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Molecular markers and genomic resources in caraway (*Carum carvi* L.): Current status, research gaps, and strategic directions for breeding

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Abstract: Caraway (*Carum carvi* L.) is an economically important spice and medicinal crop valued for its essential oil composition, particularly its high content of carvone and limonene. Despite its commercial relevance, compared with that of other Apiaceae species, the development of genomic resources remains limited. Molecular research has progressed from early dominant marker systems, including random amplified polymorphic DNA (RAPD) and inter simple sequence repeat (ISSR), to more recent SNP-based genotyping approaches that clarify population structure and flowering-type differentiation. However, key genomic resources, such as simple sequence repeat (SSR) markers, a high-quality reference genome, quantitative trait locus (QTL) mapping, genome-wide association studies (GWAS), and transcriptomic datasets, are still lacking. This review synthesises current knowledge on molecular marker applications in caraway and identifies major gaps limiting breeding progress. Evidence from related Apiaceae species indicates that systematic SSR development and integration of genome-based tools can substantially enhance breeding efficiency. Particular emphasis is placed on a phased strategy for SSR development in caraway, positioned as complementary to single-nucleotide polymorphism (SNP)-based approaches within a progressive genome-enabled breeding framework. Strengthening the molecular infrastructure of caraway will support precision breeding aimed at improving yield stability, essential oil quality, and environmental adaptability.

Keywords: Apiaceae; germplasm characterisation; microsatellites; single nucleotide polymorphism (SNP) genotyping; transcriptomics

Caraway (*Carum carvi* L.) is a biennial, or occasionally annual, herbaceous plant of the Apiaceae family. It is cultivated globally for its seeds, whose aromatic and bioactive compounds are highly valued (Bailer et al. 2001; Liu et al. 2023; Bouzaid et al. 2024). Caraway, which is traditionally utilised in culinary applications, also has diverse pharmaceutical potential, including anti-inflammatory effects, digestive stimu-

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lant effects, and antioxidant properties (Keshavarz et al. 2013; Mahboubi 2018; Hajlaoui et al. 2021). Most of its medicinal effects are associated with its essential oil, which is rich in bioactive compounds such as carvone and limonene, key contributors to the plant's pharmaceutical and commercial value (Ghannay et al. 2022; Ermenlieva et al. 2025). It is cultivated primarily in temperate regions of Europe and North America, with additional production in parts of Asia and Africa, and remains particularly relevant in organic and sustainable production systems (Johri 2011; von Maydell et al. 2020b).

Despite its economic and medicinal importance, caraway remains underdeveloped in terms of genomic resources relative to other Apiaceae crops such as carrot (*Daucus carota*), fennel (*Foeniculum vulgare*), and coriander (*Coriandrum sativum*), which have benefited from genome sequencing efforts and the integration of molecular markers into breeding programs. In contrast, structured breeding initiatives in caraway have been limited, and available molecular evidence indicates only moderate levels of genetic variation within cultivated populations (Laribi et al. 2011; Janipour et al. 2017; von Maydell et al. 2020a). Consistent with the patterns observed in many domesticated crops (Frankel et al. 1995; Dwivedi et al. 2017), its cultivated genetic base may therefore be relatively narrow, partly because of domestication bottlenecks and restricted germplasm exchange. This discrepancy between economic importance and available genomic infrastructure highlights the need for systematic evaluation of genetic diversity and strategic expansion of genomic resources in caraway. The long-term viability and adaptive potential of plant species depend fundamentally on genetic diversity (Chung et al. 2023). Genetic diversity provides the basis for adaptation to environmental change, resistance to biotic and abiotic stresses, and effective breeding for improved traits (Dwivedi et al. 2016). Reduced genetic variation may result in inbreeding depression and increased vulnerability to environmental pressures (Keller & Waller 2002; De Kort et al. 2021; Walker & Spigler 2024).

Closely related to genetic diversity is population structure, which refers to the non-random distribution of genetic variation shaped by factors including gene flow, geographical isolation, mating systems, and demographic history (Bradburd et al. 2018). Understanding population structure enables the identification of distinct genetic groups, reveals evolutionary relationships, and informs the design of effective conservation and breeding strategies (Pálsson et al. 2023).

Assessing the extent of genetic diversity within *C. carvi* is therefore essential for developing improved cultivars. It is also important for expanding adaptability across agro-ecological zones and enhancing tolerance to biotic and abiotic stresses (Frankel et al. 1995; von Maydell et al. 2020b). Traditional approaches based on morphological or phenotypic traits are limited by their sensitivity to environmental conditions, phenological variability, and the polygenic nature of adaptive traits (Collard & Mackill 2008). In contrast, molecular markers provide precise, reproducible, and environment-independent insights into the genetic architecture of plant populations (Govindaraj et al. 2015).

