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Review

The Importance of Lentils: An Overview

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Abstract: The legume family includes approximately 19,300 species across three large subfamilies, of which Papilionoideae stands out with 13,800 species. Lentils were one of the first crops to be domesticated by humans, approximately 11,000 BP. They are diploid legumes that belong to the Papilionoidea subfamily and are of agricultural importance because of their resistance to drought and the fact that they grow in soil with a pH range of 5.5–9; therefore, they are cultivated in various types of soil, and so they have an important role in sustainable food and feed systems in many countries. In addition to their agricultural importance, lentils are a rich source of protein, carbohydrates, fiber, vitamins, and minerals. They are key to human nutrition since they are an alternative to animal proteins, decreasing meat consumption. Another characteristic of legumes, including lentils, is their ability to form nodules, which gives them a growth advantage in nitrogen-deficient soils because they enable the plant to fix atmospheric nitrogen, thus contributing nitrogen to the soil and facilitating the nutrition of other plants during intercropping. Lentils have also been applied for protection against various human diseases, as well as for phytoremediation, and they also have been applied as environmental bioindicators to identify cytotoxicity. This review addresses the importance of lentils in agriculture and human health.

Keywords: bioremediation; biological nitrogen fixation; nodulation; lentil medical approaches; nutritional importance; sustainable agricultural systems

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Citation: Montejano-Ramírez, V.; Valencia-Cantero, E. The Importance of Lentils: An Overview. *Agriculture* **2024**, *14*, 103. https://doi.org/10.3390/agriculture14010103

Academic Editors: Nunzia Cicco and Adriano Sofo

Received: 22 November 2023
Revised: 30 December 2023
Accepted: 4 January 2024
Published: 7 January 2024

1. Introduction

Legumes comprise approximately 750 genera and 19,300 species. They are primarily herbs, shrubs, vines, and trees [1]. Currently, three large groups of subfamilies are recognized: Mimosoideae, with 4 tribes and 3270 species; Papilionoideae, with 28 tribes and 13,800 species; and Caesalpinoidea, with 4 tribes and 2250 species [2]. The lentil (*Lens culinaris* Medik.) is a diploid legume ($2n = 14$) with a large genome of 4063 Mbp, is phylogenetically nested within the tribe Vicieae, and belongs to the Papilionoideae subfamily of the Fabaceae family [3].

The importance of lentil cultivation lies in its resistance to drought and its ability to grow in a wide range of soils, from light to heavy, with a pH of 5.5–9; therefore, this legume production presents an encouraging panorama. Due to its low cultivation costs, it could become a magnificent option for the diversification of crops, taking advantage of marginal soils that otherwise would be left out of agricultural activities [4]. Regarding nutritional aspects, lentils contain proteins, carbohydrates, oils, and ash in proportions of 23%, 59%, 1.8%, and 0.2%, respectively, and also provide iron, calcium, phosphorus, magnesium, vitamin A, and vitamin B [5,6]. Furthermore, worldwide lentil production has increased annually to an estimated 5.6 million hectares [7]. Lentils are important in the diet of low-income populations in developing countries because they replace animal proteins [8]. Another characteristic of legumes is their ability to fix atmospheric nitrogen (N_2) through symbiosis with bacteria called rhizobia through the formation of specialized structures called nodules, which is advantageous for growth in soils with low N_2 content [9].

Lentils were possibly the first crop to be domesticated approximately 11,000 BP in the Fertile Crescent [10]. When agriculture spread from the Fertile Crescent, lentils were among the first crops introduced to Europe and Egypt [11]. However, neither archaeological nor genomic investigations have found the exact location of lentil domestication. Still, it is believed to have been near the east, in the Franchthi cave in Greece dated to 11,000 BC and at Tel Mureybet in Syria 8500–7500 years BC, in a region known as "The cradle of agriculture" [11].

Lens culinaris subsp. *Orientalis* (Boiss.) is a wild progenitor of the cultivated species (Figure 1) and is found in Asia, Central Asia, and Cyprus. Another *Lens culinaris* (Medik.) wild progenitor is *Lens nigricans* (M. Bieb.) and its domestication could be located in southern Europe [12]. Despite this, restriction fragment length polymorphism (RFLP) analysis has shown that the taxon with the greatest genetic identity to *Lens culinaris* (Medik.) was *Lens culinaris* subsp. *Orientalis* (Boiss.) followed, followed by *Lens odemensis* (L.), *Lens ervoides* (Brign.), and *Lens nigricans* (M. Bieb.) [13]. Additionally, *Lens nigricans* (M. Bieb.) shows a level of polymorphism that suggests that it may have undergone domestication [14].

