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Review article

Exploration of advanced omics tools and resources for the improvement of industrial oil crops

Badal Mahakalkar [a,1], Virender Kumar [a,1], Sreeja Sudhakaran [a,1], Vandana Thakral [a], Sanskriti Vats [a,b], Rushil Mandlik [a], Rupesh Deshmukh [a], Tilak Raj Sharma [c], Humira Sonah [a,*]

[a] Department of Biotechnology, Central University of Haryana, Mahendragarh, Haryana, India
[b] Department of Plant and Environmental Sciences, University of CopenhagenThorvaldsensvej, Frederiksberg C, Denmark
[c] Division of Crop Science, Indian Council of Agricultural Research, New Delhi, India

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ABSTRACT

The rapid advancement in the field of omics approaches plays a crucial role in the development of improved industrial oil crops. Industrial oil crops are important for many sectors like food processing, biofuels, cosmetics, and pharmaceuticals, making them indispensable contributors to global economies and these crops serve as vital elements in a multitude of industrial processes. Significant improvements in genomics have revolutionized the agricultural sector, particularly in the realm of oil crops. Cutting-edge advancements have facilitated the efficient sequencing of genomes for key commercial oil crops. This breakthrough not only enhances our understanding of the genetic makeup of these crops but also empowers breeders with invaluable insights for targeted genetic manipulation and breeding programs. Moreover, integrating transcriptomics with genomic data has assisted in a new era of precision agriculture. This approach provides an in-depth understanding of molecular mechanisms involved in traits of interest, such as oil content, yield potential, and resistance to biotic and abiotic stresses. Proteomics methods are instrumental in deciphering the intricacies of protein structure, interactions, and function, while metabolomics and ionomics shed light on the intricate network of metabolites and ions within biological systems. Each omics discipline offers unique insights, and their integration holds the promise of enriching our understanding and furnishing invaluable insights for enhancing oil crops. This review delves into the efficacy and constraints of various omics approaches in the context of refining industrial oil crops. Moreover, it underscores the importance of multi-omics strategies and explores their convergence with genetic engineering techniques to cultivate superior oil crop varieties.

1. Introduction

Oil crops have garnered significant attention in the field of industrial applications, and the incorporation of omics-scale methods has facilitated significant advancements in enhancing industrial oil crops. The integration of these omics techniques has opened new avenues for enhancing the properties of oil crops which in turn optimize their utility in various industrial applications. Further, the utilization of omics methods improves the cultivation and utilization of oil crops on an industrial scale. For instance, crop-based oil is a useful and adaptable resource that has applications in various industrial processes such as lubrication, energy production, food processing, cosmetics, and chemicals. These oils are widely used due to their widespread availability, cheap rate, and efficient properties.

Industrially important edible oils such as palm oil, coconut oil, rapeseed oil, sunflower oil, and soybean oil, play a crucial role in various applications. For instance, palm oil being easily available and due to its high stability, is used as a biofuel which replaces the dependency on non-renewable energy sources (Parveez et al., 2021). Additionally, it is used in the production of detergents, cosmetics, and lubricants (Parveez et al., 2021). Sunflower oil, commonly used in food processing, also plays a significant role in various industries by contributing to the production of paints, varnishes, cosmetics, biofuel, and lubricants (Ramadhas et al., 2004). As we go further on to non-edible oils, castor oil is employed in the production of lubricants, hydraulic fluids, paints, coatings, plastics, and adhesives (Yeboah et al., 2020). According to FAO statistics 2021 (htt

* Correspondence to: Department of Biotechnology, Central University of Haryana, Mahendergarh, Haryana 123031, India.
E-mail address: biohuma@gmail.com (H. Sonah).
[1] Authors have contributed equally.

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ps://openknowledge.fao.org/server/api/core/bitstreams/522c9fe3-0fe2-47ea-8aac-f85bb6507776/content), global oil crop production is 12 % of the world's agricultural crop production within the commodity group. Further, in the main commodity category, oil palm contributes 4 %. Oilseeds Global Market Report 2024 showed an increase of 9.6 % compound annual growth rate (CAGR) from 2023 to 2024 (https://www.thebusinessresearchcompany.com/report/oilseeds-global-market-report). India in terms of total oil crop production showed an increase in yield despite a decrease in the harvested area between 2018 and 2020. Vegetable oil has one of the greatest trade share, comprising 41 % of all agricultural products. Due to rising local demand and limited options for production development, India remains one of the world's largest importer of vegetable oil.

Significant advancements have occurred in biochemical based omics technologies, facilitating the elucidation of biosynthetic pathways in crops (Singh et al., 2022). Contemporary genetics and omics methodologies have become indispensable for comprehending gene expression and functionality (Chaudhary et al., 2015b; Joshi et al., 2024). Omics techniques serve as a bridge between gene regulation and associated genetic markers by identifying genes and biochemical pathways that are directly connected to key traits (Okoye et al., 2024). In general, oil yield results from a complex interplay of various biological processes, many of which manifest as observable physical traits that collectively influence yield and can be quantified for parental selection. However, the genetic contributions to these processes vary across populations and environments, complicating observations in traditional breeding trials and the creation of genetic marker tools. Omics technologies, like transcriptomics, proteomics, and metabolomics, allow for the simultaneous analysis of numerous biochemicals, aiding in the understanding of biological processes associated with physical traits, and have found extensive application in both plant science and human health research (de Sousa et al., 2023; Zhao et al., 2024). Omics techniques have also been employed to uncover genes associated with yield in key crop varieties, including those of oil crops (Chen et al., 2024; Li et al., 2024; Li et al., 2023b). In recent developments, biochemical levels have been increasingly associated with genetic markers, revealing their connections to physical traits such as those found in brassica plants (Ali et al., 2023), soybean (Liu et al., 2023), and maize (Sethi et al., 2023). These investigations affirm the genetic regulation of biochemical levels within cells and enhance our comprehension of the interconnected biological mechanisms contributing to crop yield. This review provides comprehensive insights into various omics approaches, highlighting their advancement, efficacy, constraints, and the significance of adopting muti-omics approaches.

2. Omics approaches: recent advancements and challenges

Technological advancements enable extensive studies that offer a holistic understanding at the omics scale. Omics is the branch of science that unveils information about biological systems through the study of different molecules and their interactions. Multi-omics approaches include genomics, transcriptomics, metabolomics, ionomics etc. In recent times, the field of omics has witnessed notable advancements, offering new insights into crop development and production. These advancements include Next Generation Sequencing (NGS) methods and Single-Cell Genomics and epigenomics. Next Generation Sequencing includes the latest genome sequencing technologies like Illumina and Nanopore, while Single-Cell Genomics involves sequencing single-cell RNA (scRNA) to study gene expression (Stuart et al., 2019). Single-cell sequencing technologies for genomics and epigenomics have created new opportunities to explore cellular heterogeneity across various biological processes. For instance, single-cell genomics and epigenomics can be successfully utilized in plant research such as meiotic recombination, epigenetic reprogramming, spermatid chromosome fragmentation, and chromatin conformational changes during fertilization (Luo et al., 2020). Furthermore, the emergence of recombinant DNA (rDNA) techniques, coupled with the completion of genome projects of plants, has led to the advancement of genetic engineering methods. These methods could greatly reduce the time required to develop new plant cultivars using cis-genesis, intra-genesis, and trans-genesis techniques (Rauf et al., 2023; Vaikuntapu and Kumar, 2023). Despite the great potential of genetic engineering, public resistance to genetically modified organisms (GMOs) has hindered the adoption of these technologies by consumers. However, the accessibility of complete genome sequences for crop plants has enabled significant progress in plant improvement while reducing environmental risks (Ali and Zhang, 2023). Advancements in DNA sequencing techniques have greatly enhanced our capacity to utilize genomics-based approaches for crop improvement (El-Esawi, 2024; Wendel et al., 2016), To date, the entire genome has been sequenced for several oilseed crops, including cotton (Lee et al., 2006; Wang et al., 2015), maize (Martienssen et al., 2004), soybean (Alsanie, 2021), rapeseed (Hu et al., 2011), and sunflower (Kane et al., 2011). The accessibility of the oilseed crops reference genome and the rapid advancements in other omics technologies, have significantly eased the process of gene cloning and functional analysis in oilseed crops. A recently developed panomics platform, used to integrate complex omics data, has emerged as an effective tool for studying crop plants (Weckwerth et al., 2020). Further, the integration of omics-driven new breeding techniques (NBTs) alongside genetic engineering holds promise as a viable alternative for enhancing the development of superior crop varieties. However, efficient high-throughput techniques for studying oil crops face challenges, such as the need to remove noise, normalizing the data, handling missing values, and further statistical analysis for result interpretation (Yang et al., 2021). Omics approaches also present challenges like data integration, standardization, and interpretation. For instance complex and polypoid genomes of oilseed crops like rapeseed and sunflower makes genome assembly, annotation, and interpertation difficult (Yang et al., 2021). Inadequate reference genomics and limited functional annotations for many oilseeds plants limits the utility of omics studies. By adressing current limitations of omics technologies in oilseed crops through intergation of muti-omics approaches and innovative technologies will accelarate future avancencement in breeding of improved oil crops varieties. The efficient analysis of high-throughput omics-scale data in the context of understanding oil crops can be considerably aided by tailoring crop specific cutting-edge computational tools, algorithms, and standardized methods.

