easily be scored and mapped in most segregating populations. It is not difficult in populations of most crop species to identify and map 10 - 50 segregating molecular markers per chromosome pair [122]. These molecular markers can accelerate the breeding via improvement of new varieties and backcross gene transfer assisted with marker and pyramiding of desirable alleles in a directed manner that would not be practical with conventional phenotypic selection procedures. Polygenic complex traits are readily established relationships between crop species that were difficult to analyse in conventional plant breeding [121]. The ability to map genes contributing to variation in complex traits with enough accuracy to be useful for plant breeding applications is possible through development of comprehensive molecular marker-based genetic linkage maps [30].

Application of molecular markers in carrot improvement

Carrot has a good deal of genetic diversity because it originated in different parts of the world. The genetic germplasm of carrot has been studied and classified based on morphologic and phenotypic difference. The high level of phenotypic plant to plant variation has been detected with genetic molecular markers within wild relatives, putative ancestors, cultivated genotypes and open pollinated cultivars. Genetic and molecular markers have been studied in derived populations in self-pollination of heterozygous carrot [39,41]. Genetic, and gene dispersal, studies have used crosses of wild carrot, cultivated carrot, land races, and open populated cultivars and shown the evaluation of genetic diversity and distinguished parent partners [123,124]. Molecular marker studies examined the relationship of carrot diversity. These molecular studies resulted in various taxonomic relations between geographical groups and carrot germplasm which will provide a holistic view of application of molecular marker systems by examining random molecular markers such as isozymes [125,126]; random amplified polymorphic DNA (RAPD) [127-132]; amplified-fragment length polymorphism (AFLP) [131,133,134]; amplication of

microsatellite polymorphic loci (SAMPL) [44-45], inter-simple sequence repeat (ISSR) [133,135], single nucleotide polymorphism (SNP) [34,51], universal rice polymorphic (URPs) [135] and simple sequence repeats (SSRs) [33] (Table 2). This broad section will great scope of importance and various utilization of molecular markers. These developed carrot markers can be successfully utilized for nutritional rich carrot varieties. Thus, will help to find suitable marker for nutritional traits.

Genome Investigated	Type of marker	References
mt, cp	RFLP	De Bonte., *et al.* [168]
Nuclear, *cp*	Isozyme	Matthews and Widholm [169]
Mt	Restriction fragment patterns	Ichikawa., *et al.* [136,137]
Nuclear	Isozyme	St. Pierre., *et al.* [125,126]
Mt	RFLP	Ronfort., *et al.* [170]
Mt	RFLP	Bowes and Wolyn [142]
Nuclear, *mt*	RAPD, AFLP	Nakajima., *et al.* [131]
mt, cp	RFLP	Vivek and Simon [44]
Nuclear	AFLP	Shim and Jørgensen [134]
Nuclear, *mt*	AFLP, ISSR	Bradeen., *et al.* [133]
Nuclear	URP, RAPD, ISSR	Jhang., *et al*. [135]

Table 2: *Used molecular markers in Daucus genetic diversity.*

Molecular evaluation of fertile, petaloid and brown anther cytoplasm were analyzed using mitochondrial fragments, and protein products, which exhibited different patterns and yield *atpA* specific gene [136-140]. Use of inter- and sub-specific crosses produced new cytoplasmic male sterility (CMS) systems [141]. The marker system great helps to understand the nutritional linkage with cytoplasmic male sterile lines of carrot.

The AFLP marker of P3B30XA is loosely linked to the *Rs* gene [44-45]. The 8 linkage groups, with an average distance of 13.1 cm, were constructed using 10 isozyme loci, 14 RFLPs, 28 RAPD markers and 6 isolated RFLP probes isolated from PCR fragments [41]. These molecular marker can be successfully utilized for screening of total soluble solids in various carrot genetic resources.

