

Article

Genetic Studies in Carrot (*Daucus carota* L.): Advancements and Trends in Research

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Abstract

The cultivated carrot (*Daucus carota* L. subsp. *sativus*) is a globally important crop valued for its high content of beta-carotene, vitamins, and other bioactive compounds. Advances in molecular genetics and genomics have driven improvements in yield, stress tolerance, disease resistance, pigment accumulation, and nutritional quality. Here we present a comprehensive scientometric analysis of 398 peer-reviewed articles on carrot genetics (1964–2023), integrating keyword co-occurrence mapping and co-authorship network analysis to identify research lines, methodological approaches, and international collaboration. The focus of research was predominantly on Plant Biology (67.59%), followed by Conservation (15.58%) and Plant Breeding (10.55%). The integration of omics technologies has yielded new insights into abiotic stress tolerance, carotenoid and anthocyanin biosynthesis, and genetic diversity; however, significant challenges remain in translating genomic resources into routine breeding practice and conservation of genetic resources. We recommend prioritizing genome-assisted breeding strategies, functional genomics and interdisciplinary, multi-omics approaches to accelerate the development of resilient and high-quality carrot cultivars under climate change.

Keywords: scientometric analysis; plant breeding; genetic diversity; molecular markers; germplasm conservation; genomic resources



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1. Introduction

The cultivated carrot (*Daucus carota* subsp. *sativus*), a member of the Apiaceae family, stands out as one of the most economically important and nutritionally valuable root

vegetables worldwide. This crop is a major dietary source of β -carotene, a precursor of vitamin A, alongside other essential nutrients, including dietary fiber, vitamin K1, potassium, and antioxidants [1]. The global relevance of carrots extends beyond nutrition, impacting agricultural economies and food security, with cultivation spanning temperate to subtropical climates [2].

Despite the extensive research conducted on carrot genetics over the past decades, a comprehensive analysis of research trends and methodological approaches in this field is yet lacking. Carrots are cultivated in almost all countries, both on small and large scale production systems. China presently accounts for almost 45% of the worldwide carrot market and is the leading country in both production (18.2 million tons annually) [3] and consumption.

The United States, Ukraine, Uzbekistan, and Russia are also among the largest carrot producers, worldwide. Over the past five decades (1967–2017), the global carrot production (combined with turnip) has expanded dramatically by 5.5-fold, rising from 7.3 to 40.3 million tons. This remarkable growth reflects both a 2.9-fold increase in the cultivated area (from 0.39 to 1.15 million hectares) and nearly twice in productivity (from 20.3 to 38.4 tons per hectare) [4], demonstrating the success of both agricultural expansion and genetic improvement efforts.

The rapid expansion of carrot cultivation has prompted extensive research to improve agronomic traits, such as yield, pest and disease resistance, abiotic stress tolerance, and enhanced nutritional quality [5,6]. Modern breeding methods, combined with advances in genomics, have significantly accelerated carrot improvement. The sequencing of the carrot genome, a landmark achievement in 2016, provided a comprehensive understanding of the genetic basis of important traits, including root color and disease resistance, facilitating precision breeding [5,7].

Molecular markers, particularly single nucleotide polymorphisms (SNPs) and simple sequence repeats (SSRs), have played a crucial role in characterizing the genetic diversity and population structure of carrot germplasm. Recent studies using high-throughput genotyping have identified genetic loci associated with key agronomic traits, thereby optimizing selection strategies for breeding programs [8,9]. Understanding this genetic variation is crucial for leveraging the extensive diversity found in wild relatives of carrot, which offer underexplored reservoirs of potentially beneficial alleles for genetic research and, perhaps, breeding purposes [10,11].

The development of carrot varieties with increased intensity of the orange color has led to modern materials with high carotene content and enhanced nutritional and functional status. Efforts for increasing color intensity in other carotenoid backgrounds have led to the development of commercially available materials with intense red or yellow roots, containing high levels of lycopene or xanthophylls, respectively. Similarly, breeding for purple pigmentation has led to cultivars with greater anthocyanin content and more stable and uniform distribution of anthocyanin pigments in the tap root tissues. Recent studies have identified key metabolic pathways and regulatory genes involved in the biosynthesis of these pigments [5,12,13].

Similarly, candidate structural and regulatory genes were identified for the biosynthesis of other important phytonutrients, such as non-anthocyanin phenolics, polyacetylenes, terpenes, and carbohydrates [14,15]. Additionally, advances in transcriptomics and metabolomics deepened our understanding of the molecular mechanisms underlying stress responses, offering new avenues for developing climate-resilient plants, highlighting their central role in plant adaptation to adverse environments [16].

Abiotic stress tolerance, especially drought and salinity, remains a critical area of research, as climate change poses significant threats to carrot cultivation. Recent genomic

and physiological studies have identified candidate genes and pathways associated with stress adaptation, highlighting potential targets for genetic improvement [17,18]. Genome-wide studies on members of AP2/ERF, NAC, bZIP, and MYB transcription factors [19–22] outlined genes that are among the main targets for breeding abiotic stress tolerance in carrot. The integration of omics such as proteomics, transcriptomics and metabolomics, has provided holistic insights into the complex stress response networks in carrots, paving the way for the development of cultivars with wider adaptation range or higher phenotypic stability under stress [16,23].

Disease and pest resistance are also a major concern in carrot breeding. Germplasm evaluations led to the identification of a few nematode (*Meloidogyne javanica* and *M. incognita*) resistant accessions, some of which were later used to develop segregating populations to genetically map nematode-resistance loci and QTL [24–26]. Similarly, through germplasm screening, carrot accessions with high tolerance to *Alternaria* leaf blight (AFB), caused by *Alternaria dauci*, were identified, and QTL for AFB resistance were genetically mapped [27]. Furthermore, specific terpene volatile compounds from the leaves have been associated with AFB resistance [28].

Despite these advancements, several challenges remain, such as the efficient integration of genomic resources into traditional breeding programs and the sustainable conservation of genetic diversity. Germplasm banks play a pivotal role in preserving the biodiversity of carrot and related taxa, facilitating the identification and utilization of novel traits from wild and domesticated *Daucus* species [29,30]. Worldwide, carrot germplasm collections maintained ex situ are substantial, with over 13,400 accessions preserved across 62 institutions. Most of the stored genetic material comes from cultivated germplasm. However, growing awareness of the significance of wild relatives in crop improvement has resulted in a rising number of *Daucus* wild accessions being safeguarded in gene banks [31].

The application of cutting-edge genomic tools and the integration of multi-omics approaches are transforming carrot research and breeding. These advances encompass not only nutritional quality and stress adaptation but also disease resistance, plant development, and agronomic performance traits that remain critical targets for variety improvement. However, the rapid improvement in methodological approaches and the high number of publications available need a proper systematic analysis to further identify patterns, gaps and future directions in research with carrots.

In this context, bibliometric and scientometric approaches provide an effective framework for synthesizing the expanding body of literature across diverse research areas, guiding future priorities, fostering international collaboration, and ensuring the sustainable development of this economically important crop. This study presents the first comprehensive scientometric analysis of carrot genetics, mapping research themes and methodological approaches from 1960 to 2023.

This work advances the field through three concise innovations. First, it divides the evolution of the research in carrot genetics into three main stages, each with distinct methodological approaches and their transition. Second, it provides multiscale maps of collaboration at author, institutional and country levels that reveal structural bottlenecks limiting international integration. Third, it offers a synthesis by topics or subjects of research that links keyword-derived clusters to concrete genetic findings and translational gaps, highlighting priorities for research in carrot breeding.