3. Genomics advances in industrial oilseed crops

Genomic research has undergone significant strides, with advancements spanning from initial genome sequencing to cutting-edge technologies such as CRISPR-Cas9 for targeted trait improvement (Fig. 1). The exponential demand for raw oil in both consumption and industries, coupled with the limited availability of fossil oil resources, urges the need for the improvement of oilseed crops. Interestingly, oil crops (i.e., soybean, palm, peanut, cotton, brassica, sunflower, castor, and linseed) hold the potential to fulfill increasing demand. With the advent of NGS technologies, genome sequencing was revolutionized, providing a cost-effective and high-throughput method to decipher the genetic codes of oilseed crops efficiently. The integration of genomic information into traditional breeding programs marked a pivotal shift in the field, as evidenced with the release of cultivars showcasing enhanced traits such as higher yield, resistance to pests and diseases, and improved oil composition (Cao et al., 2017). Also, functional genomics emerged as a powerful approach, aiming to understand gene function at a functional level. Cumulatively these genomics strategies marked the transition from theoretical insights to practical applications in agriculture, benefiting farmers and industries reliant on oilseed crops (Vollmann and Rajcan, 2010; Wittkop et al., 2009).

3.1. *Whole genome sequencing and re-sequencing efforts for industrial oil crops*

The genome of most oilseed crops, including soybean, oil palm, peanut, brassica, cotton, linseed, sunflower, sesame, castor, *Jatropha curcas* have been sequenced. These genomes are sequenced using a

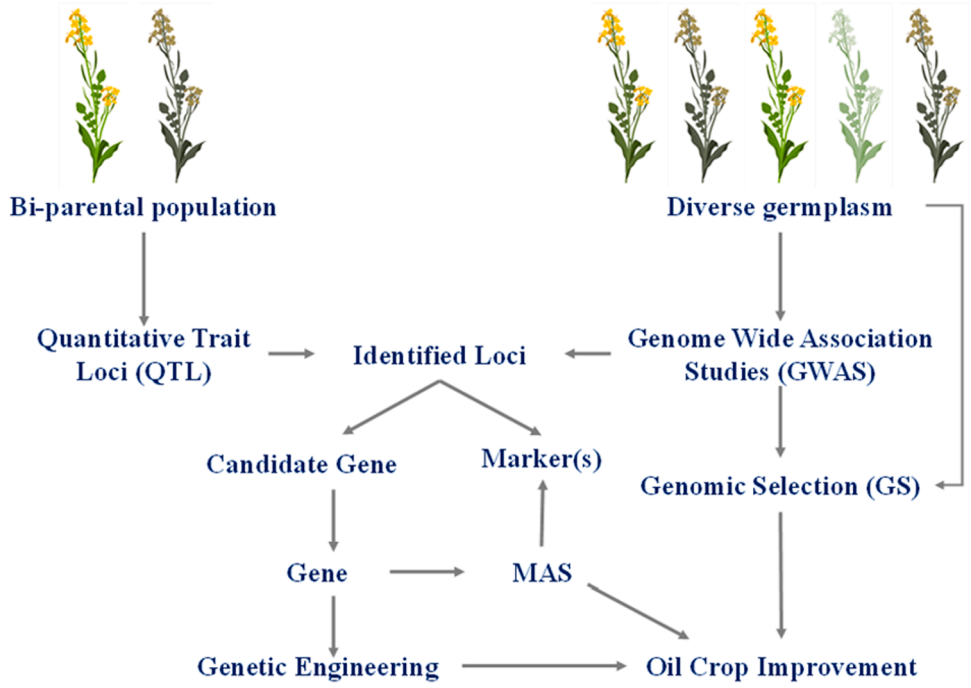

Fig. 1. Different genomic approaches utilizing genetic resources and genomic tools for the crop improvement. Quantitative trait loci (QTL) mapping explores bi-parental populations whereas Genome wide association studies (GWAS) and genomic selection (GS) strategy largely explores diverse germplasm. Information generated through QTL mapping and GWAS is further utilized to identify the genes and development of markers for marker assisted selection (MAS) based breeding.

combination of advanced high throughput sequencing techniques such as Illumina, Roche Genome Sequencer, Nanopore, and PacBio. For instance, Ha et al. (2019) employed PacBio long reads and Illumina short reads for WGS and high quality genome assembly of *J. curcas*. Furthermore, a chromosome level genome sequence assembly was reported in wild castor accession WT05 (Lu et al., 2022). However, sequencing a single cultivar/accession is not enough to provide full genomic DNA fingerprints. There are thousands of germplasm accessions, including wild and cultivated varieties, representing the genomic diversity of species probably carrying the same set of genes with nucleotide variations. Thus, whole genome re-sequencing (WGRS) provides information on the gene pool and aid in constructing the pan-genome of a species (Arsenault-Labrecque et al., 2018; Kumawat et al., 2022). The advancement of NGS has made sequencing more cost-effective, enabling large-scale genome resequencing. Most oilseed crops are re-sequenced for the identification of various complex and domestication-related traits. WGS has been utilized for various genomics techniques like QTLs mapping, Genome wide association studies (GWAS), GS, and genomic diversity identification. For instance, the whole genome resequencing of 31 wild and cultivated soybeans identified significant genomic diversity in wild type, high linkage disequilibrium, and $>$ 200k single nucleotide polymorphisms (SNPs) (Lam et al., 2010). Later, WGS of 302 accessions identified regions associated with domestication-related traits, revealing several loci related to seed oil content and fatty acid biosynthesis genes (Zhou et al., 2015). Many WGS studies in soybean and other oilseed crops have been conducted, revealing different genes associated with important traits. Similarly, the WGRS of peanuts helps to better understand polyploidization, domestication, and center of origins (Bertioli et al., 2019; Zhuang et al., 2019). Furthermore, the WGRS of 62 varieties of date palms provides insights into population structure, evolutionary history, and diversification (Hazzouri et al., 2015). However, challenges such as duplication, heterozygosity, ploidy, and repetitive DNA sequence remain in many genomes. In the future, further extensive study of WGS will contribute to generate high quality genomes and enhance the understanding of complex traits, particularly in industrial oil crops.

3.2. *Quantitative Trait Loci (QTL) mapping efforts for oil quality and quantity-related traits*

Many efforts have been made for the identification of QTLs related to seed oil quality and quantity in different oilseed crops (Chandrawati and Yadav, 2017; Li et al., 2021; Ramchiary et al., 2007; Zhao et al., 2008). In peanut, QTLs and *FAD2* homologs significantly contributing to total oil content and three vital oil quality traits (linoleic acid, oleic acid, oleic/linoleic ratio) have been mapped using two different biparental populations (Pandey et al., 2014). Similarly, Pérez-Vich et al. (2004) identified three minor QTLs on linkage groups LG3, LG11, and LG13 that are responsible for increased stearic acid content in sunflower seed oil. Furthermore, they observed QTL on LG11 is associated with the SAD6 locus, suggesting an association with the increased stearic acid content in the oil. Markers associated with these QTLs can be used as a powerful tool for breeding new sunflower varieties with elevated oil quality. In *Brassica juncea*, QTLs significant for erucic acid content, oil, and seed protein contents were identified. Tightly linked QTLs (SP-A1, SP-A9, SP-B4, O-A1, O-A9, AND O-B4) with opposing effects impose a challenge for the improvement of negatively correlated oil and seed protein content, while unlinked QTLs (SP-B6 and SP-C) offers simultaneous improvement of both traits (Mahmood et al., 2006). Also, a recent study used 11,398 SNP markers in the RIL population (*G. soja* x *G. max*) to identify QTLs for seed oil and components (Yao et al., 2020). The bottleneck arises from the negative correlation of oil and fatty acids content QTLs with other agronomic important traits (Montero et al., 2008; Montoya et al., 2013; Smallwood et al., 2017; Yan et al., 2011; Zhu et al., 2019) along with their interaction with other QTLs and environment. These complexities of QTLs make it difficult to identify candidate genes and use them for MAS (Deshmukh et al., 2014). A statistical method based on previous QTL analysis would help in the fine mapping of candidate genes. Several meta-QTLs were identified in soybeans (Kumar et al., 2022; Qi et al., 2011; Qi et al., 2018; Qin et al., 2018) which helped in the fine mapping of the candidate gene. Thus, meta-analysis in other oilseed crops would also be helpful for fine mapping of robust QTLs. Further, the limitation of the conventional QTL

mapping method is use of bi-parental mapping population (F2, Backcross: BC, Recombinant inbreed line: RIL, double haploid: DH) made between contrasting trait which takes 2–8 years for development. Other limitation of these populations is having low allelic diversity and cannot estimate the minor allele effect.