The 109 point molecular linkage map for phenotypic loci (P_1, Y_2 and *Rs*) of carrot (*D. carota* L. ssp. *sativus*) were constructed using 6 RFLPs, two RAPDs, 96 AFLPs and 2 selective SAMPL marker with polymorphism of 36, 20 and 42%, respectively. The total length of the saturated map was 534.4 cm with space of 4.9 cm. The marker size of AFLP P6B15 was 1.7 cm from P1, AFLP-P1B34 was 2.2cM from Y2, and AFLP-P3B30XA was 8.1 cm from *Rs* [44,45]. The molecular map was constructed using phenotypic loci, isozymes, RFLPs and RAPDs and 4 selfed (S1) carrot plants resulting in 5 - 8 linkage groups with 1926 markers in each map [41]. These markers can be utilized for black, yellow and reducing sugar phenotypic carrot. Thus, will helps to further dissection of nutritional characters viz., anthocyanin, lutein and total soluble sugars.

Bowes and Wolyn [142] reported that three male fertile carrot lines and 6 petaloid male sterile carrot lines originated from geographical locations exhibited clear restriction patterns of mitochondrial genomes. The phenotype (*phen1/phen1*) of annual flowering carrot were mapped using morphological markers along with RAPD, RFLP and isozyme markers. The genetic constitution of *phen1/phen1* was characterized and described as small, dark green, curled leaves, regular annual flowering without vernalization and roots appeared to be normal [41]. The phenotypic marker could great help to find differentiation of morphological and phonological characterization of carrot.

Nakajima., *et al.* [131] characterized 5 species of carrot which includes 7 carrot (*D. carota* ssp. sativus) cultivars/inbred lines, 6 wild species differentiated by both R used RAPD and AFLP. Vivek and Simon [45] identified 8 cultivated and 8 wild species relations were under 4 sections different from the conventional classified 5 sections by Sáenz Laín [143]. Nakajima., *et al.* [131] demonstrated, using AFLP markers, that 2 Japanese derived carrot cultivars were more closely related with wild carrot than European derived carrot. Bradeen., *et al.* [133] postulated that 4 wild carrot species were classified under 1 cluster of carrot species using of AFLP and ISSR markers. The 6 domi-

nant RAPD markers were identified to distinguish male-fertile and cytoplasmic sterile lines of carrot and these markers has been cloned and the end sequence characterized [130]. This interspecific hybridization and molecular markers would help to isolation of targeted nutritional genes from purple, orange, yellow and red carrot.

Vivek and Simon [44] mapped the reducing sugar phenotype (*Rs*), marker size 8.1 cm to 1 end of the linkage group C which is away from an AFLP marker but was genetically unlinked to Y_2 and P_1 [108]. The successful transfer of *Rs* gene through marker assisted selection has occurred [144]. The gene for resistance to root knot nematode was closely linked to a RAPD marker with a size of 6.5 cm [40]. The RFLP and RAPD marker can be successfully utilized for characterization of different colour of carrot. Moreover it will help to understand the reducing sugar, yellow and purple phenotypic linkage group thus led to dissect the nutritional traits of carrot.

AFLP polymorphic markers were successfully used for varietal purification and identification of geographic origin of wild carrot populations [134]. Grzebelus., *et al.* [127] identified genetic heterogeneity within and between carrot inbred lines by using 8 AFLP markers. These markers were successfully used to test purity of 8 F1 hybrids generated from 4 inbred lines including male sterile lines and maintainer lines of carrot. This AFLP marker could help to purify the varietal distinction, true hybridity test and screening and discarding of varietal duplication in carrot.

Robison and Wolyn [145] mapped more than 20 genes, and pseudogenes, on the CMS carrot mitochondrial genome using carrot mitochondrial gene fragments derived from other plant species. The identified distance was 255 kb size and the genes *cox1*, *cox2*, and *atp8* were reversibly located on subgenomic circular DNA molecules associated with repeated mitochondrial genome regions. Two contrasting unrelated carrot F_2 populations, having the same identity and size, were mapped using the same linkage group using AFLP markers [124]. This contrasting mapping population's programme will give great idea to generation of recombinant inbred lines and backcross inbred lines in carrot. Furthermore, it will give conceptualization of isolating the nutritional important genes.