For many years, molecular genetic investigations in caraway were largely restricted to dominant marker systems, particularly random amplified polymorphic DNA (RAPD) and, to a lesser extent, inter simple sequence repeat (ISSR) approaches (Seidler-Łożykowska et al. 2014; Janipour et al. 2017). This reliance reflected the limited availability of genomic resources in the species, including the absence of a high-quality reference genome assembly (von Maydell et al. 2024). RAPD markers operate independently of prior sequence knowledge and can therefore be applied in species lacking characterised genomic sequences (Williams et al. 1990; Hussain & Nisar 2020). Such properties made RAPD a practical initial tool for diversity assessment in caraway (Laribi et al. 2011). However, the dominant inheritance pattern and reproducibility constraints of RAPD markers restrict their utility for high-resolution population genetic analyses and advanced breeding applications (Powell et al. 1996; Collard & Mackill 2008).

Recent single-nucleotide polymorphism (SNP)-based studies, particularly those employing genotyping-by-sequencing, have uncovered significant population differentiation in caraway. Most notably, differentiation occurs between annual and biennial flowering types (von Maydell et al. 2020b). While these findings represent important progress, genomic resource development in caraway remains at an early stage. To date, no high-quality reference genome assembly, comprehensive quantitative trait locus (QTL) mapping studies, genome-wide association analyses (GWAS), or integrative transcriptomic resources have been reported. The absence of these advanced genomic tools limits the transition from descriptive diversity assessment to trait-associated breeding applications. Moreover, the diversification of marker

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systems remains incomplete. Among molecular markers, microsatellites are particularly valuable because of their high reproducibility, locus specificity, codominant inheritance, and significant polymorphism (Gupta & Varshney 2000; Schlötterer 2004). These characteristics make SSRs powerful tools for detecting inter- and intra-population variation. They are also effective for assessing gene flow and elucidating population structure and linkage disequilibrium (Selkoe & Toonen 2006; Bhargava & Fuentes 2010). While SSR markers have been widely used in other Apiaceae crops such as celery (*Apium graveolens* L.) (Fu et al. 2014), coriander (*Coriandrum sativum* L.) (Tulsani et al. 2020), fennel (*Foeniculum vulgare* L.) (Palumbo et al. 2018), and carrot (*Daucus carota* L.) (Cavagnaro et al. 2011; Baranski et al. 2012), and even in phylogenetically distant species such as black cumin (*Nigella sativa* L.) (Celik & Aydin 2023), their application in caraway (*C. carvi*) remains absent or extremely limited. In these related crops, SSR development has contributed not only to diversity assessment but also to genome saturation, linkage mapping, and breeding-oriented applications, further emphasising the opportunity for similar strategic implementation in caraway. This review synthesises current knowledge on molecular marker applications and genomic resources in caraway. It integrates findings from earlier marker systems, including RAPD, ISSR, amplified fragment length polymorphism (AFLP) and recent advances using SNPs, identifies major research gaps, and outlines strategic directions for SSR development and broader expansion of molecular resources. The resulting framework aims to support effective breeding strategies, strengthen germplasm conservation, and facilitate the sustainable utilisation of *C. carvi* genetic resources.

LITERATURE SEARCH STRATEGY

This review was conducted using a structured narrative approach incorporating database searches to enhance transparency and reproducibility. Literature searches were performed in Web of Science, Scopus, PubMed, and Google Scholar for publications published between 1980 and 2026. The following keyword combinations were applied: ("*Carum carvi*" OR caraway) AND ("molecular marker*" OR SSR OR microsatellite* OR SNP OR RAPD OR ISSR OR AFLP OR QTL OR GWAS OR genome assembly OR transcriptome*). The search was restricted to peer-reviewed articles published in English. In addition to database retrieval, relevant studies were identified through manual screening of reference lists from selected publications to ensure comprehensive coverage. Titles and abstracts were screened to exclude studies unrelated to molecular marker applications or genomic research in caraway and closely related Apiaceae species. Full-text articles were subsequently assessed for eligibility based on relevance to genetic diversity, population structure, marker development, or breeding-oriented genomic applications. The study selection process is summarised in Figure 1, following the PRISMA 2020 guidelines (Page et al. 2021).

A literature search was conducted across four databases, including PubMed (n = 8), Web of Science (n = 45), Scopus (n = 50), and Google Scholar (n = 110), yielding a total of 214 records. After removal of duplicate entries (n = 65), 148 unique records remained and were screened based on titles and abstracts. During this stage, 95 records were excluded because they did not meet the predefined inclusion criteria, most commonly due to a non-molecular research focus (e.g., essential oil composition or agronomic studies), absence of *Carum carvi* as the target species, or review-type publications lacking primary genetic data. The remaining 53 articles were assessed for full-text eligibility, of which 25 were excluded due to insufficient primary molecular or genomic information, limited methodological detail or sample size, or focus on species outside the scope of this review. Ultimately, 28 studies fulfilled all inclusion criteria and were incorporated into the final qualitative synthesis.