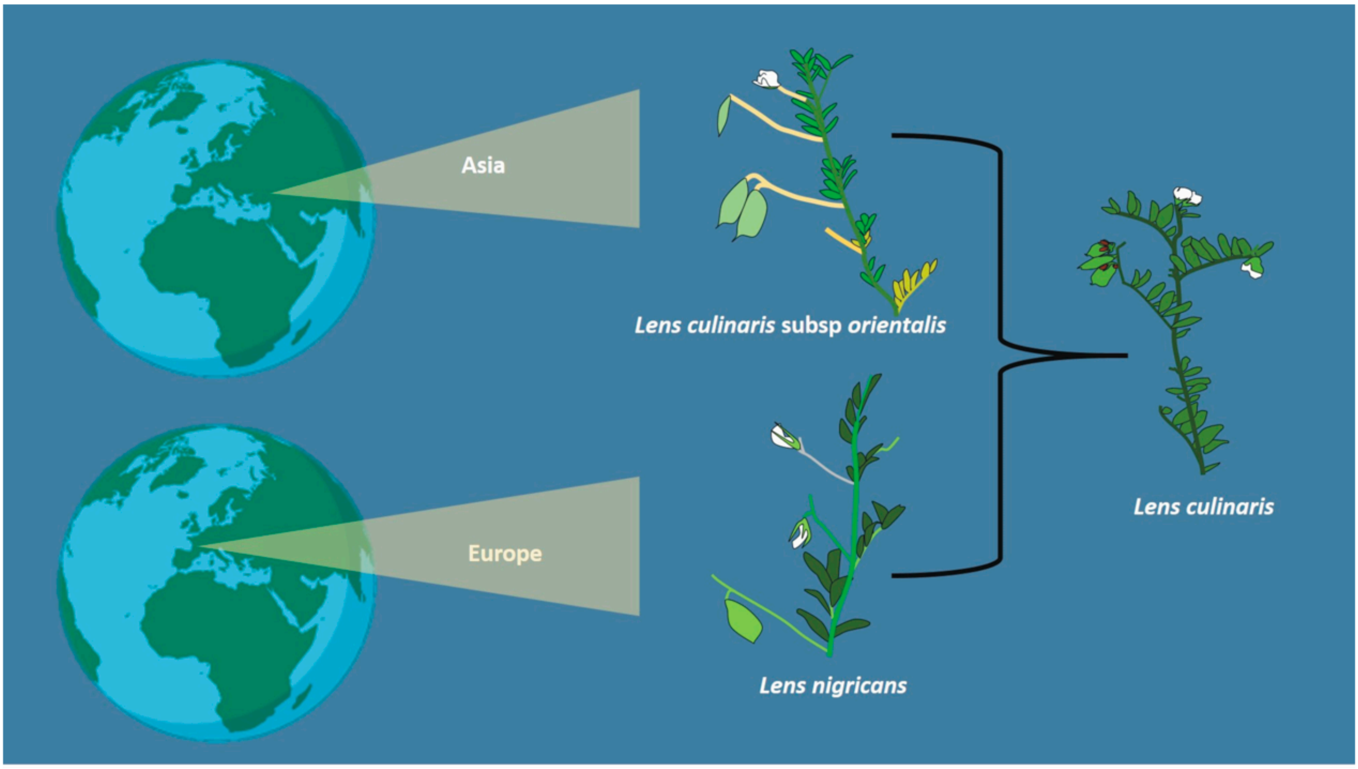

Figure 1. Origin of *Lens culinaris*. The origin of the lentil dates back to 11,000 BP in the Fertile Crescent, with *L. culinaris* subsp *orientalis* (Boiss.) being the wild progenitor. This indicates that this legume was domesticated in Asia; however, other evidence points to the progenitor of the lentil being *L. nigricans* (M. Bieb.), whose domestication occurred in Europe.

Wild species of the genus *Lens* are distributed in the Mediterranean Basin: *Lens culinaris* subsp. *odemensis* (L). is restricted to the east, from Turkey to Syria and Palestine [15], while *Lens culinaris* subsp. *tomentosus* (Ladiz.) has only been found in Libya. In contrast, *Lens ervoides* (Brign.) is distributed from Spain to Ukraine and to the south of Jordan. *Lens nigricans* (M. Bieb.) grows in small colonies on stony slopes and rocky soils and in clearings of pine forests [16]; it has a western distribution from Spain to Turkey and southern distribution to Morocco [17] but is also found in Ethiopia and Uganda. Finally, *Lens lamottei* (Czefr.) grows in Morocco [18].

Therefore, the regions with the highest species richness of the genus *Lens* (with three and four species) are the Crimean Peninsula, southeastern Turkey, and the eastern Mediterranean countries of Syria, Jordan, Israel, and Palestine. Regions with two species of the genus *Lens* include Spain, the Balkans, Albania, Greece, and western Turkey [19]. *Lens culinaris* (Medik.) is the only cultivated species [18] for which wild species, which serve as genetic reserves, are threatened by poor competitiveness and low palatability, along with the fact that they occur in small, isolated populations [17]. It is necessary to promote the maintenance and care of these lentil genetic reservoirs to preserve the evolutionary history of this legume and not only focus on its economic and agricultural impact worldwide.

Because lentils have high nutritional content and beneficial effects on soil restoration, this review focuses on the importance of this legume in human health and its application in phytoremediation processes.

2. Biological Nitrogen Fixation (BNF)

The process through which legumes can apport fixed nitrogen into soils is known as biological nitrogen fixation (BNF). BNF has contributed approximately 50 million tons of N per year to agriculture, but currently, its contribution is less than half of that provided by chemical fertilizers [20]. Nitrogenous fertilizer production requires large amounts of fossil fuels, representing approximately 2% of global energy consumption [21]. Large amounts of nitrogen applied to the soil are not absorbed by crops. Almost 25% of nitrogen fertilizers are lost via leaching during agricultural processes [22]. This generates cumulative effects that trigger contamination, thus affecting the health of the soil and environment [23]. Lentils have important functions in maintaining and improving soil [24] because they enrich soil nutrients by adding nitrogen, carbon, and organic matter, promoting the sustainable cultivation of cereals. Therefore, lentil cultivation improves soil fertility and health [25,26].

