Carrot Domestication

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Abstract

The domestication syndrome of carrot (*Daucus carota* subsp. *sativus*) includes increased carotenoid, anthocyanin, and sugar content, loss of lateral root branching, biennial growth habit, and increased size and variation of root shape. Recent advances in high-throughput sequencing and computational techniques have facilitated new ways to study the genetic and genomic changes that accompany plant domestication. While most genetic studies now support a central Asian center of domestication for carrot much remains unknown regarding the genetic mechanisms that contribute to phenotypic changes associated with domestication. Most research to study the genetics of plant domestication uses a top-down approach, which begins with a phenotype of interest and then identifies causative genomic regions via genetic analyses such as quantitative trait locus (QTL) and linkage disequilibrium (LD) mapping. An alternative approach is to start by identifying genes or genomic regions with signatures of selection and then make use of genetic tools to identify the phenotypes to which these genes contribute, also referred to as a bottom-up approach. In this chapter, we present a thorough review of genetic and genomic studies that have used both top-down and bottom-up approaches to study the domestication syndrome of carrot.

5.1 Domestication Introduction and Overview

Darwin (1868) was first to describe how human selection altered plants to meet human food, fiber, shelter, medicinal, and aesthetic needs (Gepts 2004). The process of domestication follows a similar path in most species where the plant is first cultivated and then conscious and unconscious selection occurs to modify plant characteristics to meet human needs, typically resulting in a plant that has lost its ability to survive without human intervention (Harlan 1992). Early studies of where plant domestication first occurred were dominated by the centers of origin concept. This hypothesis, initially proposed by Candolle (1884) and later refined by Vavilov (1926), posits that domestication occurred in a few discrete geographies or "centers". Recent genomic and archeological data suggest that the concept of discrete centers of origin or diversity may oversimplify the actual histories of cultivated species. In many cases,

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Fig. 5.1 Domestication syndrome in carrot during primary domestication, secondary domestication, and carrot improvement. White arrows (left to right) align with phenotypic shifts between wild and primary domesticates and secondary domesticates and secondary domesticates and improved varieties. Domestication syndrome traits associated with each stage are listed below the white arrows

the evolution of crop plants has been a more complex and continuous process (Harlan 1971; Meyer and Purugganan 2013). Although limited in universality, these concepts remain useful frameworks for finding and preserving valuable variation for plant breeding and determining the extent of genotypic and phenotypic evolution in crops (Ross-Ibarra et al. 2007).

The domestication syndrome is a set of phenotypic characteristics that are common across crop plants and include grain retention by loss of shattering (rice, barley, wheat, and soybean), reduction of lateral branching (maize and sunflower), increase in organ size (tomato, potato, and bean), and flowering-time modification (small grains, sunflower, maize, and soybean) (Harlan 1971; Meyer and Purugganan 2013; Zohary and Hopf 2000). After primary traits have been selected and fixed, the process of domestication often has directed more attention to quality traits such as color, shape, and flavor, and physiological traits contributing to uniformity (Doebley et al. 2006). The domestication syndrome of carrot (*Daucus carota* subsp. *sativus*) includes increased carotenoid, anthocyanin, sugar content, loss of lateral root branching, biennial growth habit, and increased size and variation of root shape (Fig. 5.1). After domestication, carrot improvement traits have included better flavor, nutrition, uniformity, (a)biotic stress tolerance, and male sterility for hybrid cultivar development (Fig. 5.1).

5.2 Wild Carrot Distribution

Wild carrot (*D. carota* subsp. *carota*), also known as Queen Anne's lace, is native to temperate regions of Europe and Western Asia, and has been introduced into America, New Zealand, Australia, and Japan (Bradeen et al. 2002; Iorizzo et al. 2013; Rong et al. 2010). It is speculated that the seed was the first part of the carrot plant used by humans, as observed by the presence of carrot seed at prehistoric human habitations in Switzerland and Southern Germany,

4000–5000 years ago (Neuweiler 1931). Wild carrot seed was likely used medicinally or as a spice (Andrews 1949; D. Brothwell and P. Brothwell 1969). The Romans used carrot seed as an aphrodisiac and to render the body safe from poison (Stolarczyk and Janick 2011). In fact, Roman-made pills containing carrot seed were recovered from a shipwreck that occurred approximately 130 BCE (Fleischer et al. 2010).

