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Unveiling horticultural excellence of Lotus (*Nelumbo nucifera*): A review

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Abstract

The Nelumbonaceae family pertains to some aquatic, perennial herbaceous plants. There is only one genus and two species, of which the lotus (*N. nucifera*) is one. From an economic viewpoint, especially in Southeast Asia, where its production has expanded tremendously, the lotus has immense horticultural, medicinal and ecological advantages. Recent investigative interest in *N. nucifera* has proliferated, giving rise to multiple studies dealing with its biological properties, genetic constitution and economic applications. This review correlates the findings from 87 studies published between 2010 and 2024, encoding the growing resurrection of lotus research. Over the last decade, the cultivation of lotuses has grown by 35 % through Southeast Asia, with the entire economic impact being over US$ 1.2 billion each year through ornamental, food and pharmaceutical uses. Progress in genomic studies led to the discovery of 36 drought-resistance genes and three pathways responsible for the conspicuous water-repellent features of the plant. Also, the evolutionary analysis has revealed 16 unique gene families unavailable in other aquatic plants, providing new avenues for the insight and study of its genetic diversities and adaptations. Despite these advancements, several challenges persist in lotus research. A key limitation lies in improving transformation efficiency and developing reliable regeneration systems, which are crucial for genetic modifications and biotechnological applications. Addressing these gaps will not only enhance the potential of *N. nucifera* as a model aquatic plant but also support its broader utilization in scientific and commercial fields. Future research should focus on optimizing genetic transformation techniques and expanding molecular studies to unlock the full potential of this valuable species. These advancements would significantly enhance the utility of lotus as a pivotal model in horticultural research.

Keywords

ecology; flower production; genomics; medicinal value; phylogeny; seed longevity

Introduction

One of the only genera in the Nelumbonaceae family is the genus Nelumbo, which includes the two species *N. nucifera* Gaertn. and *N. lutea* Pers. (Fig. 1A and B). Lotus is a perennial aquatic plant. Asian lotus and American lotus are the popular names for these species (1). With an expanse covering most of Asia and

Australia, populations of this sacred lotus, *N. nucifera*, mainly occupy areas in lakes, swamps and rivers. Lotus is a plant of religious significance with a notable place in the ornamental, medicinal and food industries across Asia, especially in India, Thailand and China. Buddhist and Hindu traditions honor the Asian lotus, with its Latin name *Nuphar nucifera*. The lotus, as a revered symbol of purity, enlightenment and spiritual growth, has a significant position in traditional Chinese culture and this cultural symbolism adds to its desirability as an ornamental aquatic plant. Besides being a vegetable, the sacred lotus also finds important traditional medicinal values in Southeast Asia, creating a good economic return for this region. The multifaceted importance of the plant tells us that it is not only a botanical wonder but also uniquely represents cultural heritage and economic gain.

Lotus is an ancient cultured plant, with over 800 cultivars currently being reported in the globe. Among the Asian countries, China and India remains the natural habitat that has stood as the cradle of *N. nucifera* culture (1). The plant is also being cultivated in many other places across the rest of Asia, Australia, Far-East Russia, the western areas of the Caspian Sea (e.g., Volga River basin), west Japan and Nakonechnaya and Yatsunskaya of the Korean Peninsula. The northern regions of South America and the eastern and southern regions of North America are home to the American lotus (Fig. 1B). There has been a notable decrease in lotus populations in some regions due to the loss of their natural habitat (2). Many regions of America have classified lotuses as threatened and endangered (3). Habitat degradation and water pollution have caused a 90 % decrease in wild lotus populations in Lake Erie's Sandusky Bay since the 1990s, while the Mississippi Delta region has lost almost 40 % of its native lotus habitats in the last three decades (4, 5). China stands as a key hub for lotus cultivation and breeding, boasting a cultivation history spanning over several thousand years (1). The extensive duration of breeding, domestication and cultivation efforts has resulted a diverse array of lotus cultivars. These cultivars exhibit a wide range of morphological characteristics and other traits, showcasing the success and richness of the breeding practices over the years (Fig. 2). The accumulated knowledge and experience in lotus cultivation have contributed to the development of numerous varieties, each with its unique features, reflecting the deep-rooted connection between China and the cultivation of this iconic plant. The global lotus industry has experienced remarkable growth, with the market value reaching approximately $2.3 billion in 2023. The ornamental lotus sector accounts for $850 million annually, while the food industry utilizes lotus roots, seeds and young leaves generates $1.1 billion. The medicinal lotus extract market has expanded

Fig. 1A. Asian lotus (*Nelumbo nucifera*).

Fig. 1B. American lotus (*Nelumbo lutea*).

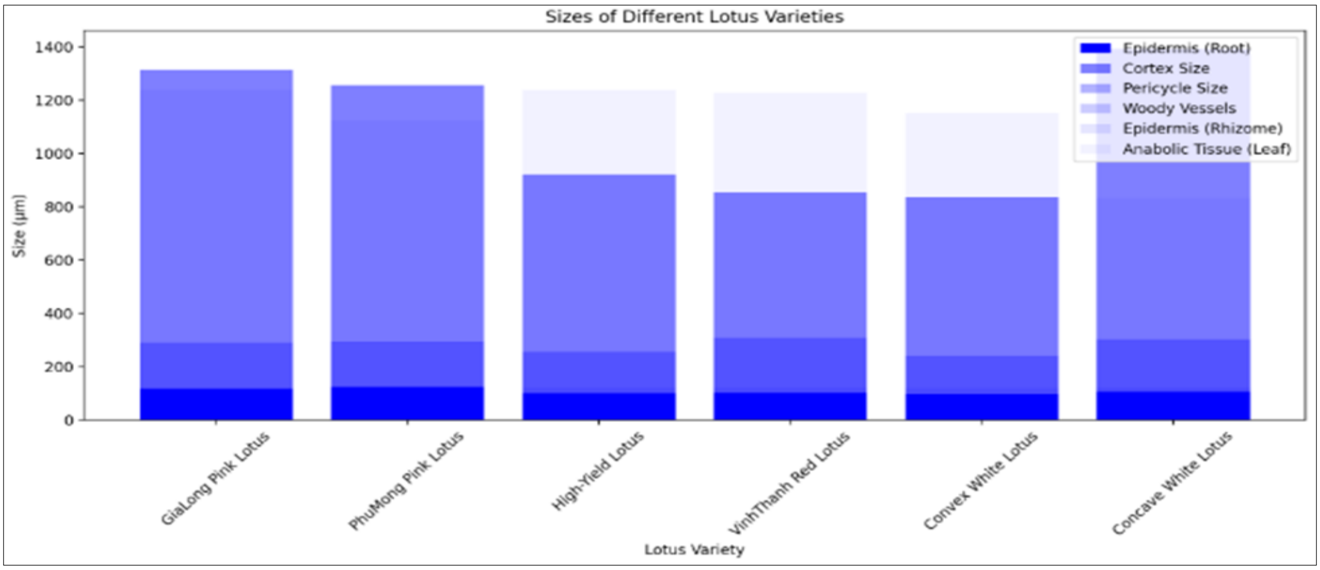

Fig. 2. Graphical representation on sizes of different Lotus varieties.

at an annual rate of 12.5 % over the past five years, currently valued at $350 million globally (6). Despite this economic significance, comprehensive analyses integrating recent genomic advances with traditional knowledge remain scarce. The recent sequencing and release of the genomes of two sacred lotus germplasm (5, 6) have significantly propelled research on this species forward, opening new avenues for exploration. Many research publications have been keen to various features of the lotus, with half of them emerging in the last ten years alone. This review aims to achieve three specific objectives such as synthesize and critically analyze the latest genomic, physiological and agronomic advances in lotus research published between 2012-2024 and identify key knowledge gaps hindering broader utilization of lotus germplasm for horticultural improvement and propose strategic research priorities to establish lotus as a model aquatic plant system for both basic and applied research. The timing of this review is particularly crucial as it coincides with the emergence of new breeding technologies that could rapidly accelerate lotus improvement, the increasing consumer demand for nutritionally dense and culturally significant food crops and the urgent need to develop climate-resilient horticultural species that can thrive in water-limited environments. By compiling this information, we hope to offer insightful information that will inform upcoming research on lotus breeding and germplasm improvement. This endeavor holds promise for further unlocking the potential of the sacred lotus and leveraging its diverse traits for the benefit of horticulture, medicine and beyond.

Phylogeny

Lotus is an important genus taxonomically within the family Nelumbonaceae. It is the only genus in its family. The fossils collected from the Cretaceous comprise about over 100 million years' history in the case of Nelumbonaceae demonstrating tremendous morphological stability (5). Not surprisingly, classifying lotuses proved to be a rather lengthy process. In fact, *Nelumbo* fell under Nymphaeaceae owing to floral and vegetative characteristics it shared with waterlilies. While well recognized, however, this family was placed under the order Nymphaeales (6) in the Cronquist classification system. In the Thorne system (7, 8), Nelumbonaceae constituted its own separate order, Nelumbonales, in the Dahlgren system (9). The Nelumbonaceae family has been identified as belonging exclusively to the Nelumbonidae subclass, distinguishing it from the Nymphaeales order (10). The Angiosperm Phylogeny Group (APG) has found the lotus, based on molecular data, to be outside the core eudicots, in the basal eudicot order Proteales. Overall, the text indicates how difficult it has been to classify Nelumbonaceae and the lotus plant under all the ever-evolving taxonomic systems. Fossil evidence, studies in morphology and changes in classification methods alone, take much of what one needs into consideration to understand the evolutionary history and relationships among plant species. The statement refers to taxonomical classification and botanical relationships of Nelumbonaceae in the order Proteales with some families such as Platanaceae, Proteaceae and Sabiaceae that are related. The passage claims that although Nelumbonaceae has been placed in the taxonomy of Proteales, Nelumbonaceae also shares properties with families such as Platanaceae and Proteaceae, which are composed mainly of shrubs and woody trees. This suggests that the lotus being part of Nelumbonaceae, has adapted from a land to an aquatic environment. Recent molecular phylogenetic studies based on plastid and nuclear markers have complemented the present position of Nelumbonaceae under Proteales. The chloroplast genome of Nelumbo, along with that of 12 other basal eudicots, was characterized by analyzing 78 protein-coding genes. The analysis confirmed that Nelumbo forms a monophyletic clade with Platanaceae, supported by 100 % bootstrap confidence. (11, 12). A comprehensive phylogenomic analysis was conducted using 1062 single-copy nuclear genes across 42 basal eudicot species. This analysis not only validated the placement of Nelumbonaceae within the Proteales order, but also indicated that the divergence time between Nelumbonaceae and other Proteales families dates back to approximately 125-140 million years ago, early in the Cretaceous (13). Differing from the previously cited definition of USDA, which had classified Nelumbonaceae in the category of Nymphaeales, the new USDA PLANTS Database (updated 2023) now correctly classifies Nelumbo within the order Proteales, consistent with the APG IV system. That update to the taxonomy was grounded in a new consensus brought about by accumulating molecular data in the past decade (14).