Generally, the interaction between legumes and rhizobia (Figure 2) begins in nitrogen-deficient soils, where legumes secrete secondary metabolites called flavonoids. These flavonoids are recognized by bacteria, which activate the synthesis and subsequent release of lipochitooligosaccharides known as nodulation (Nod) factors. Nod factors are recognized by the legume through the LjNFR (Nod Factor Receptor)/MtLYK3 (LysM Receptor Kinase) and LjNFR5/MtNFP (Nod Factor Perception) receptors [27]. The formation and maintenance of nodules are expensive for plants in terms of energy consumption; thus, this is a highly regulated process. Plants have evolved molecular pathways to control the number of formed nodules. Autoregulation of nodulation (AON) responds to rhizobial infection to maintain an adequate number of nodules; this pathway works systematically throughout the shoot [27–30]. The genes involved in the AON process are *LjHAR* (*Hypernodulation And Aberrant Root*)/*GmNARK* (*Nodule Autoregulation Receptor Kinase*)/*MtSUNN* (*Super Numeric Nodules*), homologous to the *Arabidopsis CLAVATA1* (*CLV1)* gene, which is a gene involved in the AON process and meristem maintenance. Other genes involved in this process are *GmRIC1* and *GmRIC2* in soybean and their orthologs in other species: *LjCLE-RS1* and *LjCLE-RS2* in *Lotus japonicus* Regel (K. Larsen.), *MtCLE12* and *MtCLE13* in *Medicago truncatula* (Gaertn.), and *PvRIC1* and *PvRIC2* in *Phaseolus vulgaris* (L.) The peptides encoded by these genes are transported to the shoot xylem, where they are perceived by a homodimeric or heterodimeric receptor complex present on parenchyma cells in the leaf vasculature. Mutations in these receptors result in hypernodulation [31]. To date, homologs of these genes have not been reported for lentils, but the nodulation signaling pathway seems to be conserved between different legume species, and so the lentil–rhizobia interaction process could follow the same route and the same self-regulation process [32].

On the other hand, the excessive use of nitrogenous fertilizers in agriculture, as well as the high residual levels of this macronutrient, limit the formation of nodules and N_2 fixation [33]. In different investigations, the effect of excess nitrogen on the nodulation process of legumes has been studied; using bean plants and applying grafting techniques on young plants to generate plants with a dual root system, it was shown that the side grown in N+ (>50 mg/L) had a lower production of nodules, as well as a lower weight, compared to roots grown in N− (<50 mg/L) [34]. Additionally, using the same dual root system in soybean (*Glycine max* L.) plants, it was observed that short-term nitrogen supplementation regulates specific nitrogenase activity (SNA) and therefore inhibits ethylene reduction activity (ARA), used as a reference for nitrogenase activity in the nodules, while a long-term nitrogen supplement recovers SNA and the concentration of supplemented nitrogen regulates the growth of nodules, also inhibiting ARA. Fertilizer supplementation (identified by the ^{15}N tracer method) also decreased the percentage of atmospheric nitrogen fixed by the nodules, but did not decrease the accumulation of nitrogen in the nodules [35]. As mentioned, excess nitrogen decreases the formation of nodules and one of the mechanisms through which this process occurs in soybean plants is through the acceleration of senescence due to the suppression of the expression of *GmLb* genes that encode the leghemoglobin protein, whose function is to protect bacterial symbionts from O_2 pressure, since the nitrogenase complex is sensitive to oxygen and must be maintained in anaerobic conditions [36].

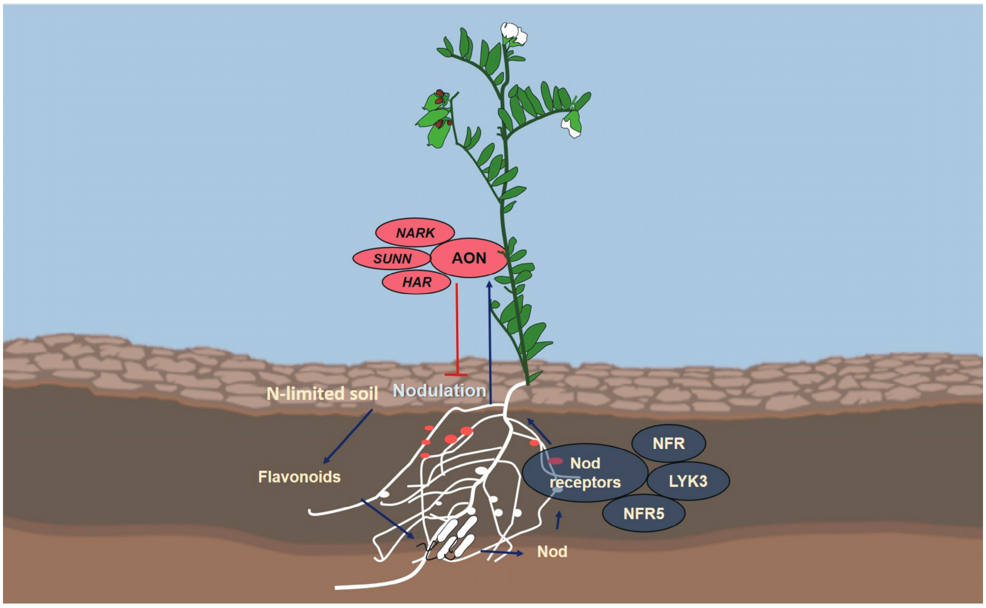

Figure 2. Legume–rhizobia interaction. During the interaction with rhizobia, legumes secrete flavonoids, which are perceived by bacteria, and the synthesis of nodulation factors (Nod) is activated. Nod factors are perceived by the roots of the legume through receptors such as NFR, LYK3, and NFR5 (Nod receptors). Because nodulation is an energetically expensive process, the plant activates a nodulation autoregulation (AON) process involving genes such as *NARK*, *SUNN*, and *HAR* that control nodule formation. Blue arrows indicate activation, while red arrows indicate repression. The excessive use of fertilizers not only generates health and pollution problems, but also affects the establishment of biological mechanisms used by legumes to cope with N_2 deficiency in agricultural soils.