Carrot genetic diversity analysis was accomplished using AFLP, ISSR and 2 SCAR markers closely linked to root color (Y_2), nematode resistance (*Mj-1*) and a chloroplast-specific conditioning genes in 124 carrot accessions [133]. There were differences between wild and cultivated accessions at a high molecular level and non-structured. Bach., *et al*. [146] studied variation between male fertile and sterile cytoplasm using RFLP markers in which 17 markers described a diverse mitochondrial genome and its applicability in carrot germplasm. They identified tightly linked RFLP markers associated with 6 conserved genes in the male fertile (K831B) and the petaloid male sterile line (K826A). Cytoplasmic male sterility markers were closely associated with MADS box genes which is homologous to GLOBOSA and DEFICIENCS [147]. Two molecular maps were constructed by Westphal and Wricke [38] and Vivek and Simon [44] for disease controlling locus. A resistance locus to the nematode *M. hapla* was identified using 200 marker isozymes, RFLP, RAPD, AFLP, RAMP and microsatellite markers derived from *D. carota* subsp. *azoricus* [148]. These various molecular markers can be utilized for temperate and tropical carrot genetic resources. It will help to find the close linkage of nutritional genes, thus led to nutra-rich carrot genotypes.

Jhang., *et al.* [135] studied genetic variability in 40 indigenous lines of subtropical carrot using 16 ISSRs, 10 URPs, 16 RAPD and 6 SSRs. The 48 markers were amplified to a size of 200 - 3500 bp in ISSR, RAPD and URPs and 100 - 300 bp in SSR markers. They demonstrated that ISSR and URPs can be successfully used in genetic diversity analysis of tropical carrots.

Developing a mapping population

The most important steps for construction of linkage maps with molecular markers are those made in developing mapping populations. The most important criteria for successful mapping are selection of parents for crossing, the size of the mapping population, how crosses are advanced, and which generations is used for molecular marker and phenotypic analyses [26]. Santos and Simon [50,123,124] described procedures used for development and multiplication of carrot mapping populations, parent of mapping populations used, and targeted traits for which they might be used for mapping. Linkage maps of crop species are often constructed with segregating populations, i.e. F_2 populations or backcrosses.

DNA polymorphisms among parents

Higher detectable DNA sequence polymorphism between parents is sufficient for genetic mapping [149]. In many allogamous species any cross that does not involve related individuals will provide sufficient polymorphism for mapping. Natural inbreeding crop species have low levels of sequence variation and it is a challengeable to find DNA polymorphism [23]. The requirement for sufficient DNA sequence polymorphism may preclude use of DNA markers in some narrow-based crosses [26]. Electrophoresis systems capable of separating DNA molecules with only a single base pair change [150] provide better methods for uncovering polymorphisms within narrow-based crosses, probes based on minisatellites [151], or simple repeated tetra-nucleotide motifs [152], can uncover polymorphisms between closely related individuals. Because these are so variable at the DNA sequence level, these sequences are likely to eventually provide markers useful for mapping in narrow-base crosses [153-155].

Choice of segregating population

Selection of suitable parents to generate genetic populations is an important step in the construction of a linkage map. The type of genetic populations differ. The simplest are F_2 populations derived from a true F_1 hybrid, and their backcross populations. For most plant species, these types of populations are easy to construct, although sterility in the F_1 hybrid can limit some combinations of parents, particularly in wide crosses. The major drawback to F_2 and backcross populations is they are ephemeral that is for seed derived from selfing the resulting individuals will not breed true. Westphal and Wricke [39] described advanced generation progeny-based phenotyping of S_1 genotyped individuals. Schulz., *et al.* [41] and Westphal and Wricke [39] described methods for developing and maintaining a carrot mapping population based on S1 plants derived by selfing; a single F_1 plant that will provide an "immortal" mapping population available for several seasons. Similar types of inbred lines utilized for generating F_2 populations, can be used for linkage mapping with many of the same advantage of S_1s [45,50]. Use of inbred populations, comprised of recombinant inbred lines (RILs), derived from individual F_2 plants are excellent to provide more permanent mapping resources [156].

Computer software for genetic linkage mapping

MAPMAKEREXP is linkage analysis software for constructing primary linkage maps of markers segregating in experimental crosses. It performs full multipoint linkage analysis for dominant, recessive, and co-dominant markers in backcrosses, F_2 and F_3 (self) intercrosses and recombinant inbred lines [157-159].

