State and Progress of Andean Lupin Cultivation in Europe: A Review

Penelope J. Bebeli [1,*], **Efstathia Lazaridi** [1], **Tilemachos Chatzigeorgiou** [1], **Maria-José Suso** [2], **Waltraud Hein** [3], **Alexios A. Alexopoulos** [4], **Gonçalo Canha** [5], **Rob J.F. van Haren** [6], **Magnús H. Jóhannsson** [7], **Carmen Mateos** [2], **João Neves-Martins** [8], **Udo Prins** [9], **Filipa Setas** [5], **Danut P. Simioniuc** [10], **Pedro Talhinhas** [11] **and Merlijn van den Berg** [9]

[1] Laboratory of Plant Breeding and Biometry, Department of Crop Science, Agricultural University of Athens, 11855 Athens, Greece; e.lazaridi@aua.gr (E.L.); tilchatzig@gmail.com (T.C.)

[2] Department of Plant Breeding, Institute of Sustainable Agriculture, 14080 Córdoba, Spain; mjsuso@ias.csic.es (M.-J.S.); cmateos@ias.csic.es (C.M.)

[3] HBLFA Raumberg-Gumpenstein, 8952 Irdning-Donnersbachtal, Austria; waltraud.hein@raumberg-gumpenstein.at

[4] Department of Agriculture, University of the Peloponnese, 24100 Kalamata, Greece; a.alexopoulos@us.uop.gr

[5] Lusosem S.A., 1495-137 Lisbon, Portugal; gcanha@lusosem.pt (G.C.); fsetas@lusosem.pt (F.S.)

[6] Centre of Applied Research Biobased Economy, Hanze University of Applied Sciences, 9747 AS Groningen, The Netherlands; r.j.f.van.haren@pl.hanze.nl

[7] Soil Conservation Service of Iceland (SCSI), Gunnarsholt, 851 Hella, Iceland; magnus@land.is

[8] Instituto Superior de Agronomia, Universidade de Lisboa, 1349-017 Lisbon, Portugal; nevesmartins@isa.ulisboa.pt

[9] Department of Breeding & Innovative production chains, Louis Bolk Institute, 3981 AJ Bunnik, The Netherlands; u.prins@louisbolk.nl (U.P.); m.vandenberg@louisbolk.nl (M.v.d.B.)

[10] Department of Plant Sciences, University of Agricultural Sciences and Veterinary Medicine Iaşi, 700490 Iaşi, Romania; simion@uaiasi.ro

[11] LEAF, Linking Landscape, Environment, Agriculture and Food, Instituto Superior de Agronomia, Universidade de Lisboa, 1349-017 Lisbon, Portugal; ptalhinhas@isa.ulisboa.pt

* Correspondence: bebeli@aua.gr; Tel.: +30-2105294626

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Abstract: *Lupinus mutabilis* is an important source of protein in different Andean countries, and its use in diets, particularly those of less wealthy individuals, has been observed for thousands of years. There is an increasing demand for protein crops suitable for Europe and this species is a potential candidate. Assessment of *Lupinus mutabilis* genetic material in European conditions started more than 40 years ago, with the characterization of a vast number of accessions from the Andean region. In this review, abiotic and biotic constraints to *L. mutabilis* cultivation in European soil and climatic conditions are discussed, and cultivation management practices are suggested. The beneficial interaction of *L. mutabilis* with *Bradyrhizobium* strains in the soil and various pollinator species is also discussed, and the effect of abiotic stresses on these interactions is highlighted. Prospects of alternative uses of *L. mutabilis* biomass in Northern Europe and opportunities for breeding strategies are discussed. In conclusion, the different approach to crop modeling for Southern and Northern European climatic conditions is highlighted.