5.3 Carrot Domestication and Dispersal

The first evidence of carrot used as a storage root crop is in the Iranian Plateau (Afghanistan, Pakistan, and Iran) and the Persian Empire (modern day Turkey) in the tenth century AD (D. Brothwell and P. Brothwell 1969; Laufer 1919). The Iranian Plateau was described as the primary center of greatest carrot diversity (Heywood 1983; Mackevic 1929; Vavilov 1951) with Turkey being proposed as a secondary center of diversity (Banga 1963a, b; Clement-Mullet 1866; Vavilov 1951). Several recent studies support a Central Asian center of domestication by showing that domesticated carrots from Central Asia are more genetically similar to wild samples from the same region, as compared to wild samples from Turkey (Arbizu et al. 2016; Ellison et al. 2018; Iorizzo et al. 2013; Rong et al. 2014). Wild carrot roots lack carotenoid and anthocyanin pigments and are therefore white. The first descriptions of domesticated carrot roots included purple and yellow types and therefore these traits were likely some of the first human selections in carrot. Purple and yellow carrots spread west to Syria, North Africa, the Mediterranean region, and Southern Europe during the eleventh to fourteenth centuries (Fig. 5.2) (Simon 2000; Smartt and Simmonds 1976). Carrot arrived in Europe in the early middle ages after the Arab conquest and the revival of horticulture under Charlemagne. Documents from Muslim Spain and Christian Europe describe carrots as purple and yellow without any mention of orange (Banga 1957b, 1963b). Carrot spread eastward to China, India, and Japan during the thirteenth to seventeenth centuries (Banga 1957a, b, 1963a, b; Shinohara 1984) (Fig. 5.2). Purple root color was apparently popular in eastern regions, yellow more popular in the west although the red (likely purple) carrots in twelfth century Spain were described as more "juicy and tasty" than the "more coarse" yellow types (Banga 1957a; Clement-Mullet 1866). The Asiatic carrot was

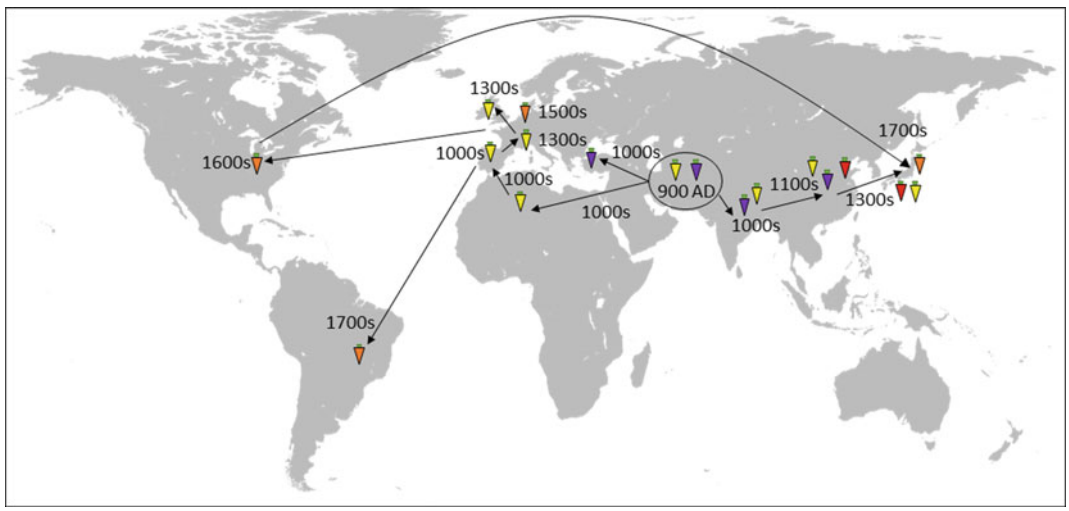

Fig. 5.2 Origin and spread of carrot throughout the world. Dates shown indicate the first known appearance of domesticated carrot within a region. Colors within the cartoon carrots indicate the most prevalent carrot pigment class found in that region at the time of first arrival

developed from the Afghan type and a true red type appeared in China and India around the 1700s (Laufer 1919).

In Europe, genetic improvement led to a wide variety of cultivars. White and orange-colored carrots were first described in Western Europe in the early 1600s (Banga 1963a, b). It is unknown why carrot breeders shifted their preference to orange types, but this preference has had a significant effect in providing a rich source of vitamin A, from α- and β-carotene, to carrot consumers ever since (Simon 2000). The modern orange carrot was stabilized by Dutch growers in the sixteenth and seventeenth centuries, supported from variety names and contemporary works of art (Banga 1957b; Stolarczyk and Janick 2011) (Fig. 5.2). Soon after orange carrots became popular, the first named carrot cultivars came to be described in terms of shape, size, color, and flavor, and the first commercially sold carrot seed became available (Banga 1957b; Simon 2000; Simon et al. 2008). Orange carrots first arrived in North America during the early seventeenth century (Rubatzky et al. 1999) (Fig. 5.2). After the eighteenth century, with the discovery of gold, there was a strong and systematic immigration from the Açores islands to the South of Brazil. Immigrants brought along many varieties of vegetables including white, yellow, purple, and red carrots from Spain, Holland, and Germany (Madeira et al. 2008) (Fig. 5.2).

