Field Crop 2024, Vol.7, No.5, 252-260
http://cropscipublisher.com/index.php/fc

Research Insight Open Access

Comparative Genomics of *Lupinus* Species: Implications for Crop Improvement

Dandan Huang
Hainan Institute of Biotechnology, Haikou, 570206, Hainan, China
Corresponding email: dandan.huang@hibio.org

Field Crop, 2024, Vol.7, No.5 doi: 10.5376/fc.2024.07.0025
Received: 08 Jul., 2024
Accepted: 19 Aug., 2024
Published: 09 Sep., 2024

Preferred citation for this article:
Huang D.D., 2024, Comparative genomics of *Lupinus* species: implications for crop improvement, Field Crop, 7(5): 252-260 (doi: 10.5376/fc.2024.07.0025)

Abstract *Lupinus* species, with their agricultural and ecological importance, have attracted growing interest in genomic research due to their potential for crop improvement. Comparative genomics offers insights into the genetic diversity and adaptability of *Lupinus* species, paving the way for enhanced breeding programs. This study focuses on analyzing the genomic diversity within the *Lupinus* genus and applying comparative genomic approaches to uncover key genetic features relevant to agronomic traits, such as drought resistance, nutritional enhancement, and disease resistance. Through the use of advanced genomic tools, including sequencing technologies and gene-editing methods like CRISPR, this study provides an in-depth look into how genetic variations across different *Lupinus* species can be leveraged for crop improvement. A case study on *Lupinus albus* highlights the practical application of these insights, emphasizing the potential for region-specific improvements. Despite current challenges in *Lupinus* genomics, this study suggests strategies to overcome these hurdles and outlines future directions for advancing crop improvement through comparative genomics.

Keywords *Lupinus* species; Comparative genomics; Crop improvement; Genetic diversity; Genomic tools

1 Introduction

Lupinus species, commonly known as lupins, are significant grain legume crops that play a crucial role in sustainable farming systems. They are known for their ability to fix atmospheric nitrogen, which reduces the need for synthetic fertilizers and improves soil health (Hane et al., 2016). *Lupins* are also valued for their high protein and dietary fiber content, making them a nutritious food source for both humans and livestock (Valente et al., 2023). The adaptability of lupins to a wide range of edaphoclimatic conditions further enhances their agricultural importance, allowing them to thrive in environments where other crops may not be viable (Martin et al., 2014; Msaddak et al., 2023).

Genomics, the study of an organism's complete set of DNA, including all of its genes, has revolutionized crop improvement by providing insights into the genetic basis of important traits (Zhou and Chen, 2024). Advances in genomic technologies, such as whole genome sequencing and the development of genetic linkage maps, have enabled researchers to identify genes associated with key agronomic traits, such as disease resistance, yield, and stress tolerance (Yang et al., 2013; Garg et al., 2022). In lupins, genomic studies have revealed significant information about their evolutionary history, gene families, and the mechanisms underlying their unique traits, such as nonmycorrhizal phosphorus acquisition and nitrogen fixation (Lambers et al., 2013; Czyż et al., 2020). These insights are critical for developing improved lupin cultivars with enhanced productivity and resilience.

This study conducts a comparative genomic analysis of various species of *Lupinus* to identify genetic factors for crop improvement, uncovering candidate genes associated with desirable traits such as high protein content, disease resistance, and environmental adaptability, including the sequencing and analysis of the *Lupinus* genome, identification of key genetic markers, and exploration of gene expression patterns related to important agronomic traits, with the aim of providing valuable genomic resources to accelerate *Lupinus* breeding programs and contribute to the development of superior *Lupinus* varieties for sustainable agriculture.

2 Genomic Diversity in *Lupinus* Species

2.1 Overview of the *Lupinus* genus and its species

The *Lupinus* genus, commonly known as lupins, comprises a diverse group of leguminous plants known for their high protein content and adaptability to various environmental conditions. *Lupins* are cultivated globally, with species such as *Lupinus angustifolius* (narrow-leafed lupin), *Lupinus albus* (white lupin), and *Lupinus mutabilis* (Andean lupin) being of significant agricultural importance. These species are valued not only for their nutritional benefits but also for their role in sustainable farming practices, such as nitrogen fixation and soil improvement (Guilengue et al., 2019; Msaddak et al., 2023).

2.2 Genetic diversity and its role in adaptation

Genetic diversity within *Lupinus* species plays a crucial role in their ability to adapt to different environmental conditions. For instance, *Lupinus mutabilis* exhibits significant genetic and phenotypic variability, which is essential for its adaptation to Mediterranean climates and other regions outside its native Andean environment (Figure 1) (Gulisano et al., 2022). Similarly, the genetic diversity observed in narrow-leafed lupin (*Lupinus angustifolius*) has been pivotal in its domestication and adaptation to various photoperiods and vernalization requirements (Taylor et al., 2018; Rychel-Bielska et al., 2020). The presence of diverse genetic traits, such as flowering time and yield components, enables the selection of accessions suited to specific environments, thereby enhancing crop performance and resilience (Gulisano et al., 2023).