Linkage mapping in carrot

A primary genetic map, consisting of easily scored polymorphism marker loci spaced through a genome, is an essential prerequisite to genetic studies in any organism. Saturated linkage maps are essential for genetic studies using quantitative trait mapping, marker-assisted selection, and positional gene cloning. It has been possible to construct linkage maps only in intensively studied organisms, such as bacteria, yeast or fruit flies, in which many visible mutations were available as genetic markers. This limitation has been overcome with development of many molecular marker techniques allowing visualization of existing polymorphism at the DNA level. Linkage mapping put marker loci (and QTLs) in order, indicating relative distances between them, and assigning them to linkage groups on the basis of recombination values from all pair-wise and 3-point combinations. The first linkage map of the human genome based on molecular markers [160] fuelled development of molecular marker-based genome maps in other organisms.

High saturated genetic linkage maps of carrot were developed by precise application of genetic markers [39-49,51,123,124,133]. These maps include isozymes, RFLPs, RAPD, microsatellites, SNPs, ISSRs, SAMPLs and morphological markers. Most of the maps have no markers in common and cannot be compared. Six linkage groups were developed using 2 populations of 'B493 × QAL' and 'Brasilia × HCM BA' with 2 codominant markers and 28 sequenced dominant AFLP [50]. This markers would be used in high carotenoids carrot lines. Development of PCR are limited due its small number based markers in carrot which are useful in comparing distantly related populations [39-41].

The first molecular linkage map of carrot was constructed using isozyme markers in backcross populations generated from self-pollinated (S1) carrot lines [39]. Westphal and Wricke [39] postulated that RFLP and RAPD markers could be more effective for construction

of linkage maps in carrot. Schulz., *et al*. [41] completed the linkage map using 4 S1 populations derived from three carrot cultivars viz., Finae, Primatoe, and Gustoe which had 10 isozyme, 14 RFLP, and 28 RAPD markers in 70 individuals and resulted in 8 linkage group with a distance of 13.1 cm. Westphal and Wricke [38] expanded the linkage map with 200 markers of AFLP, microsatellites, isozyme, RFLP and RAPD using the same mapping populations. RAPD and AFLP marker system were used to determine genetic diversity of *D. carota* and indicated that cultivated carrot were discriminated from wild *D. carota* [131].

A 109-point linkage map was constructed for phenotypic loci (P_1, Y_2, and *Rs*) of carrot using 6 RFLP, 2 RAPDs, 96 AFLPs, and 2 SAMPL providing 36, 20 and 42% of polymorphism for RFLP probes, RAPD primers, and AFLP primers, respectively. The phenotypic character of purple pigmentation (P_1), white colored roots (Y_2) and reducing sugar (*Rs*) were closely linked to AFLP markers P6B15, P1B34 and P3B30XA at distances of 1.7 cm, 2.2cM and 8.1cM, respectively [45]. This markers strategy can be utilized for screening four different contrasting carrot phenotypes,

Bradeen and Simon [43] constructed 6.6 cm size of 6 AFLP marker which were tightly linked to the Y2 locus. The markers were cloned and sequenced and were 264 bp in size. The sequence of a 2 kb fragment were developed using sequenced AFLP markers and an Y_2Y_2 allele parent to characterize the y_1y_1 parent as a template for inverse PCR. These resulted in a 310 bp size of codominant marker for Y_2 allele (172 bp size of Y_2 maker +138 bp indel) which could be utilized for identification of the **y2** allele parent.

The F_2 mapping population of 'B9304 × YC7262' were utilized with size of 103 plants for construction of a linkage map using of 106 markers which included 96 AFLPs, 6 RFLPs, 2 RAPDs and 2 microsatellite derived markers. The resulting 11 linkage groups were composed of 5 to 15 markers of 524.1 cm in length with an average distance of 4.9 cm. The estimate of carrot genome size was 900 cm from this map [44]. This linkage group would be great help to understand the linkage group with targeted traits. Thus similar approach can be successfully utilized for development of mapping population as well as mapping for targeted nutritional traits.

Reducing sugar (*Rs*) type were mapped into C group linkage with an AFLP marker of the size 8.1 cm. The *Rs* gene was distantly unlinked with Y_2 and P_1 [44,108]. This linkage group can be useful and applicable for the traits of total soluble solids as well as purple phenotype.