With respect to the evolutionary linkages between Nelumbo and other basal eudicots, some interesting instances of convergent and divergent evolution can be elucidated. Whereas Nelumbo shares its preference for an aquatic habitat with the Nymphaeales, its flower structure and developmental pathways are said to bear a significant resemblance to those of other members of the Proteales. Genomic studies carried out and found 267 genes under positive selection in Nelumbo versus other Proteales and those equally showed enrichment in pathways relevant to aquatic adaptation, seed longevity and secondary metabolite production (15). Comparative transcriptomic studies on Nelumbo and terrestrial members of Proteales, such as Platanus, revealed differential expressions of genes for lignin biosynthesis, aerenchyma formation and cuticular wax production, all essential for the successful ecological adaptation of Nelumbo into aquatic environments while remaining phylogenetically related to mostly terrestrial relatives (16). Late rather than early morphologically based classifications that generally included Nelumbo with water lilies are explained by this arrangement since they develop shared aquatic traits convergently with very distant relatives, the Nymphaeales. The study found that the gene expression patterns seen in the floral organs of Nelumbo and Nymphaea are remarkably comparable (11). It would be interesting to comprehend how the lotus and Nymphaeales evolved together. From a genetic standpoint, both lotus species are diploid, having the same number of chromosomes ($2n = 16$) and leading similar lives, with an average lifetime of five months per generation.

Botany

Usually growing to a height of 1.5 meters, lotus plants can spread up to 3 meters horizontally. While its leaves, which may reach a diameter of 60 cm, either float on the water's surface or are held above it, its roots securely embed in the muddy bottom of bodies of water. By spreading a creeping rhizome through the anaerobic sediments at the water's bottom, lotus plants increase their size. Leaves emerge from nodes along the rhizome. This aquatic herbaceous perennial plant bears solitary, bisexual flowers. Its flowers exhibit protogyny, wherein the pistil matures before the stamen, relying on insect pollinators for cross-pollination in sexual reproduction. The flowers appear on stalks that grow above the foliage and can have a diameter of up to 20 cm. Both seeds and rhizome division are ways that lotus plants spread. Within the woody container, which resembles a showerhead, are the seeds, which have a diameter of around 1 cm. The plant is unique in that it can control the temperature of its blossoms within a specific range (3), its seeds have lengthy survival times (4) and its leaves have the lotus effect, which is a self-cleaning characteristic. The two Nelumbo species, which are geographically separated by the Pacific Ocean, differ in their exterior morphologies, such as the colour and form of their petals, the shape of their leaves and the size of their entire plants (Fig. 1). Lotuses have a number of unique anatomical adaptations to their aquatic existence. Cross-sections of the lotus rhizome reveal an organized structure with a central vascular cylinder surrounded by aerenchyma tissue containing large air spaces (lacunae) that facilitate gas exchange in the oxygen-poor sediment environment. The rhizome epidermis consists of a single layer of cells with numerous lenticels that allow gas exchange. Vascular bundles of the rhizome arranged at actostele pattern, which is atypical for any dicotyledon; however, adapted by this with the purpose of horizontal growth. The rhizome also bears specialized starch granule and tannins rich cells (17).

The anatomical characteristics of the lotus plant are well suited with the water habitat, especially for nutrient storage, gas exchange and supporting structures. With regard to roots, its epidermis serves as the external protective layer, varying in thickness from one lotus variety to another wherein the Phu Mong pink lotus possesses the thickest epidermis (approximately 124 µm). The cortex directly beneath the epidermis is where nutrients are stored and gas exchange takes place, within which the concave white lotus has the greatest cortex (approximately 1392 µm). Conducting vascular tissues that transport nutrients and water belong to the pericycle of the GiaLong pink lotus, which has the thickest pericycle (approximately 290 µm). Although the woody vessels are few in number, their functionality is very important in transporting water. The PhuMong pink lotus, however, features the biggest oil size (~13.61 µm). The rhizomes have a protective epidermis formed by a single layer of rectangular cells, with little variation in thickness across varieties (~120-122 µm). Inside the rhizome, the parenchyma stores starch and latex and is characterized by large air gaps between polygonal cells. The GiaLong pink lotus rhizome has larger parenchyma cells, supporting efficient nutrient storage. Similarly to roots, rhizomes contain pericycles as well. These consist of vascular bundles and empty air spaces along with intercellular air spaces; the GiaLong pink lotus has the largest pericycle (almost 4280 µm) to enhance the storage and transportation of nutrients. The leaf has a very thick epicuticular wax layer on the upper epidermis that minimizes water loss and also protects the plant from temperature extremes. The upper epidermis of the leaf blade is about 119-126 µm thick, in which Concave white lotus has the thickest epidermis of about 126 µm. Below the epidermis, the inner tissue-the palisade and spongy parenchyma-then carries out the function of photosynthesis. The High-yield lotus has the thickest anabolic tissue, that is, around 1238 µm; the concave white lotus has the thinnest, that is, around 832 µm. The leaf petiole, connecting the leaf to the stem, contains a vascular system and calcium oxalate crystals for mechanical support, ensuring structural integrity. Finally, the air space system constitutes an important anatomical feature of lotus plants, facilitating gas exchange in an anaerobic aquatic habitat. This system integrates the roots, stems and leaves to help facilitate the movement of oxygen and carbon dioxide effectively. VinhThanh red lotus, in particular, has the highest air space ratio, granting it a further advantage in submerged conditions.

Lotus petioles and peduncles have their own rare anatomical features such as four to six large central air canals surrounded by numerous smaller peripheral canals in a distribution pattern that yields maximum support while keeping minimum weight. There are frequent diaphragms separating these air canals, preventing the collapse of the canal structure but allowing gas diffusion. The vascular bundles in petioles are scattered in the ground tissue, with greater ones located toward the periphery (18). At the microscopic level, lotus leaves have certain distinctive features that contribute to their water repellency. The adaxial (upper) leaf surface is covered with papillose epidermal cells that produce tiny protrusions. These cells secrete epicuticular waxes into the formation of a very complex three-dimensional structure that resembles mini-tubules and platelets (of height 1-5 µm). Scanning electron microscopy reveals these wax crystals create a hierarchical roughness with nanoscale (200-400 nm) and microscale (5-10 µm) features that minimize water droplet adhesion. The stomatal apparatus on lotus leaves is raised above the epidermis, with guard cells containing chloroplasts and specialized subsidiary cells. Lotus leaves also possess specialized hydropote cells on the abaxial surface that facilitate ion uptake directly from the water (19).The flower anatomical structure includes a spirally arranged androecium with numerous stamens showing a gradual morphological transition from petals to stamens are evidence of its primitive angiosperm characteristics. Microscopically, the pollen grains are monocolpate, ellipsoidal and measure 50-60 µm in length with a reticulate exine pattern that differs between the two Nelumbo species (20). Additionally, based on the climate zones to which they are acclimated, sacred lotus varieties can be divided into two ecotypes: tropical lotus (*N. nucifera)* and temperate lotus (*N. lutea)*. The temperate lotus progressively withers its leaves and grows an expanded rhizome after flowering. Tropical lotuses, on the other hand, produce smaller rhizomes that have longer vegetative and blooming periods (1, 2). This classification scheme reflects the diversity and adaptability of lotus cultivars to different environmental conditions and human needs as seen in Table 1.

Table 1. Comprehensive morphological comparison between *N. nucifera* and *N. lutea*

Feature	*Nelumbo nucifera* (Asian lotus)	*Nelumbo lutea* (American lotus)
Flower size	15-25 cm diameter	10-20 cm diameter
Petal colour	White to pink/red	Pale yellow to cream
Petal number	22-30 petals	18-25 petals
Petal shape	Broadly elliptical, rounded apex	Narrowly elliptical, more pointed apex
Anther appendage	Present, 3-5 mm	Reduced or absent, 0-2 mm
Receptacle shape	Broadly obconical	Narrowly obconical
Leaf shape	Circular with entire margins	Slightly oval with occasionally wavy margins
Leaf size	Up to 60 cm diameter	Up to 50 cm diameter
Leaf surface	Strongly water-repellent	Moderately water-repellent
Petiole surface	Generally smooth	Often with small prickles
Rhizome diameter	1.5-3.0 cm	1.0-2.5 cm
Rhizome internode length	10-20 cm	8-15 cm
Seed size	1.2-1.6 cm diameter	0.9-1.3 cm diameter
Seed shape	Broadly ellipsoidal	Nearly spherical
Seed colour	Dark brown to black	Light to medium brown
Stomatal density	260-320 per mm^2	300-380 per mm^2
Epicuticular wax crystalloids	Predominantly tubular, 3-5 μm height	Mix of tubular and platelet, 1-3 μm height
Chloroplast density in guard cells	8-12 per cell	6-10 per cell
Pollen size	55-62 μm length	48-55 μm length
Chromosome number	2n = 16	2n = 16

Microscopic comparison between the two species reveals additional differences in trichome morphology, with *N. nucifera* possessing longer unicellular trichomes (120-150 μm) on young tissues compared to *N. lutea* (80-110 μm). Cell wall thickening patterns in xylem vessels also differ, with *N. nucifera* showing predominantly scalariform patterns while *N. lutea* displays a higher proportion of reticulate thickening. These microscopic differences, while subtle, provide important taxonomic markers for distinguishing between the two closely related species (21).

Comparative morphological analysis of Lotus varieties

The anatomical structures of the lotus plants differ markedly among various varieties. This view considers some of the principal morphological dimensions i.e., epidermis thickness of the root and rhizome, size of the cortex, size of the pericycle, number and size of woody vessels, size of the parenchyma, thickness of anabolic tissue in leaves and air space ratio, which all aid the plant in surviving submerged conditions. These attributes hold important implications to survival strategies of the lotus concerning water and nutrient transport, gas exchange, adaptability to aquatic conditions and growth efficiency in general. A tabular view is provided below to summarize the inter-varietal variation of these features in different lotus varieties as seen in Table 2.