3. Lentil Nodulation

As has been mentioned throughout this work, nodulation facilitates the fixation of atmospheric nitrogen and is caused by the interaction between legumes and rhizobia, which evolved approximately 58 million years ago and occurs in 88% of all legume species [37]. The interaction of legumes and rhizobia forms nodules, which provide an ideal environment for nitrogen fixation in exchange for the photosynthates provided by the plant. This is advantageous for legumes because they can grow in nitrogen-deficient soils.

Like many other legumes, lentils can also form nodules, thus supplying nitrogen. *Rhizobium leguminosarum* bv. *Vicia* is one the most effective rhizobia for nodule formation in lentils [38]; however, other studies have suggested that lentils can also nodulate with *Rhizobium etli* [39] and *Rhizobium laguerreae*, as well as some unnamed species of the genus *Rhizobium* [40].

In addition to the interactions between legumes and rhizobia, other bacteria, known as plant growth-promoting rhizobacteria (PGPR), promote plant growth through various mechanisms, including phosphate solubilization and nitrogen fixation, as well as phytohormone production [41]. Some PGPR synthesize indole acetic acid (IAA), which controls plant growth and development by regulating the expression of various genes [42]. PGPRs also protect plants against abiotic stress by regulating tissue ethylene levels, which is achieved by producing the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase. This enzyme sequesters and breaks down ACC, an ethylene precursor, thereby preventing high concentrations of this phytohormone in plant tissues [43].

Therefore, the co-inoculation of PGPRs with rhizobia potentiates the beneficial effects on legumes and crop soils. Sepúlveda-Caamaño et al. [44] isolated PGPRs from lentils to evaluate their effect on nodulation during co-inoculation with rhizobia from nine soils in the Mediterranean area. Among the 57 strains, 17 showed ACC deaminase activity, all producing IAA, and 38 were compatible with rhizobia. Using 16S rRNA sequencing, 10 strains were identified as *Pseudomonas* spp. The strains were then inoculated into lentil seedlings to evaluate nodulation. The LY50a strain showed increased early nodulation compared with plants only inoculated with rhizobia (AG-84). In another study and field experiments, increases in fresh biomass, grain production, straw production, pods per plant, dry weight of the nodule per plant, weight of 1000 grains, and nitrogen content in the lentil grains compared with the control were observed [45].

Co-inoculation of PGPR with rhizobia helps to mitigate the environmental and economic impacts caused by using nitrogenous fertilizers. Excessive use of nitrogen generates expenses of between EUR 70 and 320 billion for the European Union due to its contribution to climate change and the loss of biodiversity. This expense is more than double the value of nitrogen fertilizers used on European farms [46].

4. Nutritional Importance of Lentils

Food scarcity causes nutritional deficiencies in humans, coupled with a deficient diet lacking macro- and micronutrients such as proteins, fats, vitamins, and minerals, resulting in protein malnutrition. Low-digestible carbohydrates, also called prebiotics, are substrates that microorganisms in the host's digestive system use to confer health benefits [47].

Microorganisms in the human body comprise four main Phyla: Firmicutes, Bacteroides, Actinomycetes, and Proteobacteria. The Firmicutes/Bacteroides ratio is an important parameter to reflect disturbances of the gut microbiota, which can cause disease [48]. The intestinal microbiota regulates nervous, endocrine, and immune system communication through the brain–gut connection, which affects the appearance and development of central nervous system diseases, especially Parkinson's and Alzheimer's diseases [49]. Additionally, metabolites produced by the microbiota, especially trimethylamine oxide, bile acids, and short-chain fatty acids, can induce the development of cardiovascular diseases, such as hypertension and atherosclerosis [50]. Finally, the gut microbiota has been associated with metabolic diseases such as obesity and diabetes, as well as gastrointestinal diseases such as inflammatory bowel disease and colon cancer [51].

A previous study in a rat model [52] reported the profile of prebiotic carbohydrates after removing protein and fats from the lentil seed (Figure 3). Among the simple sugars, sucrose was the most abundant (1.2–2.3 g/100 g), followed by glucose (21–61 mg/100 g), fructose (0.2–21.9 mg/100 g), mannose (1.2–7.9 mg/100 g), and rhamnose (0.5–1.0 mg/100 g). Among sugar alcohols, sorbitol concentrations were the highest (0.6–0.7 g/100 g), followed by mannitol (9–31 mg/100 g) and xylitol (14–31 mg/100 g). In the case of the oligosaccharides of the raffinose family, stachyose was more abundant (2236–2348 mg/100 g) than raffinose (0.4–0.6 g/100 g) and verbascose (0.6–1.8 g/100 g). In contrast, lentils contain more kestose than nistose. Other prebiotic carbohydrates present were arabinose (2.4–2.6 g/100 g), xylose (1.9 g/100 g), and cellulose (0.6 g/100 g).