Several hypotheses have been proposed to explain the origin of orange carrots: (1) Vilmorin (1859) concluded that orange carrots were selected from European wild carrots; (2) Small (1978) and Thellung (1927) discussed the possibility that orange carrot had a Mediterranean origin, resulting from a hybridization event with *D. carota* subsp. *maximus* (3) Banga (1957b) concluded that orange carrots were selected from yellow cultivated carrots; and (4) Heywood (1983) concluded that orange carrots were hybrids between European cultivated and wild carrots. A study by Iorizzo et al. (2013) demonstrated that wild carrots from Europe and samples of *D. maximus*, grouped into two separate clades that are phylogenetically distinct from all cultivated carrot, contrary to the hypotheses of Vilmorin (1859), Thellung (1927), Small (1978), and Heywood (1983). Additionally, Iorizzo et al. (2013) found orange carrots formed a sister clade with all other cultivated carrots (yellow, red, and purple) supporting the idea that orange carrot was selected from cultivated carrot. Their work provides support for Banga's hypothesis that orange root color was selected out of yellow, domesticated carrots (Banga 1957b). In fact, there now appears to be three genetic loci (*Y, Y_2, Or*) that must be fixed for the "domestication allele" to maximize carotenoid accumulation in carrot (Ellison et al. 2017, 2018; Iorizzo et al. 2016).

5.4 Historic Evidence of Carrot Domestication

The wide distribution of wild carrot, the absence of carrot remains in archeological excavations, and lack of historical documentation make it challenging to determine precisely where and when carrot domestication was initiated. A particular challenge is that of carrot and parsnip nomenclature. Carrot and parsnip have often been confused in historical references and in many cases were discussed interchangeably. In classical and medieval texts, both vegetables were commonly referred to as "pastinaca" making it difficult to know if authors were discussing carrots or parsnips. We refer the reader to Nissan (2014) for an extensive review of the etymology of the word carrot and the relationship between the word and its origins. Furthermore, there have been numerous theories regarding the first occurrence of orange carrots in works of art. Art works alone are not considered to be strong evidence for crop origins as the colors used are not always true to type and artists may use "artistic freedom" to embellish or deviate from the subject matter. We refer the reader to Stolarczyk and Janick (2011) and Vergauwen and Smet (2016) for extensive reviews of historical documentation, particularly artwork, as related to the origin of various pigmentation classes of carrot.

5.5 Genetics and Genomics of Carrot Domestication

Recent advances in high-throughput sequencing and computational techniques have facilitated new ways to study the genomic changes that accompany plant domestication. There is substantial interest in discovering the genes and genetic mechanisms that contribute to phenotypic changes associated with domestication, because their identification may facilitate trait manipulation during breeding. Most research to study the genetics of plant domestication uses a top-down approach, which begins with a phenotype of interest and then identifies causative genomic regions via genetic analyses such as quantitative trait locus (QTL) and linkage disequilibrium (LD) mapping. An alternative approach is to start by identifying genes or genomic regions with signatures of selection and then make use of genetic tools to identify the phenotypes to which these genes contribute, also referred to as a bottom-up approach (Ross-Ibarra et al. 2007).

5.6 Population Structure and Genetic Diversity

Many studies have analyzed population structure and genetic relatedness in carrot. Population structure can cause spurious correlations between the genetic background and traits of interest in association studies and therefore must be accounted for by using a mixed model approach such as proposed by Zhang et al. (2010). Furthermore, population structure and genetic relatedness can shed light on where domestication may have occurred and if gene flow is continuous between wild and domesticated populations. Finally, understanding the genetic diversity within breeding resources is important for developing carrot varieties with new beneficial alleles.

Strong population structure is commonly observed between wild and domesticated carrots (Bradeen et al. 2002; Rong et al. 2014; Shim and Jorgensen 2000) and between eastern (Central and Eastern Asia) and western (American and European) geographies (Baranski et al. 2012; Clotault et al. 2010; Ellison et al. 2018; Grzebelus et al. 2014; Iorizzo et al. 2013, 2016; Maksylewicz and Baranski 2013; Soufflet-Freslon et al. 2013). However, there is evidence of continuous gene flow where populations overlap geographically, such as in Europe and the USA where wild accessions are present in areas where domesticated carrot is grown. There is significant overlap in structure between wild and domesticated samples from the eastern group. This may be attributed to either recent admixture or to domesticated carrots sharing many of the same alleles as wild carrots from the region.

Further geographic substructure has been observed by Arbizu et al. (2016) including the Balkan Peninsula and the Middle East, North Africa exclusive of Morocco, and the Iberian Peninsula and Morocco with the two latter groups confirmed by Ellison et al. (2018). Interestingly, domesticated carrot germplasm in the USA, representing many market types, formed an unstructured population with only some evidence of structure within the hybrid imperator market class (Ellison et al. 2018; Luby et al. 2016). Ma et al. (2016) used 119 carrot accessions to investigate the relationship between Chinese carrots and western orange varieties. Their results indicated that western orange samples were clearly separated from Chinese carrots. They concluded that Chinese orange carrots were derived from Chinese red carrots according to the mixed distribution of red and orange accessions in the observed phylogeny, suggesting that Chinese orange carrots may have undergone a specific, independent process different from that of western orange.