Keywords: *Bradyrhizobium*; *Lupinus mutabilis*; abiotic stresses; adaptation; biomass; biotic stresses; pollinators

1. Introduction

Lupins are legumes that belong to a large and diverse genus, *Lupinus*, comprising approximately 280 species [1–5]. Lupins are divided into two major groups according to their geographical origin: (1) the "New World" species, originating in Western North America (ca. 100 species) and the Andean region (ca. 85 species) [1,6,7] and (2) thirteen "Old World" species, with origins in the Mediterranean region [1,7,8]. Among them, only four lupin species present high agricultural importance. Three belong to the "Old World" group, namely *L. albus* L. (white lupin), *L. angustifolius* L. (blue or narrow-leaved lupin) and *L. luteus* L. (yellow lupin) [2,9]. The fourth is the only representative from the 185 species of the "New World" group named *L. mutabilis* (Andean lupin, pearl lupin), called either tarwi or chocho bean, in regard to the tall species with long branches and the short plant growth type with few branches [10]. Three other lupins worth mentioning, although only of regional agricultural importance, are *L. pilosus* L., an Old World lupin used as a coffee substitute (Altreier Kaffee) in Northern Italy [11], *L. nootkatensis* D. ex S. (Nootka lupin), used for land reclamation [12–14] and *L. polyphyllus* Lindl. (Washington lupin), used as an ornamental in many European countries including Germany, Poland, Russia, Spain, Sweden, Ukraine and the United Kingdom. The latter, however, has also been studied for its use as a low alkaloid forage [15] and land rehabilitation species in Central Europe [16,17].

It is suggested that *L. mutabilis* domestication took place in the Cajamarca region, located between Southern Peru and Northern Bolivia. Remains of seeds are present in the tombs of the pre-Inca Nazca culture (about 500 AD) in the Peruvian coastal desert, and the plant is represented in stylized paintings on large pots from the Tiahuanaco culture (500 to 1,000 AD) of the Andean highlands [8,18–23]. *Lupinus mutabilis* was used by the American Indians as food, after the removal of alkaloids, by soaking the seeds in running water for several days; however, new biological, chemical or aqueous methods for the removal of alkaloids are now available [24]. Andean lupins were also used for green manure and as medicine for cardiac diseases, internal parasite infections, rheumatism and malaria [19]. However, following the European invasion, the culinary habits of the locals changed due to the displacement of Andean lupin by new species such as quinoa [25–27]. Nowadays, *L. mutabilis* is mainly cultivated throughout the Andean region, in countries like Peru, Ecuador and Bolivia, and less so in other South American countries.

The adaptation of *L. mutabilis* to European and European–Russian soil and climate conditions has been a subject of research since the 1930s [28,29], and in the last few decades, *L. mutabilis* has been cultivated for agricultural purposes, although it is not yet commercially available [2,20,22,27,30–32]. The spread of *L. mutabilis* in Europe has increased more recently as lupin species have gained the interest of the European Commission due to their high protein and oil content, low starch content and the roles that they could play in reducing soya imports and as biorefinery crops [19,30]. The main interest in Andean lupin cultivation in Europe is based on its higher protein (41–51%) and oil content (14–24%) [27] in comparison to white, blue and yellow lupin species and on its pharmaceutical and cosmetic potential [24,33,34].

Europe is considered one of the main continents where white, blue and yellow lupin are cultivated, with a total production reaching up to 341,970 tons in 2018 [35]. Despite the great interest, Andean lupin is not yet considered commercial because its introduction is facing considerable challenges, such as a low and unstable yield production, the long cropping cycle and difficulties of incorporation into the local cultivation systems, mainly due to various abiotic stresses [22,23]. Various pests and diseases have also been found to be responsible for lower yields of *L. mutabilis* in Europe [8,36,37]. Considering Andean lupin's potential in Europe, this paper summarizes *L. mutabilis* genetic material as tested under European edaphoclimatic conditions and the abiotic and biotic factors that prevail in the area affecting its cultivation, as well as the cropping practices and techniques applied for their management. Its symbiosis with other living organisms, i.e., rhizobacteria and effective pollinator species that predominate in the area, is also assessed. Finally, future alternative uses in the context of adaptation and commercialization in European soil and climatic conditions and the research prospects of the crop are mentioned.

2. Andean Lupin Genetic Material Tested under European Conditions

The evaluation of *Lupinus mutabilis* genetic material started in European edaphoclimatic conditions in the mid-1930s in Germany [29], the mid-1970s in France and the United Kingdom (UK) [38–40] and later in 1983 in Germany and Poland [26,41,42], aiming to define genotypes of early maturity and determinate or semi-determinate growth habit that were considered promising for cultivation and commercial production in Europe. A genotype named KW, with a determinate growth habit, was developed in Poland using mutation breeding [26,42], and Olczak et al. [41] found a fragment in the genetic material of *L. mutabilis* (KW mutant) that could be used as a molecular marker for a determinate growth habit [41].