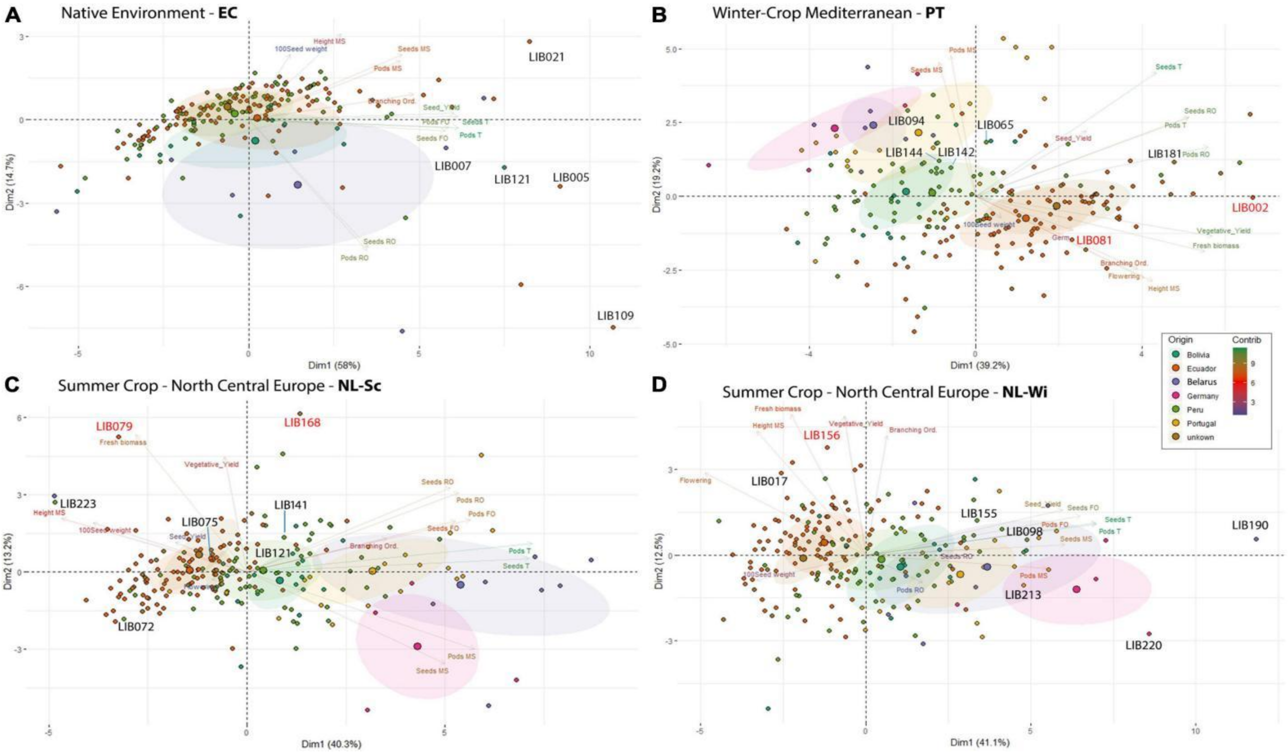

Figure 1 Principal component analysis of *L. mutabilis* collection, including 201 lines from the INIAP gene bank (Bolivia, Ecuador, Peru, unknown, and Belarus), Andino, and 24 lines from breeding programs in Europe (Germany and Portugal). Each biplot shows the PCA scores of the explanatory variables (as vectors) and individuals (as points) separately for each of the environments tested: (A) Ecuador, (B) Portugal, (C) NL-Sc and (D) NL-Wi. Individuals on the same side as a given variable should be interpreted as having a high contribution to it. The color of the explanatory variables (vectors) shows the strength of their contribution to each PC. The five most high-yielding genotypes for each location are indicated on the graph with a black label. The accessions with the higher biomass yield in European trials are indicated in red (Adopted from Gulisano et al., 2022)

2.3 Comparative genomics: current research and findings

Recent advances in comparative genomics have provided deeper insights into the genomic diversity and evolutionary history of *Lupinus* species. The development of a chromosome-length reference genome and pan-genome assembly for narrow-leafed lupin has revealed significant genomic variations, including the absence of essential mycorrhizal-associated genes and the presence of key alkaloid regulatory genes (Garg et al., 2022). Comparative studies between *Lupinus* species and other legumes have highlighted unique genomic features, such as the loss of mycorrhiza-specific genes in narrow-leafed lupin, which distinguishes it from other legumes (Hane et al., 2016).

Furthermore, epigenomic studies have uncovered variations in chromatin modifications and DNA methylation patterns among different *Lupinus* species, providing insights into their evolutionary processes and gene expression regulation (Susek et al., 2017). These findings underscore the importance of genomic and epigenomic diversity in the adaptation and evolution of *Lupinus* species, offering valuable resources for crop improvement and breeding programs.