Although a reduction of allelic diversity caused by a genetic bottleneck is a hallmark of domestication, cultivated carrot does not appear to have gone through a severe bottleneck. As compared to domesticated western carrot, there is slightly higher genetic diversity in wild and eastern germplasm with advanced breeding materials from the west containing the least amount of observed diversity. Barański et al. (2012) assessed 30 SSRs in a collection of 88

carrot accessions comprised of cultivars and landraces mainly from Asia, Europe, and North America and found genetic diversity of the Asian gene pool was higher than that of the western gene pool. Iorizzo et al. (2013) used 3326 SNPs to genotype 84 geographically well-distributed wild and domesticated carrots samples and observed no reduction of genetic diversity. Rong et al. (2014) used 622 SNPs to genotype 115 domesticated carrots, wild carrots, and other wild *D. carota* subspecies, and found genetic diversity was significantly reduced in western cultivars; however, a high proportion (85%) of genetic diversity found in wild carrot was retained in western cultivars. Consistent with these previous findings, Iorizzo et al. (2016) found nucleotide diversity estimates in wild carrots have a slightly higher level of genetic diversity than domesticated carrots as well as a clear reduction in genetic diversity in inbred breeding lines. Maksylewicz and Barański (2013) studied intra-population variation of 18 cultivated carrot populations of diverse origins using 27 SSRs and found accessions originating from continental Asia and Europe had more allelic variants and higher diversity than those from Japan and USA. Also, allelic richness and variability in landraces was higher than in F_1 hybrids and open-pollinated cultivars. Finally, Ellison et al. (2018) found little reduction in genetic diversity in 520 domesticated carrot compared to 154 wild carrot after analyzing over 30,000 SNPs.

5.7 Linkage Disequilibrium

Linkage disequilibrium (LD) between two loci decays gradually in proportion to the recombination rate and time as measured in numbers of generations. When mutations are under positive selection, the LD surrounding the mutations is maintained because of the hitchhiking effect which produces longer haplotypes at high frequencies within the population. Extended blocks of LD found in domesticated populations as compared to their wild counterparts can inform researchers of potential regions of the genome under selection. Additionally, LD decay rates are important for the design of powerful association studies as they inform necessary marker density and casual mutation discovery. Few studies to date have assessed LD in carrot. In 2010, Clotault et al. found carotenoid biosynthesis genes did not exhibit LD decay (mean $r^2 = 0.635$) within the 700–1000 bp analyzed. Soufflet-Freslon et al. (2013) observed the absence of LD decay across 4234 bp in the *CRTISO* sequence. Similarly large blocks of LD were found around the *Y* and *cult* candidate domestication genes (Iorizzo et al. 2016; Macko-Podgórni et al. 2017). The first estimates of genome-wide LD found very rapid decay in wild carrot and moderate decay in domesticated accessions. Furthermore, decay was uneven across the nine chromosomes and large blocks of LD were found to correlate with observed signatures of selection (Ellison et al. 2018). The observed rapid LD decay in carrot suggests genome-wide association studies (GWAS) should be very useful for identifying candidate genes as long as SNP density and coverage is comprehensive.

5.8 Top-Down Approach: QTL and LD Mapping

5.8.1 Anthocyanins

From a historical viewpoint, the appearance of purple-colored carrot coincided with that of the yellow carrot at the beginning of the domestication from white wild carrots in central Asia, 1100 years ago (Barański et al. 2016). In Southeastern Europe and Asia, purple carrot became an important crop during the early Middle Ages (Simon 2000; Stolarczyk and Janick 2011). Purple carrots accumulate abundant cyanidin-based anthocyanins in taproots. Discovery of candidate genes relating to anthocyanin production will be quite helpful when tracing the origins of carrot domestication.