2. Materials and Methods

2.1. Data Collection and Filtering

The dataset for this study was gathered using an automated search within the Web of Science (WoS) database (<https://www.webofknowledge.com>, accessed on 13 February

2024), specifically chosen for its multidisciplinary scope and widespread use in scientometric research [32]. The search spanned from 1960 to 2023 and included the keywords “*Daucus carota*” AND “carrots” AND “genetics” to refine the results. To ensure the relevance of the retrieved studies, only complete articles and directly related to carrot genetics were considered. English-language articles were prioritized due to their higher likelihood of citations in the global literature. Publications in other languages, conference proceedings, and reviews were excluded.

The selected studies were organized into an electronic spreadsheet (S1) using Microsoft Excel (Supplementary Materials). The dataset was divided into three main categories: (i) raw, unfiltered data; (ii) refined entries that met the selection criteria; and (iii) article classification based on specific analytical parameters. The extracted information included publication details such as authorship, journal, year of publication, research domain, affiliation, keywords, and digital object identifier (DOI).

The initial search retrieved 5227 records in total, of which 1535 were open-access publications. After filtering by document type to retain only research articles (4589 records) and restricting the dataset to publications written in English (4398 records). This language filter corresponds to 3.7% of the initial records. After duplicate removal (4 papers, 0.1%), and exclusion of studies outside the temporal scope 1960–2023 (29 papers, 0.7%), a total of 4338 remained.

After that, 44 papers (1.0%) were excluded for not representing full research articles (e.g., technical notes, “first reports”, short communications) or for not directly addressing carrot. Title and abstract screening further eliminated 3665 papers (84.5%), which did not specifically address genetic aspects of carrot. Finally, during full-text evaluation, 231 papers (5.3%) were excluded because carrot was not the main research focus or the genetic approach was insufficient, resulting in 398 eligible articles (9.2% of the initial dataset) that were included in the scientometric analysis.

It is noteworthy that exclusions were not limited to older records but also included recent publications, mainly because these addressed nutritional, processing, or other non-genetic aspects rather than carrot genetics. This outcome highlights the rigor of the screening process in retaining only studies with a direct genetic scope, regardless of publication date. To maximize consistency and inter-reviewer agreement, the dataset was independently analyzed by three researchers and the results compared to create the final dataset.

2.2. Quantitative and Qualitative Classification

To assess the development of research on carrot genetics, a chronological analysis was conducted by counting the number of publications per year. Descriptive and graphical analyses were conducted to visualize fluctuations over time. Additionally, we identified key authors, research institutions, and prominent journals contributing to the field.

For analytical consistency, we defined four major fields of study: Plant Biology, covering fundamental biological and genetic processes in carrot; Conservation, addressing the preservation and sustainable use of carrot genetic diversity, including studies on evolutionary history and genetic structure; Plant Breeding, focused on the development and improvement of cultivars, as well breeding methods; and Plant Pathology, encompassing the genetic basis of host–pathogen interactions and resistance, molecular identification/characterization of carrot pathogens, vector biology and transmission dynamics, and diagnostic or high-throughput surveys of the carrot disease complex.

To each aforementioned field were attributed subcategories as follows: (i) Plant Biology (morphophysiology, taxonomy, reproductive biology, classical cytogenetics, molecular cytogenetics, molecular); (ii) Conservation (origin, evolution, and domestication; population genetics/population genomics; ethnobotany; phylogeny; phylogeography); (iii) Plant

Breeding (pre-breeding, breeding, molecular breeding); and (iv) Plant Pathology (molecular). Studies spanning more than one domain were coded as “combinations” of two or more fields (e.g., Plant biology and conservation). Moreover, studies that employed high-throughput methods or omics approaches (genomics, transcriptomics, proteomics, metabolomics) were flagged as a cross-cutting category, regardless of their subject categorization, so that the impact of these methods could be highlighted even when applied within specific research areas.

2.3. Data Analysis

To promote reproducibility and analytical clarity, the corpus was limited to peer-reviewed original research articles in English. Therefore, conference proceedings and non-English records were excluded to reduce terminological heterogeneity and to avoid a potential geographic and language bias (see Limitations). Network construction and visualization were performed with VOSviewer v.1.6.20 using association-strength normalization. The preprocessed Web of Science export files used as VOSviewer input are provided as Supplementary File S2 (WoS export, .txt) and Supplementary File S3 (WoS export, RIS, .ris).

The keyword co-occurrence network was derived from 10,554 unique keyword entries (Author Keywords plus abstract-derived keywords) using a minimum threshold of six occurrences, which retained 85 terms for the main map. This cutoff was selected after iterative testing: lower thresholds introduced many generic or low-relevance terms with minimal interpretative value, while substantially higher thresholds (for example, 10) excluded specific but meaningful items and risked underrepresenting emerging topics. A custom thesaurus file (.txt) was applied to merge synonymous terms, standardize terminology and exclude generic tokens (for example plant, data, identification, organization) that could distort clustering.

For the author co-authorship network, publications listing more than 25 authors were excluded to mitigate hyperauthorship, following the default VOSviewer setting applied consistently across analyses. A minimum publication threshold of five documents per author (default) was required for inclusion in the main figure; this cutoff was chosen to focus the principal map on authors with a sustained contribution to carrot genetics and to improve legibility of the co-authorship topology. Total Link Strength (TLS) was computed for all authors from the full curated dataset and used to characterize connection intensity; the display thresholds applied for figure presentation do not alter the underlying TLS values. Based on these criteria, 36 of the 961 unique author entries met the labeling threshold in the main figure.

Analogous cutoffs were applied for the organizational and country-level analyses so that the main maps emphasize institutions and countries with meaningful collaborative activity rather than isolated contributions. The organizational network comprised 326 institutions, of which those with at least five documents were retained for the main figure; thirty-one institutions met this criterion. The country-level network covered 48 countries with a five-document minimum, of which 19 qualified.

All maps used full counting, association-strength normalization, the VOS layout and modularity-based clustering. In these maps node size reflects document counts and edge thickness reflects TLS; labels and name variants were harmonized using the thesaurus to merge naming variants while preserving the underlying numeric counts.

Descriptive statistical summaries, including frequency distributions, were used to evaluate publication trends. Data visualization was conducted in R [33] using the tidyverse package [34]. The results therefore provide an overview of research activity, key contributors and methodological approaches in carrot genetics across the study period.

3. Results

3.1. Temporal Trends

Research on carrots has increased over the period reviewed (Figure 1), with three distinct phases that reflect major technological and conceptual shifts in the field: an initial period of low production (1964–1989), a growth phase driven by the advent of polymerase chain reaction (PCR) and sequence-based molecular markers (1990–2009), and a recent acceleration with next-generation sequencing (2010–2023). The studies predominantly focus on Plant Biology, followed by Conservation, Plant Breeding, and Plant Pathology, highlighting sustained efforts in genetic diversity characterization and crop improvement. Molecular approaches, particularly SNPs and SSRs, have been widely adopted to address genetic diversity, population structure, and marker-trait associations. The integration of omics approaches, including genomics, transcriptomics, and metabolomics, has significantly contributed to deepening our understanding of the molecular mechanisms involved in responses to abiotic stresses, as well as in the biosynthesis of pigments such as carotenoids and anthocyanins. Despite remarkable progress, challenges persist in effectively bridging genomics with practical breeding applications and ensuring the long-term conservation of valuable genetic resources.