Santos and Simon [123] demonstrated that 84% of AFLP markers of a common size generated from the same F2 mapping populations shared greater than 91% of the DNA sequence identity. For map merging, 28 AFLP markers and 2 PCR markers, common to both mapping populations, were used to construct a mapping framework upon which additional, population-specific markers were placed.

A linkage map was constructed using F_2 mapping populations of 'B493 × QAL' and 'Brasilia × HCM' with an AFLP marker in the combinations of the *EcoRI/MseI* and *PstI/MseI* restriction enzymes. The PCR based codominant markers were used in the 2 populations. The merged linkage group length was from 68.9 cm (20 markers) to 117.6 cm (27 markers) and average distance was 3.75 cm [50]. Just., *et al.* [51] stated that in the carotenoid biosynthetic pathway, 22 carotenoid genes were identified in 8 of 9 linkage groups in the carrot genetic linkage from populations of orange × white carrot. They isolated 24 putative genes and 2 co-localized QTL for carotenoid accumulation utilizing available sequence information of carrot and other plant species.

The genetic linkage map was constructed using an F_2 mapping population of wild carrot QAL (*D. carota* subsp. *carota*) and B493 (D. carota subsp. *sativus*). These detailed genetic maps were assigned to 250AFLP markers and supplemented with gene-specific size, SNP, DcMaster and Krak transposon insertion sites. The saturated genetic map is currently comprises of 381 markers with a genome size of QAL and B493 which were 1,242.0 cm and 1,474.7 cm, respectively [51,123,124,127].

A total 440 of GSSRs, ESSR and BSSRs were developed for carrot genomic distribution, linkage mapping, genetic diversity analysis and marker transferability across the Apiaceae. Using these markers, 9 linkage groups were constructed distributed by wide SSR [33,52]. This markers would play a vital role and substitute for future carrot molecular breeding compared with other markers.

QTL mapping studies in carrot

Development of molecular marker technologies and use of markers in detecting and mapping quantitative trait loci is a powerful approach to be used to study genetic and phenotypic bases of complex traits [21,161-163]. If individual genetic components associated with a complex trait can be identified, research can focus on the function of each locus independently without confounding effects of other segregating loci [163].

Size and Type of Mapping population	Parental Lines	Mapped Markers	Total No. of Markers	No. of Linkage Groups	Map Length (cM)	References
S_1	Various	Isozyme (12)	12	4	114.0	Westphal and Wricke [39]
≥70 S_1	4 Populations	RFLP (14)	58	5-8	151.3 - 283.5	Schulz., *et al.* [41]
	(a) cv. Finaê ⊗	RAPD (12)				
	(b) cv. Primatoê ⊗	Isozyme (10)				
	(c) cv. Gustoê ⊗	RAPD Probes (6)				
	(d) cv. Gustoê ⊗	Morphological (1)				
≥70 S_1	4 Populations	RFLP (unspecified)	~200	9	Unspecified	Westphal and Wricke [38]
	(a) cv. Finaê ⊗	RAPD (unspecified)				
	(b) cv. Primatoê ⊗	Isozyme (unspecified)				
	(c) cv. Gustoê ⊗	AFLP (unspecified)				
	(d) cv. Gustoê ⊗	Microsatellite (unspecified)				
		Morphological (1)				
103 F_2	B9304 × YC7262	AFLP (96)	109	11	534.4	Vivek and Simon [44]
		RFLP (6)				
		Morphological (3)				
		RAPD (2)				
		Microsatellite (2)				
F_2	**2 Populations:**					Santos and Simon [123]
183 F_2	(a) B493 × QAL	AFLP (250)	250	9	1114.0	
160 F_2	(b) Brasilia × HCM	AFLP (287)	287	9	1188.0	
Merged	Pops (a) + (b)		138	6 (+3 un-merged)	517.6	
F_2	QAL and 493	SSR	300	9	144 - 433 bp	Cavagnaro., *et al.* [33]
		156 GSSRs				
		144 BSSRs				
72 F_2	B7262 × B493					

Table 3: *Review of published carrot genetic linkage map.*

Bradeen and Simon [43] identified 6 AFLP markers linked to the Y2 locus with a distance of 2.8 and 15.8 cm from 103 F_2 populations of a cross of 'B9304 × YC7262' which segregated for core color using bulked segregate analysis [164]. Vivek and Simon [44] identified a single AFLP marker from the Y_2 locus and assigned it to linkage group B with a size of 2.2 cm using these populations. They identified horticulturally important QTLs through segregation analysis.

