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Review

Research progress of omics technologies in forage breeding ☆

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ABSTRACT

Forages are essential to global agriculture and ecosystems, with the development of high-yield, high-quality varieties as a cornerstone of efficient agricultural practices. However, traditional genetic breeding methods, characterized by lengthy cycles and limited efficiency, fall short of meeting the demands of modern agriculture. In recent years, the rapid advancements in omics technologies, including genomics, epigenomics, transcriptomics, proteomics, and metabolomics, have significantly transformed forage research. These tools have deepened our understanding of the biological mechanisms underlying forage growth and development, aided in identifying essential genes and metabolic pathways, and accelerated the improvement of forage varieties. This review summarizes the applications and recent advances of various omics approaches in major forage species, including alfalfa (*Medicago sativa* L.), ryegrass (*Lolium perenne* L.), red clover (*Trifolium pratense* L.), white clover (*Trifolium repens* L.), and oat (*Avena sativa* L.). Additionally, we outline the advancements in these technologies for major crops and how we can learn from and apply them to improve forage yield, nutritional quality, and environmental adaptability, thereby establishing a theoretical foundation for the genetic improvement and molecular breeding of forages.

1. Background

Forages play a crucial role in global agriculture and ecosystems, being the primary feed source the primary feed source for livestock and contributing a significant contribution to ecological balance and soil health [1]. Genetic breeding has become a critical objective in modern agricultural research to improve forage yield, nutritional quality, and environmental adaptability [2].

Traditional genetic breeding methods, primarily based on phenotypic selection and genetic crossbreeding, have resulted in considerable success. However, these approaches are often limited by lengthy breeding cycles, low efficiency, and restricted genetic gains, making it challenging to meet the diverse demands of modern agriculture.

The advent of molecular biology and genetic technologies has led to the development of a suite of omics technologies, such as genomics, epigenomics, transcriptomics, proteomics, and metabolomics, which provide innovative tools for the molecular breeding of forages. These technologies enable researchers to explore the biological mechanisms of forages under diverse environmental conditions, facilitating the identification of crucial genes and metabolic pathways associated with critical agronomic traits. By incorporating these insights, a thorough understanding of the complex biological processes in forages has been developed, creating a cohesive research framework to improve forage varieties.

This review provides a systematic overview of recent advances in omics research on important forage species, including alfalfa, ryegrass, red clover, white clover, and oat, and examines their applications in molecular breeding.

2. Principles of omics studies and research hotspots in forages

2.1. Principles of various omics studies

Omics technologies provide a comprehensive framework for investigating biological systems by analyzing multiple molecular layers, including genomics, epigenomics, transcriptomics, proteomics, and metabolomics. Each technology offers unique insights into the regulation and function of biological molecules (Table 1), contributing to a holistic understanding of complex biological processes in forages.

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Table 1
Core techniques, advantages, and disadvantages of omics technologies.

Omics technology	Core techniques	Advantages	Disadvantages
Genomics	Genome-wide Association Study (GWAS), Quantitative Trait Locus (QTL) Mapping, Bulked Segregation Analysis (BSA), Whole Genome Sequencing (WGS)	Comprehensive genetic data, Identifies key traits for breeding	High cost, Requires large datasets, Limited reference genomes
Epigenomics	DNA Methylation (Bisulfite Seq), Chromatin Immunoprecipitation Sequencing (ChIP-Seq), m6A Sequencing, miRNA Profiling	Reveals gene regulation, Essential for gene-environment interactions	Complex data interpretation, Limited resolution for some regions
Transcriptomics	RNA-Seq, Single-Cell Sequencing, Spatial Transcriptomics Sequencing, Full-length Transcriptome Sequencing	Dynamic gene expression data, Identifies stress-responsive genes, High resolution in single-cell studies	Computationally intensive, May not capture all gene functions
Proteomics	Mass Spectrometry (MS), Two-Dimensional Gel Electrophoresis (2-DE), Affinity Purification-Mass Spectrometry (AP-MS)	Unveils protein functions and interactions, Insights into biological pathways	High sample complexity, Requires advanced technology
Metabolomics	Gas Chromatography-Mass Spectrometry (GC-MS), Liquid Chromatography-Mass Spectrometry (LC-MS), Neclear Magnetic Resonance (NMR), Capillary Electrophoresis-Mass Spectrometry (CE-MS)	Snapshot of biochemical state, Studies on metabolic responses	Difficult to analyze diverse metabolites, Sensitive to sample prep

Genomics is the study of an organism's complete genetic makeup. Recent advances in high-throughput sequencing, such as next-generation sequencing (NGS) [3], have made the generation of large-scale genomic data more efficient and cost-effective. In forage research, genomics is pivotal in identifying genes associated with important traits such as yield, disease resistance, and drought tolerance, which are crucial for improving forage breeding [4].

Building on genomics, epigenomics investigates heritable changes in gene function that do not involve changes to the DNA sequence itself. Modifications such as DNA methylation and histone changes influence gene expression and cellular processes, which can be shaped by environmental factors [5]. In forages, epigenomics is critical for understanding how plants respond to environmental stressors, thereby improving traits such as stress resilience and adaptability.