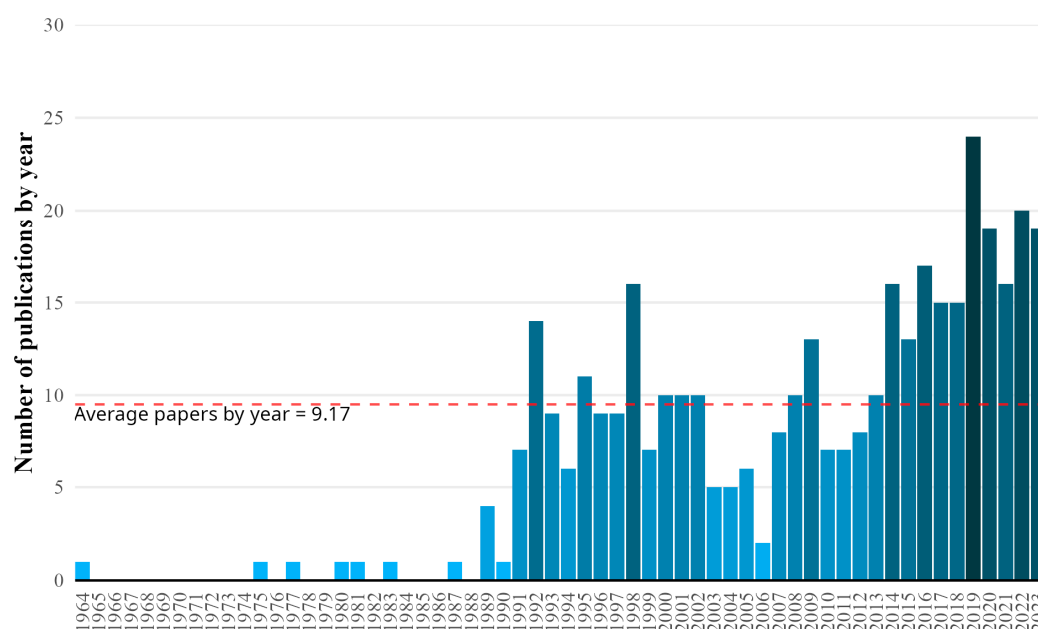


Figure 1. Temporal distribution of publications on carrot genetics, 1964–2023. Bar color intensity reflects the relative number of publications per year, with darker tones indicating higher peaks. The dashed red line represents the long-term average publication rate (9.17 papers per year). From the empirical pattern we infer three broad phases: exploratory (1964–1989), when cytological, biochemical and classical genetic studies predominated; methodological growth (1990–2009), associated with marker development and broad adoption of PCR-based approaches; and modern acceleration (2010–2023), reflecting adoption of next-generation sequencing and high-throughput genotyping and catalyzed by the availability of a reference carrot genome. The figure itself is unchanged; phase boundaries are described here as data-driven inferences supported by historical methodological milestones.

For example, although substantial progress has been made in the characterization of carotene-controlling loci, such as *Y* [5], *Y2*, *Or*, and *REC* [30], this has not yet translated to the application of molecular tools in breeding programs leading to the development of cultivars with specific carotenoid profiles, such as carrots with high α -carotene or exclusively β -carotene, phenotypes that could be of interest for various purposes [30].

Also, the identification and characterization of genes controlling anthocyanin biosynthesis, such as *DcMYB7* and *DcMYB113*, and genes conditioning the proportion of acylated vs. non-acylated anthocyanins, like the acyltransferase *DcSCPL1*, generated molecular markers tightly linked to these genes. However, the application of such markers in breeding programs, has not yet yielded new varieties containing high levels of exclusively acylated (AA) or non-acylated anthocyanins (NAA), which are of interest for the food colorant industry (due to the high chemical stability of AA) and for fresh consumption (due to the high bioavailability of NAA), respectively. Finally, the knowledge from resequencing efforts in large germplasm collections and the characterization of carrot genetic diversity [30] should be leveraged and applied by curators aiming at more efficient management and conservation of germplasm banks.

The distribution of publications across time (Figure 1) reveals a clear upward trajectory in research activity related to population genetics in carrots. From 1964 to the late 1980s, publication outputs were sporadic and remained consistently below the average of 9.17 papers per year, indicating a period of very limited availability of genomic, cytogenetic, and molecular tools to support genetic research studies.

As a result, most publications from this period relied on lengthy classical genetic and breeding approaches, further complicated by carrot's biennial life cycle. These involved directed sexual inter-crosses and progeny testing through segregation analysis of phenotypic ratios to infer aspects such as inheritance, maternal effects, and the number of genes controlling a given trait. Such studies required deep knowledge of carrot reproductive biology, practical skills in making sexual crosses and managing progenies, and several years of field trials and phenotypic evaluations. Therefore, publications during this phase were occasional.

A notable increase in publication frequency began in the early 1990s, coinciding with a broader global rise in the use of molecular tools and advancements in genetic analysis techniques. PCR-based markers, including RAPD, AFLP, and SSR, were rapidly adopted by plant scientists, including carrot researchers and breeders, contributing to the increasing publication rates observed in the following years. SSRs, in particular, progressively replaced RAPDs and AFLPs due to their higher specificity, reproducibility, and co-dominance. During this period, these marker types were widely used in carrot genetics for studies on genetic diversity, population structure, phylogeny, and linkage mapping.

Additionally, restriction fragment length polymorphism (RFLP) markers and Southern blot analyses were also extensively used to estimate gene copy number, and confirming transgene insertions in transgenic experiments, and for linkage mapping. Other types of markers that combine locus-specific sequence information followed by PCR (e.g., Sequence Characterized Amplified Region; SCAR) or PCR and digestion with restriction enzymes (e.g., Cleaved Amplified Polymorphic Sequence; CAPS) were also used for analyzing carrot loci of interest.

After relative stability in the early 2000s, a second wave of growth began post-2007, with publications at levels above the average. While this growth is coincident with the development of next-generation sequencing (NGS) platforms, a clear growth can be observed after 2013, leading to the highest publication numbers per year between 2019 and 2023. This modern acceleration phase was not only driven by technological advances, such as the continuous development of NGS platforms since 2005, that increased sequencing depth and reduced costs, but also by shifting scientific priorities. Until 2012, Plant Biology predominated, but after 2013 research diversified toward Conservation, Population Genomics, and Applied Breeding. The priorities included a stronger emphasis on dissecting the genetic basis of carotenoid and anthocyanin biosynthesis, mapping loci associated with abiotic and biotic stress tolerance, and leveraging genetic diversity for breeding programs.

Together, these shifts reflect a broader research agenda that links technological advances with strategic goals in carrot improvement and conservation.

Overall, the trend highlights a three-phase development: an initial exploratory phase (1964–1989), a growth phase marked by methodological maturation (1990–2009), and a modern acceleration phase (2010–2023) characterized by sustained and increasing research activity. The described phases reflect scientific goals shaped by distinct eras of technological input, which unequivocally shaped the research on carrot genetics, including population genetics, phylogenetics, genomics, linkage and association mapping, and gene cloning.

3.2. Keyword Co-Occurrence

As shown in Figure 2, the VOSviewer keyword co-occurrence map displays terms selected according to minimum occurrence and association strength, producing coherent clusters that summarize the field's principal research fronts.