ECONOMIC AND AGRICULTURAL IMPORTANCE OF CARAWAY

Commercial production of caraway is concentrated in Europe and Canada, where the crop is cultivated on a commercial scale and contributes to regional spice and essential oil markets (Sedláková et al. 2003; Malhotra 2012; Rahman et al. 2019). Finland and Canada are recognised among the major commercial producers that supply seeds for food processing, bakery products, and pharmaceutical applications (Kochhar 2016; Niemi & Väre 2019). Market value is largely determined by seed yield and essential oil quality, both of which directly influence commercial competitiveness. The economic relevance of caraway is closely linked to essential oil content and composition, particularly the relative proportions of carvone and limonene that define aroma

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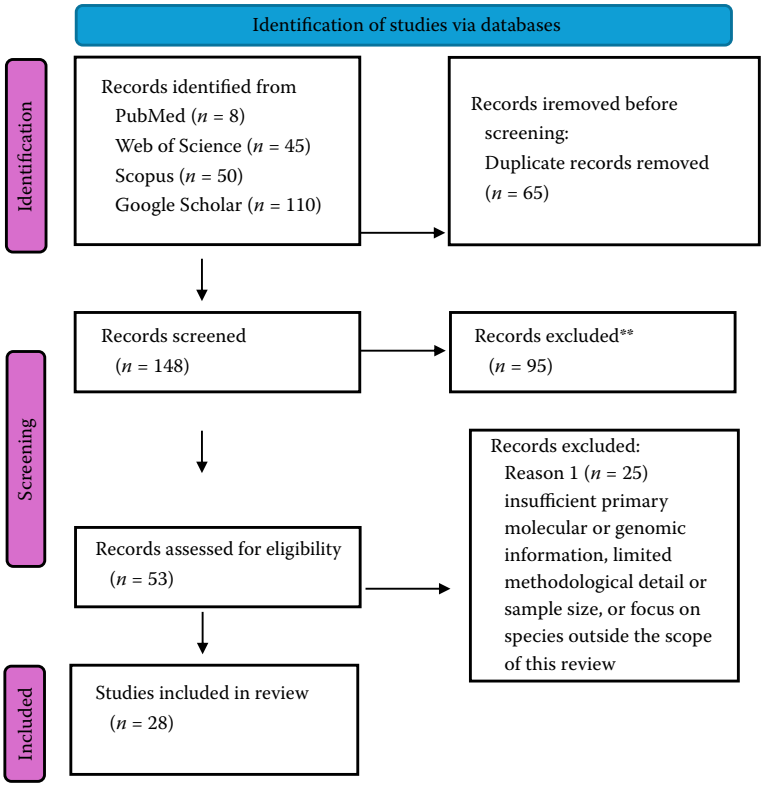

Figure 1. Flow diagram illustrating the identification, screening, eligibility assessment, and inclusion of studies considered in this review

**did not meet predefined inclusion criteria, most often due to non-molecular research focus, absence of *Carum carvi* as a target species, or review-type publications lacking primary genetic data

and industrial suitability (Aćimović et al. 2015; Mahboubi 2018; Ghannay et al. 2022). Essential oil concentration in caraway typically ranges between approximately 1–6%, depending on genotype and environmental conditions (Sedláková et al. 2003; Aćimović et al. 2015). Substantial variation among cultivars and growing regions has been documented, reflecting strong genotype–environment interactions that influence both yield and oil composition (Marcinkevičienė et al. 2021; Bouzaid et al. 2024). Such variability underscores the importance of genetic improvement aimed at stabilising productivity and essential oil quality.

Agronomically, caraway is cultivated as either annual or biennial types, with biennial forms dominating commercial production and requiring vernalization before flowering, thereby extending the production cycle over two seasons (von Maydell et al. 2020b, 2022). Yield performance is strongly influenced by sensitivity to climatic variability, weed competition, and soil conditions. Reported differences in productivity among regions highlight the influence of both environmental factors and genetic background (Sedláková et al. 2003; Marcinkevičienė et al. 2021). In addition, documented variation in essential oil composition complicates quality standardisation for industrial use (Sedláková et al. 2003; Aćimović et al. 2015). Although caraway has clear commercial importance, breeding efforts remain limited relative to those for other Apiaceae species. Improvement efforts have focused primarily on seed yield and essential oil traits; however, the genetic basis underlying these characteristics is still insufficiently characterised. Molecular analyses have revealed moderate differentiation among cultivated populations (von Maydell et al. 2020b), indicating that additional exploitation of available germplasm may contribute to further breeding advancements. Therefore, strengthening the molecular and genomic framework of caraway is essential to enable precise germplasm characterisation, identification of trait-associated variation, and development of cultivars with improved yield stability, oil quality, and environmental adaptability.