3.3. Genome-wide association studies (GWAS) focusing on traits related to oil quality and quantity

The genomic sequencing of numerous oilseed crops has laid the foundation of genotyping followed by GWAS, facilitating the correlation between high-throughput SNP markers and the phenotypic variations present within diverse germplasms (Sonah et al., 2013; Sonah et al., 2015; Vats et al., 2022). This comprehensive approach illuminates the expansive genomic diversity inherent in these crops, thereby facilitating the precise delineation of QTLs (Passianotto et al., 2017). GWAS plays an important role in understanding complex QTLs for oil composition traits. Notably, GWAS in *B. napus* unveils a novel locus on chromosome A5, proven to enhance seed oil content by 1.5–1.7 % (Liu et al., 2016). Similarly, in Chinese cultivars of soybeans, a stable QTL confined to a small region from 38.13 to 38.57 Mb on chromosome 05 was reported for seed oil content by combining linkage mapping and GWAS (Cao et al., 2017; Kumar et al., 2022). Further, Babu et al. (2021) conducted GWAS on 310 African oil palm germplasm and identified 43 significant QTLs related to oil yield traits, which in turn can provide insights into genetic basis of important traits in oil palms (Babu et al., 2021). Likewise, GWAS on 468 individuals of *Eucalyptus polybractea* identified 2.39 million SNPs associated with 12 traits related to terpene yield including eight terpene concentration related traits and four biomass related traits (Kainer et al., 2019). Repeated GWAS on a set of populations in different environments also helps to understand genotype-environment interaction. Most oilseed crops are self-pollinated, and responsible for high linkage disequilibrium (LD) (Sonah et al., 2014). The diverse germplasm has a large number of meiotic events and rapid LD decay compared to the bi-parental population. Several GWAS studies focusing on QTL mapping of oil in various oilseed crops have been conducted. These studies identified several genes associated with seed oil quality and quantity. For instance, GWAS involving 705 diverse lines of sesame identified 547 QTLs, including six multi-environmental QTLs and 76 pleiotropic QTLs associated with different traits related to seed yield. They also identified two novel genes *SiLPT3* and *SiACS8* which play a role in controlling seed traits such as capsule length and number (Zhou et al., 2018). In rapeseed, GWAS of eight seed quality traits including fatty acid contents (palmitic, steric, eicosenoic, erucic oleic, linoleic acid), oil content, and protein content was performed by Tang et al. (2019). Their findings emphasize the intricate positive and negative correlations among these seed quality traits, which provides valuable information for crop selection strategies. Further, Teh et al. (2016) conducted GWAS in oil palm and identified three key loci for high oil-to-dry mesocarp content (O/DM), which was further validated by breeding trial (Deli x AVROS), revealing a 4 % higher O/DM in palms. Many studies highlight the significance of GWAS in detecting the genomic regions associated with seed weight, seed yield, and oil quality, thereby providing valuable insights for breeding improvement in oil seed crops (Li et al., 2014; You et al., 2018). Further, the use of NGS boosts the GWAS studies, which generate thousands of cost-effective SNP markers across a large number of accessions (Sonah et al., 2015). The gene expression relationship along with GWAS is a powerful approach for the identification of expression QTLs (e-QTL). While this approach has been utilized in various crops, no studies were available for oilseed crops, especially for seed oil-related traits. The transcriptomics and qRT-PCR are useful for the confirmation of genes identified by GWAS, with subsequent validation using overexpression and silencing (Ma et al., 2019). The gene expression analysis present in GWAS QTL reveals the identified candidate gene in cotton (Islam et al., 2016). Phenotypic variation in traits under different environmental conditions significantly impacts the precise identification of QTL. Despite this challenge, most GWAS studies utilized a multi-environment approach. For instance, Pandey et al. (2014) studied 50 agronomic important traits of peanuts across 457 diverse environments, leading to the identification of 524 QTLs with a wide range of phenotypic variance. These types of studies would result in better understanding and breakthroughs of the bottleneck of breeding programs. Thus, the integration of GWAS with other techniques would be more convenient for robust QTL/gene identification. The MAGIC and NAM populations were employed for gene identification using GWAS in many crops (Gangurde et al., 2022; Islam et al., 2016). These populations provide the genetic diversity of different parents within the mapping population. The number of molecular markers, population structure, and linkage disequilibrium are some of the GWAS limiting factors that can result in false positive results. However, several strategies were developed to reduce the false positive results. The combination use of population structure kinship and linkage disequilibrium is very helpful in minimizing false positive results of GWAS. Most GWAS studies utilize a mixed linear model using kinship. The meta-GWAS analysis would result in an increase in the accuracy of GWAS as the number of studies is increasing in most crops.

3.4. Opportunity and challenges for the implementation of genomic selection

Initially, MAS was implemented for the indirect selection of desired traits, however, it proves challenging for complex quantitative traits. In marker-assisted selection, the less numbers of markers used were mostly inked to Mendelian or major QTLs. However, several minor QTLs also have a significant role in phenotypes of complex traits. The advancement of NGS (viz. WGS, WGRS, GBS, and transcriptome and epigenetic analysis) generates large numbers of sequencing data throughout the genome of several hundred accessions of a species in a cost-effective manner and ultimately generates thousands of SNP markers throughout the genome (Sonah et al., 2015). These several thousand markers can successfully calculate the genomic estimated breeding value (GEBV) of the training population. The phenotype and genotypes of the training population were used for the calculation of GEBV by applying different statistical models. This GEBV will be used to identify superior individuals in the breeding population for the next generation (Bhat et al., 2016). However, the accuracy of GEBV depends on many factors including the number of markers, environment, epistasis interaction, phenotype, and size of the training population (Arruda et al., 2015; Crossa et al., 2017; Isidro et al., 2015; Ravelombola et al., 2020). However, some studies also reported no significant accuracy among the different statistical models. The phenotype has a drastic effect on GEBV than the markers data (Marulanda et al., 2015). The multi-environment phenotype with high throughput phenotype techniques, gives precise phenotype of several thousand plants in a day without manual intervention. This coupled with the training population can result in an accurate estimation of GEBV (Singh et al., 2019). The markers associated with complex traits were reported to give more accuracy for GEBV than all markers (Li et al., 2018). In most studies, the GEBV of the training population was validated in a similar population and same generation, so the accuracy of prediction for the next generation was not known, as in crop breeding selection is made at every generation. The GS is superior to MAS even with less accuracy than GEBV (Heffner et al., 2010). Similarly, another study of 391 double haploid populations of Brassica with less accuracy of GEBV reported, GS can be valuable for complex traits. The GS can identify superior individuals even in drastic environmental conditions (biotic or abiotic stress) as the phenotype is predicted based on genotypes. The GS reduces the cost of phenotyping of a large population, which is one of the major bottlenecks of breeding programs. GS successfully implemented for quality and quantity related as well as for many disease resistance traits. Several studies reported the successful implementation of GS in oilseed crops and induced genetic

gain in next generation. In soybean, GS for yield and seed protein content of early and late line reported to check accuracy of different statistical model and no significant difference was observed among models (Duhnen et al., 2017).

The demand for vegetative oil for cooking and industries can be fulfilled by applying GS in various breeding programs, and no study of GS is available for seed oil content. The biochemical phenotype of seed oil and other seed components is costly, so GS would be more cost-effective in industrial oilseed crops to fulfill the oil demand. Perhaps GS is very useful but the development of a large number of molecular markers through sequencing is still costly and unaffordable by many labs around the world. GS would be cost-effective for those labs that maintain several thousand germplasm lines every year and multiple years data would result in more precise GEBV. The sharing of GEBV, statistical models, and valuable problematic information among the lab can result in the successful implementation of GS. The GS implementation in cross-pollinating is still challenging.

3.5. Limited genomics progress with non-edible industrial oil crops

Genomics has transformed agriculture, providing a promising pathway for improving crop productivity, resilience, and quality. However, advancements in the genomics of non-edible industrial oil crops, such as jatropha, castor bean, and camelina, have lagged behind those of major food crops like rice, wheat, and corn (Bajar et al., 2023; Koçar and Civaş, 2013). One of the primary reasons for this disparity is the difference in economic importance and research investment between edible and non-edible crops (Jha et al., 2012). Food crops have attracted increased attention because of their direct impact on global food security and human nutrition (Varzakas and Smaoui, 2024). Consequently, they have garnered substantial funding and research attention, which has led to significant advancements in their genomic understanding and manipulation. Conversely, non-edible industrial oil crops have been viewed as niche crops with limited immediate economic impact (Ciastowicz et al., 2024). While they show promise for biofuel production, industrial applications, and biodiesel manufacturing, their market size and commercial viability have remained relatively modest compared to major food crops (Arshad et al., 2023; Khurana and Bhatnagar, 2024; Kichonge and Kivevele, 2023). As a result, research funding and efforts directed towards understanding their genomics have been comparatively limited.

Moreover, non-edible industrial oil crops frequently present distinct challenges due to their genetic complexity, limited genomic resources, and specialized breeding techniques (Román-Figueroa et al., 2023). Unlike major food crops with extensive genetic and genomic databases, these industrial oil crops have received less attention from the scientific community. The pace of genetic improvement efforts in these crops is hindered by the limited availability of genomic resources, including reference genomes, genetic markers, and comprehensive trait databases (Duan et al., 2023; Li et al., 2023a). Another factor contributing to the slow progress in genomics of non-edible industrial oil crops is the absence of cohesive research networks and collaborations. Unlike the well-established research communities for major food crops, the scientific community focused on non-edible industrial oil crops is relatively small and fragmented. This fragmentation limits the sharing of resources, knowledge, and best practices, thereby hindering the advancement of genomic research in these crops. Nonetheless, despite these challenges, there have been some notable efforts in recent years to enhance the genomic understanding of non-edible industrial oil crops. Researchers are now employing cutting-edge genomic tools and technologies, including next-generation sequencing, genome editing, and high-throughput phenotyping, to uncover the genetic foundations of key traits like yield, oil content, and stress tolerance (Hussain and Fredua-Agyeman, 2023; Roshna et al. n.d.; Sachan et al., 2024). While genomics has greatly enhanced our ability to understand and manipulate major food crops, progress in non-edible industrial oil crops has lagged behind. This slower pace is due to factors such as limited research investment, genetic complexity, and fragmented research communities. However, by addressing these challenges and promoting collaborative research efforts, we can unlock the genetic potential of these crops and drive innovation in sustainable agriculture and renewable energy.