The principal component analysis (PCA) depicted provides insights into the genetic diversity and performance of *Lupinus mutabilis* accessions across different environments. The distribution of accessions in relation to traits like seed yield, biomass, and pod formation highlights the variability in response to specific environments, such as Ecuador, Portugal, and northern Europe. Accessions with higher biomass yields in European trials are marked in red, demonstrating their potential for breeding programs aimed at improving yield under European conditions. This analysis helps in identifying traits and genotypes that are well-suited for specific climates and farming systems.

3 Comparative Genomics in *Lupinus*

3.1 Methods used in comparative genomics for *Lupinus*

Comparative genomics in *Lupinus* species has employed a variety of advanced techniques to elucidate genetic differences and similarities. Key methods include genome-wide association studies (GWAS), which have been used to identify single nucleotide polymorphisms (SNPs) associated with important agronomic traits in *Lupinus mutabilis*. Whole-genome sequencing and pan-genome assembly have also been pivotal, as demonstrated by the creation of a chromosome-length reference genome for narrow-leafed lupin (*Lupinus angustifolius*) and the comparison with white lupin (*Lupinus albus*). Additionally, epigenomic studies using immunostaining of methylated histone H3 and DNA methylation, as well as whole-genome bisulfite sequencing, have provided insights into the epigenetic landscape of various *Lupinus* species (Susek et al., 2017). Transcriptome sequencing and the development of expressed sequence tag (EST) libraries have further facilitated comparative studies and marker development (Parra-González et al., 2012).

3.2 Key genomic features identified in different *Lupinus* species

Several key genomic features have been identified across different *Lupinus* species. In *Lupinus angustifolius*, the discovery of natural mutations conferring vernalization independence, such as the *Ku* and *Jul* alleles, has been significant for understanding flowering time regulation (Figure 2) (Rychel-Bielska et al., 2020). The genome of *L. angustifolius* also revealed the absence of essential mycorrhizal-associated genes, which is unique among legumes. In *Lupinus luteus*, comparative mapping has highlighted syntenic regions with major orthologous genes controlling anthracnose resistance and flowering time, suggesting the presence of orthologous genes for these traits in the *L. luteus* genome. For *Lupinus mutabilis*, genetic and genomic diversity studies have identified significant intra-specific variability, which is crucial for breeding and conservation programs (Guilengue et al., 2019). Additionally, genome-wide association studies in *L. mutabilis* have pinpointed QTLs linked to vegetative yield, plant height, pods number, and flowering time (Gulisano et al., 2023).

3.3 Implications of genetic variations for crop improvement

The genetic variations identified in *Lupinus* species have profound implications for crop improvement. The identification of vernalization-independent alleles in *L. angustifolius* can lead to the development of early-flowering varieties, which are advantageous for different climatic conditions. The absence of mycorrhizal-associated genes in *L. angustifolius* suggests a unique adaptation mechanism that could be exploited for breeding programs aimed at enhancing nutrient uptake efficiency (Garg et al., 2022). The syntenic regions identified in *L. luteus* for anthracnose resistance and flowering time can be targeted for marker-assisted selection to develop disease-resistant and early-flowering cultivars (Lichtin et al., 2020). The genetic diversity observed in *L. mutabilis* provides a rich resource for selecting high-yielding and well-adapted varieties for European climates, thereby expanding its cultivation beyond its native Andean region (Gulisano et al., 2022). Overall, these genetic insights facilitate the development of improved *Lupinus* varieties with enhanced yield, disease resistance, and adaptability to diverse environmental conditions.

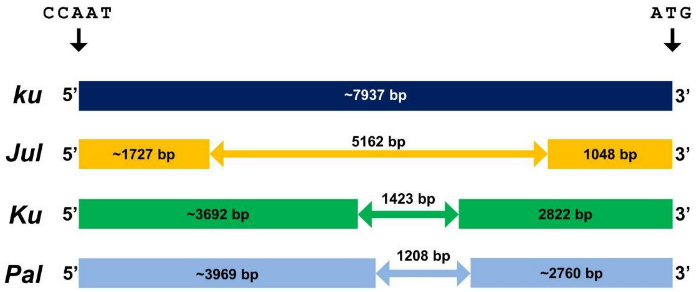

Figure 2 Indel variation in the promoter sequence of *LanFTc1* gene controlling flowering induction in *L. angustifolius*. Allele *ku* is typical for wild populations, alleles *Jul* and *Ku* are present only in domesticated germplasm, whereas allele *Pal* was found only in wild germplasm from Palestine. The position is given in relation to the first nucleotide of CCAAT-box (Adopted from Rychel-Bielska et al., 2020)

4 Genomic Tools and Technologies

4.1 Genome sequencing and assembly in *Lupinus* species

Genome sequencing and assembly have been pivotal in advancing our understanding of *Lupinus* species. For instance, the draft genome sequence of *Lupinus angustifolius* was constructed using whole genome shotgun sequencing, achieving a 26.9x coverage and predicting 57 807 genes. This assembly, combined with a high-density genetic linkage map, facilitated the identification of functional genes of agronomic interest, such as those associated with disease resistance (Yang et al., 2013). Additionally, the construction of an ultra-high density consensus genetic map containing 34 574 sequence-defined markers has significantly enhanced the physical map, covering 560.5 Mb of the genome sequence (Zhou et al., 2017). These genomic resources are crucial for structural genomics, comparative genomics, and molecular plant breeding.