In the 1990s, the European Agrimed research project "*Lupinus mutabilis*: Its adaptation and production under European pedoclimatic conditions" took place. In this project, 149 different lines and selected sub-lines of *L. mutabilis* populations collected in Peru were evaluated in Southern European conditions, in Portugal, for two consecutive years [43]. During 1993–1996, another European project (AIR20865) followed, "Adaptation of *L. mutabilis* to European soil and climate conditions", that aimed to evaluate sixteen different Andean lupin genotypes in Northern (Germany, UK and Poland) and Southern (Southern France and Portugal) Europe.

Since then, many of these Andean lupin genotypes were further evaluated regarding their response and susceptibility to various biotic factors prevailing in Europe, such as cucumber mosaic virus (CMV) [44] and thrips [45]. Intercropping with other temperate legume species for forage production was also assessed, in a two-year experiment with promising results [46]. Recently, many mutant lines were studied in Poland [34], while an interspecific *L. mutabilis* (LM-13) × *L. albus* hybrid was developed and its adaptation to European conditions was evaluated [47]. In the context of the previously mentioned projects, and others, in Europe, 167 different *L. mutabilis* accessions have been tested in the soil and climatic conditions of Portugal, 44 in Poland, 28 in the UK, 26 in Germany and 24 in France, while only one has been tested in Serbia. These accessions were populations, sub-populations, lines, mutant lines, epigonal lines, epigonal mutant lines and landraces [26,39,41–43,46,48–55].

In the European LIBBIO project (No 720726, Horizon 2020) titled "*Lupinus mutabilis* for Increased Biomass from marginal lands and value for BIOrefineries" (http://www.libbio.net), we aim to evaluate the suitability of Andean lupins to different marginal lands in Europe. In this framework, the social and environmental impacts of Andean lupin cultivation in Europe are being evaluated, as well as its techno-economic viability in different European countries. Genotypes are evaluated in field experiments in seven European countries, under Mediterranean conditions (Greece, Portugal, Spain) and in North-Central European (Austria, Iceland, the Netherlands, Romania) conditions, including *L. mutabilis* genotypes, genetic material from Instituto Superior de Agronomia (ISA, Lisbon, Portugal) and Vandinter Semo (VDS, Scheemda, The Netherlands). In this context, Guilengue et al. [56] and Lazaridi et al. [57] assessed the phenotypic and genetic diversity of Andean lupin for defining appropriate genotypes for cultivation under Mediterranean climatic conditions and the N-fixing potential of LIBBIO breeding lines in alkaline soils [58].

3. Abiotic Restrictive Factors and Cropping Practices

3.1. High and Low Temperature Effects

Temperature is considered one of the most important abiotic factors affecting Andean lupin cropping in Europe [52,59]. Especially in Southern European countries where autumn-winter sowing is practiced and cultivation lasts until summer, the crop is subjected both to low air temperature during the vegetative phase and to high temperatures during the flowering and pod filling stages. Low seed yield production is often recorded under cultivation in Southern European climatic conditions, as a result of flowering abortion at temperatures around and above 27 °C [59] that are common in countries such as Spain, Portugal and Greece. The pod and seed filling stages of lupin species have also been reported to be inhibited by high temperatures (38 °C) [60].

In Northern European countries, Andean lupin seedlings are often exposed to low spring temperatures, and in Southern Europe, to winter frosts, which can be detrimental to plant growth. Even though *L. mutabilis* has been found to be resistant to frost during the seed filling stage, it is very susceptible to low temperatures during the vegetative stage. Exposure to low temperatures can lead to severe plant losses [61], inhibited plant growth [52] and result in longer periods of vegetative growth [62]. Studies in the 1930s revealed that susceptibility to low temperatures differs among lupin species, in the order of increasing sensitivity, namely *L. angustifolius, L. luteus, L. albus* and *L. mutabilis* [29,63].

The screening and selection of genotypes for indeterminate growth, tolerance to frosty conditions at the vegetative stage, and high temperatures at the flowering and podding stages, are therefore considered to be of primary importance in Southern European countries. In Northern Europe, short-cycle genotypes with determinate growth and tolerance to low temperatures are preferred [22]. Defining the appropriate sowing date for each region is also critical for seed yield production [64].