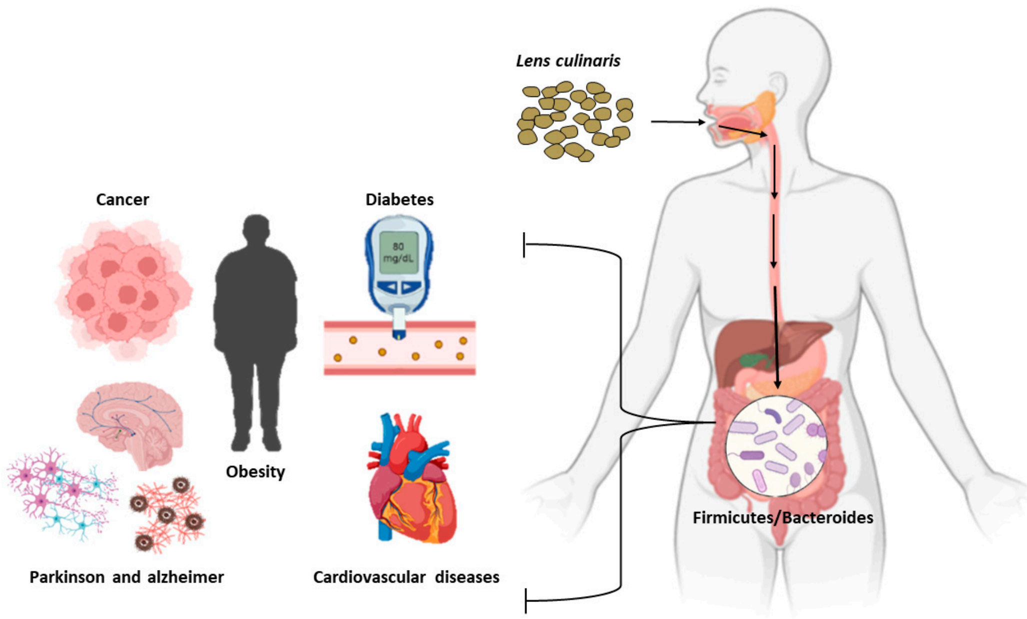

Figure 3. Effect of lentil consumption on human health. Due to lentils containing prebiotics, which serve as a substrate for microorganisms such as Firmicutes and Bacteroidetes (whose ratio is an important parameter that reflects intestinal disturbances) present in the human intestine, the consumption of this legume protects against various diseases like Parkinson's, Alzheimer's, diabetes, obesity, cancer, and cardiovascular diseases.

Considering the importance of prebiotic carbohydrates in the maintenance of the intestinal microbiota, which is involved in the development of a large number of diseases in humans, the consumption of lentils plays a key role in the protection and maintenance of intestinal microbiota health. It has been linked to a reduction in hypertension, cardiovascular diseases, diabetes mellitus, and cancer [53].

Much of the increase in lentil cultivation is due to its nutritional contribution. Lentils are an important source of protein in developing countries as well as an excellent source of complex carbohydrates, fibers, vitamins, and minerals [54]. Other abundant macronutrients in lentils are proteins, among which globulin predominates, comprising 47% of the total seed, and a high amount of albumin [55]. Therefore, a protein-rich diet based on legumes is a viable and sustainable option that helps prevent malnutrition in developing countries and is an alternative to animal proteins, which are more expensive and have greater harmful effects on the environment [56].

Among *Lens* spp., the accession ILWL47 was identified as having a high protein content, belonging to the species *Lens ervoides* (Brign.) [57]. Another lentil accession, IC317520, was identified as having high protein, sugar, and starch content. The crossing of these two varieties could generate offspring with improved nutritional content [58]. Another approach for improving lentils nutritionally and agriculturally is through mutations; a mutant variety of lentils, NIA-MASOOR-5, has a high protein content, high yield, and resistance to diseases [59]. Considering this background, we can highlight that the efforts to improve the nutritional content of lentils have focused on maintaining nutritional security, improving human health, and providing highly nutritious and low-cost foods.

5. Role of Wild Lentils in *Lens culinaris* (Medik.) Domestication

The importance of wild lentils lies in giving rise to the domesticated variety, *Lens culinaris* (Medik.). The cultivation of wild lentils is not profitable because the seeds are very small and collecting them for human use is difficult; therefore, it is considered that their domestication was through co-domestication in previously domesticated cereal crops, with the purpose of taking advantage of the space to later select and isolate seeds of relatively large sizes that would be easier to harvest [60]. Additionally, this theory is reinforced because wild lentils are not capable of growing in soils disturbed by human settlements, but they can grow perfectly in cereal fields, especially barley, which is the case for domesticated lentils [61].

The genetic traits involved in the domestication of lentils are poorly studied when compared to other legumes; however, it is known that crosses of *Lens culinaris* (Medik.) × *Lens culinaris* subsp. *orientalis* (Boiss.) are key in this process. The segregation and inheritance of various traits have been studied, such as seed coat color, epicotyl color, flower color, and pod dehiscence. Of the characteristics evaluated, the white flowers and growth and indehiscence of the pod are typical of the domestic lentil. According to this, it is believed that one of the first traits selected by man was the indehiscence of the pod, in addition to the fact that the conservation of these characteristics was easy to preserve, due to the self-pollination present in some legumes. The size of the seed is a more complicated event to determine because regarding the lentils used in the cross, some had small seeds and others had large seeds. The F1 hybrids showed variations from large to small seeds, but the size of the large seeds of the cultigen was not reached [62]. On the other hand, seed hardness in domesticated lentils is controlled by a single gene present in *Lens ervoides* (Brign.), which is the result of crossing this species with *Lens culinaris* (Medik.) [63].

In addition to *Lens culinaris* subsp. *orientalis* (Boiss.) and *Lens ervoides* (Brign.), three more species of wild lentils have been grouped: *Lens tomentosus* (Ladiz.), *Lens odemenis* (Ladiz.), and *Lens lamottei* (Czefr.); these are used to create hybrids with *Lens culinaris* (Medik.) in order to explain the genetic origin of the traits present in this domestic species. The above was achieved through the construction of two 96-plex genotyping-by-sequencing (GBS) libraries with a total of 60 accessions, where some accessions had several samples and each sample was sequenced in two technical replicates. With these data, an automated GBS was developed, and with which 266,356 genome-wide single-nucleotide polymorphisms (SNPs) were detected throughout the genome; these were filtered and 5389 were used. Subsequently, a phylogenetic tree was constructed and four sets of genes were identified that corresponded to the previously mentioned wild species [64]. Therefore, it can be considered that the lentil as we know it today is the result of the crossing of different wild species, whose traits were selected and conserved by humans.