4. Transcriptomics efforts in industrial oil crops

The RNA-seq analysis of seeds at different stages of development and seed compartments would help to understand the gene regulation and tissue-specific activity (Deshmukh et al., 2014). The RNA-seq analysis at five different stages of soybean seed development identified 124 differentially expressed genes, that significantly affect seed oil content (Yang et al., 2019). Further, the integration of transcriptomics with other techniques viz. QTL mapping and GWAS would be very effective for gene identification. The combined study of GWAS and transcriptomics, involving two varieties with low and high oil content, reported six genes significantly associated with fatty acid synthesis in flax seeds (Xie et al., 2019). RNA-seq analysis of 49 peanut accessions deferrer in oil content reported 5458 differentially expressed genes (Wang et al., 2018). Tissue-specific RNA-seq analysis of transgenic castor has been studied to understand the ricin oleic acid biosynthesis (Brown et al., 2012). The environmental effects on phenotype have been extensively documented for most traits.

Several studies are available in oilseed crops showing differential expression of genes in different conditions. These studies made a large number of publically available transcriptomics data accessible at the National Center of Biotechnology Information (NCBI) and European Nucleotide Archive (ENA)- EMBL-EBI. This data can be used for co-expression network development. Similarly, the Soybean Functional Genomics Database (SFGD) has been developed from microarray and RNA-seq data comprising 23267 genes and 1873 miRNA-target pairs. Additionally, it includes information on 221 enzymes and over 1550 genes from a group of acyl-lipid pathways (Yu et al., 2014). The public RNA-seq data along with the digital differential display, and microarray identified 184 genes specific to seed (Yin et al., 2014). However, transcriptomics studies specific to seed-related are not very much, and in the future, more transcriptomics studies would help to better understand the complexity of gene networks. In the future, single-cell transcriptomics will help in a precise understanding of gene expression in different cells of tissues and environments.

5. Proteomics efforts in industrial oil crops

Proteomics is a contemporary systems biological approach that helps to understand the structure, expression, interactions, and functions of proteins. It represents a significantly more intricate approach than genomics. (Domon and Aebersold, 2006; Lander et al., 2001). Proteomics methods directly examine the changes in protein expression and provide the exact expression profile of the target. Nowadays, proteomic approaches are used to improve and increase the yield of industrial oil crops on a large scale (Table 1). Conventional proteomic techniques such as various types of chromatography are used for the purification of proteins (Hu et al., 2013), and enzyme-linked immunosorbent assay (ELISA) and western blotting are used for the detection of selective proteins (Brun et al., 2005; Kurien and Scofield, 2006; Lequin, 2005). Further, for the separation of complex protein samples gel-based proteomic techniques such as Sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE), and two-dimensional differential gel electrophoresis (2D-DIGE) are used (Sammour, 1999). Mass spectrometry (MS) was used for the quantitative profiling of proteins whereas nuclear magnetic resonance (NMR) spectroscopy was used to predict the protein three-dimensional (3D) structure (Sinha and Mann, 2020; Yee et al., 2002). Advancement in proteomics-based technologies leads to discoveries in the fields of drug development, agriculture, and industrial applications.

Table 1
List of studies carried out in industrial oil crops using proteomic tools.

Industrial Oil crop	Botanical name	Proteomic approaches	Findings	References
Canola	*Brassica napus*	2D-DIGE	Identified 165 differentially expressed proteins in germinating seeds. Proteomic analysis showed that seeds with higher oil content show higher metabolic activity.	(Gu et al., 2019)
Canola	*Brassica napus*	iTRAQ labeling coupled to LC-MS/MS	Identified 1976 proteins involved in drought stress response.	Koh et al. (2015)
Coconut tree	*Cocos nucifera*	iTRAQ	Leaf proteomic analysis showed that the aromatic coconut variety down-regulate several differentially expressed proteins and is cold-sensitive compared to the Hainan Tall variety which up-regulates stress-responsive proteins	(Yang et al., 2020)
Flax	*Linum usitatissimum*	SDS-PAGE, LC-MS	Identified several proteins that are involved in the protein destination, primary metabolism, storage, and energy.	(Barvkar et al., 2012)
Oil palm	*Elaeis guineensis*	iTRAQ labeling coupled to 2D-LC and MALDI-TOF/ TOF MS	Temporal changes in the mesocarp proteomes were identified, that were involved in the palm oil production	(Loei et al., 2013)
Soybean	*Glycine max*	2-DE, MALDI-TOF/ TOF MS, western blotting	Stress proteins are not expressed in high-oil soybean and it contain more oleoin and vitamin E.	(Xu et al., 2015)
Sunflower	*Helianthus annuus*	2D-DIGE, LC-MS	Oil content in seeds was linked with carbohydrate metabolism and protein synthesis.	(Hajduch et al., 2007)
Tree peony	*Paeonia ostii*	Tandem mass spectrometry (MS), multiple reaction monitoring (MRM)	Integrated proteomics and the transcriptomic study revealed differences in the number and abundance of differentially expressed genes (DEG) and differentially expressed proteins (DEP) but a high level of similarity was observed in expression patterns and metabolic pathways	(Wang et al., 2019)

Proteomic approaches are widely used to study oil-related traits in industrial oil crops like soybean, sunflower, and *Brassica* to improve the quality and yield. For instance, proteomic analyses such as 2D-DIGE, and liquid chromatography-mass spectrometry (LC-MS) were employed to analyze near-isogenic sunflower varieties with varying seed oil traits. The findings revealed that high-oil varieties show an up-regulation of plastid phosphoglycerate kinase, fructokinase, and enolase proteins. Conversely, low-oil lines showed up-regulation of cytosolic phosphoglycerate kinase, phosphofructokinase, and cytosolic phosphoglucomutase (Hajduch et al., 2007). Similarly, 2D-DIGE was used to identify differentially expressed proteins in germinating seeds of *B. napus* with differing oil content to understand the seed germination process under high and low oil content (Gu et al., 2019). Koh et al. (2015) identified proteins in *B. napus* expressed during stress using isobaric tags for relative and absolute quantitation in combination with the liquid chromatography-tandem mass spectrometry (iTRAQ-LC-MS/MS) proteomic method. The initial proteome-wide iTRAQ analysis of *E. guineensis* fruit mesocarp was done by Loei and his team to comprehend the biological processes involved in the production of palm oil (Loei et al., 2013). Isobaric tags for relative and absolute quantitation labeling, combined with two-dimensional liquid chromatography (2D-LC) and matrix-assisted laser desorption/ionization-time of flight mass spectrometry (MALDI-TOF MS), reveal that heightened oxidative phosphorylation activity plays a critical role in augmenting storage oil production in high-yield oil palm trees (Loei et al., 2013). Comparative proteomics was employed to understand the lipid regulation between different types of oilseeds like soy, castor, rapeseed, and Arabidopsis (Hajduch et al., 2011; Houston et al., 2009). Further, proteomic analysis such as two-dimensional gel electrophoresis (2-DGE), 2D-DIGE, SDS-PAGE, semicontinuous multidimensional protein identification technology (Sec-MudPIT), nano electrospray ionization liquid chromatography-tandem mass spectrometry (nESI-LC-MS/MS), MALDI-TOF-MS were also used to determine the metabolism of seed development and regulation of oil production in rapeseed, peanut, castor, sunflower, and soybean (Hajduch et al., 2006; Hajduch et al., 2007; Houston et al., 2009; Kottapalli et al., 2008). Proteomics also revealed the protective effects of olive oil and corn oil on the regulation of the hepatic proteome during carbon tetrachloride (CCl4) induced liver injury (Wang et al., 2014). Recently, the integrated proteomic and transcriptomic analysis revealed candidate genes related to fatty acid metabolism and oil biosynthesis in *Paeonia ostii* (Wang et al., 2019). Overall proteomics approaches unrevealed several proteins which play an important role in growth, metabolism, stress response, and oil production in industrial oil crops.

6. Metabolomics -a promising approach to study industrial oil crops

Metabolomics is the comprehensive study of small intermediate products of metabolic reactions, commonly known as metabolites that naturally occur within the cell, tissue, biofluids, or whole organism.

Metabolites and their interactions within a biological system are collectively known as metabolomes. Metabolites present in the plant cell, tissue, or biofluids were analyzed using metabolomics techniques coupled with statistical and computational methods. Metabolomics is a robust, sensitive, and powerful approach, which helps to study the substrates and products of metabolism using analytical platforms like Fourier Transform-Mass Spectrometry (FT-MS), Fourier-Transform-Infrared Spectroscopy (FT-IR), NMR, Ultra-Performance Liquid Chromatography (UPLC), High-Performance Liquid Chromatography (HPLC), LC-MS, Gas Chromatography-Mass Spectrometry (GC-MS), and Capillary Electrophoresis-Mass Spectrometry (CE-MS) (Fig. 2) (Zhang et al., 2012). These techniques enable the separation, detection, quantification, and characterization of metabolites and related metabolic pathways. Advancements in currently available metabolomics techniques helped to study both known and unknown metabolites (Nakabayashi and Saito, 2013). Metabolomics is a promising approach to study the metabolites that influence the oil production and yield in oil crops. The combination of metabolomics with other modern approaches also improves the industrial oil crops metabolomics studies.