Transcriptomics analyzes RNA molecules, particularly messenger RNAs (mRNAs), to assess gene expression under diverse conditions. In forages, transcriptomics identifies genes that are activated or suppressed in response to environmental stress, providing insights into plant responses to variations in water availability and temperature. Techniques such as RNA sequencing (RNA-Seq) provide detailed views of gene activity, bridging the gap between genomic information and plant function [6].

Proteomics focuses on the study of proteins translated by genes. By analyzing the proteome, which includes the full set of proteins in an organism, proteomics helps uncover the functional roles of proteins in various biological pathways [7]. In forages, proteomics assists in understanding how proteins contribute to processes like nutrient uptake, growth regulation, and stress response, thereby facilitating improvements in forage productivity and quality.

Finally, metabolomics targets small molecules, known as metabolites, produced during metabolic processes. Profiling the metabolome offers a snapshot of an organism's biochemical state, reflecting the effects of genetic and environmental factors [8]. In forages, metabolomics is particularly useful for understanding how plants adapt to environmental challenges, such as drought or nutrient deficiencies, and for identifying biomarkers that enhance stress resilience and productivity.

In summary, genomics establishes the structural foundation of biological systems, whereas epigenomics and transcriptomics elucidate the regulatory mechanisms governing gene expression. Proteomics and metabolomics reveal the functional manifestations of these regulatory processes in organisms. Thus, integrating multi-omics offers a comprehensive understanding of complex biological processes and regulatory networks in forages. This holistic approach not only enhances our knowledge of forage biology but also identifies potential targets for improvement, laying a scientific foundation for advancing forage breeding and productivity (Fig. 1).

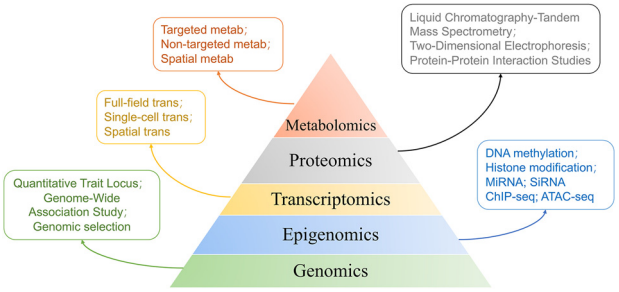

Fig. 1. The relationship between each omics and some corresponding research hotspots.

2.2. Research hotspots in omics studies on forages

The increasing global demand for high-yield, high-quality forages has made the application of omics technologies in forage research a prominent area of focus [9]. This review synthesizes 434 research articles published over the last decade, focusing on omics studies of five widely cultivated forage species: alfalfa, ryegrass, white clover, red clover, and oat. Articles were identified via a systematic search of the Web of Science database using keywords such as 'genomics', 'transcriptomics', 'proteomics', 'metabolomics', and 'epigenomics'. Following retrieval, articles were manually screened and categorized according to their topical relevance to ensure comprehensive coverage of trends and directions in forage research. We aim to clarify the current state and future prospects of forage omics research by synthesizing publication data.

To analyze publication trends, we categorized the articles into eight research dimensions. Our analysis reveals that the main research hotspots include abiotic stress, genetic evolution, metabolic pathways, and growth and development. Researches on abiotic stress leads the field, with 179 articles accounting for over 38.66% of total publications. Studies on genetic evolution and metabolic pathways comprise 80 (17.28%) and 70 (14.9%) articles, respectively. Additionally, 38 articles focus on growth and development, accounting for 8.21% of the total (Fig. 2).

Annual publication trends reveal significant growth in genomics research from 2016 to 2018, peaking at 14 articles in 2018, thereby establishing genomics as the dominant focus in forage omics studies. Pro-