Several studies have mapped purple pigmentation and anthocyanin content as well as analyzed transcriptional differences between purple and non-purple carrot taproots. Yildiz et al. (2013)

quantified the gene expression of six anthocyanin biosynthetic genes, *phenylalanine ammonia-lyase* (*PAL3*), *chalcone synthase* (*CHS1*), *flavanone 3-hydroxylase* (*F3H*), *dihydroflavonol 4-reductase* (*DFR1*), *leucoanthocyanidin dioxygenase* (*LDOX2*), and *UDP-glucose:flavonoid 3-O-glucosyltransferase* (*UFGT*), in three carrot inbreds with contrasting root color. Transcripts for five of these genes (*CHS1, DFR1, F3H, LDOX2, and PAL3*) accumulated at high levels in solid purple carrots, less in purple–orange carrot, and low or no transcript in orange carrots. In addition, they mapped the *P1* locus that conditions purple root color, to chromosome 3 near the anthocyanin biosynthetic genes, *F3H* and *FLS1*. In 2014, Cavagnaro et al. identified a total of 15 significant QTL, mapped to six chromosomes, for all anthocyanin pigments and purple epidermis pigmentation. Eight of the QTL with the largest phenotypic effects mapped to two regions of chromosome 3. Additionally, a single dominant gene conditioning anthocyanin acylation was identified and mapped. In 2016, Chen et al. cloned the *DcUSAGT1* gene from "Deep Purple" carrot taproots. *UDP-glucose: sinapic acid glucosyltransferase* (*USAGT*) helps stabilize the accumulation of anthocyanins. Expression profiles of *DcUSAGT1* showed high expression levels in the taproots of all three purple carrot cultivars tested but low expression levels in non-purple carrots. In many species, *R2R3-MYB* transcription factors form "MBW" complexes with other proteins and bind to the promoters of target genes to directly activate the transcription of structural genes in the anthocyanin pathway (Baudry et al. 2004). In 2017, Xu et al. observed that the expression pattern of *DcMYB6* was correlated with anthocyanin production. *DcMYB6* transcripts were detected at high levels in three purple carrot cultivars but at much lower levels in six non-purple carrot cultivars. Overexpression of *DcMYB6* in *Arabidopsis* led to enhanced anthocyanin accumulation in both vegetative and reproductive tissues and upregulated transcript levels of all seven tested anthocyanin-related structural genes.

5.8.2 Carotenoids

The presence and accumulation of carotenoids in carrot taproot is the hallmark of carrot domestication. Certainly, it is the most studied domestication trait and provides a clear phenotypic divide between wild and domesticated carrot. Although the historical record has several different accounts of when orange carrots first occurred, the majority of researchers and historians believe orange carrots rose in popularity in Europe hundreds of years after the first yellow and purple cultivars were observed in Central Asia. As more candidate genes relating to carotenoid accumulation are discovered, the origin of pigmentation in carrot will become elucidated.

Initial efforts to understand the phenotypic variation among white, yellow, and orange carrot storage roots identified two major loci, Y and Y_2 (Buishand and Gabelman 1979; Laferriere and Gabelman 1968). A digenic segregation pattern was observed in the F_2 when white roots were crossed to orange, with some evidence that a third gene, Y_1, was segregating. Bradeen and Simon (1998) used bulked segregant analysis and found AFLP markers flanking the Y_2 locus at a distance of 3.8 and 15.8 cM. Later, a SCAR marker for Y_2 was developed to facilitate marker-assisted selection for β-carotene (Bradeen and Simon 1998). Just et al. (2007) mapped twenty-two carotenoid biosynthetic pathway genes on a carrot genetic linkage map developed from a cross between orange-rooted and white-rooted carrot. The two major interacting loci Y and Y_2 were mapped to chromosomes 5 and 7, respectively, near carotenoid biosynthetic genes *zeaxanthin epoxidase*, *carotene hydroxylase,* and *carotenoid dioxygenase* (Cavagnaro et al. 2011; Just et al. 2009; Santos and Simon 2002). In 2016, Iorizzo et al. identified a candidate gene, *DCAR_032551*, for the *Y* locus on chromosome 5. This gene conditions carotenoid accumulation in carrot taproot and is a homolog of the Arabidopsis *PSEUDO-ETIOLATION IN LIGHT* (*PEL*) protein. *PEL* presumably acts as a

repressor of photomorphogenesis. Only carrot varieties with a loss-of-function allele of the *PEL* gene accumulate carotenoids in the root, suggesting that their high pigment contents might result from a derepressed development of carotenoid-accumulating plastids (i.e., chloroplasts in the light but chromoplasts in the dark). Ellison et al. (2017) identified a single large effect QTL on the distal arm of chromosome 7 which 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. Transcriptome analysis within this fine-mapped region identified 17 differentially expressed genes included transcription factors and genes involved in light signaling and carotenoid flux, including a member of the *Di19* gene family involved in Arabidopsis photomorphogenesis, and a homolog of the *bHLH36* transcription factor involved in maize carotenoid metabolism.