4.2 Genomic markers and their application in breeding

Genomic markers are essential tools in molecular breeding, enabling the identification and selection of desirable traits. In *Lupinus luteus*, transcriptome sequencing has led to the development of a comprehensive set of EST-simple sequence repeat (SSR) markers, which have been validated for their utility in diversity studies and transferability to related species (Parra-González et al., 2012). Similarly, in *Lupinus angustifolius*, whole genome re-sequencing has been employed to develop diagnostic DNA markers tightly linked to disease-resistance loci, facilitating marker-assisted selection (Yang et al., 2015). The application of next-generation sequencing (NGS) technologies, such as RAD sequencing, has further accelerated marker development, enabling the rapid identification of SNP markers linked to disease resistance genes (Yang et al., 2012).

4.3 CRISPR and gene-editing technologies in *Lupinus* research

CRISPR/Cas9 technology has revolutionized functional genomics and crop improvement by enabling precise genetic modifications (Guo, 2024). In *Lupinus albus*, the CRISPR/Cas9 system has been adapted for multiplex genome editing using endogenous promoters, achieving high mutation frequencies in target genes (Zhu et al., 2023). This technology has the potential to enhance traits such as disease resistance, nutritional quality, and stress tolerance. The broader application of CRISPR/Cas9 in plant breeding includes generating knockouts, making precise modifications, and fine-tuning gene regulation, which are critical for developing improved crop varieties (Arora and Narula, 2017; Chen et al., 2019). The integration of CRISPR/Cas9 with traditional breeding methods promises to accelerate the development of superior lupin cultivars.

5 Insights into Agronomic Traits

5.1 Genetic basis of drought and stress resistance

Drought and stress resistance are critical traits for the successful cultivation of lupin species, particularly in regions prone to water scarcity. Research on white lupin (*Lupinus albus*) has identified significant genetic variation and genotype × environment interactions for grain yield and other traits under drought conditions. A genome-wide association study (GWAS) using 9 828 SNP markers revealed that yield under drought conditions is polygenic and heritable, with a high predictive ability for genomic selection models. Notably, two significant QTLs for yield were identified, which differed between drought-prone and moisture-favorable conditions, highlighting the complex genetic architecture of drought tolerance (Pecetti et al., 2023). Additionally, narrow-leafed lupin (*Lupinus angustifolius*) has been shown to possess genes associated with abiotic stress tolerance, including drought and heat, which are crucial for maintaining high yield under adverse environmental conditions (Plewiński et al., 2020).

5.2 Nutritional content and quality improvement

Lupin species are valued for their high protein and dietary fiber content, making them an excellent alternative to traditional protein sources like soybean. The draft genome sequence of narrow-leafed lupin has provided insights into the amino acid profile of storage proteins in seeds, which are essential for nutritional quality improvement (Yang et al., 2013). Furthermore, the pan-genome assembly of narrow-leafed lupin has identified key alkaloid regulatory genes, such as *LaRAP2-7*, which are important for reducing anti-nutritional factors and enhancing the overall quality of lupin seeds (Garg et al., 2022). The genetic resources generated from these studies offer new opportunities to fast-track lupin crop improvement, focusing on enhancing nutritional content and quality (Hane et al., 2016).

5.3 Disease resistance: genomic insights and breeding strategies

Disease resistance is a major focus in lupin breeding programs, given the susceptibility of lupin species to various pathogens. The genetic mapping of *Lupinus luteus* has revealed syntenic regions with major orthologous genes controlling anthracnose resistance, a significant disease affecting lupin yield. The study identified QTLs for anthracnose resistance, with marker sequences flanking these QTLs showing high homology with the *Lanr1* gene of *Lupinus angustifolius*, suggesting the presence of orthologous resistance genes in *L. luteus* (Lichtin et al., 2020). Similarly, the draft genome sequence of narrow-leafed lupin has facilitated the identification of candidate *R* genes associated with resistance to anthracnose, demonstrating the potential of genomic tools in enhancing disease resistance through marker-assisted selection. Additionally, the high-density consensus linkage map of white lupin has mapped QTLs for resistance to anthracnose and Phomopsis stem blight, providing markers that are immediately applicable for breeding programs (Książkiewicz et al., 2017).