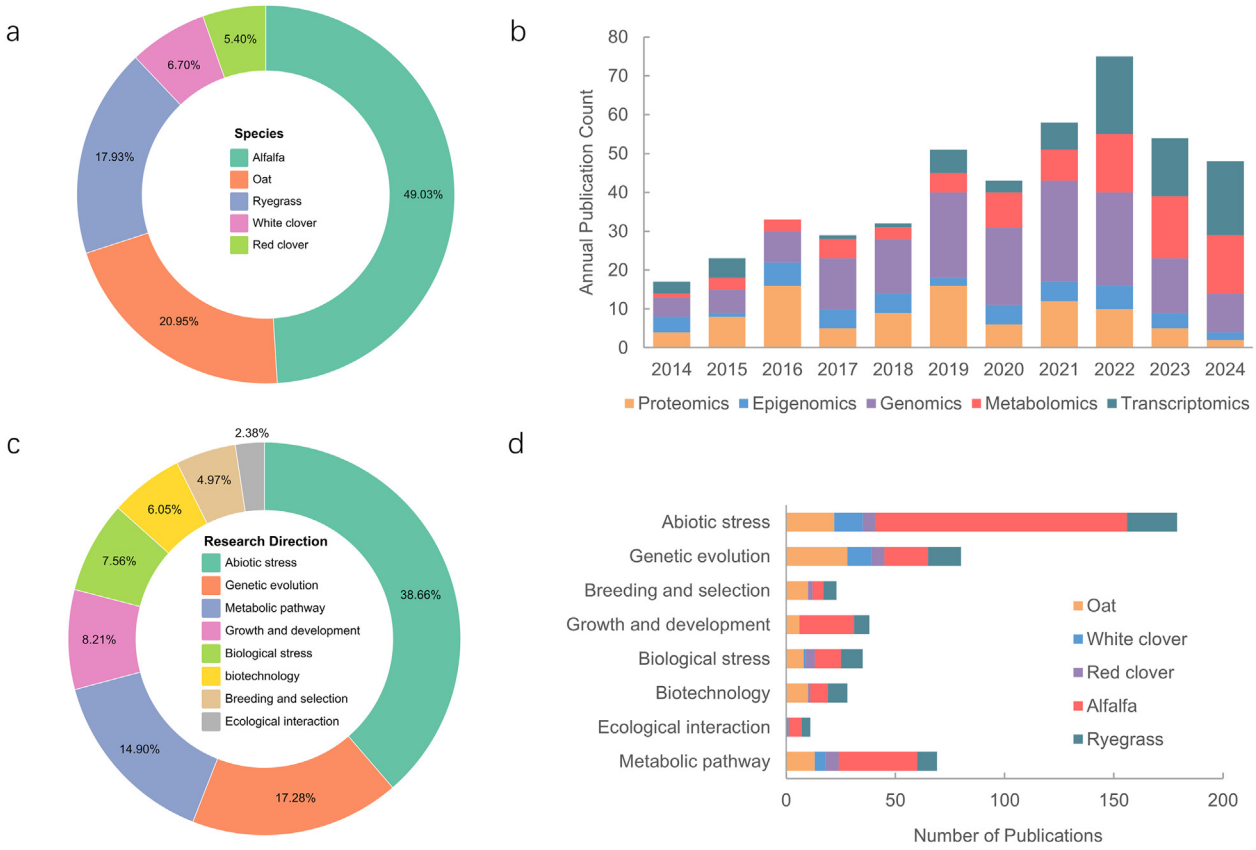

Fig. 2. Statistical chart of 10-year omics publications of five forage species (a: total number of omics research papers of the five species. b: the annual number of papers published by different omics. c: total number of publications in different research directions. d: number of papers published in different research directions of five forage species).

teomics and metabolomics researches have remained relatively stable over the years, whereas epigenomics studies are still in their early stages, presenting significant opportunities for future exploration.

Species-specific analysis shows that alfalfa has the most research attention, comprising 227 articles, or 49.05% of all publications. Oat (97 articles) and ryegrass (83 articles) follow, accounting for 20.95% and 17.93% of the total, respectively. Omics research has shown notable strengths in addressing abiotic stress and metabolic pathways. For instance, alfalfa studies on abiotic stress represent 115 articles, accounting for 64% of all publications in this research area.

Overall, current research in forage omics primarily focuses on abiotic stress, with significant contributions from studies on genetic evolution, metabolic pathways, and growth and development. Alfalfa is the most extensively studied species, particularly with respect to abiotic stress. Genomics research has seen notable growth, while proteomics, metabolomics, and epigenomics are still developing fields with potential for further exploration. These trends reflect the growing application of omics technologies in addressing key challenges within forage science.

3. Applications of omics in forages

3.1. Advances in genomics research

3.1.1. Genome assembly of forages

The decreasing cost of sequencing technologies has accelerated genomic research on forages. Genome assemblies have been completed for many forage species, including *Medicago sativa* (alfalfa), *Lolium perenne* (ryegrass), and *Avena sativa* (oat). This paper lists genome assemblies for 16 major cultivated forage species [10–22] (Table 2). These advances provide detailed insights into forage genome structures, elucidating their genetic bases and offering a robust scientific foundation for genetic improvement and breeding strategies.

3.1.2. Genome-assisted mapping in forages

The genetic diversity of forage species has profoundly influenced forage research. The relatively weak population structure and high heterozygosity can influence the effectiveness of mapping approaches. While synthetic varieties limit the availability of inbred lines, which disadvantages some genetic mapping methods, the weak population structure in forage species can be beneficial. This reduced structure helps minimize the occurrence of false positives, thereby improving the precision of genetic mapping techniques.

Quantitative Trait Loci (QTL) mapping, for instance, has identified critical loci associated with traits such as flowering time, leaf development, and cold tolerance in alfalfa [23,24]. QTL mapping has also been employed to identify loci related to seed yield traits [25]. Furthermore, QTL mapping has led to the identification of eight loci associated with resistance to anthracnose and clover rot in red clover [26].