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OVERVIEW OF MOLECULAR MARKER SYSTEMS

Molecular markers have become fundamental tools in plant genetics and breeding due to their ability to detect DNA-level polymorphisms independent of environmental influences (Collard & Mackill 2008; Govindaraj et al. 2015). In contrast to morphological and biochemical traits, DNA-based markers provide stable and reproducible information on genetic variation, facilitating the assessment of genetic diversity, population structure, and marker–trait associations. Over the past decades, several marker systems have been developed, differing in inheritance pattern, genomic coverage, technical requirements, and applicability to breeding programs (Gupta & Varshney 2000). One of the earliest DNA-based marker systems was restriction fragment length polymorphism (RFLP), which relies on variations in restriction enzyme digestion patterns and hybridisation with labelled probes (Botstein et al. 1980). RFLP markers are co-dominant and highly reliable but require large amounts of high-quality DNA and are labour-intensive, limiting their widespread application in modern breeding programs. Subsequently, dominant marker systems such as RAPD, ISSR, and AFLP were developed (Ragot & Hoisington 1993; Zietkiewicz et al. 1994; Vos et al. 1995). These techniques detect presence–absence polymorphisms and are relatively simple and cost-effective. They have been widely used for preliminary assessments of genetic diversity and population structure. However, their inability to distinguish heterozygous from homozygous states limits their ability to perform detailed population genetic and breeding analyses (Powell et al. 1996).

Co-dominant marker systems, including SSRs and SNPs, allow discrimination between allelic states at specific loci. SSRs consist of short tandem repeats that are highly polymorphic and locus-specific, making them particularly suitable for germplasm characterisation, linkage mapping, and marker-assisted selection (Gupta & Varshney 2000; Schlötterer 2004). SNPs represent single-base variations distributed throughout the genome and enable high-throughput genotyping, especially when combined with next-generation sequencing platforms (Rafalski 2002; Morin et al. 2004). Although SNPs are typically bi-allelic and individually less polymorphic than SSRs are, their abundance across the genome provides high-density coverage suitable for genome-wide association studies and genomic selection. The comparative features of the principal molecular marker systems are summarised in Table 1. Strategic selection and the development of appropriate marker systems are therefore essential for strengthening genetic analysis and facilitating genomic advancement in crops with limited molecular resources.

APPLICATIONS OF MOLECULAR MARKERS IN APIACEAE

Molecular marker development has progressed considerably in several Apiaceae species, as detailed in Table 2. In carrot and fennel, genome-scale SSR mining and draft genome assemblies have enabled linkage mapping, trait tagging, and marker-assisted hybrid breeding. Transcriptome-derived SSR markers in celery have facilitated cultivar fingerprinting and germplasm characterisation, while cross-species transfer of carrot SSRs to coriander has demonstrated the feasibility of cost-effective marker development in under-resourced species. Furthermore, SNP-based linkage mapping in carrot has enabled the identification of QTLs and candidate genes controlling quality-related metabolic traits, illustrating the transition toward genome-enabled breeding within the family (Dunemann et al. 2022). In contrast, such systematic marker diversification and integration into breeding pipelines have not yet been realised in caraway, underscoring the opportunity for targeted development of SSR resources and progressive expansion toward genome-informed breeding strategies.

MOLECULAR MARKER STUDIES IN CARAWAY

Research on molecular markers in caraway has developed gradually and remains limited compared with other Apiaceae crops. Early investigations relied primarily on dominant marker systems. Laribi et al. (2011) analysed five annual populations from Tunisia, Germany, and Egypt using RAPD markers, generating 136 bands (56 polymorphic) and revealing significant geographic structuring, with genetic variation occurring predominantly among rather than within populations. Seidler-Łożykowska et al. (2014) further estimated genetic distances among European accessions, cultivars (Rekord and Kończewicki), and breeding strains using RAPD-PCR, reporting genetic distances ranging from 0.22 to 0.67 and clustering genotypes into four groups. Beyond diversity assessment, Bocianowski and Seidler-Łożykowska (2012) examined associations between RAPD mark-

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Table 1. Comparative characteristics of major molecular marker systems used in plant genetic studies