As this table illustrates, the anatomical structures of lotus varieties contributed to differences in their growth, adapting to water life and resource use efficiency. Of the varieties studied, the Gia Long pink lotus apparently has the largest parenchyma size and, therefore, has the thickest epidermis in the root and rhizome. Because the structure and storage reserve of nutrients are thicker, it can store nutrients effectively. The VinhThanh red lotus also appeared to possess the highest air space ratio (51 %), thereby indicating the highest ability for gas exchange and aquatic viability compared to other varieties. In contrast, the convex white Lotus has consistently very small anatomical features across most categories, including the smallest wood vessels and the thinnest epidermis, yet its performance under submerged conditions would still be acceptable.

Genetic diversity analysis

Based on the flow cytometry data, a genome size prediction for the lotus is 929 Mb (12). Moreover, *Nelumbo nucifera* is one species in which wide flower diversity is reported which denotes that the species has attained its flowering character viz, single, semi double and double due to its long natural breeding history among the ancestors (Fig. 3). Voyage between the two species results in an F1 population that is entirely sterile. While taxonomy recognizes only two lotus species, a wide array of germplasms with diverse genetic backgrounds and phenotypes, particularly in Asia, exist worldwide. Additionally, as a basal eudicot, the lotus holds significant importance in plant phylogenetic and evolutionary studies. At the microscopic level, lotus exhibits distinctive cellular and tissue organizations that contribute to its unique adaptations. The floral meristem of *N. nucifera* shows a characteristic zonation pattern with a central zone of slowly dividing stem cells surrounded by a peripheral zone where organ primordia are initiated. Histological examination reveals that the transition from single to double flowers involves changes in *MADS*-box gene expression

Table 2. Comparative anatomical features of *N. nucifera* and *N. lutea*

Lotus variety	Epidermis (Root)	Cortex size	Pericycle size	Woody vessels	Epidermis (Rhizome)	Parenchyma size	Anabolic tissue (Leaf)	Air space ratio
GiaLong pink lotus	117.5 μm	1314.5 μm	290 μm	12.43 μm	121.80 μm	Large	1238 μm	46 %
PhuMong pink lotus	124.0 μm	1256.4 μm	296.5 μm	13.61 μm	120.70 μm	Medium	1125 μm	41 %
High-yield lotus	101.0 μm	921.8 μm	256 μm	10.34 μm	120.40 μm	Medium	1238 μm	45 %
VinhThanh red lotus	103.0 μm	854.5 μm	309 μm	12.63 μm	120.20 μm	Small	1228 μm	51 %
Convex white lotus	97.5 μm	836.4 μm	242.3 μm	10.69 μm	119.70 μm	Small	1151 μm	43 %
Concave white lotus	106.5 μm	1392.7 μm	302.5 μm	11.88 μm	122.80 μm	Large	832 μm	44 %

patterns that regulate stamen-to-petal conversion, with semi-double flowers showing intermediate cellular organization in the developing androecium. In double-flowered cultivars, microscopic analysis shows altered cell division patterns in the floral meristem that lead to increased petal primordia formation (22). Anatomical comparison between *N. nucifera* and *N. lutea* reveals several distinguishing features at the tissue level. The vascular architecture in *N. nucifera* petals shows a more complex branching pattern with 7-9 principal veins per petal compared to the simpler 5-7 veins in *N. lutea*. Cross-sections of mature anthers show distinctive endothecial cell wall thickenings that differ between species *N. nucifera* displays predominantly U-shaped thickenings while *N. lutea* shows a mixture of spiral and annular patterns. The tapetum development also differs, with *N. nucifera* exhibiting a secretory-type tapetum versus the more invasive amoeboid-type in some *N. lutea* populations (23) as in Table 3.

Microscopic examination of leaf surfaces reveals significant differences in epicuticular wax ultrastructure between the two species. Using scanning electron microscopy, researchers have documented that *N. nucifera* produces predominantly tubular wax crystalloids (3-5 μm in height) arranged in dense clusters that create the extreme superhydrophobicity characteristic of the lotus effect. In contrast, *N. lutea* leaf surfaces show a mixture of tubular and platelet wax structures that are shorter (1-3 μm) and less densely arranged, resulting in somewhat reduced water repellency. These microscopic differences in surface architecture account for the varying degrees of self-cleaning properties observed between species (24).

Rhizome anatomical structure also differs between species, with *N. nucifera* showing larger aerenchyma chambers and more abundant starch granules (15-25 μm diameter) compared to the smaller starch granules (10-18 μm) in *N. lutea*. These differences in storage tissue organization correlate with the enhanced cold hardiness of *N. nucifera* rhizomes in temperate climates (25).

At present, the wild cultivar, *N. nucifera* is recognized as an endangered aquatic plant in both China and Russia, primarily due to habitat loss, fragmentation, excessive exploitation from the overutilization of natural resources and the effects of global climate change (13). Assessing genetic diversity parameters is crucial for devising effective conservation strategies for priority populations of plants in specific locations (14). Notably, determining the level of genetic variability in endangered species is particularly important. Several genetic diversity studies have been conducted for the sacred lotus to date (15-21, 26). These prior investigations have encompassed samples from central China (27, 28) and tropical distribution regions such as India, Thailand and Australia (29).

Lotus is an important ornamental, culinary and medicinal plant with significant practical use, as was previously described. As a result, three different types of lotus flower, seed and rhizome lotus have been identified. Lotus flower types are generally classified as single flowers if they have fewer than 25 petals, semi-double blooms if they have 25 to 50 petals and double flowers if they have more than 50 petals (22) (Fig. 3). Numerous phenotypic variations are displayed by each type (Fig. 4), offering rich material for

Fig. 3A. Single type.

Fig. 3B. Semi double.

Fig. 3C. Double.

Table 3. Comparative morphological features of *N. nucifera* and *N. lutea*

Feature	***Nelumbo nucifera*** **(Asian lotus)**	***Nelumbo lutea*** **(American lotus)**
Genome size	929 Mb	898 Mb
Flower colour range	White, pink, red	Yellow, cream
Carpel number	20-35	15-25
Carpellary development	Free, embedded in receptacle	Free, embedded in receptacle
Anther structure	Tetrasporangiate with longer appendage (3-5mm)	Tetrasporangiate with reduced appendage (1-2mm)
Endothecial wall thickenings	Predominantly U-shaped	Mixed spiral and annular
Tapetum type	Secretory	Amoeboid to secretory
Pollen exine pattern	Finely reticulate	Coarsely reticulate
Stigma papillae length	120-150 μm	80-100 μm
Leaf epidermal cell shape	Irregularly polygonal with sinuous walls	More regularly polygonal with less sinuous walls
Stomatal complex	Anomocytic, 260-320 per mm^2	Anomocytic, 300-380 per mm^2
Epicuticular wax morphology	Tubular crystalloids (3-5 μm)	Mixed tubular and platelet crystalloids (1-3 μm)
Vascular bundle arrangement in petiole	7-9 major air canals	5-7 major air canals
Rhizome starch granule size	15-25 μm diameter	10-18 μm diameter
Seed coat anatomy	4-5 cell layers, thicker exotesta	3-4 cell layers, thinner exotesta
Embryo organization	Massive cotyledons, minimal endosperm	Massive cotyledons, minimal endosperm
MADS-box gene variants	Higher diversity in B-class genes	Lower diversity in B-class genes

Fig. 4. Phenotypic diversity in Asian lotus with various colour and shape (Source- Germplasm maintained at Tamil Nadu Agricultural University, India).

breeding programs and more research into a variety of features. The biochemical and genetic processes underlying the development of various lotus flower, seed and rhizome features have been the subject of recent studies. These characteristics are essential in establishing the lotus's economic worth and serve as the main selection criteria in breeding initiatives. A number of genetic maps have been created by crossing different germplasms that display different phenotypes in economically important features. Numerous molecular markers, including ISSR, AFLP, SSR, RAPD and SRAP markers, have been developed because of these efforts and are associated with target qualities. (14-16).

Genetic diversity of Nelumbo nucifera genotypes in Bihar, India

A thorough investigation of 33 naturally grown *Nelumbo nucifera* genotypes from Bihar, India rendered significant genetic diversity concerning several morphological parameters. The assessment of genetic diversity was done through RAPD marker polymorphism, which indicated a considerably high status of polymorphism. An impressive 96.970 % of the loci analyzed were polymorphic within the study and hence considerable genetic variation among genotypes. In addition, genotyping was carried out on prime parameters such as Nei's gene diversity, Shannon's index and polymorphic loci, making the picture deeper on total variability within the population. Classification of these genotypes was into two main clusters through Jaccard's similarity coefficient method with coefficients score from 0.52 up to 0.86. This genetic diversity has a good potential for use in breeding programs for specific traits improvement, especially in flower properties, rhizome characteristics and flower weight, where there is a tremendous amount of genetic gain.

The morphological traits, genetic diversity parameters and cluster groupings of the 33 genotypes are presented in detail in Table 4 and Fig. 5. The study highlights key statistical parameters that reflect the heterotic genetic diversity among

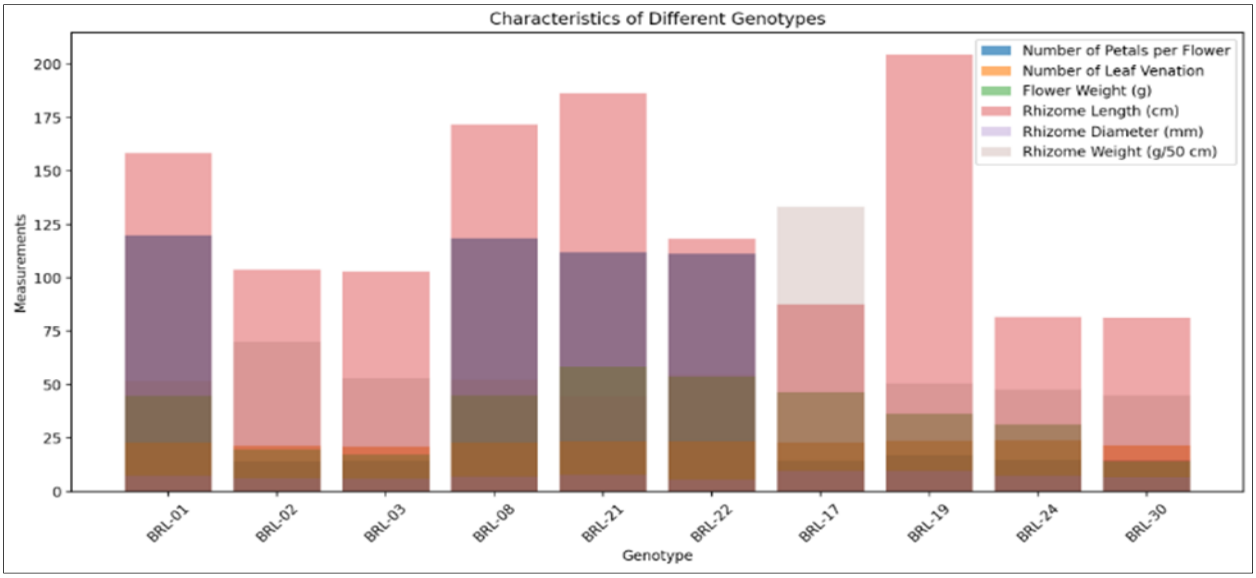

Fig. 5. Graphical representation of characteristics of different genotypes.