Although Genome-wide Association Study (GWAS) requires larger sample sizes and higher sequencing costs than QTL mapping, it provides greater precision in identifying genetic loci. For example, 53 cold-tolerance genes were identified in white clover through GWAS [27], and 49 significant loci, along with 103 candidate genes related to salt stress tolerance, were mapped in alfalfa [28].

Bulk Segregant Analysis (BSA), a cost-effective alternative to GWAS, has been increasingly used in forage research due to its lower sample size requirements and reduced costs. Compared to GWAS, BSA identifies genetic loci using fewer resources by comparing pooled samples exhibiting extreme phenotypes. For example, BSA-seq was used to identify two genes associated with male sterility in alfalfa [29]. Beyond forage crops, BSA-seq has proven effective in other species, such as identifying

Table 2
Basic information and download addresses of typical herbage genomes (for species with multiple genomes, representative genome links are provided).

Taxon	Genome size	Number of chromosomes	Assembly type	Download link
Avena sativa	10.76 Gb	21	haploid	https://www.ncbi.nlm.nih.gov/datasets/genome/GCA_023646675.1/
Cenchrus americanus	1.8 Gb	7	haploid	https://www.ncbi.nlm.nih.gov/datasets/genome/GCA_947561735.1/
Cenchrus purpureus	2 Gb	14	haploid	https://www.ncbi.nlm.nih.gov/datasets/genome/GCA_022644695.1/
Cichorium intybus	1.3 Gb	9	haploid	https://www.ncbi.nlm.nih.gov/datasets/genome/GCA_023525715.1/
Cleistogenes songorica	540.1 Mb	20	haploid	https://ngdc.cncb.ac.cn/gwh/Assembly/10365/show
Cynodon dactylon	604 Mb	18	polyploidy	https://ngdc.cncb.ac.cn/bioproject/browse/PRJCA019991
Leymus chinensis	7.99 Gb	14	haploid	https://doi.org/10.6084/m9.figshare.24032238.v1
Lolium perenne	2.55 Gb	7	haploid	https://ryegrassgenome.ghpc.au.dk/
Medicago sativa	816 Mb	8	haploid	https://modms.lzu.edu.cn/
Medicago truncatula	430 Mb	8	haploid	https://modms.lzu.edu.cn/
Onobrychis viciifolia	1821.5 Mb	28	polyploidy	https://doi.org/10.6084/m9.figshare.24155073
Panicum virgatum	1.1 Gb	18	haploid	https://www.ncbi.nlm.nih.gov/datasets/genome/GCF_016808335.1/
Poa pratensis	6.1 Gb	Scaffold level	haploid	https://www.ncbi.nlm.nih.gov/datasets/genome/GCA_947311845.1/
Trifolium pratense	413.6 Mb	7	haploid	https://www.ncbi.nlm.nih.gov/datasets/genome/GCF_020283565.1/
Trifolium repens	967.7 Mb	16	haploid	https://www.ncbi.nlm.nih.gov/datasets/genome/GCA_030408175.1/
Zoysia japonica	326.4 Mb	20	haploid	https://www.ncbi.nlm.nih.gov/datasets/genome/GCA_040438285.1/

loci linked to pigment accumulation in bitter melon [30] and pinpointing five candidate genes related to male sterility and wrinkled leaves in sesame [31].

3.1.3. Genome-assisted gene selection in forages

Genomic selection (GS) is an advanced breeding approach that utilizes whole-genome marker data to construct predictive models linking genotypes to phenotypes, enabling precise estimation of individual breeding values. This approach improves selection efficiency and accelerates breeding cycles, which is particularly advantageous for forages with complex traits and intricate genetic backgrounds.

For instance, Marty J. Faville investigated the rate of genetic gain in dry matter yield (DMY) of perennial ryegrass using GS. Five populations were sequenced by employing genotyping-by-sequencing (GBS) in a multi-population training set, and their average herbage accumulation over two years was measured [32]. Anup Dhakal explored multi-trait genomic selection (MTGS) in oats, demonstrating that incorporating grain morphology traits improved the efficiency of genomic selection for test weight and kernel plumpness [33]. F. Zhang applied machine learning approaches to predict fall dormancy (FD) in alfalfa. The study utilized support vector machine (SVM) regression in conjunction with GWAS-associated markers, achieving a maximum FD prediction accuracy of 64.1%, thus facilitating genetic research and accelerating cultivar improvement in alfalfa [34].

3.1.4. Population genetics and gene evolution in forages

Genomic studies often extend into the fields of population genetics and evolutionary dynamics. For example, F. Zhang conducted research using whole-genome resequencing to investigate the climatic adaptation and genetic susceptibility of alfalfa. They found that falcata and alfalfa contributed to the gene pool, enriching stress-response genes while also introducing genetic load. The findings highlight populations vulnerable to future climate change and suggest targeted conservation and breeding strategies to enhance resilience in alfalfa [35]. In a study on oats, Anup Dhakal revealed that the divergence between the oats and wheat tribes occurred after their split from the rice lineage, approximately 28.2 to 47.9 million years ago, with oats and rye showing closer genetic relationships. Divergence within oats occurred roughly 8.7 million years ago [33].