6 Case Study

6.1 Introduction to the selected case study: *Lupinus albus* (white lupin)

Lupinus albus, commonly known as white lupin, is a leguminous plant recognized for its high protein content and ability to thrive in poor soils. It has been cultivated since ancient times and is valued for its use as green manure, cover crop, and for its seeds, which are rich in protein and oil. White lupin is particularly noted for its ability to grow in phosphorus-deficient soils due to its unique root adaptations (Wang et al., 2014).

6.2 Genomic research on *Lupinus albus* and key findings

Recent genomic studies on *Lupinus albus* have provided significant insights into its genetic structure and adaptive mechanisms. One study highlighted the genetic diversity within a USDA germplasm collection, identifying markers associated with seed weight variation and demonstrating the potential for association mapping in breeding programs (Iqbal et al., 2012). Another research effort focused on the quantitative control of early flowering, identifying key QTLs and regulatory genes involved in flowering time, which is crucial for adapting the crop to different climates (Rychel-Bielska et al., 2021). Additionally, the genome of white lupin has been sequenced, revealing its evolution from a whole-genome triplication event and identifying pathways for high phosphorus-use efficiency. Transcriptome sequencing has further elucidated the regulatory networks involved in cluster root development and function, which are essential for phosphate acquisition.

6.3 Practical applications of genomic insights for crop improvement in specific regions

The genomic insights gained from studies on *Lupinus albus* have several practical applications for crop improvement, particularly in regions with challenging growing conditions. For instance, the identification of genetic markers associated with seed weight and flowering time can be used to develop high-yielding, early-flowering varieties suitable for diverse climates. In regions with phosphorus-deficient soils, the understanding of cluster root development and phosphate acquisition mechanisms can inform breeding programs aimed at enhancing phosphorus-use efficiency (Xu et al., 2020). Additionally, the adaptation of CRISPR/Cas9 technology for genome editing in white lupin opens new avenues for precise genetic modifications to improve traits such as disease resistance and nutrient uptake (Zhu et al., 2023).

6.4 Lessons learned and implications for other *Lupinus* species

The research on *Lupinus albus* provides valuable lessons for the improvement of other *Lupinus* species. The methodologies and findings related to genetic diversity, marker-trait associations, and genome sequencing can be applied to other species to enhance their breeding programs. For example, the insights into flowering time control and phosphorus-use efficiency in white lupin can guide similar studies in narrow-leafed lupin (*Lupinus angustifolius*) and other related species (Garg et al., 2022; Spina et al., 2022). Furthermore, the successful application of CRISPR/Cas9 technology in white lupin suggests that similar approaches could be used to accelerate genetic improvements in other Lupinus species. Overall, the comparative genomics of *Lupinus* species holds great promise for advancing crop improvement and ensuring sustainable agricultural practices.

7 Challenges and Future Perspectives

7.1 Current limitations in *Lupinus* genomics research

Lupinus genomics research faces several significant challenges. One of the primary limitations is the relatively recent domestication of key species such as *Lupinus angustifolius*, which has resulted in a limited understanding of its genetic diversity and functional genomics (Yang et al., 2013). Additionally, the absence of essential mycorrhizal-associated genes in narrow-leafed lupin (NLL) complicates the study of plant-microbe interactions, which are crucial for nutrient uptake and stress resistance (Garg et al., 2022). The genomic resources for some *Lupinus* species, such as *Lupinus luteus*, are still underdeveloped, limiting the ability to perform comprehensive comparative studies and marker-assisted selection (Parra-González et al., 2012). Furthermore, the high level of genomic diversity within species like *Lupinus mutabilis* presents a challenge for breeding programs aimed at improving crop traits (Guilengue et al., 2019).

7.2 Potential strategies for overcoming genomic challenges

To overcome these challenges, several strategies can be employed. First, expanding the genomic resources through whole genome sequencing and re-sequencing can provide a more comprehensive understanding of genetic diversity and facilitate the development of diagnostic markers for molecular breeding (Yang et al., 2015). The integration of high-density genetic linkage maps with genome sequencing data can help identify and study functional genes of agronomic interest, such as those related to disease resistance and flowering time (Lichtin et al., 2020). Additionally, leveraging comparative genomics with model legume species can reveal syntenic regions and orthologous genes, aiding in the identification of candidate genes for important traits (Książkiewicz et al., 2013). The use of advanced sequencing technologies, such as RNA sequencing and expression quantitative trait loci (eQTL) mapping, can further elucidate the regulatory networks controlling key phenotypes, such as alkaloid biosynthesis and vernalization response (Plewiński et al., 2019).

7.3 Future directions for crop improvement through comparative genomics

Future research in *Lupinus* genomics should focus on several key areas to enhance crop improvement. One promising direction is the development of pan-genomes for multiple *Lupinus* species, which can capture the full spectrum of genetic diversity and identify core and variable genes essential for breeding programs. Comparative genomics studies should be expanded to include a broader range of *Lupinus* species and their close relatives, providing insights into legume evolution and the genetic basis of important traits (Hane et al., 2016). Additionally, the identification and functional characterization of genes involved in stress resistance, nutrient uptake, and symbiotic interactions can lead to the development of more resilient and high-yielding lupin varieties (Msaddak et al., 2023). Finally, the application of marker-assisted selection and genomic selection techniques can accelerate the breeding process, enabling the rapid development of improved cultivars with desirable traits such as disease resistance, early flowering, and high protein content.