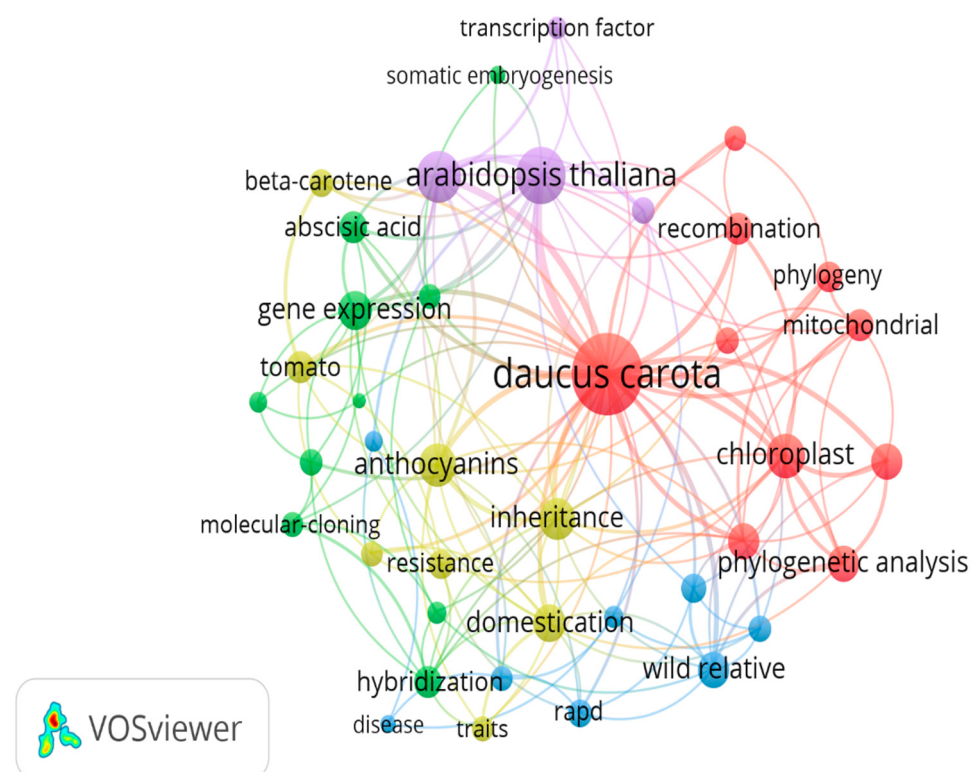


Figure 2. Keyword co-occurrence network for publications on carrot genetics (1964–2023). Data include Author Keywords and KeyWords Plus from 398 articles. Synonyms were merged with a thesaurus (for example, carrot, carrots, *Daucus carota*). Node size represents term frequency. Edge thickness indicates total link strength. Colors denote clusters identified by VOSviewer.

In Figure 2, the prominent *Arabidopsis thaliana* node reflects the frequent use of orthology for functional annotation in carrot and the fact that KeyWords Plus is derived from the titles of cited references, where *Arabidopsis* studies are highly prevalent. Its prominence therefore indicates a methodological dependence on a model organism rather than a shift away from carrot-focused research. When the analysis is restricted to Author Keywords only, the *Daucus carota* specific core remains and the *Arabidopsis thaliana* node contracts, confirming that the primary focus of the field is on *D. carota*. The remaining clusters capture the major research fronts in carrot genetics, pigment biosynthesis and accumulation (especially β -carotene and anthocyanins), domestication and inheritance (often linked to pest and disease resistance), gene expression and plant growth, and tissue culture and

somatic embryogenesis. At the center of these themes, *D. carota* remains the integrative hub connecting the network.

3.3. Categories of Studies

The distribution of population genetics studies on carrots, categorized into four primary research areas, is presented in Figure 3. A notable observation is the predominance of Plant Biology, which accounts for 67.59% of the studies, indicating that most investigations focus on genetic diversity, population structure, and evolutionary dynamics in carrots. It reflects studies on topics that have their implications or applications to conservation and preservation, underscoring that the figure represents scientific studies rather than actual management efforts.

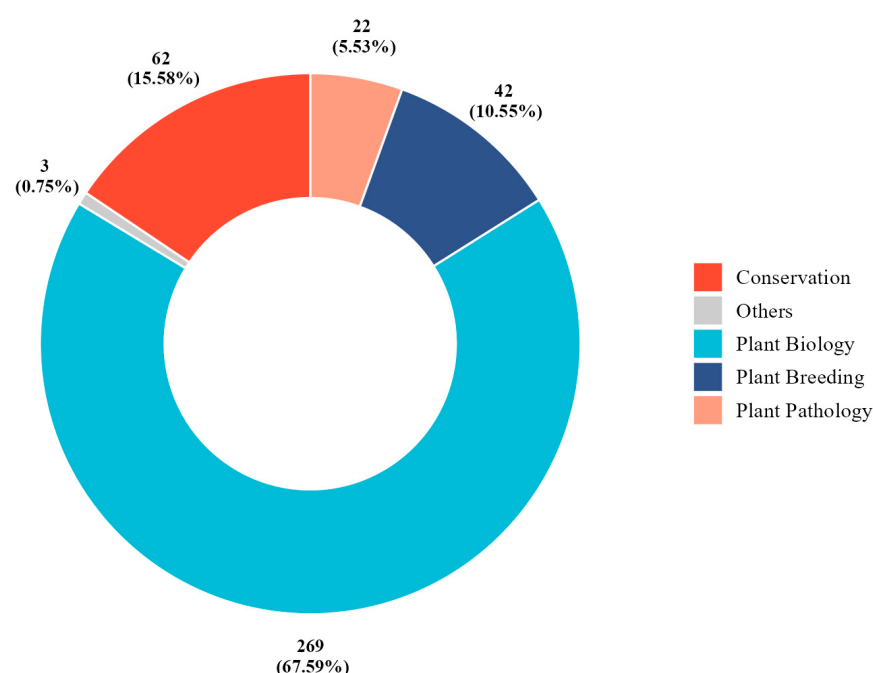


Figure 3. Categorization of genetic studies on carrots. Numbers represent the counts of studies per category and their respective proportion to the total number of papers analyzed.

Conservation represents the second-largest category, comprising 15.58% of the studies. This proportion indicates a substantial effort into preserving genetic resources, likely driven by the need to safeguard genetic diversity against environmental changes and agricultural intensification. The prominence of this category aligns with global efforts to conserve plant genetic resources and foster crop resilience. The studies emphasize the importance of regions such as the Mediterranean, North Africa, and Central Asia as centers of diversity, and use integrated approaches combining morphology and molecular markers to understand population structure, domestication history, and gene flow among populations.

Plant Breeding occupies 10.55% of the research landscape. This category includes studies focused on enhancing yield, quality, and stress tolerance-related traits, as well as those addressing marker-trait associations, introgression, heritability, and environmental adaptability. The category highlights the translation of genetic insights into agricultural innovation.

The most important traits of the studies are root shape and size; carotenoids, anthocyanins, and sugar content; and resistance to diseases and pests. Modern approaches, such as Marker-Assisted Selection (MAS) and genomic selection, Cytoplasmic Male Sterility-based hybridization, the use of NGS technologies, and automated image analysis, are

also frequently employed, reflecting the integration of traditional methods with molecular tools to develop improved carrot cultivars. Given the inherent time-gap between knowledge development and their practical applications in breeding programs, a panorama on concrete results, such as improved cultivars, is not readily evident yet. However, the identification of key genes conditioning important traits, e.g., genes controlling pigment biosynthesis, accumulation and chemical composition- as well as the characterization of the causal mutations in these genes, represent unprecedented molecular tools for precise MAS and the development of carrots with more specific phenotypes and nutritional profiles.