6. Lentils in Sustainable Agricultural Systems

The lentil is an edible legume with great nutritional value and cultivated worldwide for its nutritional contribution. Its worldwide harvested area increased from 4.1 million hectares in 2011 to 5.6 million hectares in 2021, and during this time its production increased from 4.3 to 5.6 million tons (Table 1). Additionally, it is a nutritious feed for animals and contributes to the growing demand for forage [65].

Table 1. Lentil production and area harvested in 2011 and 2021 in major growing countries.

Country	2011			2021		
	Production (t × 1000)	Area Harvested (ha × 1000)	Yield (t ha^{-1})	Production (t × 1000)	Area Harvested (ha × 1000)	Yield (t ha^{-1})
Canada	1574	1005	1.57	1606	1716	0.94
India	944	1597	0.59	1490	1734	0.86
Australia	288	173	1.67	854	501	1.70
Türkiye	406	215	1.89	263	297	0.89
Nepal	207	208	1.00	246	202	1.22
Bangladesh	80	83	0.97	186	146	1.27
Russia	33	30	1.11	176	161	1.09
China	150	60	2.50	165	65	2.54
USA	215	166	1.29	151	222	0.68
Ethiopia	128	110	1.16	123	87	1.41
Syria	112	140	0.80	94	111	0.84
Iran	50	103	0.49	80	133	0.60
Kazakhstan	7	7	1.07	56	72	0.77
Morocco	45	58	0.78	42	42	1.00
Argentina	24	17	1.40	20	28	0.72
Mexico	8	7	1.21	10	9	1.12
World	4382	4119	1.06	5610	5586	1.00

Source FAOSTAT (15 December 2023) [7].

In contrast, nitrogen deficiency in agricultural soils is a time-consuming problem, which has been combatted by applying chemical fertilizers. This is a costly practice, both economically and due to the environmental effects of excess reactive nitrogen on air, soil, and water quality. It also affects ecosystems and biodiversity, in addition to altering the balance of greenhouse gases [46]. Lentil cultivation helps fix N_2 and reduces the use of synthetic nitrogen fertilizers, thus reducing greenhouse gas emissions [66]. This improves the mineral nitrogen content in the soil, which remains after lentil cultivation [67] because the roots can decompose in agricultural soil, thus serving as a source of nitrogen for subsequent generations of crops. Additionally, rotating legumes with non-legume crops is a natural method of fertilization [68]. This process improves the fertility of soil and aids its recovery.

Damage caused to the soil and microbiome by applying fertilizers has been clearly established [69]. Weese et al. [70] evaluated two sites: one in which ammonium nitrate was used as a fertilizer for 22 years and an adjacent site in which no nitrogen fertilizers were applied. They observed that when inoculating the legumes *Trifolium repens* L., *Trifolium hybridum* L., and *Trifolium pratense* L. with sludge from fertilized soils, the biomass and chlorophyll contents of these plants were reduced compared to inoculation with samples from unfertilized soils. The results were similar when plants were inoculated with rhizobia isolated from fertilized soils; the plants had reduced biomass (17–30%), leaves (10–28%), stolons (8–21%), and chlorophyll (6–17%) compared to plants inoculated with bacteria isolated from unfertilized soils.

Owing to the benefits that they bring to soil, lentils are commonly intercropped with other plants of agricultural interest (Figure 4).

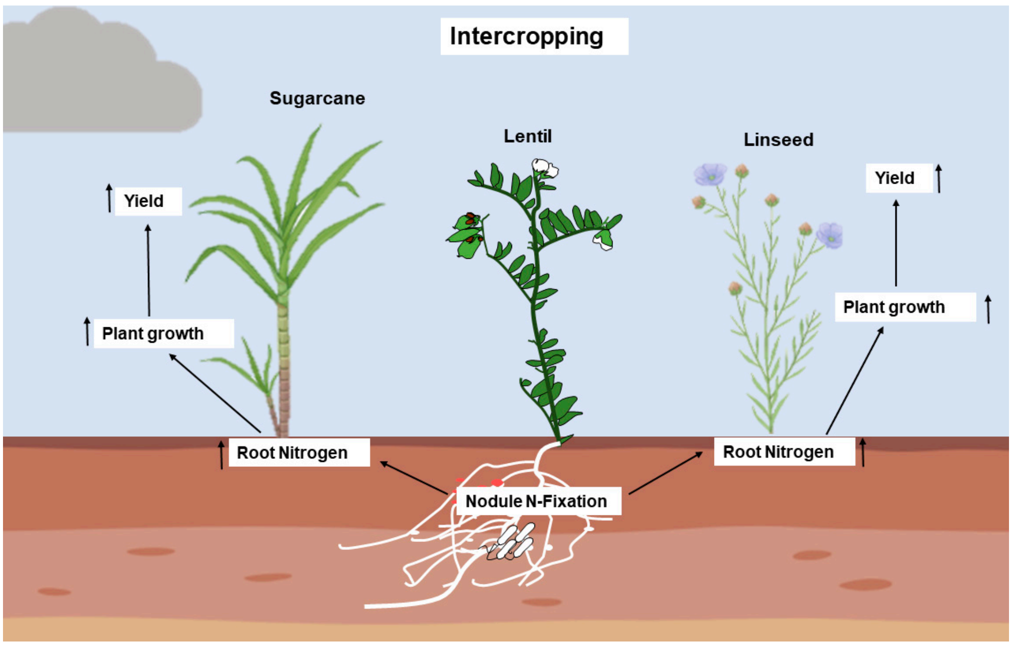

Figure 4. Intercropping of lentils. The cultivation of lentils with other plants of economic interest is a beneficial strategy in which non-nodule-forming plants obtain a greater amount of nitrogen, which is provided by the legume and is reflected in a higher production yield. The black arrows indicate an increase in the parameter mentioned.