Similarly, research on sheepgrass has shown that its polyploid genome emerged around 5.29 million years ago, originating from an *Ns-subgenome* related to *Psathyrostachys* and an unknown *Xm-subgenome* [15]. Junyi He's study on sainfoin genome construction identified gene expansion as a significant factor driving increased proanthocyanidin gene expression and production, contributing to sainfoin's enhanced proanthocyanidin content [17].

3.2. Advances in epigenomics research in forages

3.2.1. Epigenomics research on stress responses in forages

Epigenomics plays a critical role in forage research to uncover mechanisms of long-term gene regulation. For instance, DNA methylation patterns can indicate genes that are permanently 'silenced" or 'activated' under specific environmental stresses, providing insights into persistent stress tolerance in forages. Similarly, histone modifications elucidate regulation of gene expression during various growth and developmental stages. Non-coding RNAs, such as microRNAs (miRNAs), also participate in gene regulation via epigenetic pathways, influencing processes such as stress responses, development, and immune defense in forages. Collectively, these regulatory mechanisms enhance the plant's adaptability and resilience under diverse environmental conditions.

Current epigenomics studies on forages primarily focus on stress responses. For instance, Yajiao Liu and colleagues identified differentially expressed long non-coding RNAs (lncRNAs) in alfalfa under salt and alkali stress using RNA sequencing. These lncRNAs regulate fatty acid metabolism, phenylpropanoid and flavonoid biosynthesis, and plant hormone signaling pathways [36]. Nan Hang demonstrated that transgenic ryegrass expressing *Os-microRNA408* exhibited enhanced drought tolerance due to changes in leaf morphology and improved antioxidant capacity, highlighting *miR408* as a promising target for improving drought resilience [37]. Similarly, Yang Ji identified miRNA-mRNA regulatory networks in *Dactylis glomerata* under drought conditions, discovering miR164c-3p as a key miRNA related to drought resistance [38].

3.2.2. Epigenomics in forage grass growth and development

Epigenomic studies on plant growth have yielded valuable insights, however, research on forage grasses remains limited. Wenna Fan identified dormancy-related miRNAs such as *miR172*, *miR166*, and novel-*miR_1* in alfalfa through small RNA sequencing [39]. Maria Florek demonstrated that 5-azacytidine-induced DNA demethylation altered chromosomal methylation, affecting seed germination, growth, and cellular structure in hybrid oats [40]. Additionally, Guangyan Feng analyzed *Dactylis glomerata* to reveal complex regulatory networks during vernalization and heading stages [41].

Epigenomic research has progressed more extensively in other crop species. Hao Wu used ATAC-seq to explore how *NKD1, NKD2*, and *OPAQUE2* regulate maize endosperm, uncovering reciprocal effects on target site accessibility [42]. Ying Zhang revealed a synchronization mechanism in rice involving H3K9ac modifications, transcription factor binding, and gene expression [43]. Similarly, Jianzhong Hu linked increased m6A modification during tomato fruit expansion to higher mRNA abundance, emphasizing its regulatory role [44].

Although these studies primarily focus on crops, similar epigenomic mechanisms, such as modifications in DNA accessibility and mRNA reg-

ulation, might also be relevant to forage species, particularly in regulating stress responses and growth. Nevertheless, specific epigenomic investigations in forage species remain limited, underscoring the need for further research to elucidate these potential mechanisms.

3.3. Advances in transcriptomics research in forages

3.3.1. Transcriptomics in forage stress resistance

Transcriptomics, among the most widely applied omics technologies, has substantially advanced genetic breeding in forages, particularly in research on stress resistance. The success in this area reflects its importance and relative accessibility, as stress response samples are more accessible to collect at critical treatment stages than those for growth and metabolic pathway studies.

For instance, Quan Gu and colleagues examined the role of melatonin (Mel) in reducing cadmium (Cd) stress in alfalfa. Their findings indicated that Mel regulates genes related to ribosomal proteins, E3 ubiquitin-protein ligase, and pectin lyase, which promotes protein folding and sucrose accumulation to alleviate Cd stress [45]. Junming Zhao investigated the effects of exogenous chitosan (CTS) on perennial ryegrass under water stress, revealing that CTS enhances drought tolerance by modulating expression of antioxidant enzymes and photosynthesis-related genes [46]. Khan I. et al. conducted transcriptome analysis to demonstrate that silver nanoparticles alleviate oxidative damage caused by salt stress and improve the growth and physiological characteristics of *Pennisetum glaucum* L. by regulating genes associated with plant hormone signaling and secondary metabolism [47].