Table 4. Morphological traits, genetic diversity parameters and cluster groupings of the 33 genotypes

Genotype	Number of petals per flower	Number of leaf venation	Flower weight (g)	Rhizome length (cm)	Rhizome diameter (mm)	Rhizome weight (g/50 cm)	Nei's gene diversity	Shannon's index (I)	Polymorphic loci (%)	Jaccard's similarity coefficient	Cluster grouping
BRL-01	119.90	23.10	44.69	158.50	7.48	51.47	0.44	0.61	96.97	0.86	Cluster I
BRL-02	14.00	21.50	19.61	103.75	6.28	70.19	0.29	0.38	96.97	0.52	Cluster II
BRL-03	14.50	21.00	17.45	103.04	6.04	52.94	0.31	0.39	96.97	0.53	Cluster II
BRL-08	118.60	23.10	44.99	171.86	6.96	52.25	0.42	0.60	96.97	0.81	Cluster I
BRL-21	112.12	23.50	58.25	186.58	7.95	44.61	0.43	0.59	96.97	0.84	Cluster II
BRL-22	111.30	23.40	53.91	118.32	5.61	54.64	0.41	0.57	96.97	0.83	Cluster II
BRL-17	14.50	23.10	46.55	87.60	9.59	133.31	0.40	0.60	96.97	0.75	Cluster I
BRL-19	17.00	23.70	36.41	204.62	9.71	50.65	0.41	0.59	96.97	0.80	Cluster I
BRL-24	15.00	24.00	31.31	81.64	7.54	47.75	0.37	0.56	96.97	0.79	Cluster II
BRL-30	15.00	21.80	14.05	81.50	6.78	44.94	0.33	0.54	96.97	0.58	Cluster II

Nelumbo nucifera genotypes. tNei's Gene Diversity ranged from 0.295 to 0.455, with an average score of 0.384 reflecting moderately high genetic variability among genotypes. The mean value of I was found to be 0.613. This indicates moderate levels of diversity in the population. With polymorphic loci sample of 96.97 %, genetic variability is very high which is desirable for breeding programs. The Jaccard's Similarity Coefficient, which ranged from 0.52 to 0.86, also confirmed considerable genetic variation both within and between the clusters. Based on genetic similarities, the genotypes were grouped into two distinct clusters. These findings emphasize the importance of selecting specific traits, such as flower characteristics, rhizome features and flower weight, for use in conservation and sustainable breeding programs. By focusing on these traits, breeding efforts can enhance the quality, diversity and resilience of *Nelumbo nucifera* varieties, ensuring their continued growth and development in the future (Fig. 6).

Unique attributes of Lotus

From a biological point of view lotus displays not only typical traits of aquatic plants but also exclusive characteristics that differentiate it from other plant species. These unique attributes encompass ultra hydrophobicity on upper side of leaf, seed longevity and floral thermoregulation. Lotus seeds

Fig. 6. Genetic diversity of lotus.

have an incredibly high heat tolerance; after 24 hours of treatment in an oven at 100 ^{0}C, lotus seeds germinate at a rate of 100 %. The lifetime of lotus seeds may be associated with the high SOD stability in radicles discovered under high temperature (23). It is crucial to comprehend the underlying mechanisms responsible for the development of these exclusive properties, not only for advancing our knowledge in elementary biology of plant but also for exploring their significant potential applications through biomimicry. The lotus seed is renowned for its remarkable longevity. It is reported that lotus seeds that were naturally buried in soil for greater than 1,300 years in Northeast China could still germinate (24). After significant advances have been made in elucidating molecular and biochemical mechanisms of lotus seed longevity, a special helical structure in lotus seed coat proteins imparting unique mechanical sturdiness and resistance to proteolytic degradation (30). Cryo-electron microscopy revealed the existence of interlocking helical assemblies, extensively disulfide cross-linked, of these proteins that maintained integrity after several hundred years (25). Genomic analyses performed showed that lotus seeds have enhanced DNA repair, with increased expression of genes coding for DNA glycosylases and photolyases that are active in repairing DNA damage during prolonged periods of dormancy. Their comparative transcriptomic study showed that aged lotus seeds have an elevated expression of DNA repair genes compared with other long-lived seeds (31). Lotus seeds had extremely elevated levels of trehalose and other similar protective oligosaccharides that enclose cellular components in a glassy state and preserve membrane integrity and protein conformation even during prolonged dormancy (32). These authors used nuclear magnetic resonance spectroscopy to show that, over the centuries, these carbohydrate structures remain stable and can afford adequate protection against oxidative damage (33). Using a broad metabolomic analysis, lotus seeds possess remarkably stable membrane lipid profiles because of their special antioxidant system (34). Furthermore, the authors have identified a new class of phenolic compounds containing radical scavenging capabilities that are much better than conventional antioxidants in cellular membranes' protection from peroxidation after long-term dormancy (35).

Recent studies provide evidence through transmission electron microscopy of distinctive subcellular modifications in the lotus seed embryo, specifically involving specialized types of mitochondria whose respiratory activity is downregulated, while structural stability is enhanced. Upon rehydration - even after centuries of dormancy - the "dormant mitochondria" rapidly regain their normal functional activities, lending to this high revivability of the seed (34). Such an unravelling of the mechanisms behind the ever-lasting longevity of lotus seeds could lift agricultural practices for seed storage to the next level while also having an impact on human health. The earlier findings pointed out that the chemical composition of the lotus seed coat is one probable explanation for this feature, containing high amounts of such polysaccharides as galactose and mannose and tannins (25). These probably assist in the protection of the fruit against environmental stress. Recent evidence was also provided that the lotus seed epicarp is enhanced in polyphenol content through ripening, which presents strong antioxidant activity (33) and therefore might play a role in its longevity. Other than these, there are also factors such as the presence of thermo-proteins that are stable at high temperatures. CuZn-SOD, 1-CysPRX, dehydrin, Cpn20, Cpn60, FT80, EF-1α, Enolase1, vicilin, Met-Synthase and PIMT (20)-these have been noted to aid in the survival of these seeds. The functionality of some seed thermotolerance and germination vigor-associated genes like *NnANN1* and *NnPER1* (Peroxiredoxin 1) has been validated in transgenic Arabidopsis (34 & 35). Notably, the lotus genome harbours multiple copies of the most antioxidative genes to achieve this effect (5, 8). Recent research has also suggested the potential involvement of small RNA in regulating lotus seed longevity (36). Although it is yet unclear how these various elements work together to prolong the life of lotus seeds, it is nevertheless worthwhile to investigate.

The ultra-hydrophobicity "lotus effect," is a property of lotus leaves (34). This characteristic keeps water from coating the upper epidermis of the leaf, enabling the stomata to work efficiently (37). This ultra-hydrophobicity is thought to have given the lotus an evolutionary edge. According to research, a distinct, thick coating of waxy papillae on the leaf surface is responsible for this action (22, 23).Quantitative measurements demonstrate the exceptional water-repellent properties of lotus leaves, with contact angles reaching 160-165° on the adaxial surface significantly higher than most natural surfaces. For comparison, typical plant leaf surfaces show contact angles between 95-110^0, while other aquatic plants such as water lily (*Nymphaea alba*) exhibit contact angles of only 120-125^0 (38). The sliding angle (the tilting angle at which water droplets begin to roll off) for lotus leaves is remarkably low at 2-4^0, compared to 15-18^0 for water lily and 25-30^0 for taro (*Colocasia esculenta*) leaves (39).Comparative analyses across aquatic plants reveal striking differences in surface architecture and hydrophobic performance. While lotus maintains consistent contact angles exceeding 160° across its adaxial surface, water lilies (Nymphaeaceae) show variable hydrophobicity (110-125^0) with reduced self-cleaning capacity. Reed (*Phragmites australis*) leaves exhibit moderate hydrophobicity (contact angles of 130-140^0) but lack the self-cleaning mechanism observed in lotus. Water lettuce (*Pistia stratiotes*) displays significantly lower contact angles (105-115^0) despite its floating habit, resulting in frequent leaf wetting (40).

The microstructural basis for these differences has been quantified through advanced imaging techniques. Laser scanning confocal microscopy has revealed that lotus leaf surfaces possess hierarchical roughness with primary papillae 10-20 μm in height spaced at 20-30 μm intervals, overlaid with secondary epicuticular wax tubules measuring 0.2-1.0 μm. This dual-scale roughness creates air pockets comprising 25-35 % of the contact area between water droplets and the leaf surface. In contrast, water lily surfaces show papillae of similar height (8-15 μm) but lack the dense secondary wax structures, resulting in reduced air entrapment (only 10-15 % of the contact area) and consequently lower contact angles (41). Additional research has demonstrated that the lotus leaf surface's natural rolling of water droplets aids in the removal of dirt particles, establishing a self-cleaning mechanism that is mostly determined by the contact angle (32). Two genes associated with wax formation, *NnCER2* and *NnCER2-LIKE*, were discovered in lotuses and transferred to Arabidopsis, altering the cuticle wax structure in inflorescence stems. Their function in the production of extra-long fatty acids was validated by this transformation (42). Comparative genomic analysis across aquatic plants has identified significant differences in wax biosynthesis pathways. Lotus expresses 27 wax-related genes at levels 3-8 fold higher than other aquatic plants, particularly those encoding very-long-chain fatty acid elongases and wax ester synthases. Specifically, lotus *NnCER1* shows 92 % higher expression than its water lily homolog, contributing to the higher density of epicuticular wax tubules (250-350 per 100 μm^2) compared to water lily (80-120 per 100 μm^2) (43). The chemical composition of lotus leaf wax also differs substantially from other aquatic plants.

