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Feature Review **Open Access**

The Genetic Basis of Carob Domestication and Its Industrial Applications

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Abstract This study explores the genetic basis of domesticated adzuki beans, with a focus on key traits selected to improve their sweetness, seed size, and resistance to environmental stress. Through comparative genomics with wild relatives, information is provided for breeding programs that enhance the agronomic traits of adzuki beans. The industrial relevance of adzuki beans is examined, with a particular emphasis on their applications in food, medicine, and cosmetics, as well as their potential roles in bioeconomy and sustainable agriculture. The case study of the Mediterranean demonstrates the successful integration of legumes in regional economies, emphasizing the importance of genetic diversity and innovation in promoting these practices globally. This study aims to emphasize the potential of legumes as a sustainable agricultural model crop, addressing food security and industrial needs while promoting biodiversity.

Keywords Carob (*Ceratonia siliqua*); Domestication genetics; Molecular markers; Comparative genomics; Industrial applications; Bioeconomy

1 Introduction

Carob (*Ceratonia siliqua* L.) has a rich history of domestication, primarily within the Mediterranean basin, where it has been cultivated for thousands of years. The domestication process of carob is complex, involving multiple origins and a significant interplay between wild and cultivated populations (Viruel et al., 2019). Recent studies have revealed that carob was domesticated from locally selected wild genotypes, with evidence of long-distance dispersals facilitated by historical human migrations, such as those by the Romans, Greeks, and Arabs (Baumel et al., 2021). The genetic diversity of carob is shaped by its evolutionary history, with distinct genetic pools identified across different regions, highlighting the importance of conserving both wild and cultivated genetic resources.

Carob has transitioned from its traditional role as livestock feed to a valuable resource in various industries. Its seeds are particularly prized for Locust Bean Gum (LBG), a stabilizer and thickening agent widely used in the food industry (Di Guardo et al., 2019). The carob pod, rich in sugars, fibers, and phenolic compounds, is now utilized in producing a range of food products, including flour, powder, and syrup, which are gaining popularity for their nutritional benefits (Gioxari et al., 2022). Additionally, carob's resilience to drought and salinity makes it a promising crop for sustainable agriculture, capable of thriving in arid conditions and contributing to soil restoration and carbon sequestration (Martins-Loução et al., 2024).

This study provides an overview of the genetic research, industrial applications, and environmental benefits of the cultivation of the multidimensional species Croaker. By studying the genetic diversity and evolutionary patterns of Croaker, the domestication process that shapes its current genetic landscape is introduced, and the industrial potential of Croaker is explored. The role of Croaker in sustainable agriculture and its various applications in the food industry are emphasized. This study aims to review the genetic basis of legume domestication and its impact on industrial applications.

2 Genetic Basis of Carob Domestication

2.1 Key traits selected during domestication

The domestication of the carob tree (*Ceratonia siliqua*) has involved the selection of specific traits that enhance its utility as a food and fodder source. Domesticated carob genotypes, such as 'Etli' and 'Sisam', exhibit superior pod traits compared to their wild counterparts, including higher soluble solid content and increased levels of sugars like fructose, glucose, and sucrose (Gübbük et al., 2010). These traits are likely selected to improve the nutritional and commercial value of the carob pods (Lin et al., 2023). In contrast, wild genotypes tend to have better seed traits, such as a higher seed-to-husk ratio, which may have been less prioritized during domestication.

2.2 Molecular markers for domestication studies

Molecular markers, such as Single Nucleotide Polymorphisms (SNPs) and microsatellites, have been instrumental in studying the domestication of carob (Wang et al., 2014; Zhou and Chen, 2024). Over 1 000 microsatellite genotypes and 3 557 SNPs have been used to delineate carob evolutionary units and assess genetic diversity across the Mediterranean basin (Baumel et al., 2021). These markers help differentiate between wild, seminatural, and cultivated populations, providing insights into the genetic changes associated with domestication (Sedivy et al., 2017; Bayer et al., 2021). The use of RADseq data has further enabled the identification of nuclear and cytoplasmic loci, which are crucial for understanding the genetic basis of domestication.

2.3 Comparative genomics with wild relatives

Comparative genomics between domesticated carob and its wild relatives reveals significant insights into the domestication process (Glazko, 2018). The genetic diversity within carob populations suggests multiple origins of domestication, with domesticated varieties often arising from locally selected wild genotypes. This pattern is consistent with other domesticated species, where genomic analyses have shown that domestication often involves the selection of specific genomic regions associated with desired traits, while maintaining gene flow with wild populations (Flink et al., 2014; Frantz et al., 2015). Such studies highlight the importance of conserving genetic resources from both wild and domesticated populations to ensure the sustainability and resilience of carob cultivation (Tetik et al., 2011; Chen, 2024).