In this post-genomic era, metabolomics plays a vital role in analyzing metabolites, understanding the metabolic pathways, identifying biomarkers, biochemical effects, metabolite fingerprinting, and extensive metabolite profiling (Weckwerth, 2010). Researches efforts in metabolomics studies paved the way to improve oil quality, production, and yield-related traits in oil crops. Metabolome analysis in *Camelina sativa* helps to understand the regulation of triacylglycerol (TAG) biosynthesis and identify bottlenecks that limit seed and oil yield. The data obtained from metabolomics profiling of wide-type *Camelina* seeds helped to select two candidate enzymes (glycerol-3-phosphate dehydrogenase triacylglycerol (GPD1) and diacylglycerol acyltransferase 1 (DGAT1) in the TAG synthesis pathway, which can be manipulated to increase seed and oil yield (Abdullah et al., 2018). Understanding the dynamic changes of metabolic flux is crucial for improving both the quality and quantity of seed oil. Tan and his co-workers identified and characterized 443 metabolites from canola seeds and silique walls using GC-MS to understand the dynamic changes of seed metabolic flux during the oil accumulation process (Tan et al., 2015). Moreover, Neoh et al. (2013) studied the profile of oil palm metabolites under six fruit developmental stages to better understand the biosynthesis mechanism of lipids using multi-platform metabolomics techniques (GC-MS, LC−MS, and CE−MS). The outcome of the research provides beneficial information about regulatory mechanisms influencing enhanced oil yield in industrial oil palm populations and it also provides metabolite yield markers for breeding programs (Neoh et al., 2013). Further, the combination of GC-MS and principal component analysis (PCA) identified the variation of metabolites between non-infected and *Ganoderma boninense* infected oil palm roots. Metabolites like dimethyl benzene-1,4-dicarboxylate, methyl (9*Z*,12*Z*)-octadeca-9,12-dienoate, methyl (*Z*)-octadec-6-enoate, (*E*)-icos-5-ene, ergost-5-en-3-ol, (3β), stigmast-5-en-3-ol, (3β), stigmasterol, methyl 3-(3,5-ditert-butyl-4-hydroxyphenyl)propanoate, methyl octadecanoate, 2-(hydroxymethyl)-2-nitropropane-1,3-diol, and methyl hexadecanoate which plays role in pathogen defence were found to be abundantly present in infected oil plam roots (Isha et al., 2020). In soybean, metabolomics techniques were used to detect metabolites in response to different abiotic stresses such as drought, salinity, heat, heavy metal, flooding, and chilling (Feng et al., 2020). Industrial oil crops play an important role in the oil economy and this is achieved by the metabolomics integrated with other omic technologies which revealed the regulatory steps that play key role in improving the oil yield in crops.

7. Ionomics progress in industrial oil crops

Ionomics refers to the comprehensive investigation of all ions present

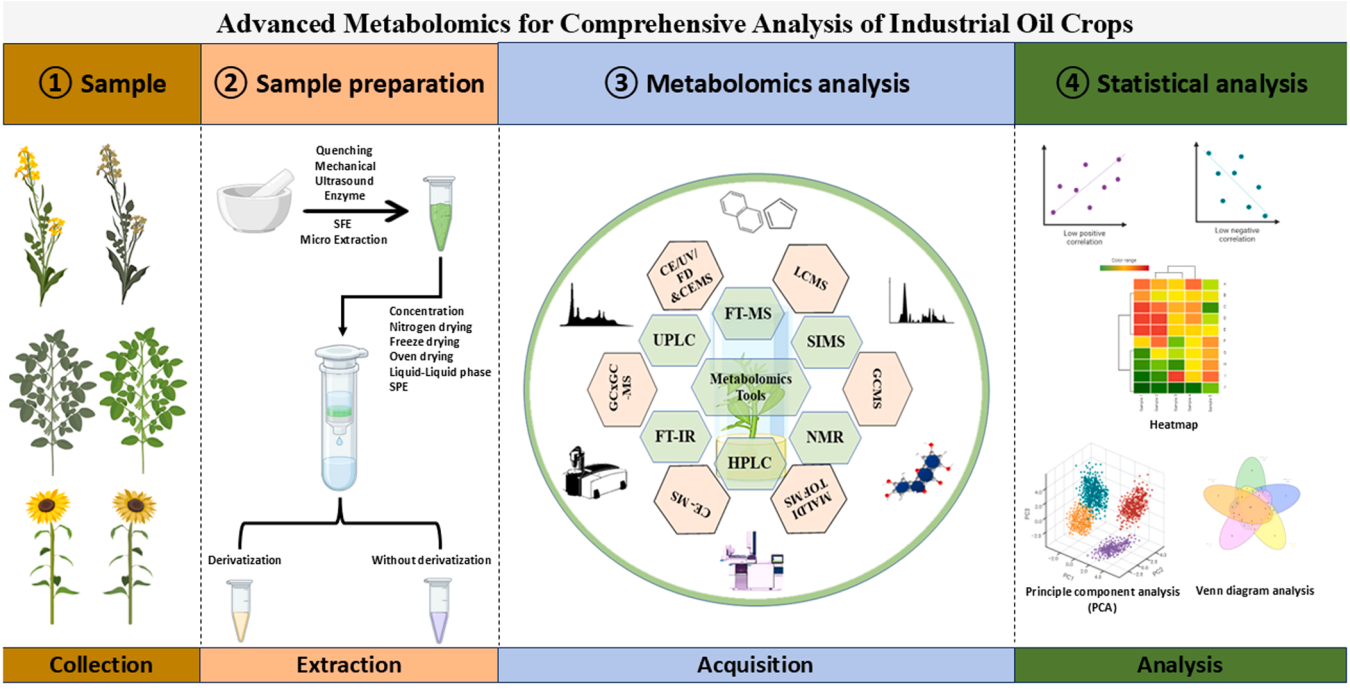

Fig. 2. Schematic representation of advanced metabolomics techniques for comprehensive analysis of industrial oil crops. 1) Sample collection is one of the crucial step that involve rapid freezing and storage until, 2) sample processing involving steps like extraction, filtration, and derivatization, as per the instruments used for the 3) Metabolomic analysis which includes instruments like Liquid Chromatography-Mass Spectrometry (LC-MS), Gas Chromatography-Mass Spectrometry (GC-MS), Comprehensive Two-Dimensional Gas Chromatography-Mass Spectrometry (GC×GC-MS), Fourier Transform Mass Spectrometry (FTMS), Nuclear Magnetic Resonance (NMR), High-Performance Liquid Chromatography (HPLC), Ultra-Performance Liquid Chromatography (UPLC), Secondary Ion Mass Spectrometry (SIMS), Capillary Electrophoresis-Ultraviolet-Fluorescence Detection (CE-UV-FD), and Capillary Electrophoresis-Mass Spectrometry (CE-MS), and finally the data need to be analysed with different 4) statistical methods including univariate, multivariate, and machine learning approaches, depending on the nature of the data and research objectives.

in living organisms, including how ion production changes in response to external stimuli and during different developmental stages, and genetic modifications using high throughput elemental profiling (Fig. 3). Along with nucleic acid, proteins, and carbohydrates, ions are critically involved in almost every process. They regulate numerous biochemical pathways and thus regulate various cellular functions. They are responsible for maintaining cell integrity, transporting minerals, and serving as co-factors for enzymes that catalyze crucial regulatory pathways. Consequently, variations in ion production can result in changes to metabolic pathways. To thoroughly examine these changes, it's crucial to analyze how alterations in one ion's production affect the production of other ions. Both physiology and biochemistry of plants control this dynamic network of elements which are ultimately controlled by the genome. Thus, the ionomic-based study provides a better and more effective way to understand the mechanism of gene regulation (Baxter, 2010; Salt et al., 2008; Zargar et al., 2016). Furthermore, ionomics also enables genetic dissection using different approaches such as natural and induced genetic variation via mutagenesis, association mapping, and reverse genetics.

Ionomics-based studies are useful in revealing the cross-talk between the elements during the uptake and metabolic utilization of minerals. In *B. napus,* ionomics studies have been utilized to determine the plant nutritional status. Notably, deficiency in one element can lead to the deficiency of other elements due to positive or opposite interactions between the elements. In this study, a total of eighteen interactions at the uptake level have been identified including pairs like K & Na, S & Mo, and Fe, Zn & Cu. The uptake of Mo is most frequently affected as it is increased under S-, Fe-, Cu-, Zn-, Mn-, or B-deprivation which could be the consequence of different metabolic disturbances (Maillard et al., 2016). Another study on sunflowers conducted by Júnior et al. (2014) focuses on the effect of cadmium and its correlation with other elements including copper, iron, magnesium, manganese, phosphorus, and zinc. According to this study, sunflowers are not only cd-hyperaccumulators but also hypertolerant. Although it does affect the uptake and translocation of other essential elements. Accumulation of Cd results in the depletion of the content of P, Fe, Mg, and Mn necessary for photosynthesis and thus creates chlorosis. Thus, these types of studies are useful for understanding the correlation between enzymes, proteins, and metals and their role at physiological level. In soybean, ionomics is used to analyze the Cd uptake and its accumulation in seeds which was first