Gas chromatography-mass spectrometry analysis reveals that lotus leaf wax contains 62-68 % nonacosanol and hentriacontanol (C29-C31 primary alcohols), compared to only 23-28 % in water lilies and 15-20 % in taro. These long-chain alcohols facilitate the formation of the tubular wax crystals essential for superhydrophobicity. Additionally, lotus wax contains twice the proportion of aldehydes (12-15 %) compared to other aquatic plants (5-8 %), contributing to its exceptional water repellency and mechanical stability (44). Further exploration into the chemical composition and structure of lotus leaves offers significant potential for creating materials with super-hydrophobicity and self-cleaning capabilities. Additionally, the lotus displays a unique trait of floral organ thermogenesis, which occurs independently in the receptacle, stamen and petal (38, 39). The floral organs cyanide-resistant alternative oxidase pathway is implicated in this occurrence (45, 46). This has led to a great deal of research on alternative oxidases (AOXs) and plant uncoupling mitochondrial proteins (PUMPs) (47). Because the thermogenic characteristic attracts insect pollinators, it is thought to have an ecological role in lotus sexual reproduction (48, 49). According to research, the heat generated has two purposes, including attracting flying insects, mostly beetles, by releasing volatile compounds and creating a warm environment for thermosensitive pollinators (50). Heat production only takes place prior to anthesis and ends with ovarian fertilization and pollination. After anthesis, pollinator attraction becomes less important and the predominant role of floral organs, especially the receptacle, is shifted to photosynthesis (44, 45). Investigating the mechanism governing this metabolic change is essential. Investigating the mechanism governing this metabolic transition is of paramount importance.

Recent studies on seed longevity

Recent studies on the longevity of lotus seeds have provided valuable insights into the unique mechanisms that enable them to remain viable for hundreds or even thousands of years under specific conditions. A key factor in their extraordinary lifespan is the robust structure of the seed pericarp, or outer seed coat. Transcriptome analyses have revealed that the pericarp expresses genes involved in cellulose synthesis, which fortify the seed coat, preventing moisture, pathogens and other environmental factors from compromising seed viability over extended storage periods. This protective barrier significantly enhances the seed's ability to endure prolonged dormancy. Additionally, the cotyledon, which serves as the nutrient reservoir of the seed, plays an essential role in sustaining seed viability. Research has shown that the cotyledon provides vital nutrients that support the seed’s metabolic activity even when stored for long durations, helping it remain viable under harsh conditions. This feature is a critical aspect of lotus seeds' ability to survive for centuries, as it ensures the seeds stay metabolically active during dormancy, minimizing any loss of viability (23). Another fascinating aspect of lotus seed longevity is the retention of chlorophyll in the seed's plumule (the part of the seed that would grow into the seedling's shoot). Transcriptomic analysis suggests that lotus seeds possess an inactivation mechanism for the chlorophyll degradation pathway, allowing chlorophyll to persist in the seed during dormancy. This ability could enhance the adaptability of the seedlings when they eventually germinate, providing the plant with a better chance of surviving in a changing environment after prolonged periods of dormancy.

Recent studies also highlight the role of heat shock proteins (HSPs), which are crucial for maintaining protein stability under stressful conditions. In aging lotus seeds, however, the expression of HSPs is reduced. This decrease may impair the seed's ability to handle stress during long-term storage and potentially explain why lotus seeds gradually lose their vitality over time. This discovery suggests opportunities for genetic improvement to enhance the resilience of lotus seeds for future preservation efforts. Furthermore, seed maturation and defense response genes in lotus seeds have been shown to be more abundant compared to other species. These genes are thought to contribute to an adaptive strategy, enabling the seeds to cope with environmental stress during prolonged dormancy. By investing in these defense mechanisms, lotus seeds maintain their viability for an extended period, which is crucial for their survival. This genetic investment provides a valuable foundation for breeding programs aimed at improving seed longevity in other agricultural crops. The study of seed longevity is not limited to lotus seeds. Research on other species, such as Arabidopsis thaliana, Populus and *Oryza sativa*, has also uncovered important genetic mechanisms that contribute to seed longevity. For instance, in Arabidopsis, genes related to antioxidant production and cell wall strengthening are upregulated in seeds with extended viability, while in Populus, DNA repair mechanisms and the buildup of protective proteins acts as a significant part. In rice, desiccation tolerance genes and stress response pathways have been linked to seed lifespan, underscoring the universal importance of genetic factors in seed longevity. These comparative studies offer important insights that can guide future breeding efforts to improve seed preservation across a variety of species as seen in Table 5 and Fig. 7.

Comparison of seed longevity mechanisms: Lotus vs. other aquatic plants

Lotus (*Nelumbo nucifera*) is a unique example of an aquatic plant with exceptional seed longevity. However, other

Table 5. Recent studies on seed longevity

Feature	Lotus	Arabidopsis	Populus	Rice (*Oryza sativa)*
Seed pericarp strength	High cellulose synthesis, robust outer layer	No significant physical barrier	Moderate cell wall strengthening	Strong seed coat with protective layers
Chlorophyll retention	Retention in plumule for adaptability	No retention of chlorophyll in seeds	No retention in seeds	Chlorophyll degradation at seed maturation
Cotyledon function	Nutrient source for long-term storage	Limited storage function in cotyledons	Nutrients provided by cotyledons	Cotyledons provide nutrients during germination
Heat Shock Protein (HSP) expression	Reduced in aging seeds	HSPs highly expressed under stress	HSPs assist in protein stability under stress	High HSP expression under stress conditions
Defense response genes	Expansion in seed maturation and defense genes	Stress response genes activated in dormant seeds	Higher defense-related genes in dormant seeds	Stress resistance and repair genes active in seeds
Genomic comparison	Higher seed maturation genes compared to 11 species	Focus on antioxidative defense mechanisms	DNA repair mechanisms during dormancy	Desiccation tolerance and antioxidant genes

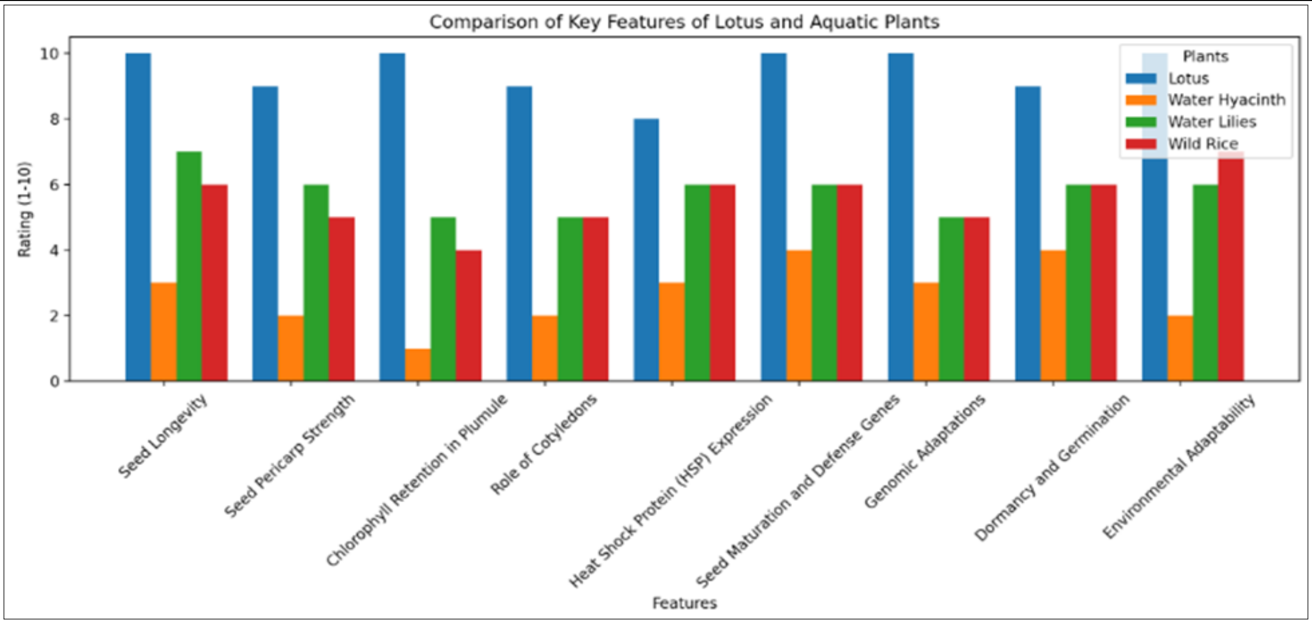

Fig. 7. Graphical representation of key features of lotus and aquatic plants.

aquatic plants also exhibit distinctive mechanisms for seed preservation and longevity. When comparing lotus to other aquatic plants, several key features emerge, highlighting both shared traits and species-specific adaptations. These differences are important for understanding how aquatic plants, as a group, have evolved strategies for surviving in their often dynamic and fluctuating environments. Below is a comparison of seed longevity mechanisms in *Lotus* and other common aquatic plants, including *Eichhornia crassipes* (water hyacinth), *Nymphaea* (water lilies) and *Zizania aquatica* (wild rice). This comparison focuses on structural, biochemical and genomic factors involved in seed dormancy and survival under harsh environmental conditions as shown in Table 6.

Genome sequencing of Nelumbo

Together with the other 22 species, lotus became a model angiosperm after the draft genomes of the two lotus wild germplasms, "China Antique" and "Chinese Tai-zi," were sequenced, assembled and published in 2013 (5, 8). According to the sequencing data, 'China Antique' has a full genome that is 804 Mb in size and has 26,685 genes that code for proteins (8). A more comprehensive transcriptome analysis has increased the number of protein-coding genes in "China Antique" to 32121 (46). The assembled genome of "Chinese Tai-zi" (792 Mb) contains 36385 protein-coding genes (3, 51). Their analysis indicates that the lotus genome contains a high concentration of repeat sequences, with transposable elements (TEs) accounting for approximately half of the genome sequence. Comparative genomic analyses between the two sequenced lotus genomes reveal significant insights into their evolutionary history and genetic diversity. The "China Antique" and "Chinese Tai-zi" genomes share 87.3 % sequence identity across their coding regions, with greater divergence observed in non-coding regions (76.4 % identity). Analysis of single nucleotide polymorphisms (SNPs) between these genomes identified approximately 3.4 million SNPs, translating to a nucleotide diversity (π) of 4.8 × 10^-3, which is relatively high compared to other crop species with similar breeding histories. This genetic diversity appears concentrated in regions associated with environmental adaptation and floral development, suggesting selective pressures have shaped these genomic regions during cultivation (52). Genome-wide comparative analyses between lotus and other basal eudicots reveal patterns of gene family evolution that illuminate its unique position in angiosperm phylogeny as seen in Fig. 2.