3.3.2. Transcriptomics in forage growth and development

Transcriptomics plays a pivotal role in elucidating forage growth and development. The key is sampling during critical developmental stages and ensuring reproducibility. Giulio Testone et al. employed transcriptome assembly and RNA-seq to investigate gene expression differences between curly (frisée) and smooth-leaved (escaroles) endive varieties. They identified 3177 SNPs distinguishing the two varieties and 26 genes involved in sesquiterpene lactone (STL) biosynthesis [48]. Similarly, Zhongzhiyue Jin analyzed leaves from 46 sainfoin germplasm accessions and identified *OvMYBPA2*, a gene critical for proanthocyanidin biosynthesis [49]. Man Zhang investigated how oats react to long and short photoperiods, finding that long photoperiods promote flowering by regulating hormonal signaling pathways (e.g., ABA, auxin), circadian rhythms, and sucrose metabolism pathways [50].

Transcriptomic studies in forage species face specific challenges. Laboratory and greenhouse conditions often fail to replicate natural grassland environments, leading to potential sampling biases. Additionally, the high genetic diversity and variable growth stages in forage species result in inconsistent gene expression, which affects the reproducibility of transcriptomic data. To address these challenges, it is crucial to carefully consider sampling strategies to improve data reliability. Furthermore, for forage species with high heterozygosity and large genomes, increasing the sequencing depth can enhance transcriptomic accuracy. For instance, increasing the commonly utilized sequencing depth from 6 Gb to 10 Gb could substantially enhance sequencing precision and data quality.

3.3.3. Potential research value of single-cell and spatial transcriptomics in forage studies

Single-cell transcriptomics and spatial transcriptomics are emerging as transformative tools in transcriptomics research. Single-cell transcriptomics enables the analysis of gene expression heterogeneity across individual cells during different developmental stages or environmental conditions, offering new insights into cell differentiation and function. On the other hand, spatial transcriptomics localizes gene expression within tissues, uncovering the spatial distribution and functional interactions of different cell types.

For example, Yuxin Fu used single-cell transcriptomics to study maize endosperm cell differentiation, identifying 12 cell clusters and constructing a gene regulatory network with 181 regulatory factors. This framework enhances our understanding of cereal endosperm development and function [51]. Similarly, Xiehai Song applied spatial transcriptomics to investigate bud regeneration in tomato callus, identifying diverse cell populations and factors essential for primordium formation. The study also showed that light enhances bud regeneration by promoting mesophyll cell development and coordinating sugar signaling [52].

Currently, research on single-cell and spatial transcriptomics in forage crops is still limited. Using single-nucleus RNA sequencing, Zhijian Liu and colleagues investigated the response of *Medicago truncatula* to nod factors, revealing rapid early gene expression reprogramming and dynamic regulation of defense genes. They also demonstrated that MtFER is phosphorylated by LYK3 and plays a crucial role in rhizobial symbiosis [53].

Overall, single-cell and spatial transcriptomics provide high-resolution insights into gene expression, but they present challenges in forage species. Single-cell transcriptomics demands large sample sizes and replicates, which can be difficult due to the small size of forage tissues, especially when studying meristematic tissues. Spatial transcriptomics, while capable of analyzing multiple samples on a single chip, faces the challenge of maintaining consistent tissue sectioning to ensure all samples are in the same plane, which is critical for accurate spatial analysis. Despite these challenges, both technologies provide valuable molecular details that traditional methods cannot achieve.

3.4. Advances in proteomics research in forages

3.4.1. Proteomics in nutritional quality regulation of forages

The protein content of forages significantly influences their nutritional value. Proteomics plays a pivotal role in identifying key proteins involved in growth and development, optimizing cultivation management, and enhancing nutritional composition. Zhihao Dong and colleagues demonstrated through proteomics that tissue damage in red clover silage induces differential protein accumulation. This process promotes the degradation of intracellular organelle proteins and increases the accumulation of chloroplast thylakoid membrane proteins, which affects silage quality [54]. Similarly, Rajiv Kumar et al. employed proteomics to study five native forage plants from the high-altitude pastures of the Western Himalaya. The results showed that both yellow-flowered alfalfa (*Medicago sativa* subsp. *falcata*) and clover are rich in enzymes related to photosynthesis and the Calvin cycle. The increased photosynthetic efficiency may be the reason for their ability to accumulate more carbohydrates [54].

3.4.2. Proteomics in stress resistance regulation of forages

Proteomics is invaluable in understanding stress resistance mechanisms in forages. For instance, Zhou Li explored how changes in endogenous polyamine (PA) levels affect the drought adaptability in white clover. Proteomic analysis revealed that inhibition of PA synthesis reduced accumulation of key proteins related to ribosomal structure, amino acid transport, and metabolism, thereby decreasing drought resistance [55]. Lingling Chen investigated the role of boron in regulating seed yield and germination in alfalfa. The study found that boron deficiency impaired stress resistance, while excessive boron disrupted sugar utilization in flowers and caused lipid peroxidation in seed membranes. Four key boron-responsive proteins, including ADF-like protein, IMFP, NAD (P)-binding Rossmann-fold protein, and NAD-dependent ALDHs, were identified as critical for maintaining boron balance [56].