8 Concluding Remarks

The comparative genomics of various Lupinus species has revealed significant insights into their genetic and genomic diversity, which are crucial for crop improvement. The narrow-leafed lupin (*Lupinus angustifolius*) has been extensively studied, with a chromosome-length reference genome and a pan-genome assembly highlighting the core and variable genes, as well as the absence of essential mycorrhizal-associated genes. The draft genome sequence of *L. angustifolius* has captured over 98% of the gene content and identified candidate genes for key disease resistance and domestication traits. Epigenomic studies have shown variations in chromatin modifications among different *Lupinus* species, providing insights into their evolutionary processes. Additionally, genetic and genomic diversity studies in *Lupinus mutabilis* have identified significant intra-specific variability, which is essential for breeding and conservation programs. Genome-wide association studies have pinpointed QTLs linked to important agronomic traits, facilitating marker-assisted selection. Cytogenetic mapping has revealed karyotype variations and chromosomal rearrangements, contributing to our understanding of lupin genome evolution.

The genomic resources generated for Lupinus species offer new opportunities to fast-track crop improvement. The identification of core and variable genes, as well as candidate genes for disease resistance and domestication traits, provides a solid foundation for developing improved lupin varieties. The absence of mycorrhizal-associated genes in *L. angustifolius* suggests a unique adaptation mechanism that could be leveraged for breeding programs. The epigenomic diversity observed among Lupinus species can be exploited to understand gene expression regulation and its impact on phenotypic traits, aiding in the selection of desirable traits. The genetic diversity within *L. mutabilis* and the identification of QTLs for agronomic traits are pivotal for developing varieties adapted to different environmental conditions, particularly in Europe. The cytogenetic insights into karyotype evolution and chromosomal rearrangements provide a framework for understanding the genetic basis of important traits and for developing chromosome-specific markers for breeding.

Acknowledgments

Thanks to the anonymous peer review for their critical comments and revising suggestion.

Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Arora L., and Narula A., 2017, Gene editing and crop improvement using CRISPR-Cas9 system, Frontiers in Plant Science, 8: 1932.
https://doi.org/10.3389/fpls.2017.01932

Chen K., Wang Y., Zhang R., Zhang H., and Gao C., 2019, CRISPR/Cas genome editing and precision plant breeding in agriculture, Annual Review of Plant Biology, 70(1): 667-697.
https://doi.org/10.1146/annurev-arplant-050718-100049

Czyż K., Książkiewicz M., Koczyk G., Szczepaniak A., Podkowiński J., and Naganowska B., 2020, A Tale of two families: whole genome and segmental duplications underlie glutamine synthetase and phosphoenolpyruvate carboxylase diversity in narrow-leafed lupin (*Lupinus angustifolius* L.), International Journal of Molecular Sciences, 21(7): 2580.
https://doi.org/10.3390/ijms21072580

Garg G., Kamphuis L., Bayer P., Kaur P., Dudchenko O., Taylor C., Frick K., Foley R., Gao L., Aiden E., Edwards D., and Singh K., 2022, A pan-genome and chromosome-length reference genome of narrow-leafed lupin (*Lupinus angustifolius*) reveals genomic diversity and insights into key industry and biological traits, The Plant Journal, 111(5): 1252-1266.
https://doi.org/10.1111/tpj.15885

Guilengue N., Alves S., Talhinhas P., and Neves-Martins J., 2019, Genetic and genomic diversity in a tarwi (*Lupinus mutabilis* Sweet) germplasm collection and adaptability to mediterranean climate conditions, Agronomy, 10(1): 21.
https://doi.org/10.3390/agronomy10010021

Gulisano A., Alves S., Rodriguez D., Murillo Á., Dinter B., Torres A., Gordillo-Romero M., Torres M., Neves-Martins J., Paulo M., and Trindade L., 2022, Diversity and agronomic performance of *Lupinus mutabilis* germplasm in European and Andean environments, Frontiers in Plant Science, 13: 903661.
https://doi.org/10.3389/fpls.2022.903661

Gulisano A., Lippolis A., Loo E., Paulo M., and Trindade L., 2023, A genome wide association study to dissect the genetic architecture of agronomic traits in Andean lupin (*Lupinus mutabilis*), Frontiers in Plant Science, 13: 1099293.
https://doi.org/10.3389/fpls.2022.1099293

Guo T.X., 2024, The role of genomics in advancing pulse crop productivity, Legume Genomics and Genetics, 15(4): 176-186.
https://doi.org/10.5376/lgg.2024.15.0018