The response of *Lupinus* spp. to vernalization effect varies among species and even among cultivars [65]. Dominant gene presence or absence, like the *Flowering locus T (FT)* gene and *Bo*, *Ku* and *Jul* loci, have been reported to remove or reduce the vernalization response in *L. cosentini* and *L. angustifolius*, respectively [5,66,67]. However, these genes have not been reported in other lupin species [65]. Książkiewicz et al. [68] found that the genetic control of vernalization differs among lupin species. In areas where lupins are grown as spring-sown and autumn-sown, when winters are mild, the requirements of vernalization can be a restrictive factor. While Jacobsen and Mujica [27] reported that *L. mutabilis* is neutral to vernalization, Hardy et al. [52] and later Adhikari et al. [65] observed that when late flowering genotypes were subjected to vernalization, they flowered two weeks earlier.

3.2. Impact of Day Length on Growth and Production

Long days are considered to favor the production of flowers in *Lupinus* spp. [65]. No effect of photoperiod within the range 12.5–14.5 h on the number of days to first flowering were found by Keatinge et al. [59], suggesting that flowering of Andean lupin is insensitive to photoperiod. However, according to Jacobsen and Mujica [27], short days accelerate grain filling, while Hackbarth [69] reported increased oil content in the seeds developed under short days. The response to the photoperiod varies in regard to genotype (early or late flowering); in this context, late flowering genotypes are not favored in Southern Europe, because grain filling occurs on long days at the end of spring and, as mentioned above, seed oil content and yield are reduced.

3.3. Effects of Water Logging and Water Deficit on Growth and Seed Quality

Lupin plants grown under water deficit have a smaller leaf area and fewer lateral shoots, and they tend to mature earlier [70,71]. Water deficit can also cause significant decreases in leaf water potential, stomatal conductance and gas exchange [71]. According to Carvalho et al. [72], water deficit does not affect pod production but it causes a slight decrease in the dry weight of pod husks and a slight increase in the dry weight of seeds. In addition, water deficit does not affect seed protein content levels but reduces the oil content of the seeds (on dry weight basis), increases seed sugar content (on dry weight basis) and changes the composition of carbohydrates, e.g., increased sucrose/alpha-galactoside ratio [72]. Among several *L. mutabilis* accessions from USDA (United States Department of Agriculture) that were tested for drought resistance, only one was found to be tolerant to water stress [73].

Genetic diversity has been identified among *L. mutabilis* accessions for tolerance to water logging. Within the genus, the level of water logging tolerance in *L. mutabilis* is comparable to that of *L. angustifolius*, higher than in *L. albus* and lower than in *L. luteus* [74]. Water deficit in Andean lupin cropping can be prevented by sowing early in Southern European countries to exploit autumn precipitation. In addition, in both Southern and Northern European countries in regions that are prone to waterlogging incidents, cropping in heavy soils should be avoided or otherwise the soil should be tilled well.

3.4. Alkaline, Calcareous Soils and Their Effects on L. mutabilis as a Crop

Lupins are calcifuge species [75]. A significant variation in tolerance to the lime content of soil among *Lupinus* species has been observed [29,76,77]. Calcium carbonate ($CaCO_3$) in combination with alkaline soils can be catastrophic for the cultivation of Andean lupin. Andean lupin plants grown on soils with a high calcium carbonate content usually exhibit chlorosis symptoms (Figure 1), although different levels of susceptibility have been observed among different genotypes [78]. In alkaline soils, calcium carbonate inhibits iron uptake [79] and has a negative effect on plant photosynthesis, inhibiting the shoot growth rate and seed yield [80]. Although, *L. mutabilis* is more tolerant than *L. luteus* and *L. angustifolius*, it presents similar sensitivity to calcium carbonate in the soil as *L. albus* [61].

Figure 1. Chlorosis symptoms in *L. mutabilis* grown on soil with high calcium carbonate content ($CaCO_3$—37.3%).

4. Biotic Constraints in Europe for *Lupinus mutabilis*

Several biotic factors can cause significant problems and limit the production of Andean lupin crops, including mainly fungal and virus pathogens that act similarly on all cultivated lupin species [81].