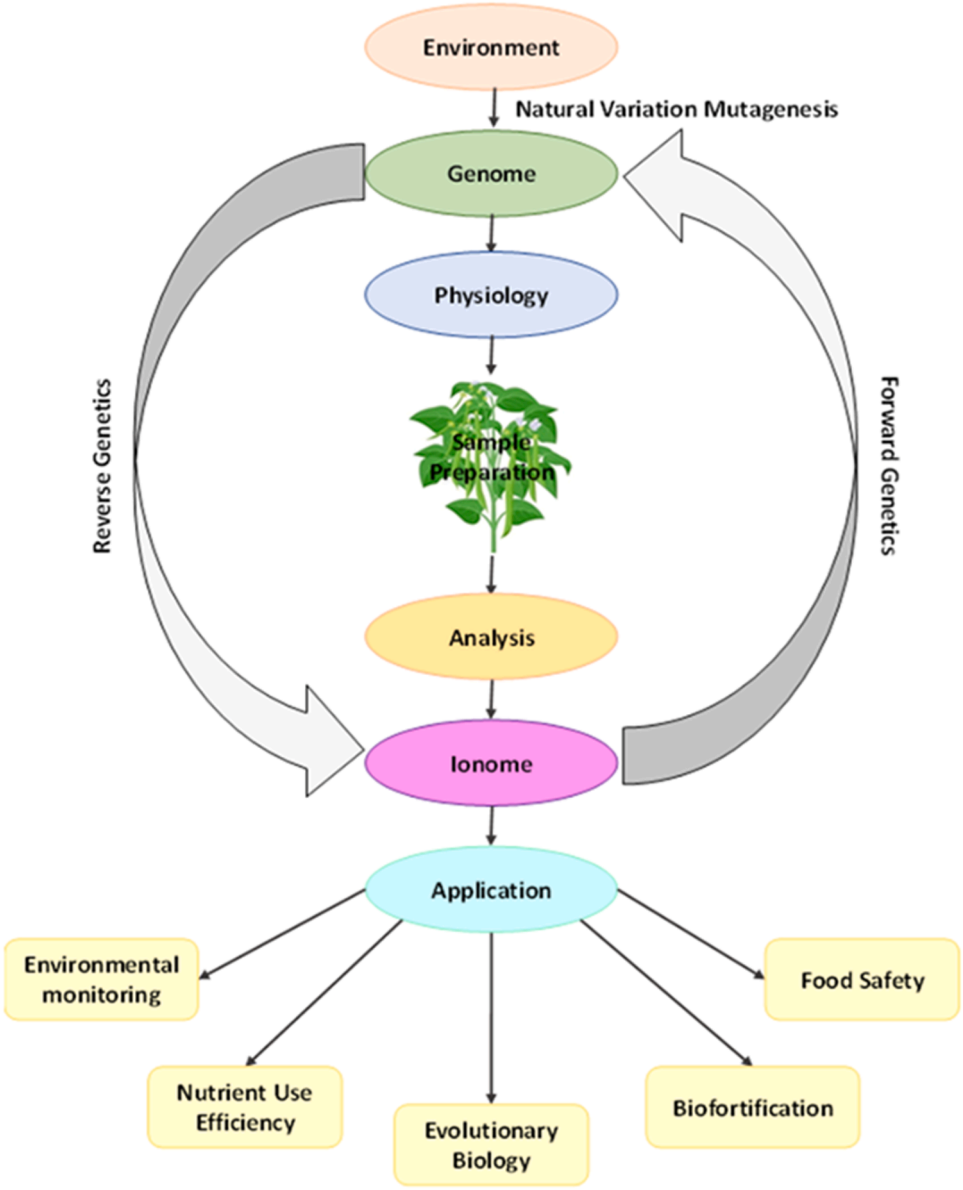

Fig. 3. Comprehensive steps in ionomic studies and the biological processes influencing the plant ionomes.

reported by Arao et al. (2003) in different Japanese cultivars, later on a similar approach was employed in Canadian cultivars. A wide variation in the accumulation of Cd in stem, leaves, pods, and seeds suggests that plant has different mechanisms of root uptake and translocation to different parts. Thus, providing a platform that helps to understand the heavy metal uptake and their accumulation in relation to food safety concerns.

It also provides insight into the improvement of crops against various biotic and abiotic stresses. For instance, silicon has been proven as a beneficial element as it provides resistance against various biotic and abiotic stresses including water stress, high salinity, heavy metal stress, and UV-b (Liang et al., 2007). Initially, soybean has been considered a poor accumulator of silicon because of existing genetic differences in the germplasm and lack of study. However, advancements in ionomics technologies made it possible to identify silicon transporter genes in soybean (Deshmukh et al., 2013). This study helps in improving the understanding of soybean ionome and its subsequent employment in the management of abiotic stress tolerance.

Apart from these, ionomics approaches are used to identify quantitative trait loci related to mineral composition beneficial to humans and animals. Initially, ionomics based approaches have been used to differentiate mutants and natural alleles in the model organism Arabidopsis (Lahner et al., 2003) and yeast (Eide et al., 2005), now this approach has been extended to a broad survey of plant species. With the help of ionomics it is possible to detect genes affecting the composition of elements in soybean seeds (Lahner et al., 2003). Previously, ionomic study was used to analyze the concentration of 17 different elements in diverse accessions and 3 RIL populations of Arabidopsis grown in different environmental conditions. This led to the identification of more than 100 QTLs for different elemental accumulation (Buescher et al., 2010). To date, ionomics approaches have been employed to analyze the nutritive value of soybean products (Deshmukh et al., 2014). Further, in *B. oleracea*, *B. rapa,* and *B. napus,* genetic loci affecting the mineral composition have also been identified using ionomics approaches. Thus ionomics proves to be an advantageous approach not only to understand complex biological systems but also in the identification of loci/genes.

8. Integrated omics approaches

The progress in omics approaches has led to the accumulation of an enormous amount of information in all dimensions of plant science, being used incredibly to generate improved crop varieties. Omics approaches have provided improved information about gene structure, gene function, metabolic pathways, and regulatory networks. Even though several omics-based networks are available, a complete understanding of metabolic pathways on the cellular and molecular level cannot be done based on individual genomic, transcriptomic, or metabolomic data (Chaudhary et al., 2015a). The integrated approach is essential for defining gene function, and characterization of interactions between different biological pathways (Fig. 4) (Fukushima et al., 2009). For instance, QTL and GWAS can be utilized to locate the chromosomal regions relating to specific phenotypes. These chromosomal regions contain numerous genes, which cannot be deciphered via QTL or GWAS alone (Deshmukh et al., 2014). The integrated omics approaches, together with WGRS data and the transcriptomic data related to seed development for varied germplasm and RILs can be used to identify novel variant linked coexpression networks related to seed composition traits, including seed oil (Chaudhary et al., 2015a). Kusano et al. (2015), assessed genetically modified (GM) and non-GM soybean lines using the combination of ionomics and metabolomics. The seed-filling process has also been studied by integrating metabolomic and transcriptomic analysis (Li et al., 2015). The integrated omics approach has also been utilized by Sonah et al. (2015) for the discovery of candidate genes or loci related to seed oil, weight, and protein content in soybeans. A chromosomal locus known as an eQTL explains genetic variation linked to population-level differentiation in gene expression. The two types of eQTL-cis-eQTL and trans-eQTL have an impact on global gene regulation and local expression, respectively (Zhao et al., 2023). Disease-resistance gene loci and the hotspots of the regulators that govern biological pathways and processes were successfully found using eQTL analysis across time points (Gélinas Bélanger et al., 2024). Further, eQTL analysis can directly recommend candidate genes for desired features when paired with phenotypic QTL (pQTL), correlation, regulatory network, co-expression, linkage mapping, and association mapping (Ming et al., 2023). The *Ibmyb1–2* gene was found to be in charge of triggering anthocyanin biosynthesis in potatoes using an integrated method of association mapping, regulatory network, and eQTL analysis (Bowers et al., 2024). Recently, the genes linked to the *B. napus* flowering time regulation module were identified using a combined TWAS and eQTL technique (Tan et al., 2022). The aforementioned examples demonstrate

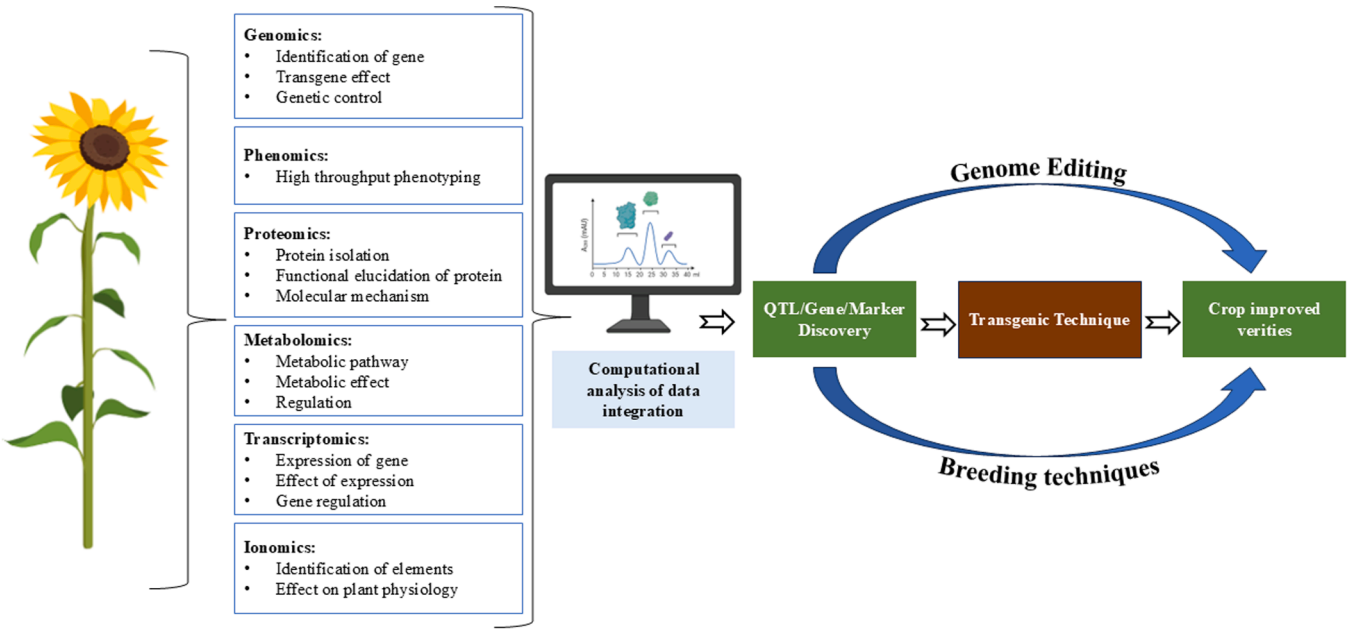

Fig. 4. Overview of the utilization of different cutting-edge integrated omics approaches for the enhancement of industrial oil crops.

how integrated use of omics can be utilized for the effective elucidation of genes of interest. In addition, computational resources can help store, catalog, and analyze data, and make the generated information easily accessible through databases. Soybean knowledge base (SKB;http://soykb.org), and *Camelina* genome portal (http://camelinagenomics.org/index.php?a=view) are examples of data integration for oil crops. Many other such databases dealing with metabolites, proteins, genes, molecular markers, sRNAs, microRNAs, and phenomic information, are present in the public domain for various crops, which prove vital for the effective utilization of omics data for the production of improved crop varieties (Fig. 4).