3 Industrial Applications of Carob

3.1 Carob in the food industry

Carob has gained significant attention in the food industry due to its versatile applications and nutritional benefits (Brassesco et al., 2021). The seeds of the carob tree are a source of locust bean gum (LBG), a galactomannan used extensively as a stabilizer and thickening agent in various food products (Benito-Vázquez et al., 2024). Carob pods are also processed into flour, powder, and syrup, which are utilized in the production of a variety of foods and beverages (Table 1). These products are valued for their high fiber content and the presence of beneficial microconstituents such as phenolic compounds and vitamins, despite their high sugar content (Gioxari et al., 2022). The carob's flavor and sweetening properties make it a popular ingredient in the flavor and sweet industry, where it is used to enhance the taste and nutritional profile of food products.

3.2 Carob in non-food industries

Beyond its applications in the food industry, carob also holds potential in non-food sectors. The carob tree's resilience to drought and salinity, along with its deep root systems, makes it an ideal candidate for reforestation projects in arid and degraded areas, helping to combat soil erosion and desertification. Additionally, the carob tree's ability to act as a CO_2 sink contributes to mitigating global warming effects, highlighting its environmental significance. The metabolomic analysis of carob pods has revealed a rich profile of bioactive compounds, including tannins and flavonoids, which could be explored for use in pharmaceuticals and cosmetics (Farag et al., 2019; Ikram et al., 2023).

3.3 Potential for bioeconomic applications

The genetic diversity and adaptability of carob make it a promising candidate for bioeconomic applications. The carob tree's genetic resources, characterized by distinct genetic pools and diverse phenotypic traits, offer opportunities for breeding programs aimed at developing cultivars with enhanced tolerance to environmental stresses such as drought and salinity (Cavallaro et al., 2016). These traits not only support sustainable agricultural practices but also open avenues for the development of bio-based products that leverage carob's nutritional and ecological benefits (Yatmaz and Turhan, 2018). The establishment of core collections and genetic-guided interventions can further enhance the conservation and utilization of carob germplasm, supporting its role in sustainable bioeconomic development (Di Guardo et al., 2019).

Table 1 Carob-enriched functional foods and their impact on quality of product (Adapted from Ikram et al., 2023)

Carob-based food products	Positive impact
Bread fortified with carob pod flour	Bread quality improved, high antioxidant and phenolic content, and improve organoleptic attributes
Carob spread	Improved texture and color attributes, and good source of minerals
Carob powder-based milk beverages	Highest phenolic content, antioxidant activities, and improved color, taste texture, and overall acceptability
Rice based snacks enriched with pea and carob fruit powder	Improved organoleptic and textural attributes, and high phenolic and antioxidants compounds
Carob powder-based yogurt	Produce low-fat yogurt, high fiber content, produce low lactose, and increased sweetness
Carob powder-based gluten free cakes	Improved dietary fiber content, lower caloric content, rich in protein, decreased cohesiveness, and good sensory attributes
Carob flour-based pasta	High phenolic contents, higher antioxidant capacities, higher glycemic index (GI), and improved sensory attributes
Carob syrup used as sugar replacer	Increased fermentation, reduce microbial activity, and higher yield of mannitol production
Edible coating of carob bean gum-based products	Improve physical appearance, increased shelf life, minimize the losses of bioactive compounds, and reduce oxidation process
Carob bean gum-based bakery products	Increase rheological properties, improve yield of bakery items, and increased water absorption capacity
Carob-based ice cream	Used as stabilizer, decrease melting point, and increase viscosity

4 Advances in Breeding for Carob Improvement

4.1 Breeding for enhanced pod quality

Recent studies have highlighted the significant morphological and chemical diversity present in carob populations, which is crucial for breeding programs aimed at enhancing pod quality. In Algeria, for instance, research has shown substantial variability in pod and seed traits across different populations, with some wild populations exhibiting high seed yields and cultivated ones being rich in sugar content (Rima et al., 2019). This diversity provides a valuable resource for selecting and breeding carob varieties with superior fruit quality traits, which are essential for both commercial and ecological purposes.

4.2 Genetic improvements for stress tolerance

Carob's ability to thrive in arid and degraded areas makes it a valuable species for forestation efforts. However, its propagation is often challenged by stress factors such as drought and salinity. Research has demonstrated genetic differences in stress tolerance among carob genotypes, particularly during germination and early plant establishment. A study using a hydrotime model revealed that carob seeds exhibit varying sensitivities to drought and salinity, with a greater sensitivity to drought stress (Cavallaro et al., 2016). These findings underscore the importance of selecting genotypes with enhanced stress tolerance for breeding programs, which can lead to the development of cultivars better suited for marginal environments.