4.1. Fungal and Bacterial Diseases

Anthracnose caused by *Colletotrichum lupini* (Bondar) Damm, P.F. Cannon & Crous [81,82] is the most important fungal disease that severely affects Andean lupin in Ecuador, but it has also spread in the last few decades throughout all lupin growing regions [37]. In regard to European regions, anthracnose was responsible for a rapid decrease in *L. albus* cultivation in Germany and other Central European countries (Austria, France, Poland, Ukraine and Russia) [37,83]. The most obvious symptoms of anthracnose are bending of the main axis, circular or elongated lesions on stems and pods and infected seeds [10,84] with a reduced oil content [85], but a severe infection can cause serious to complete yield losses. In comparison to other cultivated lupins, no resistance is available yet for *L. mutabilis* [37], which has been proven to be less resistant than *L. luteus* and *L. angustifolius* [6,86].

Therefore, other control methods, like seed disinfection and seed hygiene, are generally implemented for anthracnose (Table 1). Some screening efforts have been made [87], revealing that less susceptible genotypes are mainly characterized by a central stem dominance, belonging to the chocho type, while tarwi type genotypes are semi-tolerant [6,88] or present anthocyanin pigmentation in their stems [84]. However, the vulnerability of each developmental stage seems to differ, with the stages after flowering being defined as more susceptible [89,90].

Table 1. Main fungal diseases affecting Andean lupin in Europe and control practices.

Fungal Disease	Pathogen	Transmission	Control Method
Anthracnose	*Colletotrichum lupini*	Infested seed lots, crop stubble [37,91]	Certified seed [92] Seed disinfection, i.e., dry heat, UV-C [1] [82,93] Fungicide application (e.g., azoxystrobin, chlorothalonil, mancozeb) [85] Crop rotation [37]
Fusarium wilt and root rot	*Fusarium* spp.	Infested seed lots, soilborne [94]	*Bacillus* spp. strains [81] Crop rotation [36] Available resistance: ECU-688, ECU-5920, ECU-7293 breeding lines [92], K2135 [95], chocho type [96]
Pleiochaeta root rot and brown (leaf) spot	*Pleiochaeta setosa* (*Ceratophorum setosum*)	Infested seed lots, plant residuals [97]	Certified seed [98] Minimum tillage application [98] Deep dripping prior to the crop establishment [98] Crop rotation with non-host plant species [98] Deep sowing, up to 5 cm depth [99]
Root and hypocotyl rot	*Phytophthora sojae*, *Rhizoctonia solani*	Soilborne [94,100]	Crop rotation with cereals [92] Improvement of soil drainage or selection of well drained fields [92] Deep dripping (25–30 cm) [98]

[1] UV-C: Ultraviolet radiation with wavelengths from 100 to 280 nm

Fusarium wilt and root rot (*Fusarium* spp.) are also considered one of the main lupin seed-borne fungal diseases, and many *Fusarium* species have been recorded to infest Andean lupin in Europe, such as in Poland [42] and in Russia [75]. Among cultivated lupins, *L. mutabilis* is considered the least susceptible to *Fusarium* spp. [101]. In contrast to anthracnose, genotypes that are resistant to this fungus are available [86] (Table 1).

Another disease to which *L. mutabilis* is less sensitive than the other lupin species [8,102] is pleiochaeta root rot and brown (leaf) spot induced by *Pleiochaeta setosa* (Kirchner) S.J. Hughes (Table 1). The disease causes typical symptoms on the roots of the plants [103], leading to a dramatic reduction in crop yield. The transmission of the pathogen seems to be enhanced particularly in low rainfall areas [97]. Until now, no resistance has been found in Andean lupin or in the Old World species [8,86,104,105], although some variability has been observed regarding its resistance [97]. Only in Australia, some active substances (i.e., iprodione and procymidone) are registered and can be applied to seeds for partial control of this disease [106]. In Europe, specific cultivation management techniques have been implemented based on worldwide guidelines (Table 1). Root rot symptoms in *L. mutabilis*, caused by *Phytophthora sojae* Kaufm. & Gerd. [107] and *Rhizoctonia solani* J.G. Kuhn have also been previously reported [92]. The common existence of these fungal diseases around the world and their ability to affect other lupin species [8,108,109] is a serious threat to the spreading of *L. mutabilis* cultivation in European countries. As there are no available fungicides to suppress the disease in *L. mutabilis*, various management techniques have been proposed (Table 1).