Intercropping refers to cultivating two or more crops simultaneously, without row arrangements, on the same land. Productivity during intercropping can be measured using the land equivalent ratio (LER), defined as the land area required to produce, from sole crops, the same yield as that achieved by intercropping [71]. Crop mixes include cereals, legumes, and oilseed crops at different ratios [72]. Lentils have been successfully intercropped. Lentil/wheat (*Triticum aestivum* L.) ratios of 2:1, 10:3, 10:2, and 10:1 had

LER values ranging from 1.21 (10:1 ratio) to 1.45 (10:3 ratio) [73], and lentil/mustard (*Brassica juncea* L.) ratios of 4:1, 3:1, and 2:1 with different plant densities peaked at an LER value of 1.54 (4:1 ratio) [74]. Nitrogen, phosphorus, and potassium available after crop harvest were also increased in lentil/mustard systems. Likewise, the water use efficiency was higher than that in lentil and mustard monocultures [75]. Linseed (*Linum usitatissimum* L.) at lentil/linseed ratios of 6:1, 4:1, 3:1, and 2:1 peaked at an LER value of 1.54 (4:1 ratio) [76]. Sugarcane (*Saccharum* hybrid cultivar) showed a higher equivalent yield in systems intercropped with lentils than in sugarcane alone [77]. The highest yields recorded in intercropping systems with lentils have been attributed to nitrogen fixation [72].

Based on the above, intercropping lentils with other species improves the production and yield of plants of agricultural and nutritional interest in addition to improving the soil. Therefore, this technique is an alternative to using chemical fertilizers.

7. Lentil Crop Constraints in a Changing Environment

The lentil crop is subjected to several biotic and abiotic stresses that limit its production. Lentil seed yields of 3.3 and 2.8 t ha^{-1} have been obtained in research fields in New Zealand and Canada [78,79], but according to FOA data [7], the world average yield in 2021 was 1.10 t ha^{-1}. Enormous yield gaps are observed between major producer countries, ranging from 2.54 t ha^{-1} in China to 0.60 t ha^{-1} in Iran (Table 1). Different factors explain these yield gaps. Lentil is employed as a rotation crop in the post-rainy season using residual soil moisture [80,81] and water disposition is key in yield improvement. For example, Oweis et al. [82] reported that supplementary irrigation increased lentil grain yield from 1.04 to 1.42 t ha^{-1} in a Mediterranean environment under rainfed conditions. In addition to drought, lentil faces other constraints that drive significant production losses, including high and low temperatures, soil factors, diseases such as wilt, root rot, and rust, insect pests, and parasitic weeds [80,81].

In climate change scenarios, drought and high temperatures are considered priority constraints to be addressed, especially in Mediterranean-type climates where lentil production is affected by heat waves and erratic rainfall [80]. In the context of climate change, Delahunty et al. [83] employed a commercial lentil cultivar and two landraces to test the interactions of high temperatures, variable water supply, and atmospheric CO_2. They found that high temperatures decrease grain production, that water supply did not mitigate the effects of high temperatures, and, significantly, that the genotypes differentially responded to high temperatures. These findings support the strategy to increase the adaptation of lentils to high temperatures through existing lentil germplasm. In the same context, Wright et al. [84] (2020) phenotyped 324 genotypes in eight lentil producer countries, identifying eight lentil groups based on sensitivity to temperature and photoperiod.

Lentil varieties currently cultivated have a narrow genetic base due to domestication; this limits the prospects of further adaptation of lentils to changing climatic conditions [85]. In this sense, landraces, especially crop wild relatives (CWRs), are important sources of genetic variability. The employment of landraces and CWRs combined with systematic phenotyping can potentially develop climate-change-resilient lentil genotypes [86,87].

The lentil breeding traits valuable for disease resistance and adaptation to abiotic stresses are frequently quantitative. The identification of quantitative trait loci (QTLs) as markers for the selection and breeding of germplasm can now be performed by integrating genomics technologies that include large transcriptomic datasets, expressed sequence tags (ESTs), and single-nucleotide polymorphisms (SNPs) [88,89].

Safeguarding the agrobiodiversity of Lens species, landraces, and varieties is crucial for protecting the future of lentil breeding in a changing environment. Important efforts have been invested to conserve lentil germplasm; more than 58,000 accessions are spread across 103 countries. The largest collection (14,157 accessions) is maintained in the International Center for Agricultural Research in the Dry Areas (ICARDA), which has collected germplasm from 26 countries [88]. Other initiatives, such as LEGU-MED, are focused on producing integrative plans to valorize legume agrobiodiversity, including, specifically in the Mediterranean Basin, emphasizing biodiversity-based farming systems to enhance the provision of ecosystem services [90].

8. Lentil Medical Implications

The benefits of lentils are not limited to agriculture or human nutrition. Wang et al. [91] identified 12 lectins with different carbohydrate specificities and assessed their anti-SARS-CoV-2 activity against mutant strains and epidemic variants using a pseudovirus-based neutralization assay. Lentil-derived lectins, which specifically bind to oligomannose-like glycans and GlcNAc at the non-reducing terminus, show broad and potent antiviral activity against a panel of mutant and variant strains, including artificial, wild-type, and epidemic variants B.1.1.7, B.1.351, and P.1. Lentil lectin also displays antiviral activity against SARs-CoV and MERS-CoV. This lectin also blocks the binding of ACE2 to the S trimer and inhibits SARS-CoV-2 during the early stages of infection. Supplying mice with it resulted in no cytotoxic activity or weight loss. Based on these results, the authors highlighted the importance of their work in developing new strategies against SARS-CoV-2.