The combination of Plant Biology and Conservation constitutes only 0.75% of the studies. This minimal overlap points to a potential gap in the literature, where a comprehensive understanding of how biological processes and concepts aid conservation strategies is lacking. Plant Pathology accounts for 5.53% of the publications. Although this percentage may seem low, the studies are highly diverse and cover a wide range of economically relevant diseases and approaches. They include resistance mapping against root-knot nematodes (*Meloidogyne* spp.), the molecular characterization of phytoplasmas and their insect vectors, the detection and diversity of fungal pathogens such as *Alternaria dauci*, *Pythium* spp. and *Diaporthe*, and the identification of carrot-associated viruses and novel viromes. Other works addressed bacterial pathogens (*Pseudomonas*, *Streptomyces*, *Aliarcobacter*) and even genetic engineering approaches to enhance resistance to foliar fungi. This breadth indicates that, despite representing a relatively small share of the literature, pathology studies encompass key threats to carrot production and provide essential tools for breeding programs and disease management.

The subclassification of population genetics studies is presented in Figure 4. This subclassification (Figure 4A,B) shows a predominance of the Molecular Genetics category (249 studies), followed by Population Genetics (26), Pre-breeding (15), and Reproductive Biology (26). Other categories include Phylogeny (14) and Molecular Cytogenetics (12). Less represented disciplines are Phylogeography (5), Classical Cytogenetics (5), Origin/Evolution/Domestication (7), and Classical (6). This predominance reflects the growing incorporation of molecular techniques, such as DNA sequencing and the use of genetic markers, in elucidating the genetic structure, variability, and evolutionary history of the species, while the underrepresentation of other categories indicates areas that remain underexplored.

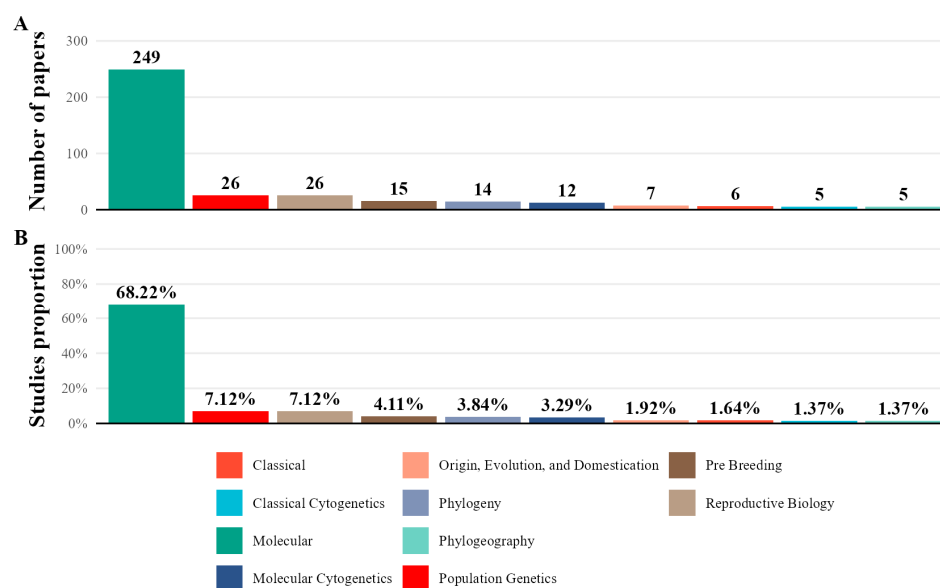


Figure 4. Subclassification of carrot genetics studies. Plot (A) shows raw counts of studies per subclass. Plot (B) shows the proportion of each subclass.

3.4. Organizational, Co-Authorship Network and Journals

The co-authorship network, which reveals collaboration patterns among researchers, is shown in Figure 5. When the co-authorship network was generated, only 31 of these 36 authors formed a consistently connected component (Supplementary Table S4 provides the complete list of authors, including the number of documents attributed to each and their total link strengths). Therefore, we visualized only 18 connected authors, as displaying disconnected nodes would not meaningfully represent collaboration structure and would reduce the clarity of Figure 5. An expanded version of this network is provided as Supplementary Figure S5.

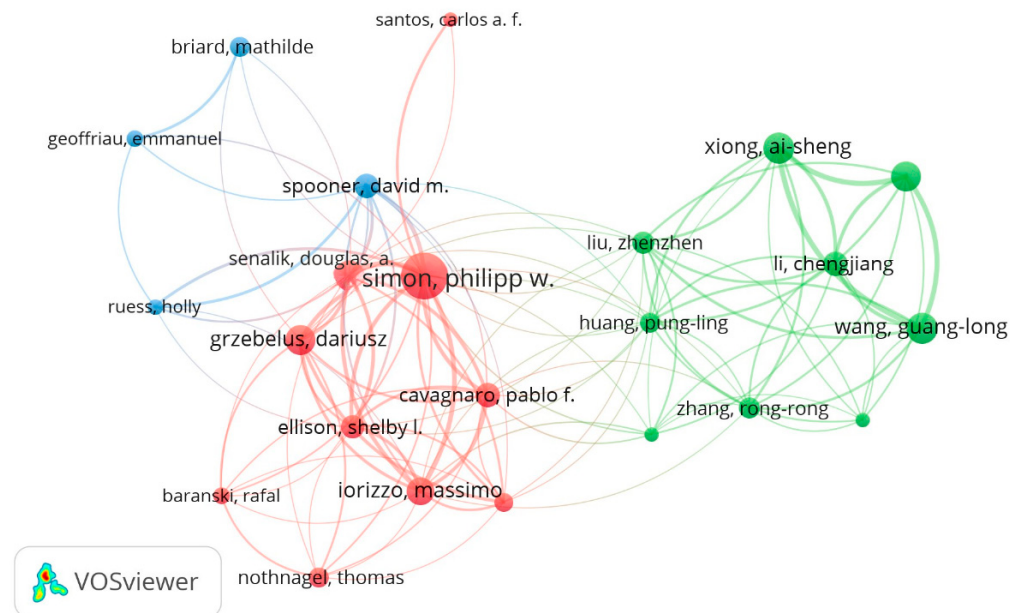


Figure 5. Co-authorship network for the carrot-genetics corpus used in this study. Nodes are authors, node size is proportional to publication count, and edge thickness reflects co-authorship strength. Colors indicate clusters detected by VOSviewer. Author names were harmonized to reduce variants.

The network resolves into two major, weakly connected clusters. The western cluster is centered on Simon, Philipp W., with strong links to Iorizzo, Massimo; Grzebelus, Dariusz; Cavagnaro, Pablo F.; Nothnagel, Thomas; Barański, Rafał; Senalik, Douglas A.; and Ellison, Shelby L. A French subgroup (Briard, Mathilde; Geoffriau, Emmanuel; Le Clerc, Valérie; Peltier, Didier) forms a coherent unit with limited connections to the core; Spooner, David M. appears at the periphery of this component.

The second cluster corresponds to the Chinese community, led by Xiong, Ai-Sheng, with dense internal collaboration among Wang, Guang-Long; Xu, Zhi-Sheng; Li, Chengjiang; Zhang, Rong-Rong; Huang, Pung-Ling; Liu, Zhenzhen; Wu, Xue-Jun; Tian, Yong-Sheng; and Tan, Shan-Shan. Cross-cluster links are sparse, indicating limited co-authorship between the Chinese and western groups. All visible nodes are labeled; the VOSviewer watermark was removed for clarity.