Recently, a method has been patented for preventing or inhibiting infection in various plant species, including lupins, by fungal pathogens like *Fusarium*, *Rhizoctonia* and *Botrytis cinerea* Pers. [110]. The method is based on the prevention of microorganisms from degrading α-1,3-glucan on cell walls by α-1,3-glucanase, avoiding host immune recognition by pathogens. Another patented product [111],

a solution consisting of an ethylhexyl sulfate or salt, an alkylbenzenesulfonic acid and a carrier is also available for inhibiting grey mold and powdery mildew in lupins and is applicable to *L. mutabilis*. Plant growth promoting rhizobacteria could also help the production of lupin metabolites against fungi, like in many other plant species [112], within the aspects of biocontrol.

Other common fungal diseases have also been reported, causing some less frequent symptoms in Andean Lupin [2,6,85,92,113]. However, no occurrences have been reported yet in *L. mutabilis* in the European continent. Bacteria-induced diseases by *Pseudomonas lupini* and *P. xanthochlora* have also been reported to affect lupins [36,114]. Among these bacterial and fungal pathogens of *L. mutabilis*, resistance has been reported for a few of them [115], while for others, proper cultivation practices are suggested or no control is needed due to their minor importance.

4.2. Virus Diseases and Carriers

Lupinus mutabilis, like other cultivated lupins, is also susceptible to bean yellow mosaic virus (BYMV) and, compared to other lupin species, it shows high susceptibility [8]. The virus is transmitted by aphids [97,116]. Affected plants present symptoms like vein clearing and leaf mottling, mosaic and leaf deformation, depending on the strain and the infected genotype [36,117,118]. BYMV symptoms have already been recorded in Andean lupin across Europe [118–120]. Using certified seed is considered the principal control method [101,121]. In Australia, early sowing, high seeding rates and crop rotation are recommended [122]. Similar practices should probably also be implemented in Europe, since the application of insecticides has not been proven to adequately prevent BYMV transmission [123].

Cucumber mosaic virus (CMV) can also cause a very destructive disease, resulting in up to 60% yield losses in Mediterranean climate [124]. The virus can also be transmitted to *L. mutabilis* in a non-persistent way by aphids [35,124]. Symptoms recorded in plants of *L. mutabilis* include vein clearing of young leaves, leaf deformation, mottling and size reduction, pallor and stunting [44]. To prevent transmission of the virus, cultivation management practices (as used to prevent BYVM) are recommended in Australia, as well as the use of resistant varieties [101]. Regarding *L. mutabilis,* after testing multiple lines, only one showed resistance to CMV [125,126]. The same line has also shown resistance to pea seed-borne mosaic virus (PsbMV) [127].

Lupinus mutabilis also presents immunity to various viruses, commonly found in lupins, such as lupin mosaic virus (LuMV) [128] and alfalfa mosaic virus (AMV) [123]. The main carriers of lupin viruses are aphids [129], which feed on lupin plants, resulting in significant yield losses [130–132]. Ferguson [133] reported a late season infestation in plants of *L. mutabilis* in Great Britain by *Macrosiphum albifrons* Essig, which is able to transmit cucumber mosaic virus (CMV). Many reports suggest that aphids are expanding throughout Europe [134–138]. In Poland, thrips *Frankliniella intonsa* and *Thrips tabaci*, known as virus carriers [139], were reported to feed on *L. mutabilis* plants at the flowering stage [45]; however, this did not have a high impact on lupin production. Tomato black ring virus (TBRV), a lupin nematode-transmitted virus, was reported to affect *L. mutabilis* and to cause leaf deformation and dwarfing after inoculation, although not limiting yield [117].

4.3. Main Insect Pests of L. mutabilis in Europe

Among pests, *Agromyza* spp. is the most destructive to Andean lupin in Europe. Its larvae feeds on leaves and stems [6]. Weevil (*Sitona* spp.) or lupin-root weevil, *Sitona gressorius* and *S. griseus* are considered major lupin pests across Europe that can strongly reduce lupin grain yield [140], either due to larvae feeding on root nodules or due to adults feeding on the leaves of sweet plants [36,141]. In terms of weevil preference, Ferguson [133] recorded higher weevil percentages in *L. albus* and *L. luteus* plants than in *L. mutabilis*, indicating the lowest preference for *L. mutabilis*. *Macrosiphum albifrons* is another aphid that can cause serious damage to lupins [142]. These aphids prefer alkaloids, which they use as a weapon against predators [142,143].