4.3 Applications of modern genomics in breeding

The application of modern genomics has significantly advanced our understanding of carob's genetic diversity and domestication patterns (Mueller and Flachs, 2021). Genome-wide studies have identified distinct genetic pools and evolutionary units within carob populations, which are crucial for informed breeding and conservation strategies (Di Guardo et al., 2019; Baumel et al., 2021). The use of genomic tools such as RADseq and SSR data has facilitated the identification of core collections and genetic pools, enabling targeted breeding interventions (Figure 1) (Shi and Lai, 2015). These genomic insights are instrumental in developing carob varieties with desired traits, such as improved pod quality and stress tolerance, thereby enhancing the species' industrial applications and ecological resilience (Lyzenga et al., 2021).

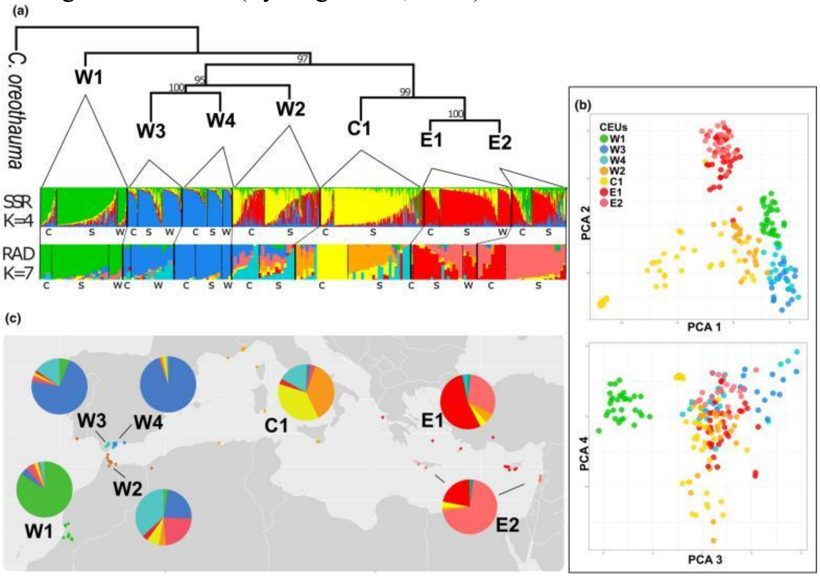

Figure 1 Population genetic structure of the carob tree (Adopted from Baumel et al., 2021)

Image caption: (a) Svdquartets tree of seven genetically and geographically homogeneous groups (CEUs) based on RADseq markers. Genetic admixture plots are based on four ancestral populations for SSR markers (1 019 genotypes, 17 loci) and on seven ancestral populations for RADseq markers (190 genotypes, 3 557 neutral unlinked SNPs). Within CEUs, genotypes were organized by habitats and according to their admixture coefficient (c=cultivated, s=seminatural and w=wild). (b) PCA scatterplots of RADseq genotypes (accumulated variance of the first four components = 15.2%). (c) Map of genetic admixture based on RADseq markers (Adopted from Baumel et al., 2021)

5 Case Study

5.1 Historical overview of carob in mediterranean agriculture

The carob tree has a long history of cultivation in the Mediterranean region, dating back to antiquity. It was initially domesticated in the Middle East around 6 000~4 000 BC and subsequently spread across the Mediterranean basin through human activities, including trade and migration by Romans, Greeks, and Arabs (Baumel et al., 2021). The carob tree has been a staple in Mediterranean agriculture, primarily used for forage and food, and has adapted well to the region's thermophilous woodlands (Mahdad and Gaouar, 2023). The domestication process involved selecting wild genotypes and dispersing domesticated varieties, which led to a diverse genetic pool across the region.

5.2 Industrial applications in mediterranean economies

In recent years, the carob tree has gained significant industrial importance beyond its traditional uses. Its seeds are a source of locust bean gum, a valuable thickening agent used in the food industry (Di Guardo et al., 2019). Despite a reduction in cultivated areas, the carob tree's resilience to drought and salinity makes it a promising crop for sustainable agriculture in the face of climate change (Gioxari et al., 2022). Additionally, carob's potential for carbon sequestration and its use in reforestation and soil restoration projects highlight its environmental benefits (Figure 2).