Santos and Simon [123] mapped 287 AFLP markers using 160 F2 populations of the 'Brasilia × HCM' cross of medium orange color and high carotene. The markers were associated with α- and β-carotene, lycopene, and the precursors ζ-carotene and phytoene QTL conditioning each trait measured. In total, 8, 3, 1, 4 and 5 QTLs were detected for α-carotene, β-carotene, lycopene and the precursors ζ-carotene and phytoene which accounted for 40, 20, 7.2, 16.3 and 28%, respectively, of total phenotypic variation; QTLs of 'Brasilia' and 'HCM' exhib-

ited 3.7 to 13.2% total variation. Twenty major QTLs have been identified for orange carrots and which control carotenoid content [123]. Buishand and Gabelman [14] reported that for these QTLs, the major genes (*Y* and *Y2*), and clusters of genes, were involved in a common carotenoid biosynthetic pathway from a population of orange (yyy_2y_2) and white carrots ($YYY2Y_2$) with yellow and pale orange color.

Santos and Simon [123] identified SNP based markers were closely linked to the Y_2 gene; Bradeen and Simon [43] also developed maps to this region. They considered ZDS2 and ZEP as candidate genes for Y_2 QTL. Phenotype yellow (xanthophyll) and orange (α- and β-carotene) were conditioned by Y_2 [14]. The Y_2 gene was derived from yellow segregants of the 'B493 × QAL' population. Since it maps to this important region Y_2 may be responsible for at least some QTL effects observed by Santos and Simon [50]. Santos and Simon [123] identified quantitative trait loci (QTLs) for total carotenoids affecting concentrations of carotenoids in the range 15.8, 21.7, 26.4, 37.7, and 44.2% of the total phenotypic variance for lycopene, α-carotene, β-carotene, ζ-carotene and phytoene, respectively. Just., et al. [51,165] reported that 22 genes involved in carotenoid biosynthesis and metabolism, provided gene-specific codominant polymorphisms for 8 of 9 linkage groups. These identified carotenoids QTL's can be useful for development of carotenoids rich cultivars through marker assisted selection.

One major QTL has been identified for β-carotene, total carotene and lycopene accumulation in the F2 population of P50006 and HCM A.C. using sequence related amplified polymorphism (SRAP) markers which explain 12.79, 12.87, and 14.61% of total phenotypic variation. The SRAP marker was tightly linked in 9 linkage groups of 502.9 cm in size with a mean interval of 5.5 cm. The genetic variability of these 3 QTLs was due to additive genetic variance. A pair of epistasis QTL for β-carotene and lycopene accumulation explained 15.1 and 6.5% of total phenotypic variation, respectively. The SRAP markers linked to these QTLs could be used in selection or QTL pyramiding for high carotenoids and lycopene content in carrot breeding [53]. Ellison., *et al.* [55] developed two closely linked codominant markers, 4135 *Apol1* and 4144 *ApeKI*, to more accurately select y_2y_2 plants with increased β-carotene accumulation. These markers have been tested not only within the mapping population, but also in a group of unrelated genetic materials, and have proven to be very accurate in predicting orange and no orange phenotypes [166,167]. Further they identified that the single large effect QTL on the distal arm of chromosome 7 overlapped with the previously identified β-carotene accumulation QTL, Y_2. Fine mapping efforts reduced the genomic region of interest to 650 kb including 72 genes.

Conclusion

Research based on genetic information in the review will provides knowledge on various aspects of carrot morphology and physiology. Further work will provide information about carrot color as sources of natural food color, genetics of carrot color, development of mapping populations, application of various markers, linkage and QTL mapping analysis in carrot. This information will help to understand genetics and molecular breeding of carrot which will lead could lead to development of multi-colored multivitamin nutritional carrot hybrids/varieties.

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