Type of marker	Genomic abundance	Degree of polymorphism	Inheritance (dominant/ co-dominant)	Reproducibility	Locus specificity	Cost per assay	References
RFLP	**High**: RFLPs are abundant in most genomes	**Medium**: RFLPs reveal a moderate level of polymorphism	**Co-dominant**: both alleles are detectable in heterozygotes	**High**: Southern blot profiles are very reproducible between labs/samples	**Yes**: each RFLP probe hybridises to a specific genomic locus	**High**: expensive (enzymes, probes, radioisotopes, and labour make each assay costly)	Burr et al. (1983); Kochert (1991); Powell et al. (1996)
RAPD	**High**: random primer binding sites are abundant throughout the genome	**High**: RAPD can detect high levels of polymorphism in many genomes	**Dominant**: band presence/absence does not distinguish homozygote vs. heterozygote	**Low**: RAPD patterns have poor reproducibility (sensitive to PCR conditions).	**No**: RAPD primers amplify random anonymous loci	**Low**: inexpensive (requires only cheap primers and standard PCR reagents)	Ragot and Hoisington (1993); Ayliffe et al. (1994); Adeeba et al. (2014)
AFLP	**Very high**: AFLP can generate numerous fragments across the genome in one assay	**Very high**: AFLP detects very high polymorphism by assaying multiple loci simultaneously	**Dominant**: fragments are scored present/ absent; heterozygotes not differentiated	**High**: AFLP yields highly reproducible and reliable banding patterns with standard protocols	**No**: AFLP produces many anonymous fragments from multiple loci per run	**Medium**: moderate cost (some special reagents/kits needed, but one AFLP run yields many markers)	Vos et al. (1995); Powell et al. (1996); Leipold et al. (2020)
ISSR	**High**: inter-SSR regions are ubiquitous and randomly distributed throughout genomes	**High**: ISSR markers display high polymorphism in genetic diversity studies	**Dominant**: like RAPD, scored by band presence/absence (cannot detect heterozygous state)	**Medium**: ISSR results have intermediate reproducibility (anchored primers improve consistency, but some profiles vary)	**No**: one ISSR primer yields multiple bands from different loci (a multilocus profile)	**Low**: cheap (only a single primer and basic PCR; no specialized consumables required)	Zietkiewicz et al. (1994); Reddy et al. (2002); Feroz et al. (2022)
SSR	**Medium**: SSR loci are moderately abundant (less common than SNPs)	**High**: SSR markers are highly polymorphic (hypervariable repeat-length variation)	**Co-dominant**: allele size differences allow heterozygote detection	**High**: SSR markers are generally very reproducible under standard PCR conditions	**Yes**: SSR primers target unique loci (flanking sequences must be known)	**Medium**: moderate (PCR is cheap, but SSR primer development is expensive and time-consuming)	Panaud et al. (1996); Temnykh et al. (2000); Feroz et al. (2022)
SNP	**Very high**: SNPs are the most abundant genetic variations	**Very high**: collectively, SNPs offer very high numbers of polymorphic sites genome-wide	**Co-dominant**: genotype calls distinguish both alleles (homozygous vs. heterozygous)	**High**: SNP genotyping is extremely reproducible and error-resistant with modern techniques	**Yes**: SNP assays focus on a single nucleotide locus in the genome	**Low**: low cost per data point (once developed, SNP genotyping is highly cost-effective at scale)	Vignal et al. (2002); Hong et al. (2012); Tian et al. (2021)

RFLP – restriction fragment length polymorphism; RAPD – random amplified polymorphic DNA; AFLP – amplified fragment length polymorphism; ISSR – inter simple sequence repeat (ISSR); SSR – simple sequence repeat; SNP – single-nucleotide polymorphism

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ers and 22 quantitative traits, identifying multiple significant marker-trait relationships explaining up to 47.6% of phenotypic variation, representing an early attempt to integrate molecular markers into breeding-oriented analysis. In their more recent publication, Bocianowski et al. (2019) utilised the same 22 quantitative traits and described their association with more than 100 markers for at least one trait. The percentage of total phenotypic variability of individual traits explained by individual markers ranged from 25.3% to 96.0%. Janipour et al. (2017) expanded these efforts by applying both RAPD and ISSR markers to Iranian populations, generating 126 and 79 fragments, respectively, and reported moderate genetic diversity with clear geographic clustering. Collectively, dominant-marker studies have consistently indicated moderate but structured diversity; however, their limited allelic resolution has constrained their utility for advanced genomic and breeding applications. To date, the only research devoted to the study of the karyotype in caraway and the use of AFLP and ISSR markers was conducted by Ibrahim et al. (2019), focusing on three species of the Apiaceae family – caraway, cumin, and coriander. It was found that caraway and cumin are closer to each other than coriander, both at the chromosome level and at the molecular level (AFLP/ISSR). Coriander is genetically more distant and probably

Table 2. Representative applications of SSR and SNP-based molecular markers in selected Apiaceae crops, illustrating the relevance of the integration of genetic resources and breeding to caraway improvement

Crop (scientific name)	Marker type	Application	Breeding relevance	Reference
Daucus carota L. (carrot)	SNP-based linkage mapping and QTL analysis	identification of QTLs and candidate genes controlling polyacetylene accumulation	trait dissection, candidate gene identification, quality improvement through marker-assisted breeding	Dunemann et al. (2022)
Daucus carota L. (carrot)	genome-wide SSR (chromosome-anchored)	*in silico* SSR mining and genome saturation	physical map development, germplasm characterisation, gene tagging, molecular breeding; cross-species transferability	Uncu and Uncu (2020)
Daucus carota L. (carrot)	genomic and EST-derived SSR	linkage mapping, diversity analysis, marker transferability	genetic map integration, trait tagging, comparative mapping across Apiaceae	Cavagnaro et al. (2011)
Foeniculum vulgare Mill. (fennel)	genome-based SSR	draft genome assembly and SSR validation	hybrid breeding support, parental line selection, marker-assisted breeding	Palumbo et al. (2018)
Apium graveolens L. (celery)	EST-SSR (transcriptome-derived)	genetic diversity and cultivar fingerprinting	germplasm characterisation, cultivar identification, population structure analysis	Fu et al. (2014)
Coriandrum sativum L. (coriander)	EST-SSR (transcriptome-derived)	genetic diversity and preliminary sketch of the transcriptome	identification of genes responsible for various economical traits, MAS breeding	Tulsani et al. (2020)
Coriandrum sativum L. (coriander)	cross-species SSR (from carrot)	SSR transferability testing	demonstrates feasibility of low-cost SSR development in under-resourced Apiaceae crops	Choudhary et al. (2017)