3.5. Advances in metabolomics research in forages

3.5.1. Metabolomics in stress resistance regulation of forages

As the downstream layer of omics research, metabolomics reveals metabolic changes under various conditions, aiding in the understand-

ing of growth and development mechanisms while guiding upstream gene expression studies. Although metabolomics studies are often integrated with other omics approaches, standalone metabolomics research provides valuable insights into stress responses.

Kun Wang and colleagues examined metabolite and phytohormone responses in three alfalfa root types (rhizomatous, tap-rooted, and creeping-rooted) under drought conditions. Their findings revealed a significant upregulation of metabolites and phytohormones such as indole-3-acetic acid (IAA) and abscisic acid (ABA), enhancing drought adaptability [57]. Anne-Antonella Serra studied the metabolic responses of perennial ryegrass when exposed to subtoxic levels of chemical stressors, observing significant alterations in nitrogen metabolism and photorespiration, including changes in asparagine, alanine, and glycerate levels [58]. In oats, Javier Sánchez-Martín found that early drought stress triggers the accumulation of salicylic acid (SA), which aids in stomatal closure, photorespiration, and antioxidant defense, helping to maintain water balance and mitigate photoinhibition [59].

3.5.2. Metabolomics in regulation of metabolic pathways in forages

Metabolomics is also crucial in elucidating secondary metabolite pathways in forages. For instance, Sainan Ma analyzed the metabolomes of two white clover varieties, 'Purple' and 'Haifa' to investigate the mechanisms of anthocyanin and proanthocyanidin (PA) biosynthesis. The study identified pelargonidin as the main pigment in purple clover and suggested that PA synthesis involves a variety of anthocyanin derivatives [60].

In alfalfa, metabolomics was employed to examine the biochemical basis of petal coloration in purple and yellow petals. Results showed that anthocyanin accumulation was higher in purple petals, while yellow petals contained more carotenoids and xanthophylls [61]. Additionally, Lv et al. [62] conducted a study on the response of *Stylosanthes guianensis* to low phosphorus stress using metabolomics, lipidomics, and gene expression analysis, identifying the genotype with high phosphorus utilization efficiency CF047827. The study also confirmed the critical role of the purple acid phosphatase gene *SgPAP27a* in enhancing phosphorus utilization efficiency.

3.5.3. Importance of multi-omics in forage research

Integrating multiple omics approaches, such as genomics, transcriptomics, proteomics, and metabolomics, enables a comprehensive analysis of the intricate biological mechanisms underlying forage growth and environmental response. Compared to single-omics studies, multi-omics integration provides a deeper and more comprehensive understanding of these processes. For example, while transcriptomics can reveal changes on gene expression, it cannot fully capture the dynamics of downstream proteins and metabolites. Multi-omics approaches analyze changes in genes, transcripts, proteins, and metabolite levels, providing a comprehensive view of growth, metabolic regulation, and stress-response mechanisms. Such insights are critical for improving breeding efficiency and developing high-yield, high-quality, and stress-resistant forage varieties.

Multi-omics applications have begun to demonstrate their potential in forage research. For instance, Yuntao Wang used a combination of transcriptomics and metabolomics to study how phosphate fertilizer impacts alfalfa. The research revealed that phosphate enhances root structure and increases soluble sugar and protein contents, improving the plant's overall quality and yield [63]. Xiaoyang Xu performed integrated proteomic and metabolomic analyses to explore how the phenolic compound O-coumaric acid (OCA) in hairy vetch inhibits alfalfa root growth. The study found that OCA modulates lignin biosynthesis, altering cell wall structure and leading to plant wilting [64].

Similarly, Lingdong Meng employed transcriptomics and metabolomics to investigate how red clover responds to lead (Pb) stress. At low Pb concentrations, red clover promotes citrate synthesis and maintains photosynthetic pigment levels, supporting stem growth. However, high Pb concentrations reduced carbohydrate contents and stunted stem growth [65]. Cheng Li utilized metabolomics, transcriptomics, and proteomics to examine how ryegrass responds to soil contaminated with cadmium (Cd) and polycyclic aromatic hydrocarbons (PAHs). The study revealed that Cd and PAHs significantly influenced linoleic acid metabolism and phenolic compound synthesis pathways, identifying several signature metabolites [65].

Through multi-omics approaches, researchers can unravel complex biological responses and regulatory networks in forages, providing valuable insights for targeted breeding programs. This integrated methodology enhances the understanding of forage biology and provides practical solutions to improve forage quality, stress resistance, and yield.

4. Insights from advances in crop genomics for forage research

Technological advancements in crop genomics, particularly in the fields of genomics, phenomics, and population genomics, have highlighted the unique advantages of crops for precise breeding and genomic research [66], providing valuable insights for forage research.

In genomics, crops have demonstrated superior higher resolution. For instance, Zijian Wang constructed a near-complete genome assembly of Chinese spring wheat using Oxford Nanopore (ONT) and PacBio HiFi technologies, filling gaps in the genome [67]. In contrast, forages, due to their high heterozygosity and complex genomic structures, face significant challenges in achieving comparable genome assembly and accuracy in genome assembly and functional annotation. To improve genome analysis accuracy, forages could adopt advanced sequencing methods, such as the Telomere-to-Telomere (T2T) approach, which integrates technologies like ONT and PacBio HiFi, to enhance genome assembly precision and completeness.