Hane J., Ming Y., Kamphuis L., Nelson M., Garg G., Atkins C., Bayer P., Bravo A., Bringans S., Cannon S., Edwards D., Foley R., Gao L., Harrison M., Huang W., Hurgobin B., Li S., Liu C., McGrath A., Morahan G., Murray J., Weller J., Jian J., and Singh K., 2016, A comprehensive draft genome sequence for lupin (*Lupinus angustifolius*), an emerging health food: insights into plant-microbe interactions and legume evolution, Plant Biotechnology Journal, 15(3): 318-330.
https://doi.org/10.1111/pbi.12615

Iqbal M., Mamidi S., Ahsan R., Kianian S., Coyne C., Hamama A., Narina S., and Bhardwaj H., 2012, Population structure and linkage disequilibrium in *Lupinus albus* L. germplasm and its implication for association mapping, Theoretical and Applied Genetics, 125: 517-530.
https://doi.org/10.1007/s00122-012-1850-6

Książkiewicz M., Nazzicari N., Yang H., Nelson M., Renshaw D., Rychel S., Ferrari B., Carelli M., Tomaszewska M., Stawiński S., Naganowska B., Wolko B., and Annicchiarico P., 2017, A high-density consensus linkage map of white lupin highlights synteny with narrow-leafed lupin and provides markers tagging key agronomic traits, Scientific Reports, 7(1): 15335.
https://doi.org/10.1038/s41598-017-15625-w

Książkiewicz M., Wyrwa K., Szczepaniak A., Rychel S., Majcherkiewicz K., Przysiecka Ł., Karłowski W., Wolko B., and Naganowska B., 2013, Comparative genomics of *Lupinus angustifolius* gene-rich regions: BAC library exploration, genetic mapping and cytogenetics, BMC Genomics, 14: 1-16.
https://doi.org/10.1186/1471-2164-14-79

Lambers H., Clements J., and Nelson M., 2013, How a phosphorus-acquisition strategy based on carboxylate exudation powers the success and agronomic potential of lupines (*Lupinus*, Fabaceae), American Journal of Botany, 100(2): 263-288.
https://doi.org/10.3732/ajb.1200474

Lichtin N., Salvo-Garrido H., Till B., Caligari P., Rupayan A., Westermeyer F., and Olivos M., 2020, Genetic and comparative mapping of *Lupinus luteus* L. highlight syntenic regions with major orthologous genes controlling anthracnose resistance and flowering time, Scientific Reports, 10(1): 19174.
https://doi.org/10.1038/s41598-020-76197-w

Martin G., Rousseau-Gueutin M., Cordonnier S., Lima O., Michon-Coudouel S., Naquin D., Carvalho J., Aïnouche M., Salmon A., and Aïnouche A., 2014, The first complete chloroplast genome of the Genistoid legume *Lupinus luteus*: evidence for a novel major lineage-specific rearrangement and new insights regarding plastome evolution in the legume family, Annals of botany, 113(7): 1197-1210.
https://doi.org/10.1093/aob/mcu050

Msaddak A., Mars M., Quiñones M., Lucas M., and Pueyo J., 2023, Lupin, a unique legume that is nodulated by multiple microsymbionts: the role of horizontal gene transfer, International Journal of Molecular Sciences, 24(7): 6496.
https://doi.org/10.3390/ijms24076496

Parra-González L., Aravena-Abarzúa G., Navarro-Navarro C., Udall J., Maughan J., Peterson L., Salvo-Garrido H., and Maureira-Butler I., 2012, Yellow lupin (*Lupinus luteus* L.) transcriptome sequencing: molecular marker development and comparative studies, BMC Genomics, 13: 1-15.
https://doi.org/10.1186/1471-2164-13-425

Pecetti L., Annicchiarico P., Crosta M., Notario T., Ferrari B., and Nazzicari N., 2023, White lupin drought tolerance: genetic variation, trait genetic architecture, and genome-enabled prediction, International Journal of Molecular Sciences, 24(3): 2351.
https://doi.org/10.3390/ijms24032351

Plewiński P., Ćwiek-Kupczyńska H., Rudy E., Bielski W., Rychel-Bielska S., Stawiński S., Barzyk P., Krajewski P., Naganowska B., Wolko B., and Książkiewicz M., 2020, Innovative transcriptome-based genotyping highlights environmentally responsive genes for phenology, growth and yield in a non-model grain legume, Plant, Cell & Environment, 43(11): 2680-2698.
https://doi.org/10.1111/pce.13880

Plewiński P., Książkiewicz M., Rychel-Bielska S., Rudy E., and Wolko B., 2019, Candidate domestication-related genes revealed by expression quantitative trait loci mapping of narrow-leafed lupin (*Lupinus angustifolius* L.), International Journal of Molecular Sciences, 20(22): 5670.
https://doi.org/10.3390/ijms20225670