Many carrot carotenoid studies have focused on a candidate gene approach utilizing known carotenoid biosynthetic genes, with particular interest in *phytoene synthase* (*PSY*), the proposed rate limiting enzyme in the carotenoid pathway (Santos et al. 2005). Maass et al. (2009) overexpressed *crtB*, a bacterial *PSY* gene, in white carrots, to increase PSY protein amounts. This resulted in increased carotenoids deposited in crystals, similar to carotenoid amounts and sequestration mechanisms found in Arabidopsis when *AtPSY* is overexpressed in green and non-green cells. Wang et al. (2014) utilized three backcross inbred lines (BC2S4) with different colored roots derived from a cross between an orange inbred line and related wild species to investigate the role of the duplicated *DcPSY* genes in root carotenogenesis. Expression levels of *DcPSY1* and *DcPSY2* were generally positively correlated with carotenoid content during root development. There were higher quantities of *DcPSY1* transcripts in carrot leaves compared with roots suggesting that *DcPSY1* seems to be more important in carotenoid accumulation in photosynthetic tissues. Similarly, Bowman et al. (2014) found increased *phytoene synthase 1* (*PSY1*) and *phytoene synthase 2* (*PSY2*) expression in orange carrot roots compared with yellow and white carrots.

Clotault et al. (2012) analyzed partial sequence from carotenoid biosynthetic pathway genes *IPI, PDS, CRTISO, LCYB, LCYE, CHXE,* and *ZEP* in 46 individuals representing a wide diversity of cultivated carrots. An excess of intermediate frequency polymorphisms, high nucleotide diversity, and/or high differentiation (F_{ST}) was found in cultivated *CRTISO*, *LCYB1,* and *LCYE* suggesting balancing selection may have targeted genes acting centrally in the carotenoid biosynthetic pathway. Rong et al. (2014) sequenced the root transcriptomes of cultivated and wild carrots and looked for expression patterns that differed radically between them. They found elevated expression of carotenoid-binding-protein genes in cultivars which could be related to the high carotenoid accumulation in roots. In 2014, Arango et al. found overexpression of *CYP97A3* in orange carrots strongly reduced α-carotene and total root carotenoids in the root and correlated with reduced PSY protein levels while *PSY* expression was unchanged. Furthermore, they identified a deficient *CYP97A3* allele containing a frame-shift insertion in orange carrots. Association mapping analysis using a large carrot population revealed a significant association of this polymorphism with both α-carotene content and the α-/β-carotene ratio and explained a large proportion of the observed variation in carrots. Jourdan et al. (2015) developed an unstructured population of 380 samples and genotyped 109 SNPs located in 17 carotenoid biosynthesis genes to test their association with carotenoid contents and color components. Total carotenoids and β-carotene contents were significantly associated with genes *zeaxanthin epoxydase* (*ZEP*), *phytoene desaturase* (*PDS*), and *carotenoid isomerase* (*CRTISO*) while α-carotene was associated with *CRTISO* and *plastid terminal oxidase* (*PTOX*) genes. Ma et al. (2017) looked at six different carrot cultivars to simultaneously analyze carotenoid contents by high-performance liquid chromatography and quantify the expression levels of genes involved in carotenoid biosynthesis of carrot by quantitative PCR. They

found that genes involved in xanthophyll formation were expressed at high levels in yellow carrot cultivars. However, these genes were expressed at low levels in orange carrot cultivars.

Most recently, Ellison et al. (2018) used a diverse collection of domesticated varieties and wild carrot accessions to conduct an association analysis for orange pigmentation and revealed a significant genomic region that contained the *Or* gene. In other species, the *Or* gene differentiates non-colored plastids into chromoplasts, which provide the deposition sink for carotenoid accumulation (Lu et al. 2006). Analysis of sequence variation at the carrot *Or* locus revealed a non-synonymous mutation co-segregating with carotenoid content. This mutation was absent in all wild carrot samples and nearly fixed in all orange domesticated samples. The *Or* domestication allele appears to have been selected after the initial domestication of yellow carrots in the east, near the proposed center of domestication in Central Asia.

5.8.3 Flavor

Free sugars (sucrose, glucose, and fructose) are the major reserves in mature carrot roots (Alabran and Mabrouk 1973). Total sugar content is moderately heritable in carrot ($h^2 = 0.40$) and has a large effect on flavor which is highly correlated with sweetness ($R^2 = 0.95$) (Simon 2000). The type of sugar accumulated in carrot roots is conditioned by a single dominant gene, *Rs* (Freeman and Simon 1983). Carrots with the *Rs/-* genotype predominantly accumulate the reducing sugars glucose and fructose, while *rs/rs* carrots accumulate sucrose. The *Rs* allele occurs in nearly all wild carrots with only rare incidence of the *rs* allele (Freeman and Simon 1983). Yau et al. (2003, 2005) found an *rs/rs* inbred line that harbored a naturally occurring 2.5 kb insertion in the first intron of *acid soluble invertase isozyme II*. Co-dominant, PCR-based markers for *acid soluble invertase isozyme II* allowed genotyping of the *Rs* locus in 1-week-old carrot seedlings whereas mature carrot roots were needed to make this evaluation previously. More recently, Liu et al. (2018) surveyed the contents of soluble sugar and sucrose in four carrot cultivars at five different developmental stages. Three *DcSus* genes (*DcSus1*, *DcSus2*, and *DcSus3*), were identified and cloned in carrot. They found that during carrot root development, the soluble sugar content and sucrose content showed increasing trends, while *DcSus* activities had persisting declinations, which may be due to the decreasing expression levels of genes encoding sucrose synthase.