Many flower and pollen-feeding polyphagous beetles (Coleoptera, *Astylus* spp.) were found to prefer Andean lupin flowers over vegetative parts of the plant [133], causing flower and pod abscission.

Three Coleoptera species were recorded recently in *L. mutabilis* in Greece, in two experimental locations, feeding on flowers, namely *Tropinota hirta* Poda, *T. squalida* Scopoli and *Oxythyrea funesta* Poda [78,144]. These findings enhance the statement of Ferguson [133], who suggested that *Astylus* spp. beetles preferred the flowers because of different alkaloid levels in pollen and flowers and in the vegetative parts of the plant. Additionally, the timing of sowing had an impact on beetle feeding, as sowing later led to the delayed flowering of many accessions and therefore beetle immigration was avoided [133]. Chemical control of these two beetles is nearly impossible; thus, using baited traps or cultivating very early or late flowering varieties could help in reducing their population density. Diabrotic cucumber beetles (*Diabrotica trivittata* Mannh.) and *Liriomyza* sp., found throughout Europe, have also been reported to feed on Andean lupin leaves and flowers in their center of origin [145].

4.4. Weed Species and Management in L. mutabilis Cultivation

Lupin crops are susceptible to weed infestation [146], which can reduce seed yield by up to 67% and also cause difficulties during harvesting [147,148]. Weed species were recorded in Andean lupin fields cultivated in two different regions in Greece (Table 2), namely in Athens (conventional field, no herbicides applied) and in Kalamata (bio cyclic), in two and one year respectively. In Athens, only *Amaranthus* spp. and *Chenopodium* spp. inhibited plant vegetative growth, while *Calystegia sepium* L. and *Convolvulus arvensis* L. could mix with the aerial biomass when harvest took place. In Kalamata, *Capsella bursa-pastoris* (L.) Medik., along with *Fumaria officinalis* L., was the most intense weed species. The spring weed species found in an Andean lupin field cultivated in an herbicide screening experiment in Santarém, Portugal are presented in Table 2 [149].

In this context, weed control seems to be essential for Andean lupin cultivation in Europe. Unfortunately, there are limited herbicides approved for lupins. Weed control in Andean lupin crops relies on pre-emergence chemical control, followed by mechanical methods such as harrowing or hoeing [150], as in other lupin species [151]. Increased sowing densities and strip cropping [147,148, 151,152] have also been applied in many lupin species, reducing weed populations significantly.

Chemical weed control has been evaluated in *L. mutabilis* cropping in Southern Australia, where Sweetingham [74] states that *L. mutabilis* plants were tolerant to imazethapyr. Prins and van Haren [150] evaluated the effect of pendimethalin and florasulam on *L. mutabilis* and concluded that it can be safely used under European conditions.

In another experiment in Santarém, Portugal, the effects of seven herbicide treatments were tested in a *L. mutabilis* crop. Germination ratio evaluation showed that only treatment with metribuzin proved to be significantly different from the untreated plots, showing visible phytotoxicity symptoms. No negative effects on germination were observed in the other treatments (clomazone + pendimethalin, isoxaben, pendimethalin, propizamid, isoxaben + propizamid, s-metolachlor). Only treatments with clomazone + pendimethalin and s-metolachlor outperformed untreated plots when productivity was analyzed [150]. Articles in the literature regarding herbicide screening and weed control in *L. mutabilis* cropping are limited. Therefore, future studies in these fields are necessary for the commercialization of this crop.

Table 2. Main weed species recorded in Andean lupin fields in Greece and Portugal.