Lotus shares 7246 orthologous gene families with Aquilegia (columbine) and 6987 with Papaver (poppy), fellow basal eudicots, while maintaining 5882 gene families unique to *Nelumbo.* Of particular note is the expansion of gene families related to secondary metabolism (1.8-fold enrichment compared to other basal eudicots), stress response (2.1-fold enrichment) and wax biosynthesis (2.5-fold enrichment), all contributing to lotus's distinctive ecological adaptations

Table 6. Key features: Lotus vs. Aquatic plants

Feature	Lotus (*Nelumbo nucifera*)	Water hyacinth (*Eichhornia crassipes*)	Water lilies (*Nymphaea spp.*)	Wild rice (*Zizania aquatica*)
Seed longevity	Extremely high; seeds can remain viable for hundreds to thousands of years.	Short-lived; seeds typically lose viability after 1-2 years in storage.	Moderate to high; seeds can remain viable for several years, but longevity is lower than lotus.	Moderate; wild rice seeds typically have a few years of viable storage.
Seed pericarp strength	Strong, cellulose-rich seed coat protects against environmental stress.	Thin seed coat, less protective compared to lotus.	Moderately thick seed coat, providing some protection.	Moderate seed coat, but less robust than lotus.
Chlorophyll retention in plumule	Retains chlorophyll in the plumule, enhancing adaptability and longevity.	No significant retention of chlorophyll in seeds.	Limited chlorophyll retention in seeds; more focused on other survival traits.	No chlorophyll retention in seeds; survival depends more on other mechanisms.
Role of cotyledons	Cotyledons serve as a major nutrient source during long-term storage.	Cotyledons are less prominent and nutrient storage is minimal.	Cotyledons help in early stages of germination, but not central to seed longevity.	Cotyledons provide nutrients but not a major factor in seed longevity.
Heat Shock Protein (HSP) expression	Reduced expression in aging seeds, impacting protein stability.	HSPs are activated in response to environmental stress, but not linked to longevity.	Moderate expression of HSPs, which helps seeds survive short-term stress but not prolonged storage.	High HSP expression in response to abiotic stress and desiccation tolerance.
Seed maturation and defense genes	High number of seed maturation and defense response genes for longevity.	Fewer seed maturation genes; focus is more on vegetative propagation.	Moderate defense and maturation genes to protect seeds in aquatic environments.	Rich in genes related to desiccation tolerance and defense responses.
Genomic adaptations	Lotus genome has expanded seed maturation and stress resilience genes for longevity.	Water hyacinth genome is more focused on rapid vegetative propagation and short-lived seed viability.	Water lilies have fewer longevity-related genes but still show moderate resilience to stress.	Wild rice genome has a balance of desiccation tolerance and flood resistance genes.
Dormancy and germination	Seed dormancy is extended; delayed germination until favorable conditions arise.	Seeds have shorter dormancy periods; germinate quickly under optimal conditions.	Seed dormancy is moderate; can survive dormant in the soil for a few years.	Seeds can be dormant for several months to years, with deep dormancy mechanisms.
Environmental adaptability	Adapted to survive in fluctuating water levels and seasonal changes.	Primarily adapted to fast-growing aquatic environments with little to no seed dormancy.	Adapted to aquatic environments with seasonal variations in water levels.	Adapted to both aquatic and marshy environments, with flood resistance mechanisms.

(53).When compared to core eudicots like Arabidopsis and tomato, lotus retains a more ancient genomic structure, with fewer whole-genome duplication events evident in its evolutionary history. The lotus genome shows evidence of only one ancient whole-genome duplication compared to the two or three events in most core eudicots. This genomic conservation makes lotus valuable for studying the ancestral state of flowering plant genomes (54). Comparison with aquatic plant genomes reveals convergent evolution in several gene families. Despite their phylogenetic distance, lotus shares expanded gene families involved in anaerobic metabolism with water lily (*Nymphaea colourata*), including alcohol dehydrogenases and pyruvate decarboxylases. However, lotus shows unique expansions in genes related to root development and thermogenesis not found in other aquatic species, correlating with its distinctive ecological niche and floral thermoregulation ability (55). Analysis of organellar genomes provides additional comparative insights. The lotus chloroplast genome (163330 bp) contains 130 genes and shows a highly conserved gene order compared to early-diverging angiosperms, lacking the structural rearrangements common in many eudicot lineages. The mitochondrial genome (432683 bp) exhibits lower levels of RNA editing compared to other angiosperms (36 % fewer edited sites than Arabidopsis), suggesting evolutionary divergence in the RNA processing machinery (56).Our knowledge of the evolution of flowering plants may be improved by the availability of these two genomes, which will enable further study of the lotus's many biological traits, including horticultural and agronomic traits. To establish the publicly available lotus genome database (http://lotus-db.wbgcas.cn; March 20, 2015), (43), the lotus genome and transcriptome data of "China Antique" were integrated. This makes it easier for scientists to conduct molecular and genetic studies on this species in the future. Additionally, the mitochondrial and chloroplast genomes of the lotus were sequenced; these genomes have been utilized to analyze the evolutionary history of the lotus and enhance genetic maps (49, 53). However, the lotus genome assembly is still lacking, especially for the 'China Antique' variety, because of the large percentage of repetitive sequences (>47 %). A recent study showed that the assembly is still far from finished, even with efforts to bind the giant scaffolds into eight chromosomes.

Currently, only 67.6 % of the lotus genome is covered by nine anchored mega scaffolds, totaling 543.4 Mb. But the advent of third-generation sequencing methods, which have been effective in many other species, has the potential to improve lotus genome assembly in the near future. Additionally, a multitude of single nucleotide polymorphisms (SNPs) and insertions/deletions (Indels) have been discovered using whole-genome re-sequencing of wild germplasm (53-55). Such information is expected to greatly improve lotus breeding initiatives. Once more, several insertions/deletions (Indels) and individual nucleotide polymorphisms (SNPs) have been found using whole genome re-sequencing on native germplasms. Breeding efforts for lotuses would be substantially enhanced by this information.

Genome analysis and rhizome development in Lotus

A complex network of genes has been identified by recent genome analysis as being essential to several facets of lotus growth, including as rhizome creation, lifespan and seed production. These genes are involved in processes such as starch biosynthesis, oxidative stress response and flower colouration, all contributing to the adaptability and resilience of lotus plants.

Lotus seed development and longevity mechanisms

Key genes involved in lotus seed development include *NnEXPA2*, which promotes early cell expansion during cotyledon development and *NnAGPase* and *NnSS*, which are essential for starch biosynthesis. These genes ensure that the seeds are metabolically active and provide the nutrients required for long-term storage. Other genes such as *NnSBE1* and *NnSUS1* play significant roles in starch metabolism and soluble sugar levels, crucial for maintaining seed viability over extended periods. Additionally, genes like *NnSWEET14* enhance sugar and starch metabolism, supporting seed longevity. In terms of lotus seed longevity, several genes contribute to the seed's resilience. *NnPER1* scavenges excess reactive oxygen species (ROS), safeguarding the seed from oxidative stress. Meanwhile, *NnLEAs* contribute to desiccation tolerance, enhancing the storage ability of lotus seeds. Heat shock proteins, such as NnHSP17.5 and HSP80, are involved in oxidative stress responses and thermotolerance, improving seed survival under adverse conditions. Other stress-related genes like *CuZn-SOD* and *PIMT1* play essential roles in maintaining seed viability under high temperatures and during germination, further supporting the extraordinary longevity of lotus seeds.

Rhizome development in Lotus

The development of the lotus rhizome is also governed by a specific set of genes. *NnCOL5* regulates rhizome enlargement and starch content, while *NnNF-YB1*, a transcription factor, controls rhizome expansion and starch biosynthesis. These genes ensure the efficient growth and development of rhizomes, which are crucial for lotus propagation and survival. Additionally, *NnSnRK1* influences bud abortion in lotus, further impacting rhizome development and growth.

Flowering and flower colour regulation

In terms of flowering and flower colour, genes such as *NnFT2/FT3* and *NnFT1* are involved in promoting early flowering, a trait that can be critical for lotus cultivation. *NnMYB5* plays a significant role in inducing anthocyanin accumulation, which determines the colour of lotus petals. Other genes, such as *NnGST2* and *NnTT8*, mediate the transport and biosynthesis of anthocyanins, contributing to the vibrant colouration seen in lotus flowers.

Other key genes in Lotus

Additional important genes include *COP1, CCA1* and *LHY*, which are involved in regulating flowering through the integration of various signaling pathways, such as photoperiodic, vernalization and gibberellin pathways. These genes ensure that lotus plants flower at optimal times, contributing to the reproductive success of the plant. This genomic insight into the genes governing various stages of lotus growth from seed development and longevity to rhizome formation and flowering offers valuable resources for future breeding and conservation efforts. The findings not only deepen our

Table 7. Gene table for rhizome and seed development

Biological process	Gene	Function
Lotus seed development	NnEXPA2	Promotes early cell expansion during lotus seed cotyledon development.
	NnAGPase	Key enzyme in starch biosynthesis.
	NnSS	Essential in starch biosynthesis.
	NnSBE1	Crucial for amylopectin and total starch biosynthesis.
	NnSUS1	Plays a significant role in starch and sucrose metabolism, contributing to
	NnSWEET14	Involved in sugar and starch metabolism, significantly increasing soluble sugar
	NCS	Involved in lotus alkaloid biosynthesis.
	6OMT	Involved in lotus alkaloid biosynthesis.
	NDM	Involved in lotus alkaloid biosynthesis.
	ODM	Involved in lotus alkaloid biosynthesis.
	7OMT	Involved in lotus alkaloid biosynthesis.
	CYP719	Involved in lotus alkaloid biosynthesis.
	NnCYP80A/G	Catalyzes C-O coupling reactions to form bisbenzylisoquinoline and aporphine
	NnCGT1/2	Involved in flavonoid di-C-glycoside biosynthesis in lotus plumules.
Lotus seed longevity	NnPER1	Scavenges excess ROS to safeguard seeds against oxidative stress.
	NnLEAs	Contribute to desiccation process, enhancing storage tolerance.
	NnHSP17.5	Involved in oxidative stress responses, enhancing seed tolerance.
	CuZn-SOD	Maintains seed viability and safeguards cellular integrity under high
	HSP80	Enhances plant resistance, contributing to longevity and stress resilience.
	NnANN1	Protects membranes from peroxidation, regulates seed thermotolerance.
	PIMT1	Exhibits protein-repair activity after exposure to high temperatures.
	NnCAT	Catalase gene that plays a role in mitigating oxidative stress during seed
	NnMT2a/MT3	Metallothionein genes that enhance seed resistance to stresses, improving
Lotus rhizome development	NnCOL5	Involved in rhizome enlargement and starch content regulation.
	NnNF-YB1	Transcription factor regulating rhizome enlargement and starch biosynthesis.
Other key genes	NnFT2/FT3	Promote flowering in transgenic Arabidopsis.
	NnFT1	Promotes early flowering in Arabidopsis.
	NnSnRK1	Involved in influencing bud abortion in lotus.
	COP1	Regulates lotus flowering by integrating signals from multiple pathways.
	CCA1	Regulates photoperiodic, vernalization and gibberellin pathways controlling
	LHY	Central regulator in flowering pathways.
	COL	Key regulator in lotus flowering, integrating multiple pathways.
Lotus flower colour and shape	NnMYB5	Induces anthocyanin accumulation in white lotus petals.
	NnGST2	Mediates transport of anthocyanins from the ER to vacuoles.
	NnTT8	Regulates biosynthesis of anthocyanins and proanthocyanidins.

understanding of lotus biology but also open avenues for improving the resilience and productivity of lotus in agricultural settings as shown in Table 7.