The country network (Figure 6) highlights the United States as the primary collaboration hub, with strong ties to Poland, France, Germany, the United Kingdom, Spain, and Argentina, and consistent bridges to China (and to Japan and India). A dense European cluster (France–Italy–Germany–UK–Spain–Netherlands–Denmark–Poland) is internally well connected and tightly linked to the US. South America participates mainly through Argentina (and Brazil), which co-authors frequently with the US and Europe. Turkey and South Korea also connect into the main component. Overall, the map reveals a transatlantic backbone (US–Europe) complemented by growing Asia–Europe/US links. Supplemen-

tary Table S6, listing all countries and their Total Link Strength (TLS), is provided in the Supplementary Materials.

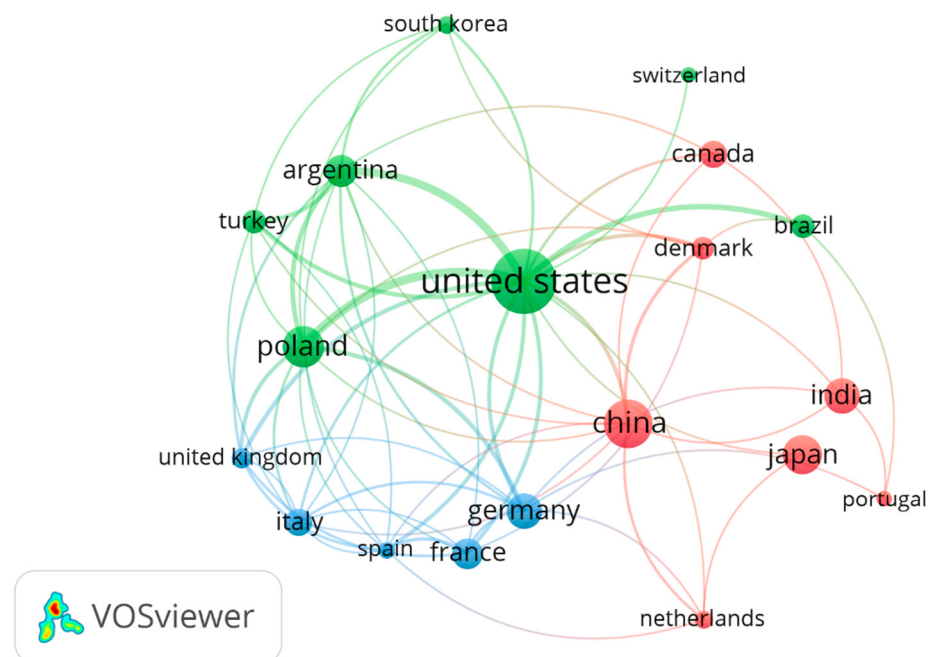


Figure 6. International co-authorship network by country, visualized in VOSviewer. Node size represents the number of documents; edge thickness denotes total link strength. Colors indicate collaboration clusters, and internode distances reflect relatedness in the VOS layout (closer = stronger/more frequent collaboration). Country names were harmonized for consistency; only countries meeting the inclusion threshold are displayed.

The organization-level network (Figure 7) reveals a core, well-connected component dominated by University of Wisconsin–Madison (UW-MADISON) and the United States Department of Agriculture (USDA), which show the strongest connectivity. This core is tightly linked with the University of California (UC), the University of Agriculture in Krakow (UNIV-AKRAKOW), and the French block formed by Institut Agro (INSTITUT AGRO; including Agrocampus Ouest), Institut National de Recherche pour l’Agriculture, l’Alimentation et l’Environnement (INRAE) and Université d’Angers (U-ANGERS).

Additional European partners such as the Julius Kühn-Institut (JKI; Germany) and the University of Warwick (WARWICK; UK) connect to the core, while the South American cluster involves the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET; shown truncated as “consejo nacional de investigac”), the Instituto Nacional de Tecnología Agropecuaria (INTA) and the Universidad Nacional de Cuyo (UNCUYO). Other visible contributors include North Carolina State University (NCSU; USA), Università di Pavia (PAVIA; Italy), Friedrich Miescher Institute for Biomedical Research (FMI; Switzerland), Yüzüncü Yıl University (YYU; Türkiye), RIKEN (Japan) and University of Tsukuba (UT-SUKUBA; Japan), and Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA; Brazil).

Several Chinese institutions appear as weakly or non-interlinked components and therefore do not appear in the main graph under the chosen thresholds. In particular, Nanjing Agricultural University (NAU) and the Ministry of Agriculture and Rural Affairs (MARA) form a dense micro-component, while Chinese Academy of Sciences (CAS) remains isolated; Texas A&M University (TAMU; USA), Simon Fraser University (SFU; Canada), Leibniz University Hannover (LUH; Germany) and University of Guelph (GUELPH; Canada) also appear as small or detached nodes. To preserve legibility, Figure 7 displays the principal connected component; an expanded view including these discon-

nected clusters is provided as Supplementary Figure S7, where the Chinese group can be seen explicitly.

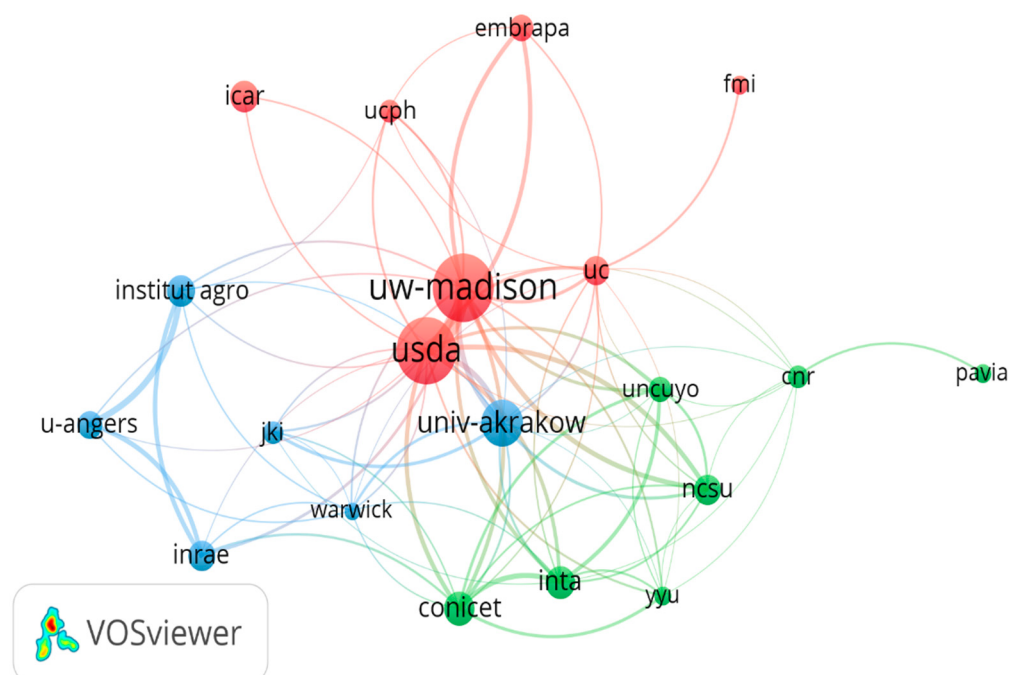


Figure 7. Organizational co-authorship network visualized in VOSviewer. Node size represents the number of documents (Weights = Documents); edge thickness denotes total link strength (co-authorship intensity). Colors indicate collaboration clusters, and spatial proximity reflects association strength in the VOS layout. Organization names were harmonized and abbreviated via a thesaurus to avoid duplicates.