9. Genetic engineering and genome-editing tools for industrial oil crops

The information generated by omics tools is insignificant without its appropriate utilization for the production of superior varieties. Modification of oil crops has occurred throughout history through breeding and more recently by genome modification methodologies. Limitations are of course there in terms of the extent of exploitable genetic variations available with natural or mutagenized varieties of sexually compatible species for plant breeding programs. Transgenic technologies also help in producing precise changes in the desired trait without linkage drag, and in a short duration. Numerous transgene-based approaches have been applied in the past for the augmentation of seed oil content. Genetic engineering plays a vital role in modifying metabolic pathways to increase oil content and alter fatty acid composition (Fig. 5). Introducing or silencing key genes that are important for lipid biosynthesis can enhance oil content and thereby meet industrial requirements. A previous study showed that seed oil content can be increased by the overexpression of the yeast *glycerol-3-phosphate dehydrogenase* (*gpd1*) gene in *B. napus*. The overexpression of this gene results in a remarkable increase in glycerol-3-phosphate levels in developing seeds which in turn leads to an increase in seed oil content (Vigeolas et al., 2007). Similarly, transgenic rapeseed transformed with yeast *sn-2 acyltransferase* (*SLC1–1*) also results in increased seed oil content (Taylor et al., 2002). Similarly, the overexpression of *Glycerol-3-phosphate acyltransferase* (*GPAT*) (Jain et al., 2000), *diacylglycerol acyltransferase* (*DGAT*) (Roesler et al., 2016), and other enzymes from the Kennedy pathway for TAG synthesis also has resulted in a successful increase of the total oil content.

Lipid biosynthesis pathways are tightly regulated and quite complex. Therefore, overexpressing key genes may not result in desired changes in the levels of lipids. Altering transcription factors involved in the regulation of key genes lipid biosynthesis provide an option to bring about significant changes in lipid composition and total lipid content (Tan et al., 2011). *Leafy cotyledon1 (LEC1)* and *LEC1-LIKE (L1L)* are some of the key transcription factors already been utilized in plants such as maize (Shen et al., 2010), and canola (Elahi et al., 2016; Tan et al., 2011). While transcription factor modification is often accompanied by growth abnormalities, these can be overcome by seed-specific manipulation, as has been done in canola (Tan et al., 2011). Extending the duration of oil production is another method where transcription factors can be utilized. For instance, Kanai et al. (2016) expressed *WRINKLED1* (*WRI1*) under *FUSCA3 (FUS3)* promoter, resulting in higher TAG accumulation in the transgenic seeds in wild-type and *12s1.4* mutants. Additionally, reducing lipid breakdown can also ultimately result in increased lipid accumulation. RNAi suppression of Sugar-Dependent 1 (SDP1), a major lipase involved in oil degradation, has increased lipid content by upto 8–30 % in *B. napus* and *J. curcas* (Kelly et al., 2013; Kim et al., 2014). These findings suggest that targeting transcription factors and suppressing lipolysis hold significant potential for yielding higher total oil content in seeds.

Redirecting metabolic flux is another aspect that can be utilized for enhancing the production of desirable FAs as has been achieved in *C. sativa* by Nguyen et al. (2015). Omega-7 monounsaturated FAs were enhanced in *C. sativa* by upto 60–65 % of total FAs by the seed-specific suppression of *3-keto-acyl-ACP synthase II* and the *FatB 16:0-ACP thioesterase* (Nguyen et al., 2015). Seed-specific RNAi-mediated suppression of cytosolic phosphatases has also resulted in up to 4 % increase in oil

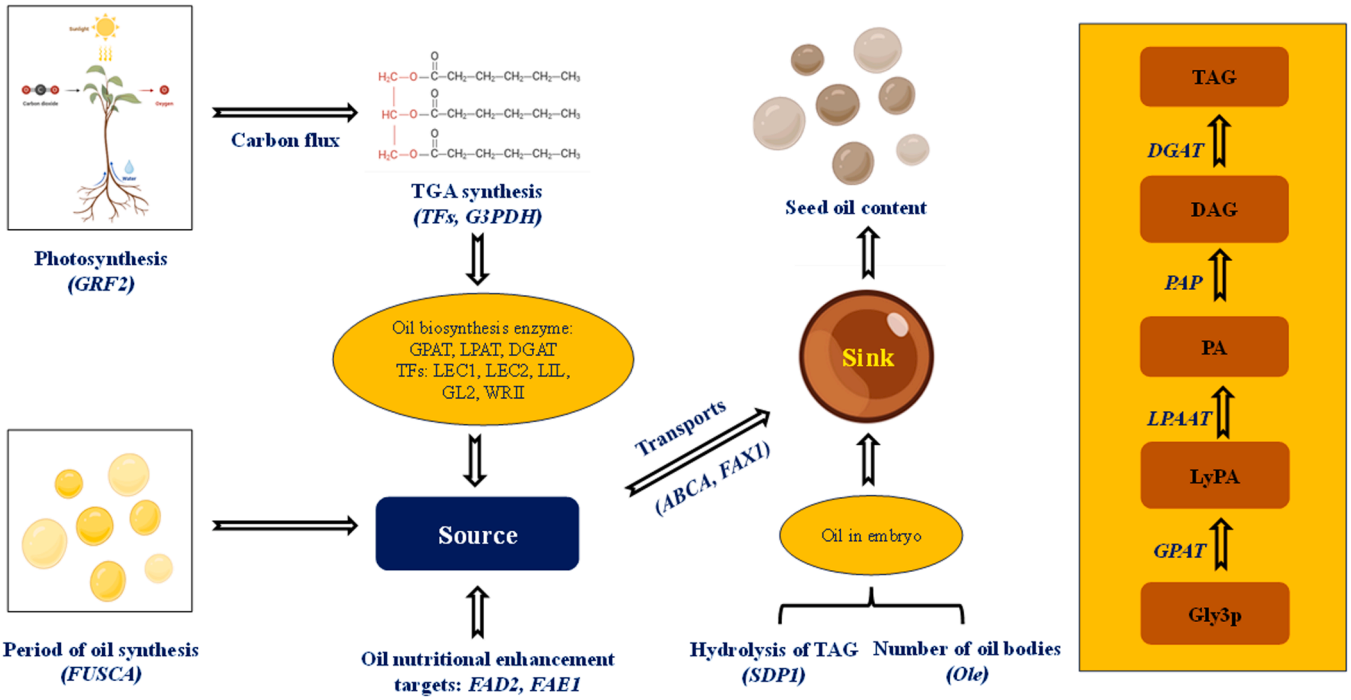

Fig. 5. Overview of factors governing the synthesis, transport, and accumulation of seed oil in plants. The studied genes are involved in the Kennedy pathway (Kennedy, 1961), which plays a critical role in lipid biosynthesis. Key enzymes include glycerol-3-phosphate acyltransferase (GPAT), lyso-phosphatidic acid acyltransferase (LPAAT), and diacylglycerol acyltransferase (DGAT), each contributing to the stepwise formation of triacylglycerol can be targeted for genome editing to enhance the seed oil content.

content but at the expense of seed protein (Meyer et al., 2012). Overexpression of specific oleosin proteins, the most abundant proteins in seed oil bodies, playing a vital role in oil body formation, is also an option (Liu and Liu, 2013). The strategies discussed above involve genetic engineering of single genes, but oil content is a polygenic trait. Therefore, stacking of genes or transgene pyramiding provides a viable solution as the synergistic effect of multiple genes may result in higher yields of lipids (Vanhercke et al., 2013; Wan, 2015).

The fatty acid composition is also an important factor in determining oil quality and health benefits. Genetic engineering offers more opportunities for the generation of precise and accurate mutations. Consequently, the manipulation of fatty acid profiles is a desirable objective of metabolic engineering studies. Such an anticipated alteration is reduced PUFA content and enhanced oleic acid content. Oleic acid enhances the thermal stability of the oil, making it more desirable for edible purposes, and thus enhancing oleic acid content is one of the main goals of oilseed crop engineering (Matthäus, 2006). The preferred target for such manipulation is *FAD2* and *FAE1* which have been utilized in many industrial oilseed crops, such as cotton (Liu et al., 2002), sunflower (Lacombe et al., 2009), *Camelina (*Nguyen et al., 2013*)*, rapeseed (Peng et al., 2010), and soybean (Wagner et al., 2011; Zhang et al., 2014).