Another study in the medical area evaluated the effect of free polyphenols or those bound to lentil shells and their digestive products on the anti-inflammatory mechanism based on the NF-kB and Keap1-Nrf2 pathways in HT-29 model cells. In total, 27 polyphenols and 5 non-phenolic constituents were identified in the free and bound fractions. Catechin glucoside, kaempferol tetraglucoside, procyanidin dimer, and dihydroxybenzoic acid-O-dipentoside were the main polyphenols in the digestive products. These digestive products reduced inflammatory mediators and presented anti-inflammatory activity by inhibiting Nf-kB and activating Keap1-Nrf2. These results indicate that lentil shells are a good source of anti-inflammatory ingredients [92].

Moreover, lentil phenolic compounds protected liver cells against cytotoxicity-induced oxidative stress. The effects of lentil phenols on stress-induced hepatotoxicity in AML12 and BALB/c mouse hepatocytes were evaluated. Treatment with H_2O_2 caused a marked decrease in cell viability. However, pretreatment with phenols (25–100 μg/mL) for 24 h preserved 50% cell viability at 100 μg/mL. Phenols drastically reduce ROS levels, partly by inducing the expression of antioxidant genes. Additionally, pretreatment with phenols (400 mg/kg) for two weeks reduced serum alanine transaminase and triglyceride levels by 49% and 40%, respectively, and increased glutathione peroxidase expression and activity in CCl4-treated BALB/c mice. These results suggest that lentil phenols protect liver cells against oxidative stress, partially through the induction of the cellular antioxidant system, thus representing a potential source of nutraceuticals with hepatoprotective effects [93].

9. Use of Lentils in Soil Bioremediation

Other uses of lentils are in the bioremediation area; however, this is not directly related to nitrogen. Sulfonylureas are popular herbicides used to control weeds, which, despite helping with agricultural problems, also affect the development of crops grown in soils treated with these herbicides. Therefore, Rainbird et al. [94] evaluated the phytoremediation capacity of lentils grown in uncontaminated soil and soil contaminated with Chlorsulfuron, with or without PulseAider supplementation. The results showed that the presence of lentils increased the degradation of Chlorsulfuron and the degradation rate increased in the presence of PulseAider. This study offers a feasible and economical solution for residual remediation of sulfonylurea herbicides.

As lentils can be used as phytoremediators, they can also be applied as environmental bioindicators to identify cytotoxicity. Among herbicides, paraquat is the most used and third best-selling herbicide worldwide, applied in more than 120 countries, despite being banned in the European Union and being a threat to ecosystems. Mercado and Caleño [95] evaluated the genotoxic effects of paraquat on *L. culinaris* in 2021. The lentil seeds were subjected to six paraquat concentrations (0.1, 0.5, 1, 1.5, 1.5, 2, and 3 ppm) and distilled water was used as a control. Root development was measured every 24 h for 72 h. After 3 days, the root tips were analyzed to determine mitotic index inhibition and the type and rate of chromosomal abnormalities. A decrease in root growth of more than 50% and a 2.9-fold inhibition of the mitotic index in the 3 ppm treatment, compared to the control, was observed. The concentration of 2 ppm presented all the abnormalities with a frequency of 84 $\pm$ 2.5 micronuclei, 106 $\pm$ 3.5 nuclear lesions, 14 $\pm$ 4.7 absence of nuclei, 8 $\pm$ 2.7 telophase bridges, and 7 $\pm$ 2.7 binucleate cells, among others. Studies on lentils in different areas continue to grow, highlighting the importance of this legume in research and as a crop of economic and nutritional interest.

10. Conclusions

The lentil is a legume that grows under various environmental conditions, making it an important crop worldwide. Additionally, lentil production has increased, as has the interest in this legume. Several studies have highlighted the nutritional importance of this legume, mainly owing to its protein content, which is why special attention has been paid to the generation of lines with higher protein content to maintain food safety, especially in developing countries. Lentils have also been shown to have antiviral, anti-inflammatory, and hepatoprotective functions, opening a new line of study to explore more applications of this legume. Another great interest in legumes, such as lentils, lies in their ability to fix atmospheric nitrogen through rhizobia–legume interactions via the formation of nodules, which facilitates the intercropping of the lentil with other plants of economic interest to improve their yield and health. Lentils also participate in soil phytoremediation by eliminating herbicides. In the context of climate change, it is essential to safeguard the agrobiodiversity of *Lens* species and landraces as germplasm is necessary to increase the adaptation of lentils to high temperatures and drought.

Therefore, it is necessary to continue conducting studies focused on promoting the yield of crops of economic interest to continue developing sustainable agriculture techniques and reduce the use of chemical fertilizers that generate environmental and economic impacts.

Author Contributions: Conceptualization, V.M.-R. and E.V.-C.; investigation, V.M.-R.; resources, E.V.-C.; writing—original draft preparation, V.M.-R.; writing—review and editing, E.V.-C.; funding acquisition, E.V.-C. All authors have read and agreed to the published version of the manuscript.

Funding: V.M.-R. was funded by Estancias Posdoctorales por México-CONACYT (México, grant number 628900) and E.V.-C. was funded by Valencia-Macías Fundation (México, grant number 11.1).

Institutional Review Board Statement: Not applicable.

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Conflicts of Interest: The authors declare no conflicts of interest.

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