Table 1 presents the most highly cited publications in carrot genetics, listing first authors and citation counts.

Table 1. Five most cited articles on carrot genetics extracted from the Web of Science database for the period 1960–2023.

First Author	DOI	Journal	Citations *	Main Contribution	Year
Iorizzo, Massimo [5]	10.1038/ng.3565	Nature Genetics	381	High-quality genome assembly and insights into carotenoid accumulation, as well as asterid evolution	2016
Kumar, S [35]	10.1104/pp.104.045187	Plant Physiology	340	Overexpression of a betaine aldehyde dehydrogenase improved salt tolerance	2004
Iorizzo, Massimo [36]	10.1186/1471-2164-12-389	BMC Genomics	179	A transcriptome assembly of carrot	2011
Iorizzo, Massimo [37]	10.3732/ajb.1300055	American Journal of Botany	164	Genetic structure and domestication of carrot	2013
Clotault, Jeremy [38]	10.1093/jxb/ern210	Journal of Experimental Botany	163	Transcriptional regulation of carotenoid biosynthesis in carrot root development	2008

* Number of citations from Web of Science.

Across the 398 articles, research is distributed over 149 journals, underscoring the field's multidisciplinary nature. The most frequent publication outlets are Theoretical and Applied Genetics (27 papers), Plant Molecular Biology (14), and Plant Cell Reports (11), followed by Frontiers in Plant Science, Plant Physiology and PLOS ONE (10 each). In contrast, the most-cited carrot-genetics papers (Table 1) are concentrated in broader or higher-impact venues—e.g., Nature Genetics, Plant Physiology, BMC Genomics, American Journal of Botany, and Journal of Experimental Botany, illustrating that citation impact does not necessarily coincide with the journals that publish the largest volume of studies.

3.5. Molecular Tools and Statistical Approaches for Genetic Analyses

Among the 398 selected articles, molecular tools or statistical methods employed for genetic analyses were distributed as follows. PCR-based methods (grouping RT-PCR, qPCR and real-time PCR) were reported as experimental approaches in 125 studies (31.4%). Marker-based approaches comprised SSR microsatellites (25 studies, 6.3%), AFLP (20 studies, 5.0%), RAPD (19 studies, 4.8%) and SNP-based assays (19 studies, 4.8%). Sequencing and genotyping platforms were represented primarily by RNA-Seq (21 studies, 5.3%) and GBS (genotyping-by-sequencing; 8 studies, 2.0%), with only isolated references to generic NGS. Mapping and analysis approaches were mainly represented by QTL mapping (18 studies, 4.5%). Transformation methods were conducted mostly by *Agrobacterium*-mediated approaches (24 studies, 6.0%). These results derive from a standardized extraction and normalization of the Tools/Methods field across the dataset; articles may report multiple methods at once and therefore contribute to more than one category.

Within the full set of 398 articles, 65 studies (16.3%) reported at least one omics-based approach. The distribution of omics occurrences is as follows (counts are non-exclusive; a single study may report more than one omics platform): Genomics (32 occurrences, 8.04% of the full dataset), Transcriptomics (28 occurrences, 7.04%), combined Genomics and Transcriptomics (3 occurrences, 0.75%), Metabolomics (2 occurrences, 0.50%), and combined Proteomics and Transcriptomics (1 occurrence, 0.25%).

4. Discussion

The development of research on carrot genetics reflects broader technological transitions that have shaped plant genomics over the last decades. Three main publication phases can be distinguished. Early work from the 1960s to the end of the 1980s was limited by the available tools at the time, based on cytological and biochemical variation. The second wave of publications (1990 to 2010) was largely marked by the screening of carrot germplasm using classic molecular markers, mostly PCR-derived. A marked increase in the publication output occurred after 2010, matching with the dissemination of next-generation sequencing (NGS) technologies and the availability of high-throughput genotyping platforms.

The sequencing and publication of the carrot genome in 2016 [5] represented a milestone that catalyzed new research directions by providing a comprehensive reference for molecular and comparative analyses. Nonetheless, similar publication growth patterns have been observed in other crops, indicating that this expansion is part of a global movement driven by technological advances rather than a carrot-specific phenomenon. Studies on cassava (*Manihot esculenta*) [39] and sugarcane (*Saccharum* spp.) [40] have shown parallel increases in genomic research following the release of reference assemblies, strengthening the thesis that sequencing breakthroughs act as triggers for scientific acceleration across plant species.

The keyword co-occurrence analysis documents a shift from classical diversity and taxonomic subjects toward molecular and functional genomics without erasing earlier lines of inquiry. Clusters centered on diversity, genetic resources and germplasm confirm

the continued importance of conservation and breeding. Marker-related acronyms or abbreviations such as SNP and QTL are present and reflect the adoption of marker-based approaches, whereas marker assisted selection is not commonly represented as an explicitly labeled keyword in our extraction. Terms such as transcriptome, genome and omics indicate increasing uptake of multi-layered analytical approaches.

The classification into categories and subcategories of study confirmed the prevalence of Plant Biology, with emphasis on genetic diversity, structure, and evolutionary dynamics. According to our bibliometric dataset, the Conservation category encompassed studies ranging from population genetics/genomics (26) and phylogeny (14) to phylogeography (5) and domestication (7). These studies are primarily anchored in genetic and evolutionary analyses, while ethnobotanical approaches remain scarce. Conservation research aligns with global priorities in safeguarding crop genetic resources and resilience, particularly in Mediterranean, North African, and Central Asian centers of diversity, often integrating morphological and molecular tools to assess population structure, domestication, and gene flow. The 15% representation of conservation studies likely reflects increasing concern over genetic erosion and the value of wild relatives as reservoirs of adaptive traits.

The predominance of Plant Biology (approximately 67.6% of the records) indicates that carrot genetics has been strongly anchored in fundamental biological inquiry. It most likely reflects several interacting factors. First, research trends and funding streams have historically favored basic research into gene function, metabolic pathways and genetic architecture, which generate publications in journals classified under Plant Biology. Second, subject categories of the Web of Science and journal indexing tend to assign fundamental studies to broad biological classes, which can mask applied work that is published in more specialized or multidisciplinary outlets. Third, our thesaurus-guided consolidation and the focus on author and abstract keywords favor detection of molecular and functional terminology, potentially reducing the relative visibility of engineering, post-harvest or nutrition studies that emphasize protocol, product, or agronomic descriptors rather than gene-level keywords.

The subclassification presented in Figure 4 shows the predominance of Molecular Genetics (249 studies), evidencing the extensive use of molecular markers to unravel the genetic structure and evolutionary history. In contrast, relatively few publications in Phylogeography, Classical Cytogenetics, and Origin/Evolution/Domestication reveal an underexplored space for integrative research that connects genomic data with historical and spatial dimensions.

Studies on the genetic control of root pigments outline the progress toward improving specific traits. Investigations of carotenoid and anthocyanin biosynthesis evolved from QTL mapping to the identification of causal genes and mutations underlying color phenotypes [5,41–51]. These advances have elucidated key regulatory factors, such as MYB, ARF, and AP2/ERF transcription families, which link pigment accumulation to developmental and stress response pathways [19–22]. This knowledge has guided marker-assisted selection and parental choice in breeding programs, particularly through loci such as *Y*, *Y2*, and *Or* that determine carotenoid profiles. Functional characterization of transcription factors has supported the development of high-anthocyanin genotypes with enhanced antioxidant capacity, demonstrating the growing integration between molecular discovery and applied improvement.