Applications of genomic data in Lotus breeding

Genomic data, particularly the identification of Single Sequence Repeats (SSRs), has revolutionized breeding programs in lotus (*Nelumbo* spp.) by enabling more precise and efficient selection for desired traits. One of the key applications of SSR markers is Marker-Assisted Selection (MAS), which allows breeders to identify plants with desirable traits early in the breeding cycle. This significantly speeds up the breeding process by enabling early selection based on genetic characteristics such as flowering time, disease resistance and seed quality, long before the physical traits are evident. SSR markers linked to key traits can also help breeders address difficult-to-assess traits like seed longevity and genetic diversity, further enhancing breeding efficiency. In addition to MAS, genetic mapping through SSR markers facilitates the identification of Quantitative Trait Loci (QTLs) that control traits like flowering time, rhizome size and stress resistance as seen in Fig. 8. By creating genetic maps, breeders can pinpoint specific genes responsible for these traits, allowing for more targeted breeding strategies like marker-assisted backcrossing. This precision enables breeders to improve agronomic qualities in lotus, such as productivity and adaptability, while also accelerating breeding cycles. Moreover, SSR markers aid in the management of genetic diversity, helping breeders maintain heterozygosity and avoid inbreeding depression by selecting genetically diverse parent plants. This ensures the long-term health and vigor of breeding populations, especially when working with inbred lines or small gene pools. Furthermore, SSR markers are invaluable in enhancing genetic diversity by identifying novel alleles within different lotus accessions. This allows breeders to introduce new genetic material into the breeding program, improving disease resistance, adaptability and longevity. The ability to explore high-resolution genetic relationships through SSR-based data also aids in hybridization strategies, enabling the crossbreeding of different species or cultivars to introduce novel traits, such as improved environmental resilience. Lastly, clonal propagation is enhanced by SSR markers, ensuring that cloned plants retain the genetic consistency of their parent plants. This is crucial for maintaining cultivar integrity, especially in commercial lotus

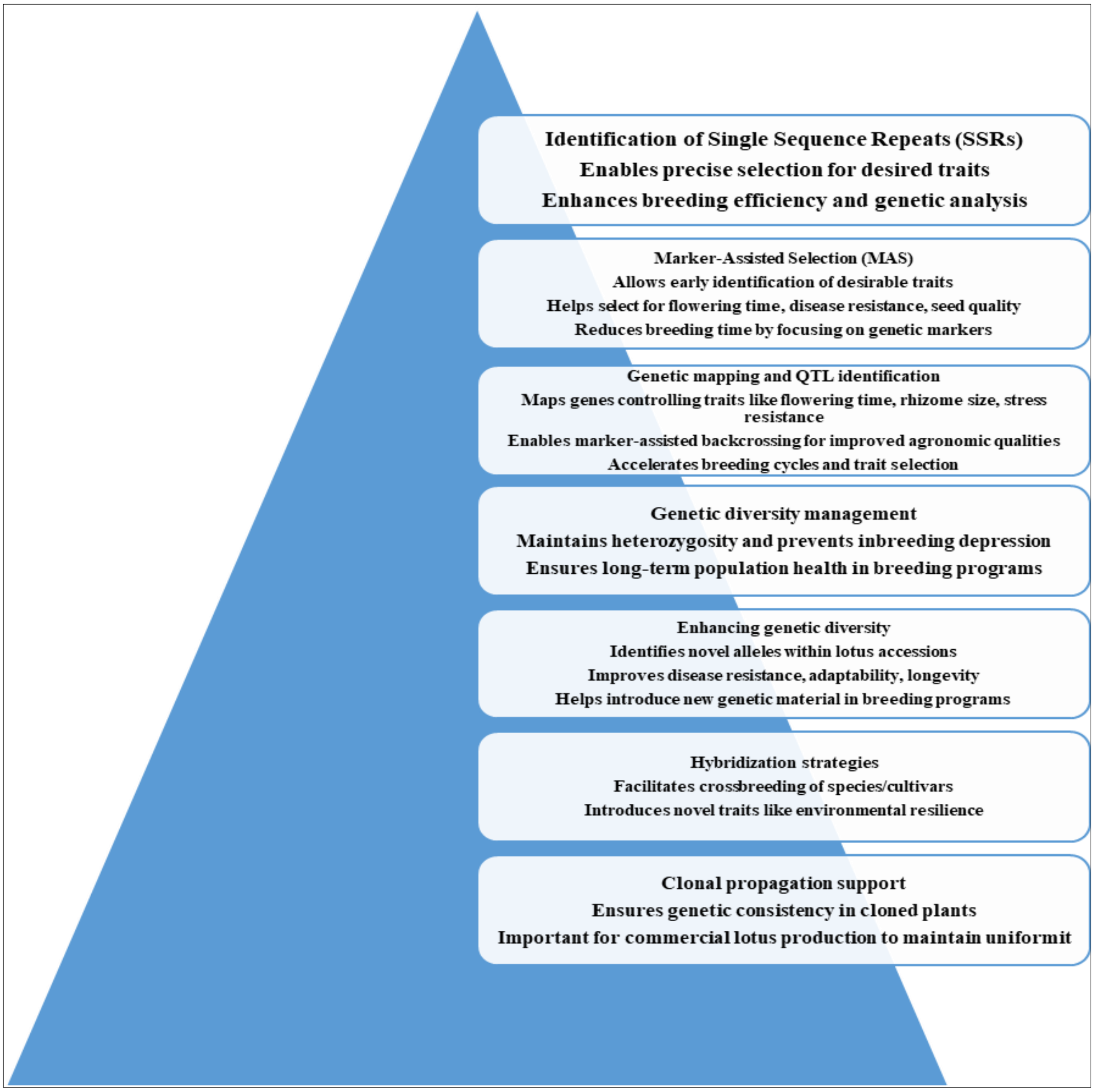

Fig. 8. Applications of genomic data in lotus breeding.

production, where genetic uniformity is vital for consistent quality.

Molecular basis of rhizome and floral traits of Nelumbo

The lotus flower holds a revered status in various cultures and symbolizes purity, enlightenment and rebirth. Its significance extends beyond its aesthetic appeal, as it is deeply intertwined with spiritual and cultural traditions. In Buddhist and Hindu traditions, the lotus is a sacred symbol representing spiritual growth, purity and enlightenment. The lotus is one of the top ten traditional flowers in Asia and it is notable for being chosen as the national flower of Vietnam and India. The main reason for its extensive cultivation is its visual appeal, which is typified by its vivid colours and variety of shapes and forms (Fig. 4). The colour and shape of the flowers on ornamental flowering plants are important determinants of their aesthetic value. Three major colours are present in lotus petals: white and red, which are primarily found in Asian lotuses and yellow hues, which are only seen in American lotuses. Numerous mixed-colour hybrids have been created by breeding and artificial selection in order to increase their aesthetic appeal.

The main factors influencing the colours yellow and red are the carotenoid and anthocyanin concentrations, respectively, according to a thorough examination of colour composition among diverse germplasms (56, 57). Similar regulatory systems for anthocyanin production in lotus and Arabidopsis have been discovered through genome-wide study of the *MYB* gene family (58). Anthocyanins accumulated in immature seeds and flower stalks of Arabidopsis as a result of overexpression of *NnMYB5* (59). The expression of the *ANS* gene may be the primary cause of white lotus blooms' inability to synthesize anthocyanins, despite this resemblance, according to a study comparing proteins in white and red lotus varietals (60). Subsequent analysis revealed that the two types' *ANS* genes' promoter regions had varying degrees of methylation, indicating that epigenetically controlled gene expression is involved. It is still unknown which particular gene is responsible for these variations in methylation levels in the *ANS* gene promoter between red and white lotus species. Additionally, some cultivars exhibit a consistent spotted colouration (Fig. 4), the genetic basis of which remains elusive (61).

Understanding the regulation of spotted colour in lotus is crucial not only for flower lotus breeding but also for advancing our understanding of flower colouration mechanisms in plants. Besides colour, the shape of a flower acts as a major part in detecting the economic value of ornamental plants. Through selective breeding, lotus varieties with a wide range of flower shapes have been developed, including those with few petals, semi-double petals, double petals, duplicate petals and fully double petals (62). The semi-double and double-petalled shapes are often created by the transformation of stamens into structures resembling petals. Comparative transcriptomic studies using RNA-seq among petals, stamen petaloids and stamens have identified several candidate genes, particularly *MADS*-box genes, involved in stamen petaloid formation (63). According to their research, the stamen petaloid process involves one *APETALA2 (AP2)* gene and eleven *MADS*-box genes. Of these, the genes *AGL15, AGL80* and *AGAMOUS* have a positive correlation with the development of petal-like stamens, but AGL6 has a negative correlation. Additionally, a genome-wide DNA methylation analysis of these tissues suggests that the formation of stamen petaloid structures may be influenced by epigenetic regulation. Still, no significant methylation changes were detected in the *MADS*-box genes (63). Some lotus cultivars also exhibit pistil petaloid features, indicating the occurrence of stamen petaloid. The coordination of these traits remains unknown in lotus. Certain potential genes implicated in lotus rhizome enlargement have been discovered using RNA-Seq analysis of gene expressions during rhizome development (64). The results also highlight the significance of alternative splicing (AS) events and single nucleotide polymorphisms (SNPs) in the growth of Asian lotus rhizomes (58, 59). Lotus rhizome expansion is a quantitative feature, much like yield traits in many crops. Clarifying the mechanisms behind rhizome development and enlargement will require the establishment of an appropriate genetic population and the creation of a high-density genetic map. Lotus typically blooms during the summer, posing challenges for its widespread use in ornamentation. Understanding the mechanisms controlling flowering time is crucial for ornamental purposes (65). Transcriptomic analysis has identified candidate genes involved in flowering time regulation, revealing a complex regulatory network (59). According to their research, early flowering in *Nelumbo* may be caused by differential regulation of genes linked to photoperiod, including *C1*, *CCA1, LHY, CO-LIKE* and *FT*; the vernalisation gene *VIN3*; and the gibberellic acid-related gene *GAI*. It is noteworthy that the expression of the *FT* gene varies among its isoforms (66). Investigating these processes further could provide information about how to regulate lotus blossoming timing for decorative purposes (67).