SNP – single-nucleotide polymorphism; QTL – quantitative trait locus; SSR – simple sequence repeat; EST – expressed sequence tag; MAS – marker assisted selection

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has a different and more complex karyotype. This finding may support both further phylogenetic studies of the family and better use of SSR markers within it.

Substantial methodological advancements have been achieved with the adoption of SNP-based genotyping through genotyping-by-sequencing. Von Maydell et al. (2020b) genotyped 137 accessions using more than 13 000 SNPs, distinguishing two subpopulations corresponding to annual and biennial flowering types. Despite this difference, approximately 92% of the genetic variation was found within groups, suggesting that domesticated caraway retains considerable diversity without evidence of a severe breeding bottleneck. In a breeding context, high-throughput SNP genotyping was applied to estimate outcrossing rates in polycross systems, revealing an average outcrossing rate of 66.5%, and supporting the feasibility of synthetic variety development (von Maydell et al. 2020a). Further trait-oriented analysis identified 60 SNP markers significantly associated with vernalization requirements, from which 19 diagnostic markers were developed to facilitate selection against the recessive biennial allele (von Maydell et al. 2022). Complementing these cultivated-material studies, de Haro Reyes et al. (2025) analysed 198 individuals from 16 Nordic wild populations using genotyping-by-sequencing (GBS)-derived SNPs and reported consistent within-population diversity alongside clear east–west geographic structuring, emphasising conservation priorities. Collectively, the available studies demonstrate that the genetic diversity of caraway is structured by both geography and life cycle, yet molecular applications remain largely focused on diversity and preliminary trait association. Notably, SSR markers have not yet been developed in caraway, and comprehensive genomic resources, including a reference genome assembly, QTL mapping, GWAS, and transcriptomic datasets, remain absent, highlighting important opportunities for targeted molecular advancement.

Strategic development of SSR markers in caraway

Despite recent progress in SNP-based genotyping in caraway (von Maydell et al. 2020b, 2022), SSR markers remain undeveloped in *C. carvi*, representing a notable gap in the molecular toolkit available for this species. In related Apiaceae crops, systematic SSR development has supported linkage mapping, germplasm characterisation, hybrid breeding, and marker-assisted selection (Cavagnaro et al. 2011; Palumbo et al. 2018; Uncu & Uncu 2020). The absence of comparable resources in caraway limits its integration into structured molecular breeding pipelines (Collard & Mackill 2008). Given the current level of genomic infrastructure in caraway, targeted SSR development represents a practical and scalable intermediate step toward broader genomic advancement (Varshney et al. 2009).

Cross-species transfer as an initial strategy

A practical and cost-effective initial approach for developing SSR resources in caraway involves testing cross-species transferability of microsatellite markers developed in closely related Apiaceae species, particularly carrot and fennel. Successful amplification of SSR loci across Apiaceae has been demonstrated in several studies, although transferability rates generally decline with increasing phylogenetic distance (Varshney et al. 2005; Cavagnaro et al. 2011; Choudhary et al. 2017). Within the family, cross-amplification of carrot-derived SSR markers has been reported in multiple species, including coriander and cumin, supporting the feasibility of this strategy in under-resourced taxa (Cavagnaro et al. 2011; Kumar et al. 2014; Choudhary et al. 2017).

Carrot represents the most extensively characterised Apiaceae species with respect to SSR development. Large-scale marker discovery efforts, including expressed sequence tag (EST)- and bacterial artificial chromosome (BAC)-end-derived SSRs, have generated substantial marker resources and demonstrated considerable transferability across the family (Cavagnaro et al. 2011; Baranski et al. 2012). These studies reported moderate cross-species amplification success within Apiaceae, illustrating the potential to obtain informative loci even in species lacking reference genome assemblies.

Screening a subset of genome-anchored or genic SSR markers from well-characterised Apiaceae crops for amplification and polymorphism in caraway could therefore provide an initial panel of informative loci. Even a modest number of transferable markers may support preliminary germplasm fingerprinting, assessment of allelic diversity, and population structure analysis, as demonstrated in related species using genome-anchored SSR markers (Uncu & Uncu 2020). Such an approach offers a rapid and economical entry point for strengthening the molecular toolkit of caraway prior to the development of species-specific SSR resources.