Transgenics have little acceptance in the majority of countries and strict regulations constrain their public release. Genome editing methodologies, including Zinc Finger Nuclease (ZFNs) (Bibikova et al., 2003), Transcription Activator like Effector Nucleases (TALENs) (Christian et al., 2010), and clustered regularly interspaced short palindromic repeats/CRISPR associated protein (CRISPR/Cas) technology (Jinek et al., 2012; Ran et al., 2013), provide a viable alternative to transgenics, especially since the advent of ribonucleoproteins (RNPs) (Malnoy et al., 2016). Among the genome editing techniques, CRISPR/Cas is the most sought after owing to the ease of application and better mutation rates. CRISPR/Cas has also been effectively used to improve the yields and quality of oils, including the important industrial oils (Table 2). For instance, CRISPR/Cas9 system was employed to knockout *seed fatty acid reducer* genes (*BnSFAR4* and *BnSFAR5*) to improve oil yield in rapeseed (Karunarathna et al., 2020a). Similarly, CRISPR/Cas9 technology used to target *△12-fatty acid desaturase II* (*FAD2*) genes in soybean to elevate seed oil contents (Do et al., 2019b; Wu et al., 2020). The multitude of CRISPR/Cas tools (Fig. 6) presents a great opportunity to industrially exploit the information generated via omics approaches, in addition to the production of a novel knowledge base. Genetic engineering and genome-editing tools represent powerful tools for the improvement of industrial oil crops, offering opportunities to enhance yield, quality, and resilience while enabling the development of novel traits and bioproducts. With continued research, collaboration, and regulatory oversight, these technologies hold the key to unlocking the full potential of industrial oil crops for sustainable agriculture, renewable energy, and industrial applications.

10. Conclusion

The utilization of advanced omics approaches holds immense potential for improving industrial oil crops. Advancements in different omics approaches such as genomics, transcriptomics, proteomics, metabolomics, and ionomics have deepened our understanding of the genetic basis of desirable traits and complex molecular interactions within these crops. This provides an opportunity to accelerate breeding programs to meet the increasing global demand for industrial oil production. Also, extensive research with the use of multi-omics tools can fully harness the potential of industrial oil crops, leading the way for

Table 2
Advancements in oil quality and yield through genome editing techniques.

Genome editing platforms	IndustrialOil Crops	*Gene(s)*	Effects on oil production and quality	References
ZFNs	*Brassica napus*	*KASII*	Upto 12.6 % reduction in palmitic acid in T_1 leaves; Upto 2 % increase in C18 fatty acids.	(Gupta et al., 2012)
TALENs	*Glycine max*	*FAD2-1 A and FAD2-1B*	Oleic acid increased from 20 % to 80 % and linoleic acid decreased from 50 % to under 4 %.	(Haun et al., 2014)
TALENs	*Glycine max*	*FAD2–1A; FAD2–1B; FAD 3 A*	*fad2–1a fad2–1b fad3a* mutants: linolenic acid decreased- 2.5 %; linoleic acid decreased- from 5.1 % to 2.7 %; oleic acid increased- from 77.5 % to 82.2 %.	(Demorest et al., 2016)
TALENs	*Arachis hypogaea*	*FAD2*	0.5–2-fold increase in the oleic acid content.	(Wen et al., 2018)
CRISPR/Cas	*Brassica napus* cv. Westar	*FAD2*	The oleic acid (C18:1) and linoleic acid (C18:2) contents of the BC1S1 seeds that were homozygous for the fad2_Aa allele were approximately 80 % and 9 %, respectively, while those of the BC1S1 seeds carrying the WT FAD2_Aa allele were approximately 73 % and 16 %, respectively.	(Okuzaki et al., 2018)
CRISPR/Cas	*Brassica napus*	*BnSFAR4; BnSFAR5*	Erucic acid content was slightly reduced; *BnSFAR5* double mutants display seed oil increase by 10.4 % and 11.2 % in T_3 and T_4 seeds, respectively; In *BnSFAR4* mutants display seed oil increase by 9.7–14.5 % and 12.9 % in T_3 and T_4 seeds increased respectively	(Karunarathna et al., 2020b)
CRISPR/Cas	*Glycine max*	*FAD2–1 A; GmFAD2–1B*	Oleic acid content to over 80 %, whereas linoleic acid decreased to 1.3–1.7 %	(Do et al., 2019a)
CRISPR/Cas	*Glycine max*	*FAD2–1A (Glyma.10G278000); FAD2–2A (Glyma.19G147300)*	In T_2 generation, oleic acid content increased from 17.10 % to 73.50 %; the protein content increased from 37.69 % to 41.16 %; the linoleic acid content decreased from 62.91 % to 12.23 %. In the T_3 generation, the oleic acid content increased from 19.15 % to 72.02 %; the protein content increased from 37.52 % to 40.58 %; the linoleic acid content decreased from 56.58 % to 17.27 %.	(Wu et al., 2020)
CRISPR/Cas	*Camelina sativa*	*DGAT; PGAT*	Altered seed physiology and reduced oil content	(Aznar-Moreno and Durrett, 2017)
CRISPR/Cas	*Camelina sativa*	*FAE1*	VLCFAs reduced from 22 % to less than 2 %; C18 unsaturated fatty increased.	(Ozseyhan et al., 2018)
CRISPR/Cas	*Camelina sativa*	*FAD2*	Oleic acid increased- from 16 % to 50 %; linoleic acid decreased- from ~16 % to < 4 %; linolenic acid decreased- from ~35 % to < 10 %.	(Jiang et al., 2017)
CRISPR/Cas	*Oryza sativa*	*FAD2–1*	*fad2–1* homozygous mutants: Oleic acid content increased by ~100 %; linoleic acid, palmitic acid contents decreased.	(Abe et al., 2018)

*CRISPR/Cas9: Clustered Regularly Interspaced Short Palindromic Repeats/CRISPR associated protein; DGAT: diacylglycerol acyltransferase; FAE1: Fatty Acid Elongase1; FAD: Fatty Acid Desaturase; KASII: β-ketoacyl-ACP Synthase II; PGAT: Phospholipid:diacylglycerol acyltransferase; SFAR: SEED FATTY ACID REDUCER; TALEN: Transcription activator-like effector nucleases; VLCFAs: Very long-chain fatty acids; ZFNs: Zinc-finger nucleases.

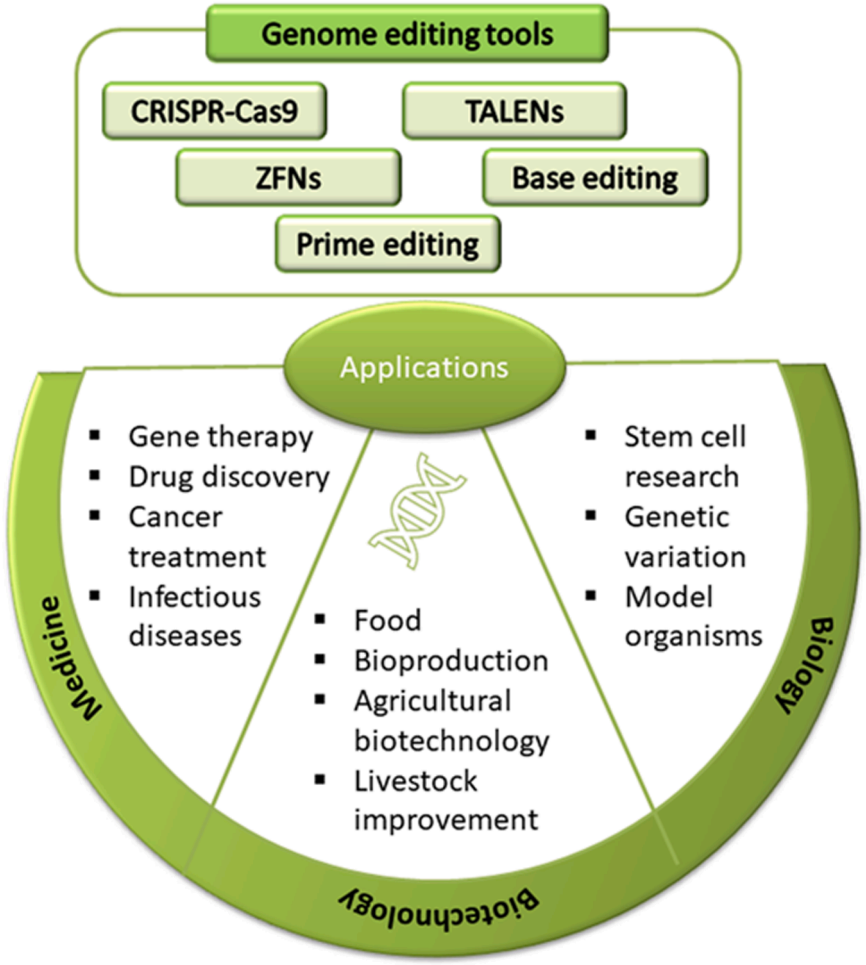

Fig. 6. Overview of genome editing tools and applications (CRISPR-Cas9- Clustered Regularly Interspaced Short Palindromic Repeats and CRISPR-associated protein 9, TALENs- Transcription Activator-Like Effector Nucleases, ZFNs- Zinc Finger Nucleases).

substantial agriculture, bioenergy production, and other industrial applications. This review provides a comprehensive overview of different omics approaches for improving the quality and quantity of industrial oil crops. The insights shared here can guide future explorations aimed at transforming these crops, ultimately contributing to global food security, environmental sustainability, and economic development.

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CRediT authorship contribution statement

Vandana Thakral: Writing – review & editing. **Rushil Mandlik:** Writing – review & editing. **Sanskriti Vats:** Writing – original draft. **Tilak Raj Sharma:** Supervision. **Rupesh Deshmukh:** Supervision. **Humira Sonah:** Supervision, Conceptualization. **Badal Mahakalkar:** Writing – original draft. **Sreeja Sudhakaran:** Writing – original draft. **Virender Kumar:** Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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