In carrots, terpenes are an important group of secondary metabolites that are important for taste and flavor but are also known to influence bitterness and harshness (Kramer et al. 2012). Indeed harsh flavor is highly correlated ($R^2 = 0.93$) with total volatile terpenoid content (Simon 2000). Keilwagen et al. (2017) used metabolite profiling to identify 31 terpenoid volatile compounds in carrot leaves and roots in a panel of 85 carrot accessions and genotyping-by-sequencing (GBS) was used to provide dense genome-wide marker coverage (>168,000 SNPs). A total of 30 QTL were identified for 15 terpenoid volatiles. Most QTL were detected for the monoterpene compounds ocimene, sabinene, β-pinene, borneol, and bornyl acetate. In total, 27 genomic regions across the nine carrot chromosomes associated with distinct mono- and sesquiterpene substances and terpene synthase candidate genes.

5.8.4 Flowering

Wild carrot is mostly biennial, but both annual and short-lived perennial forms often occur. As a biennial species, carrot plants develop leaves and storage roots during the first year of growth, and flowering is induced after a long vernalization period. In some cases, wild carrot and landraces adapted to warmer climates require less vernalization and can be classified as early flowering or annuals (Alessandro and Galmarini 2007). Eastern carrots have a greater tendency toward early flowering than western carrots, likely due to the somewhat warmer climates over the eastern production range. Once flowering occurs, the

xylem quickly becomes lignified before the floral stalk elongates and the taproot becomes woody and inedible. During carrot domestication and improvement, there has been strong selection against premature flowering as it results in a complete loss of the commercial value of the crop. Despite its economic importance only a few studies have looked into the genetic control of flowering in carrot.

In 2013, Alessandro et al. created an F_2 population, derived from the intercross between the annual cultivar "Criolla INTA" and a petaloid male sterile biennial carrot. They evaluated early flowering habit, named Vrn1, which was found to be a dominant trait conditioned by a single gene. Vrn1 mapped to chromosome 2 with flanking markers at 0.70 and 0.46 cM. Ou et al. (2016) used RNA-seq in a wild carrot species sensitive to flower induction by vernalization and photoperiod and an orange cultivar to identify flowering-time genes and use digital gene expression (DGE) analysis to examine their expression levels. Homologs of *COL2*, *CONSTANS-LIKE 5* (*COL5*), *SUPPRESSION OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*), *FLOWERING LOCUS C* (*FLC*), and *GIBBERELLIC ACID INSENSITIVE* (*GAI*) were differentially expressed between the early flowering wild carrots and domesticated carrots. Shen et al. (2018) used a set of backcross inbred lines developed by crossing a wild carrot with an orange cultivar to map days to initial flowering (DIF), main stalk length (MSL), and seed weight per plant (SWP). Two, four, and two QTLs associated with DIF, MSL, and SWP were discovered, respectively, with 14.6–23.8% phenotypic variance. The QTL for DIF mapped to chromosomes 1 and 5.

5.8.5 Root Shape

The ability to form a fleshy storage root, with reduced lateral branching, was undoubtedly one of the first selected domestication traits in carrot. Later, during carrot improvement, a vast array of carrot shapes and sizes become important for classifying market types grown in different regions of the world, many of which are still used today. Until recently, very few carrot root shape studies were conducted likely due to the difficulty of phenotyping root traits. Fortunately, modern advances in automated image analysis have started to help unravel complex traits such as root system architecture.

Macko-Podgórni et al. (2017) identified a candidate domestication syndrome gene, *DcAHLc1*, carrying three non-synonymous single nucleotide polymorphisms and one indel that systematically differentiates wild and cultivated accessions. This gene belongs to the *AT-hook motif nuclear localized* (*AHL*) family of plant regulatory genes which are involved in the regulation of organ development, including root tissue patterning. *AHL* genes work through direct interactions with other AHL family proteins and a range of other proteins that require intercellular protein movement. They speculate that *DcAHLc1* might be involved in the development of the carrot storage root, as the localization of the gene overlapped with one of the QTL for root thickening. Turner et al. (2018) developed an automated analysis platform that extracts size and shape components for carrot shoots and roots. This method reliably measures variation in shoot size and shape, petiole number, petiole length, and petiole width, root length, and biomass. They used the imaging pipeline to phenotype an F_2 mapping population consisting of 316 individuals which segregated for root and shoot morphologies and identified co-localization of quantitative trait loci for shoot and root characteristics on chromosomes 1, 2, and 7, suggesting these traits are controlled by genetic linkage and/or pleiotropy. Machaj et al. (2018) reported the first comparative transcriptome analysis between wild and cultivated carrot roots at multiple developmental stages. Comparisons of expression between cultivated and wild carrot found that transcription factors and genes encoding proteins involved in post-translational modifications were mostly upregulated, while those involved in redox signaling were mostly downregulated. Also, genes encoding proteins

regulating cell cycle, involved in cell divisions, development of vascular tissue, water transport, and sugar metabolism were enriched in the upregulated clusters of cultivated carrot.