5.3 Lessons learned and broader implications

The domestication and industrial utilization of the carob tree in the Mediterranean offer several lessons and broader implications. Firstly, the genetic diversity of carob populations underscores the importance of conserving both wild and cultivated genotypes to ensure the species' resilience and adaptability (Kyratzis et al., 2021). Secondly, the carob tree's ability to thrive in arid and semi-arid conditions positions it as a key crop for addressing food security and environmental sustainability in the region (Martins-Loução et al., 2024). Lastly, the integration of carob into modern industrial applications demonstrates the potential for traditional crops to contribute to economic development and innovation. These insights emphasize the need for continued research and investment in carob cultivation and utilization to fully harness its benefits.

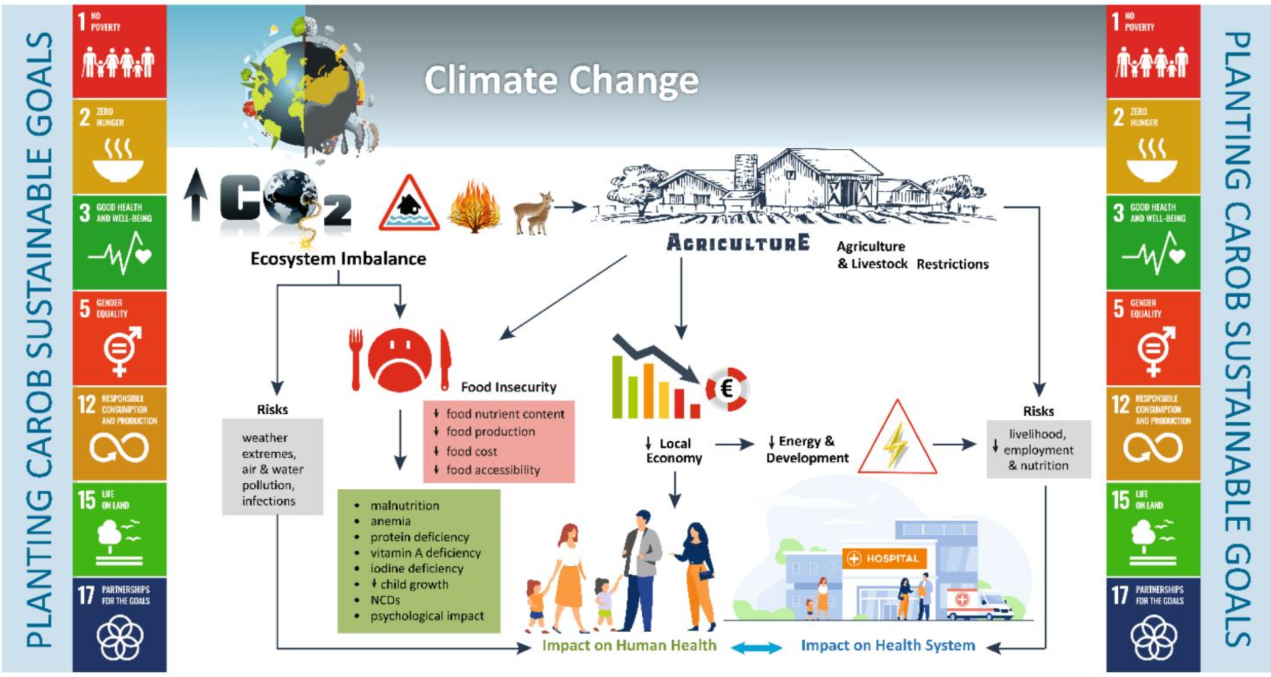

Figure 2 Interplay between climate change, food security, nutrition and human health (Adopted from Gioxari et al., 2022)

Image caption: Planting carob trees might be a promising course of action to achieve the following sustainable development goals (SDGs) across the Mediterranean area: SDG1, to eradicate extreme poverty; SDG2, to end poverty; SDG3, to achieve good health and well-being; SDG5 to empower women in economic life; SDG12, for the responsible consumption and production; SDG15, for protecting, restoring and promoting the sustainable use of terrestrial ecosystems and reversing land degradation; and SDG17, for partnerships to achieve the goal (Adopted from Gioxari et al., 2022)

6 Challenges in Carob Research and Industrialization

6.1 Limited genetic resources and knowledge gaps

Carob research faces significant challenges due to limited genetic resources and knowledge gaps. The genetic diversity of carob is not fully understood, which hampers breeding and conservation efforts. Studies have shown that there is a need for a comprehensive understanding of carob's genetic structure to facilitate effective germplasm conservation and management (Di Guardo et al., 2019). The lack of detailed genetic information limits the ability to select and breed carob varieties with desirable traits, such as drought resistance and high nutritional value. Furthermore, the genetic erosion of carob due to declining cultivation and attention exacerbates these challenges, making it crucial to prioritize research on genetic diversity and conservation (Kyratzis et al., 2021).