Transcriptome-based SSR mining

A more targeted strategy for SSR development in caraway involves mining microsatellite loci from

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transcriptomic data. Transcriptome-derived SSRs are associated with expressed genes and may therefore provide functional relevance in addition to polymorphism (Varshney et al. 2005; Ellis & Burke 2007). Advances in RNA sequencing (RNA-seq) technologies have enabled rapid identification of genic SSR markers in numerous crop species without requiring a complete reference genome assembly (Wang et al. 2009; Taheri et al. 2018). In caraway, RNA sequencing of contrasting genotypes, such as annual versus biennial flowering types or high- versus low-oil-content lines, could generate a valuable resource for identifying functionally associated SSR loci.

Because EST-SSRs are frequently located within coding or regulatory regions, they may be directly linked to genes influencing agronomically important traits, including essential oil biosynthesis, stress responses, and flowering regulation (Gupta & Varshney 2000; Varshney et al. 2005). Within the Apiaceae family, transcriptome-based SSR development has been successfully implemented in carrot, celery, coriander, and other representatives, demonstrating both marker polymorphism and cross-species transferability (Cavagnaro et al. 2011; Tulsani et al. 2020). These studies illustrate that EST-SSR mining represents a feasible and scalable medium-term objective for species with limited genomic infrastructure, offering an intermediate step between dominant marker systems and full genome-based resource development.

Genome-based SSR development, validation, and strategic integration in caraway

In the longer term, the establishment of a high-quality reference genome would enable systematic genome-wide identification of SSR loci. Genome-based SSR discovery has proven effective in several Apiaceae crops, where chromosome-anchored markers have facilitated linkage mapping, comparative genomics, and integration with high-density SNP datasets (Cavagnaro et al. 2011; Palumbo et al. 2018; Uncu & Uncu 2020). Genome-wide SSR mining enables the identification of single-locus markers distributed evenly across linkage groups, thereby supporting map saturation and trait-linked analyses. The physical anchoring of SSR loci enhances their utility in QTL mapping and comparative genome studies, particularly when they are integrated with SNP-based platforms (Collard et al. 2005; Varshney et al. 2009). Regardless of the discovery strategy, whether cross-species transfer, transcriptome-based mining, or genome-wide identification, rigorous marker validation remains essential. SSR markers are typically evaluated across representative panels of cultivated and wild accessions to determine polymorphism information content, allele number per locus, amplification reproducibility, and stability across laboratories (Powell et al. 1996; Gupta & Varshney 2000; Varshney et al. 2005). Population genetic parameters, including observed and expected heterozygosity and conformity to Hardy-Weinberg equilibrium, provide additional measures of marker robustness and informativeness (Hartl & Clark 2007). Markers demonstrating consistent amplification and sufficient allelic diversity are generally retained for downstream applications. The assembly of validated loci into multiplex PCR panels further enhances efficiency and cost-effectiveness in breeding programs.

The development of a standardised SSR marker panel would enable immediate applications in caraway breeding. These include germplasm fingerprinting, parental line characterisation, hybrid purity assessment, monitoring of outcrossing dynamics, and preliminary linkage analyses. In breeding contexts where high-throughput SNP genotyping infrastructure is limited, SSR markers offer a multi-allelic and locus-specific alternative suitable for small- to medium-scale programs (Collard & Mackill 2008). SSR markers are generally considered complementary to SNP technologies, as the two marker systems operate at different analytical scales and offer distinct advantages (Varshney et al. 2009). Given the current genomic status of caraway, a phased implementation strategy is most realistic. Initial efforts may focus on cross-species SSR screening and polymorphism testing in related Apiaceae species. Subsequent transcriptome-based SSR discovery can expand marker coverage within expressed genes. In the longer term, genome-based SSR mining and integration with SNP datasets would enable map saturation and trait-associated analyses. Such a stepwise approach enables progressive strengthening of molecular capacity without requiring immediate large-scale genomic investment, thereby aligning resource allocation with breeding priorities.

SSR vs SNP: Comparative applications in caraway breeding

Single nucleotide polymorphisms and simple sequence repeats represent two complementary classes of co-dominant molecular markers that differ in terms of their genomic distribution, analytical resolution,

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and infrastructural requirements (Gupta & Varshney 2000; Rafalski 2002; Varshney et al. 2009). In caraway, SNP-based genotyping, particularly through genotyping-by-sequencing, has enabled genome-wide assessment of population structure, estimation of outcrossing rates, and identification of loci associated with vernalisation requirements (von Maydell et al. 2020a, 2022). The high density and genome-wide coverage of SNP markers make them particularly suitable for linkage mapping, QTL analysis, and, in the longer term, genomic selection frameworks (Rafalski 2002; Collard & Mackill 2008).