Conservation-focused research (16%) emphasizes phylogenetic and domestication processes that explain the genetic diversity of carrots [52–57]. Studies have documented variation across cultivated and wild carrots [58,59], clarified evolutionary relationships [60], and described genetic signatures of domestication [30,37,61], illustrating how an evolutionary understanding informs conservation and breeding strategies. Population genetics

remains relatively limited (29 studies) despite its importance for understanding adaptation and gene flow [61]. This scarcity likely reflects the logistical and analytical challenges of large-scale sampling and modeling, especially for wild relatives and landraces. Expanding such efforts is essential to uncover adaptive variation that can enhance resilience to environmental change.

Plant Breeding research, although representing a smaller proportion, has contributed decisively to developing cultivars with improved pigment content and stress tolerance [5,30]. Classical studies on vernalization, inheritance, and cytoplasmic factors [62–64] laid the foundation for modern hybrid breeding using CMS systems. Advances in genetic mapping and genomic selection now enable more precise selection for quantitative traits, linking molecular findings with field performance. Plant Pathology studies, though fewer, remain crucial to sustain productivity, having identified loci for resistance to nematodes, fungi, viruses, and insect vectors [65–68]. Integration between genetic mapping, virology, and entomology offers opportunities for more comprehensive disease management strategies.

The methodological trajectory in carrot genetics is parallel to the global trends on plant molecular research. Isozyme and linkage maps [69] were followed by RFLP, RAPD, AFLP, and SSR markers, and gradually replaced by SNP genotyping and NGS-based analyses. These transitions increased the resolution and facilitated more detailed studies with insights into metabolic and regulatory pathways. The growing application of functional genomics and metabolomics [14,15,70] has deepened our understanding of secondary metabolism, including terpenes, polyacetylenes, phenolics, sugars, and pigments on carrots. Research on herbicide resistance [71] and somatic hybridization [72] further illustrates how biotechnological tools diversify breeding possibilities in this crop. Integrative metabolomic-transcriptomic studies now link allelic variation to metabolite accumulation [14,70], while proteomics adds another layer of information on post-translational regulation and stress response [16]. Together, these approaches advance a biological systems-level understanding that supports breeding efforts to enhance nutritional quality and flavor of carrots.

It is important to note that the bibliometric dataset used in this study was restricted to publications written in English and indexed in Web of Science. Consequently, the co-authorship and country-level networks primarily represent collaborations within the English-language scientific community. Studies published in other languages, as well as regional journals with limited indexing, may therefore be underrepresented, which should be considered when interpreting geographic and institutional patterns of collaboration.

The collaboration network topology has concrete effects on the emergence and spread of research themes and on its scientific impact. Dense co-authorship clusters tend to accelerate local uptake of particular methods and concepts because frequent collaboration increases mutual citation, facilitates hands-on methodological training, and produces coherent local research agendas. By contrast, weak links between regions reduce thematic cross-fertilization and can slow the diffusion of methodological innovations. In practical terms, nodes with high Total Link Strength play an outsized role in disseminating new techniques and shaping community norms. When these hubs are inward oriented, important advances may remain concentrated within specific regions or language communities rather than becoming part of a global research conversation.

The dense intranational connectivity that we observed in China likely reflects several interacting causes. Domestic funding programs and large-scale national projects create incentives for internal consortia and to foster collaboration within the country. Language and publication practices, including the use of national journals and Chinese language outlets, reduce visibility in anglophone citation networks. Data management and repository policies that favor domestic infrastructures may also limit seamless international reuse. To

promote greater integration while preserving the strengths of national networks, we recommend practical measures such as funding calls that require international co-leadership, mobility and joint training programs that foster methodological exchange, adoption of interoperable metadata standards and incentives to deposit primary data in widely used international repositories, and thematic workshops or special journal issues that encourage joint submissions from international teams.

The distribution of journals reinforces the integration of carrot genetics into mainstream plant breeding and molecular biology communities, as reflected in outlets such as Theoretical and Applied Genetics, Euphytica, Plant Breeding, Molecular Breeding, and Frontiers in Plant Science. Prominent contributors appear across several of these journals, exemplifying sustained collaboration within a compact but active research network.

The methodological analysis indicates that while classical PCR-based molecular markers are still widely used, omics approaches are yet limited. Genomics and transcriptomics prevail, but metabolomics and proteomics remain underrepresented. Expanding multi-omics integration could substantially strengthen the comprehension of the genotype–phenotype interaction and accelerate the practical application of genomic knowledge. This need is particularly relevant for connecting metabolic and agronomic traits, where systems-level data can guide both breeding and conservation priorities.

Building on the thematic and methodological gaps identified in this scientometric assessment, we propose five priority areas to increase the translational impact and global coherence of carrot genetics research. First, a systematic integration of multi-omics datasets is needed to connect sequence variation with expression profiles and metabolic phenotypes. Coordinated efforts combining genomics, transcriptomics and metabolomics will enable more robust genotype-to-phenotype inference. Second, a comprehensive genetic characterization and conservation sequencing of wild *Daucus* germplasm should be prioritized to expand allelic resources for breeding and conservation; targeted sequencing of wild relatives and underutilized landraces will inform ex situ and in situ strategies.

Third, the development and validation of carrot-specific transformation and gene-editing protocols are essential to enable functional genetics and accelerate trait validation. Standardized transformation pipelines and shared protocols will reduce technical barriers. Fourth, the establishment of translational pipelines that explicitly integrate molecular markers into breeding decisions is required. This includes standard protocols for phenotyping, marker-assisted selection and genomic selection frameworks tailored to root quality, pigment composition and stress resilience. Finally, initiatives to strengthen cross-regional collaboration and harmonize metadata standards will enhance reproducibility and data reuse. Practical means for that include multinational funding calls with shared leadership, mobility and training programs, interoperable metadata schemas, and incentives for deposition of primary data in international repositories. Collectively, these priorities address methodological needs and structural barriers and create a roadmap to translate molecular discoveries into resilient and high-quality carrot cultivars.

5. Conclusions

To translate the scientometric findings into actionable research agendas, we clearly connect the main challenges identified in this study with targeted priorities. First, the observed disconnection between foundational plant biology research and effective conservation or applied breeding highlights the need for integrative pipelines that link molecular discovery to practical outcomes. Second, the limited uptake of omics approaches within breeding programs indicates a gap between methodological capability and translational use. Third, the underrepresentation of wild *Daucus* germplasm constrains the available allelic diversity for both conservation and pre-breeding efforts.

Addressing these challenges requires coordinated, concrete actions. We recommend systematically integrating multi-omics datasets with standardized phenotyping and analytical frameworks to strengthen genotype-to-phenotype inference and support marker-assisted and genomic selection. We further recommend a focused program of genomic characterization for wild relatives and underused landraces to expand allelic resources and to inform evidence-based conservation and sampling strategies. Finally, we urge the establishment of collaborative frameworks to foster cross-regional data sharing and methodological harmonization, including interoperable metadata standards, multinational funding mechanisms that require international co-leadership, and training exchanges to disseminate best practices. Together, these endeavors will accelerate the translation of molecular insights into resilient, high-quality carrot cultivars and will improve the global coherence of research and conservation efforts in *D. carota*.

Supplementary Materials: Supplementary Material associated with this article, including the complete bibliometric dataset used to generate the figures, is available on Figshare (<https://figshare.com/s/02d8756d189469f038e6>), as specified in the Methodology section.

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