6.2 Environmental and agronomic challenges

Carob cultivation is also hindered by environmental and agronomic challenges. The species is predominantly grown in rainfed conditions, making it susceptible to climate change impacts such as reduced water availability and increased soil salinity (Costa-Pérez et al., 2023). These environmental stresses affect seed germination and early plant establishment, which are critical for successful cultivation (Cavallaro et al., 2016). Additionally, the traditional agronomic practices may not be suitable for modern large-scale production, necessitating the development of new cultivation techniques that can enhance yield and quality under varying environmental conditions (Van Tassel et al., 2020).

6.3 Economic and market constraints

Economic and market constraints further complicate the industrialization of carob. Despite its high industrial demand, there has been a significant reduction in the area cultivated for carob, primarily due to economic factors and competition with other crops (Martins-Loução et al., 2024). The lack of established markets and trade networks for carob products limits its commercial potential. Moreover, the development of new carob-based products requires substantial investment in research and marketing to increase consumer awareness and demand. These economic challenges highlight the need for strategic planning and investment to enhance the marketability and profitability of carob as a crop.

7 Future Directions

7.1 Innovations in genomics and breeding

Recent advancements in genomics have opened new avenues for the breeding and conservation of the carob tree. The use of genome-wide diversity studies and Single Nucleotide Polymorphisms (SNPs) has provided insights into the genetic structure and domestication patterns of carob, revealing multiple origins of domestication and highlighting the importance of preserving genetic diversity across different regions. These genomic tools can be leveraged to develop breeding programs aimed at enhancing traits such as drought and salinity tolerance, which are crucial for the carob's adaptation to arid environments. Additionally, the establishment of core collections based on genetic diversity analyses can facilitate targeted breeding efforts and conservation strategies (Di Guardo et al., 2019).

7.2 Expanding industrial applications

The carob tree has traditionally been valued for its use in food and fodder, but its industrial applications are expanding significantly. The seeds of the carob tree are a source of locust bean gum, a valuable thickening agent in the food industry. Moreover, the carob pod's nutritional profile, rich in fiber and phenolic compounds, presents opportunities for developing health-promoting food products (Gioxari et al., 2022). The carob's potential in reforestation and soil restoration projects also underscores its role in environmental sustainability. Future research should focus on optimizing agronomic practices to enhance fruit yield and quality, thereby meeting the growing industrial demand.

7.3 Enhancing global collaboration

To fully realize the potential of carob domestication and industrial applications, enhancing global collaboration is essential. This involves sharing genetic resources and research findings across countries, particularly those in the Mediterranean basin where carob has a long history of cultivation. Collaborative efforts can facilitate the development of standardized protocols for germination and stress tolerance testing, which are critical for selecting resilient genotypes (Cavallaro et al., 2016). Furthermore, international partnerships can drive investment in research and development, addressing knowledge gaps and promoting the sustainable exploitation of carob as a valuable economic and environmental resource.

8 Concluding Remarks

The genetic basis of carob domestication reveals a complex history of multiple domestication events across the Mediterranean basin. Studies have shown that carob was domesticated from locally selected wild genotypes, with significant genetic diversity maintained across different regions. The carob tree's genetic structure is characterized by distinct genetic pools, particularly in northeastern Spain and other Mediterranean regions, which are crucial for conservation and breeding efforts. Additionally, carob's resilience to drought and salinity stress, as well as its adaptability to various agro-environmental conditions, underscores its potential as a sustainable crop for arid regions.

Future research should focus on expanding the genetic and phenotypic characterization of carob germplasm to enhance breeding programs aimed at developing stress-tolerant cultivars. There is also a need for comprehensive studies on the carob tree's ecological role and its potential in carbon sequestration, which could contribute to climate change mitigation strategies. Policymakers should prioritize the conservation of carob genetic resources, particularly in regions identified as genetic refugia, to ensure the sustainability of this valuable crop. Furthermore, investment in agronomic practices and infrastructure is essential to improve carob cultivation and meet industrial demands.

Carob holds significant promise as a versatile and sustainable resource for the future. Its adaptability to harsh environmental conditions and its diverse industrial applications make it a valuable crop for economic development and environmental sustainability. By addressing current knowledge gaps and investing in research and conservation, the full potential of carob can be harnessed to benefit both local economies and global environmental efforts.

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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.

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