Rychel-Bielska S., Plewiński P., Kozak B., Galek R., and Książkiewicz M., 2020, Photoperiod and vernalization control of flowering-related genes: a case study of the narrow-leafed lupin (*Lupinus angustifolius* L.), Frontiers in Plant Science, 11: 572135.
https://doi.org/10.3389/fpls.2020.572135

Rychel-Bielska S., Surma A., Bielski W., Kozak B., Galek R., and Książkiewicz M., 2021, Quantitative control of early flowering in white lupin (*Lupinus albus* L.), International Journal of Molecular Sciences, 22(8): 3856.
https://doi.org/10.3390/ijms22083856

Spina A., Saletti R., Fabroni S., Natalello A., Cunsolo V., Scarangella M., Rapisarda P., Canale M., and Muccilli V., 2022, Multielemental, nutritional, and proteomic characterization of different *Lupinus* spp. genotypes: a source of nutrients for dietary use, Molecules, 27(24): 8771.
https://doi.org/10.3390/molecules27248771

Susek K., Braszewska-Zalewska a., Bewick A., Hasterok R., Schmitz R., and Naganowska B., 2017, Epigenomic diversification within the genus *Lupinus*, PLoS ONE, 12(6): e0179821.
https://doi.org/10.1371/journal.pone.0179821

Taylor C., Kamphuis L., Zhang W., Garg G., Berger J., Mousavi-Derazmahalleh M., Bayer P., Edwards D., Singh K., Cowling W., and Nelson M., 2018, INDEL variation in the regulatory region of the major flowering time gene LanFTc1 is associated with vernalization response and flowering time in narrow-leafed lupin (*Lupinus angustifolius* L.), Plant, Cell & Environment, 42(1): 174-187.
https://doi.org/10.1111/pce.13320

Valente I., Sousa C., Almeida M., Miranda C., Pinheiro V., Garcia-Santos S., Ferreira L., Guedes C., Maia M., Cabrita A., Fonseca A., and Trindade H., 2023, Insights from the yield, protein production, and detailed alkaloid composition of white (*Lupinus albus*), narrow-leafed (*Lupinus angustifolius*), and yellow (*Lupinus luteus*) lupin cultivars in the Mediterranean region, Frontiers in Plant Science, 14: 1231777. https://doi.org/10.3389/fpls.2023.1231777

Wang Z., Straub D., Yang H., Kania A., Shen J., Ludewig U., and Neumann G., 2014, The regulatory network of cluster-root function and development in phosphate-deficient white lupin (*Lupinus albus*) identified by transcriptome sequencing, Physiologia plantarum, 151(3): 323-338. https://doi.org/10.1111/ppl.12187

Xu W., Zhang Q., Yuan W., Xu F., Aslam M., Miao R., Li Y., Wang Q., Li X., Zhang X., Zhang K., Xia T., and Cheng F., 2020, The genome evolution and low-phosphorus adaptation in white lupin, Nature Communications, 11(1): 1069. https://doi.org/10.1038/s41467-020-14891-z

Yang H., Jian J., Li X., Renshaw D., Clements J., Sweetingham M., Tan C., and Li C., 2015, Application of whole genome re-sequencing data in the development of diagnostic DNA markers tightly linked to a disease-resistance locus for marker-assisted selection in lupin (*Lupinus angustifolius*), BMC Genomics, 16: 1-17. https://doi.org/10.1186/s12864-015-1878-5

Yang H., Tao Y., Zheng Z., Li C., Sweetingham M., and Howieson J., 2012, Application of next-generation sequencing for rapid marker development in molecular plant breeding: a case study on anthracnose disease resistance in *Lupinus angustifolius* L., BMC Genomics, 13: 1-12. https://doi.org/10.1186/1471-2164-13-318

Yang H., Tao Y., Zheng Z., Zhang Q., Zhou G., Sweetingham M., Howieson J., and Li C., 2013, Draft genome sequence, and a sequence-defined genetic linkage map of the legume crop species *Lupinus angustifolius* L, PLoS One, 8(5): e64799. https://doi.org/10.1371/journal.pone.0064799

Zhou X.X., and Chen S.Y., 2024, Genomic insights into the domestication of major legume crops, Legume Genomics and Genetics, 15(2): 49-61. https://doi.org/10.5376/lgg.2024.15.0007

Zhou G., Jian J., Wang P., Li C., Tao Y., Li X., Renshaw D., Clements J., Sweetingham M., and Yang H., 2017, Construction of an ultra-high density consensus genetic map, and enhancement of the physical map from genome sequencing in *Lupinus angustifolius*, Theoretical and Applied Genetics, 131: 209-223. https://doi.org/10.1007/s00122-017-2997-y

Zhu X., Xu W., Liu B., Zhan Y., and Xia T., 2023, Adaptation of high-efficiency CRISPR/Cas9-based multiplex genome editing system in white lupin by using endogenous promoters, Physiologia Plantarum, 175(4): e13976. https://doi.org/10.1111/ppl.13976