5.9 Bottom-up Approach: Signatures of Selection

One of the most observed trends during crop domestication is a reduction of genetic diversity caused by a genetic bottleneck (Doebley et al. 2006). Since selected genes experience more severe bottlenecks than unselected ones, the reduction of genetic diversity becomes uneven along chromosomes and creates distinct genetic characteristics that can be used to identify selective sweeps. Within domesticated populations, low genetic diversity (π), Tajima's D, and runs of extended haplotype homozygosity (EHH) can be used to find recent positive selection (Nielsen 2005). When the population data of both wild ancestors and modern domesticated accessions are available, the selective sweeps can be identified by comparing distinct genetic characteristics between two populations. A straightforward method is to scan the genome for regions with significant reduction of genetic diversity ($\pi_{wild}/\pi_{cultivar}$). Population differentiation statistics, such as F_{ST} which measures variation of allele frequency between two populations, can also be used to identify selection (Shi and Lai 2015). Additionally, a cross-population composite likelihood ratio (XP-CLR) approach jointly calculates multiple locus allele frequency differentiation to identify selective sweeps between two groups (Chen et al. 2010). With the newly sequenced carrot genome (Iorizzo et al. 2016) and the cost of genotyping rapidly declining, genome-wide scans for signatures of selection are now possible in carrot. Identified regions can be crossed referenced with genes found using traditional top-down approaches or scanned for potential candidates using the carrot genome.

Grzebelus et al. (2014) identified 27 DArT markers that showed signatures of selection and localized two of these markers to chromosomes 2 and 6. Macko-Podgórni et al. (2014) selected one of the DArT markers showing the strongest evidence for directional selection from the Grzebelus et al. (2014) work and converted it into a co-dominant cleaved amplified polymorphic site (CAPS) marker named *cult* which was used to differentiate wild and domesticated accessions. The *cult* marker was validated on 88 domesticated and wild carrot accessions. Macko-Podgórni et al. (2017) mapped *cult* to the distal portion of the long arm of carrot chromosome 2, where it overlapped with a plant regulatory gene (*DcAHLc1*) involved in the regulation of organ development, including root tissue patterning and confirmed that this gene had been selected, as reflected in both the lower nucleotide diversity in the cultivated gene pool, as compared to the wild, as well as high F_{ST}.

To identify genomic regions associated with domestication events, Iorizzo et al. (2016) analyzed genome-wide F_{ST} between wild and domesticated eastern accessions and found local differentiation signals on chromosomes 2, 5, 6, 7, and 8. Peaks on chromosomes 2, 5, and 7 overlapped with previously mapped domestication QTL for root thickness (*cult*) (Macko-Podgórni et al. 2017) and carotenoid content, (*Y* and Y_2) (Cavagnaro et al. 2011; Just et al. 2009). Ellison et al. (2017) found a drastic decrease in nucleotide diversity in the fine-mapped Y_2 region in orange cultivated accessions.

In the most extensive investigation of genome-wide selective sweeps to date, Ellison et al. (2018) surveyed F_{ST}, nucleotide diversity, and XP-CLR ratios in 500 kb genomic bins across the genomes of 520 cultivated and 154 wild carrot accessions. Twelve genomic regions were significant for all three methods of selective sweep detection. The candidate carotenoid gene, *Or*, was located in one of these 12 genomic locations. Interestingly, two DArT markers that showed signatures of selection in Grzebelus et al. (2014) overlapped with genomic regions on chromosome 2 and 6. Chromosome 2 was previously shown to carry the *Vrn1* trait (Alessandro et al. 2013) which was likely a target to favor biennial growth habit during the course of carrot domestication.

5.10 Concluding Remarks

The study of carrot domestication will continue to be an important area of focus in which the location, timing, and genes under selection will be under examination. There are new resources for domestication studies that were once limited to major crops but are now readily available for all crop species. Historical efforts to collect and preserve wild relatives, landraces, and cultivated varieties have strengthened the world's public genebanks, and the onset of low-cost sequencing and global interest in these genetic collections have initiated a transition from long-term storage facilities to active exploration. Within the next few years, over a thousand carrot wild relatives, landraces, and modern cultivars will be genotyped and available to the public scientific community. Although the focus of these efforts will be to enable plant breeders, these resources will be equally useful for studies of domestication, population genetics, genome evolution, and diversity in carrot.

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