In Genome-Wide Association Studies (GWAS), crops benefit from the use of refined mapping populations, such as long-term inbred lines and backcross populations, which enable higher mapping resolution [68]. For example, Rong Zeng et al. conducted a GWAS analysis on 205 maize inbred lines, successfully identifying gene loci related to cold tolerance, thus revealing the molecular mechanisms underlying maize adaptation to cold environments [69]. These high-resolution gene mapping research are made possible by the precise breeding management techniques employed in crop research. In contrast, forages face significant challenges in utilizing GWAS due to the lack of high-quality mapping populations. This is primarily because most forage species are self-incompatible and experience inbreeding depression, which hinders the development of inbred lines and mapping populations. Therefore, advanced breeding management improving is crucial for enhancing the accuracy of genomic studies and achieving breeding objectives in forages (Fig. 3).

The application of phenomics, especially drone- and high-resolution imaging-based methods, particularly the use of drones and high-resolution imaging, has led to significant breakthroughs in crop researches [70]. These technologies enable high-throughput phenotypic data collection, real-time monitoring of plant growth, and the assessment of key traits such as stress tolerance [71]. Forages can also benefit from these phenomics technologies, although the diversity and complexity of their ecological environments present challenges for large-scale phenotypic assessments. By improving sample consistency and refining sampling strategies, forage research can gradually enhance the application of phenomics, promoting studies on critical traits such as stress resistance and biomass yield.

Although forage omics research still lags behind crop research in some areas, it possesses unique advantages and substantial potential. Forage species generally exhibit strong adaptability to various growth environments, allowing them to thrive in diverse ecosystems and display considerable genetic diversity and breeding potential. Moreover, forages exhibit rapid growth, and many species are perennials, facilitating sample collection for omics research. The genomes of most forages

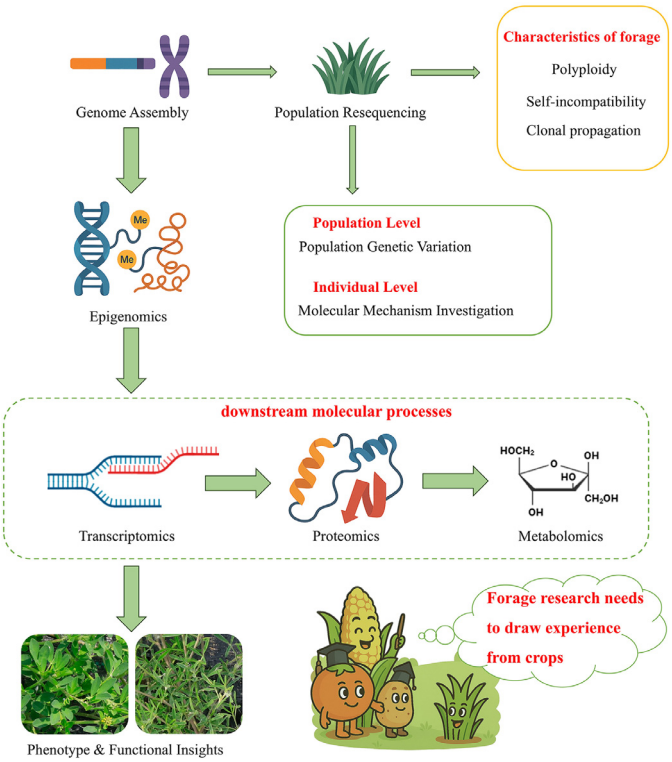

Fig. 3. The characteristics and relationships of forage omics research.

are generally compact, making them suitable for genetic analysis, such as gene mapping. With the establishment of effective hybridization or self-pollination breeding methods, combined with modern gene mapping technologies, the efficiency and precision of forage breeding could be significantly enhanced.

5. Outlook

In conclusion, although forage omics research is still in the early stages of development, its potential is considerable. With the continuous advancement of technologies such as genomics, transcriptomics, and proteomics, the breeding and improvement of forages will open up new opportunities. In the future, by integrating multi-omics approaches, researchers will be able to gain deep insights into the molecular mechanisms underlying forage growth, stress tolerance, and nutritional quality. Furthermore, breakthroughs in single-cell and spatial omics technologies will deepen our understanding of forages at the cellular level, providing more precise insights for breeding. As technological advancements continue and data analysis tools are optimized, forage omics research will be crucial in enhancing forage productivity and supporting sustainable agriculture.

CRediT authorship contribution statement

Yiwei Bai: Writing – original draft, Conceptualization. **Yunwei Zhang:** Supervision, Data curation. **Tianzuo Wang:** Supervision, Methodology. **Xiaojing Bi:** Writing – review & editing, Visualization. **Hui Wang:** Writing – review & editing, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no conflicts of interest in this work.

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