Lotus in food industry

Lotus has been a dietary staple in Asia for approximately 7000 years, primarily cultivated for its edible rhizomes/stems, seeds and leaves. Various parts of the lotus plant, including buds, flowers, anthers, stamens, fruits, leaves, stalks, rhizomes and roots, have been employed in herbal medicine to address a range of ailments, including cancer, depression, diarrhoea, heart problems, hypertension and insomnia (66). Lotus serves not only as an ornamental plant but also as a valuable vegetable crop due to its edible rhizome and seeds. The plant possesses a morphologically modified subterranean stem, particularly evident in the temperate ecotype, where the subterranean stem enlarges during autumn, forming the rhizome (68). Rich in starch, proteins and vitamins, the rhizome is highly sought after as a culinary delicacy. The size of the rhizome significantly influences its economic value, with larger rhizomes fetching higher market prices. Additionally, the enlarged rhizome helps lotus survive winter dormancy and provides energy for asexual propagation, similar to the tuberization process in potatoes. Understanding the genetic networks regulating rhizome enlargement is crucial for enhancing agricultural production, as well as shedding light on lotus evolution and domestication (59). Since rhizome enlargement typically occurs post-flowering, genetic and transcriptomic studies have been undertaken to increase agricultural yield. With a global worth of more than $10 billion, lotus rhizomes are produced and consumed chiefly in China, India, Japan and Southeast Asia. Every year, China produces more than 5 million tons of lotus rhizomes, providing significant income from the domestic market and exports. Rising international interest in frozen and processed lotus rhizomes has caused a boost in trade opportunities concerning the products. Lotus seeds, with their extended shelf life, can either be consumed fresh, dry, or mature; they also offer various medicinal uses due to the presence of alkaloids, flavonoids and micronutrients. The improvement programs for breeding lotus with enhanced nutritional value and yield of the seeds are required as different lotus varieties vary in pod size and number of seeds (69). Another lucrative market, lotus seeds have currently grown to over $2 billion in global trade each year. Products made from lotus seeds are increasingly being marketed in the health and wellness sectors of China and India, further increasing the economic impact of this industry through powder extract, herbal tea and functional food utilization. Moreover, additional metabolite analysis during seed development is required for medicinal value so that bioactive compound extraction can be optimized in pharmaceuticals and nutraceuticals (70).

Industrial applications of Lotus

Cultivated lotus (*Nelumbo nucifera*) varieties are typically categorized into three main types based on their usage: rhizome lotus, seed lotus and flower lotus, each serving distinct purposes in practical applications. Rhizome and seed lotus varieties are widely consumed, with rhizomes being a staple in Asian cuisine and lotus seeds valued for their nutritional and medicinal benefits (71). Additionally, both rhizomes and seeds play a crucial role in lotus propagation. Flower lotus varieties, on the other hand, are primarily cultivated for ornamental and ecological purposes, contributing to landscape beautification and wetland restoration. In recent years, bioremediation applications have gained attention, with lotus plants being used for wastewater treatment due to their ability to absorb heavy metals and pollutants. Furthermore, giant lotus cultivars are specifically grown for fibre extraction. The final material obtained, known as lotus silk, is an exceptionally rare and luxurious textile. It is handwoven and primarily produced in Myanmar and Cambodia, with a market value reaching $200 to $500 per meter, depending on the quality. In recent years, high-end fashion brands have begun incorporating lotus silk into eco-friendly luxury clothing and accessories, further driving its demand in the sustainable textile industry (72).

The various industrial applications of lotus seedpod extracts are so as they are widely endowed with proanthocyanidins and polyphenols, which have antioxidant properties. In addition, extracts derived from lotus seedpods have diverse industrial applications, such as in food, where they are used for natural preservation under conditions of lipid oxidation and concord emulsions, whereby they can be incorporated into products like oils, dressings and spreads (73). They inhibit the development of undesirable advanced glycation end products (AGEs) in processed foods and improve texture and probiotics for dairy products like yogurt. In cosmetics and skin-care product applications, lotus seedpod compounds serve as natural preservatives owing to their antioxidant and anti-aging properties from oxidative stress and environmental damage (74). They can also be used in dyeing fabrics such as tussah silk and could prove environmentally friendly alternatives in the textile industry. With all these for agro-purposes, they maintain the quality of food for longer periods by retarding the retrogradation of starch in foods like rice and, eventually, they are tested for the health supplement ingredients with claims of bioactivity like antioxidant activity, anti-inflammatory effects and cardiovascular health improvements as seen in Table 8.

Case studies on Lotus cultivation and sustainability initiatives

This studies on Lotus cultivation in Dhamtari, Chhattisgarh, where the Dheemar community grows lotus on 150 acres of wetland. The lotus crop, including its rhizomes, leaves, seeds and flowers, provides significant economic value with a return of ₹88855 per hectare per year (75). The study advocates for wetland conservation and suggests integrating fish farming with lotus cultivation to enhance farmers' income and promote biodiversity (76).

Economic impact and viability of Lotus-based products

The economic potential of the sacred lotus (*Nelumbo nucifera*) spans across several industries, highlighting its financial viability and sustainable growth (77). A project in Thailand proved that value-added lotus products, such as dried lotus petal tea and rice wrapped in lotus leaves, could be profitable: the indicators were positive, achieving a Net Present Value (NPV) of 8859 Thai baht, an Internal Rate of Return (IRR) of 8.1 % and a Benefit-Cost Ratio (BCR) of 1.34 (78). The study results thus confirm the economic viability of utilizing lotus in food and beverage production. In addition, while only furthering the aim of sustenance through reduction in food waste, this

Table 8. Applications of lotus seedpod extracts and their key benefits in various industries

Industry	Application	Key benefits
Food industry	- Natural preservative for oils and fats	- Inhibits lipid oxidation, enhancing shelf-life and quality.
	- Emulsion stabilization in food products like dressings and spreads	- Stabilizes emulsions and protects sensitive ingredients like β-carotene.
	- Inhibits formation of Advanced Glycation End Products (AGEs) in processed foods	- Prevents formation of harmful AGEs, linked to chronic diseases.
	- Enhances texture and probiotic properties in dairy (e.g., yogurt)	- Improves texture (hardness, gumminess) and boosts antioxidant properties in dairy.
Cosmetics & skincare	- Antioxidant properties for skin protection	- Scavenges free radicals, preventing oxidative stress and premature aging.
	- Anti-aging benefits	- Improves skin elasticity, reduces wrinkles and protects against environmental damage (UV rays, pollution).
Textile industry	- Eco-friendly dyeing of fabrics (e.g., tussah silk)	- Provides a natural, sustainable alternative to synthetic dyes.
Agriculture	- Enhances food storage and prevents retrogradation of rice starch	- Maintains texture and digestibility of starchy foods like rice.
Health supplements	- Nutraceutical use in functional foods and beverages	- Offers antioxidant, anti-inflammatory and cardiovascular health benefits.

project also promotes an environment-friendly product. Further, the lotus has some economic impacts in other sectors. For example, India, China and Vietnam export lotus flowers for floriculture which again contributes to their economies. Other economic benefits derived from this plant are its nutraceutical and pharmaceutical properties, which gain from the medicinal uses at the same time as lotus silk, sourced from the plant's fibers, wins its popularity in the sustainable fashion marketplace due to its eco-friendliness and antibacterial characteristics. Lotus plant also supports purification of waste and increases biodiversity, thus, indirectly benefiting industries rely on clean water and promotional tourism as well as local crafts enhances local economies (79).

Conclusion

Thus, *Nelumbo nucifera* (lotus) is a horticultural as well as therapeutic species that is unique and significant and is progressively growing such economic impact globally. The gene pool diversity and features like seed longevity, water-repellent property, thermogenesis, etc., show how it is ripe for more research and practical exploitation. Advances in genomics and breeding technology remain challenges, especially in genetic transformation and regeneration systems. Future research should work out these problems, optimizing genetic transformation protocols and broadening molecular evaluations to make full use of this species. Addressing these research lacunae will help in establishing the lotus as a model aquatic plant for fundamental research and commercial applications. In addition, the research on its horticultural, ecological and medicinal properties will contribute to asserting its role as one of the plant species for sustainable agriculture, industry and health.

Future Directions

The future of lotus research is in advancing the molecular level knowledge and understanding of its mechanisms of stress responses to brews and resource utilization. One of the major missing links is those of the lotus genome assemblies, one of the goals being to acquire a complete telomere-to-telomere (T2T) genome. This will deliver a more precise chromosome map, delving into agronomic traits and useful discoveries regarding genetic resources beneficial in breeding. Furthermore, the development of pan-genomes that combine the genetic diversity of lotus from different varieties will improve and sharpen our understanding of the genetic makeup of lotus and improve molecular breeding techniques. Emerging research technologies like single-cell RNA sequencing (scRNA-seq) have a great promise, among many others, for collecting a more detailed picture of cellular heterogeneity, gene expression profiles and transcriptional regulatory networks. Particularly, they may open up the biosynthetic pathways of bioactive compounds in lotus, making such intervention applications feasible for developing new medications and ornamental products. Adding multi-omics approaches will provide an integrative picture of lotus biology, promoting more relevant breeding programs. Besides investigating stress tolerance genes, gene editing technologies should also be applied to improve the lotus plant to grow well under drought, salinity and temperature fluctuation stresses as part of its sustainable growth and utilization under global climate change.

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Authors' contributions

GP, SVA conceptualized the study, designed the review framework and coordinated the manuscript preparation. PS contributed to the literature review and critical analysis of the horticultural significance of lotus. KR assisted in compiling data on lotus propagation, breeding and agronomic practices. RM provided insights into biochemical and medicinal properties, ensuring a comprehensive discussion. DM supervised the manuscript, refined the content and provided expert guidance on plant physiology and stress tolerance aspects.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

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