However, SNP-based approaches often rely on next-generation sequencing platforms and associated bioinformatic pipelines, requiring substantial data processing capacity (Morin et al. 2004; Varshney et al. 2009). In contrast, SSR markers provide a locus-specific, multi-allelic system that can be implemented using standard PCR-based methodologies without the need for advanced sequencing infrastructure (Gupta & Varshney 2000; Schlötterer 2004). The multi-allelic nature of SSRs often provides high discriminatory power per locus, which is advantageous for germplasm fingerprinting, cultivar identification, seed purity testing, and routine breeding applications (Powell et al. 1996; Collard & Mackill 2008). In crops where genomic resources are still emerging, SSR markers therefore remain practical and cost-effective tools. SNPs are well suited for high-resolution genomic analyses and large-scale trait dissection once sufficient genomic resources are available, including genome-wide association studies and genomic selection (Heffner et al. 2009). SSRs, by contrast, provide an efficient platform for structured germplasm management and medium-scale marker-assisted selection. For caraway, where a reference genome and comprehensive mapping resources are currently lacking, a combined strategy is advisable: continued expansion of SNP-based datasets to support genome-wide analyses, alongside targeted SSR development to strengthen breeding-oriented workflows. Such integration would enhance analytical flexibility while reducing dependence on a single technological platform.

Future genomic roadmap for caraway breeding

Advancing caraway breeding beyond descriptive diversity analysis requires the progressive establishment of comprehensive genomic resources. Although SNP-based genotyping has enabled initial genome-wide assessments of population structure and flowering-type differentiation (von Maydell et al. 2020b), the absence of a high-quality reference genome remains a central limitation. A chromosome-scale genome assembly would provide the structural framework necessary for precise marker localisation, identification of gene-rich regions, and systematic repeat annotation, including genome-wide SSR mining (Michael & Jackson 2013; Varshney et al. 2021). Such a resource would also facilitate comparative genomics within Apiaceae and accelerate the discovery of candidate genes. The development of structured mapping populations is another essential step. Biparental populations enable QTL mapping for key agronomic traits, including flowering behaviour, seed yield, oil content, and essential oil composition (Collard et al. 2005). In related Apiaceae crops such as carrot, SNP-based linkage mapping has already enabled identification of QTLs and candidate genes associated with quality-related metabolic traits (Dunemann et al. 2022), illustrating the feasibility of such approaches within the family. Beyond biparental mapping, genome-wide association studies in diverse germplasm panels can provide higher-resolution marker-trait associations when sufficient marker density and population structure control are available (Yu et al. 2006; Korte & Farlow 2013).

Transcriptomic resources represent an additional priority for elucidation of gene expression patterns underlying essential oil biosynthesis and stress responses. RNA sequencing enables identification of differentially expressed genes and regulatory pathways associated with metabolite accumulation and adaptive traits (Wang et al. 2009). Integration of transcriptomic and genomic data supports functional annotation of candidate genes and improves biological interpretation of QTL or GWAS signals. In the longer term, genomic selection (GS) frameworks may further enhance breeding efficiency by predicting breeding values using genome-wide marker information (Heffner et al. 2009; Crossa et al. 2017). Although genomic selection requires large training populations and dense marker coverage, incremental development of genomic resources can progressively build toward this objective. A phased implementation strategy, beginning with SSR establishment, expanding through SNP-based mapping, and culminating in integrative genomic analysis, offers a realistic and scalable pathway for modernising caraway breeding. Collectively, these developments would enable the transition from phenotypic selection and limited marker-based diversity studies toward

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a genomics-informed breeding framework capable of improving yield stability, essential oil quality, and environmental adaptability.

CONCLUSION

Caraway represents an economically valuable yet genomically underdeveloped member of the Apiaceae family. Although early studies using dominant markers and more recent SNP-based approaches have provided important insights into genetic diversity, population structure, and flowering-type differentiation, the overall molecular framework of the species remains limited. In particular, the absence of SSR marker resources, a reference genome assembly, and comprehensive trait-mapping studies constrains the transition from descriptive genetic analysis to precision breeding. Comparative evidence from related Apiaceae crops demonstrates that the systematic development of SSR markers, the integration of linkage maps, and the application of SNP-based QTL analyses can substantially strengthen breeding pipelines. In this context, targeted SSR development in caraway represents a practical and scalable intermediate step that is capable of supporting germplasm characterisation, cultivar identification, and breeding-oriented applications while broader genomic resources are being progressively established.

Future advancements will require coordinated expansion of genomic infrastructure, including genome assembly, structured mapping populations, genome-wide association studies, transcriptomic characterisation, and ultimately, genomic selection frameworks. A phased and integrative strategy combining complementary marker systems offers a realistic pathway toward modernising caraway breeding. Strengthening the genomic foundation of this crop will facilitate improved yield stability, essential oil quality, and environmental adaptability, contributing to the sustainable utilisation and long-term genetic improvement of caraway.

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