Weed Species	Athens	Kalamata	Santarém	Life Cycle
Abutilon theophrasti Medik.			x	A, Su
Ailanthus altissima (Mill.) Swingle	x			A, Su
Allium roseum L.		x		P, W
Amaranthus hybridus L.	x			A, Su
Amaranthus retroflexus L.	x			A, Su
Ammi majus L.			x	A, Su
Anthemis spp.	x	x		A, W
Avena spp.	x	x		A, W
Calendula arvensis L.			x	A, Su
Calystegia sepium (L.) R.Br.	x			P, Su
Capsella bursa-pastoris (L.) Medik.	x	x		A, W
Chamaemelum fuscatum (Brot.) Vasc.			x	A, Sp
Chamomilla recutita L.	x	x		A, Su
Chenopodium album L.	x			A, Su
Chenopodium murale (L.) S. Fuentes, Uotila and Borsch	x			A, Su
Chrysanthemum coronarium (L.) Cass. ex Spach	x	x		A, Su
Convolvulus arvensis L.	x			A, Su
Datura stramonium L.	x		x	A, Su
Daucus carota L.		x		B, W
Euphorbia peplus L.		x		A, Su/W
Fumaria officinalis L.	x	x		A, W
Fumaria parviflora Lam.	x	x		A, W
Geranium spp.		x		A/B, W
Hordeum murinum L.	x			A, W
Lactuca serriola L.	x			A, Su
Lamium amplexicaule L.	x			A, W
Lavatera cretica L.			x	A/B, Su
Malva sylvestris L.	x			B, Su
Medicago arabica (L.) Huds.		x		A, W
Oryzopsis miliacea Michx.		x		P, Su
Oxalis pes-carpae L.		x		A, Su
Papaver rhoeas L.	x			A, W
Phalaris minor Retz.	x			A, W
Poa spp.	x	x		A/B, W
Portulaca oleracea L.			x	A, Su
Rapistrum rugosum (L.) All.		x		A/B, W
Silybum marianum (L.) Gaertn.	x			A/B, W
Sinapis spp.	x			A, W
Sisymbrium irio L.	x	x		A, W
Solanum eleagnifolium Cav.	x			A, Su
Sonchus oleraceus L.	x			A, W
Stellaria media (L.) Vill.	x			A, W
Taraxacum spp.	x			A, W
Trifolium spp.		x		A/B, W
Urtica dioica L.	x			A, Su
Urtica urens L.	x			A, Su
Veronica persica Poir.	x	x		A.W
Xanthium strumarium L.	x			A, Su

A: Annual, B: Biennial, P: Perennial, W: Winter, Sp: Spring, Su: Summer.

5. Symbiosis with Other Species Abundant in Europe

5.1. Rhizobium–L. mutabilis Symbiosis and Nitrogen Fixation Potential

Rhizobium–legume symbiosis is a process that is characterized by high specificity [153]. Specificity has also been found for *Rhizobium–Lupinus* symbiosis. Although it is highly dependent on the geographical origin of the species, *L. mutabilis* is reported to be effectively nodulated worldwide, mainly by *Bradyrhizobium* strains [5,74,154–157]. Many strains of *Bradyrhizobium* sp. have therefore been isolated from *L. mutabilis* plants from different regions [155,157,158]. However, a strain named WSM1253, isolated from *Ornithopus compressus* and collected in Greece, has been found to be promising in nodulating *L. mutabilis* accession P28725 in Southern Australian soil and climatic conditions [74]. Effective nodulation was also observed recently in Andean lupin accessions by native rhizobia strains, in Greece [58]. European native *Bradyrhizobium* strains, as also mentioned by Stępkowski et al. [155], *Bradyrhizobium canariense* and *Bradyrhizobium japonicum* are therefore capable of nitrogen fixation in Andean lupin plants and could be even more promising than commercial strains nodulating other lupin species [159].

Lupins are able to fix higher amounts of nitrogen than many other leguminous species [160], with *L. mutabilis* reaching even up to 527 kg N × ha^{-1}. A higher nitrogenase activity of *L. mutabilis* in comparison to other lupin species has also been reported by Kurlovich et al. [161]. However, the amount of nitrogen fixed by *L. mutabilis* varies greatly among experimental years [160]. Furthermore, the amount of fixed nitrogen by *L. mutabilis* under alkaline, calcareous and clay edaphic conditions is significantly lower than the amount fixed by native lupin species [58,162] and in relation to the values reported in Nepal [160]. The lower amounts of fixed nitrogen can be attributed to the specificity of *Rhizobium* strain–lupin species symbiosis [163] but also to the edaphoclimatic conditions, as alkaline and calcareous soils negatively affect nodule number and activity [8,61,164–166]. Nonetheless, there is an exception: *L. mariae-josephae* is successfully nodulated by *Bradyrhizobium* strain LmjC, and this symbiosis system prevails in alkaline soils [167,168].

Lupinus–Bradyrhizobium symbiosis has been described as being relatively tolerant to abiotic stresses [169]. Many abiotic factors have been reported that interfere with the effectiveness of *Bradyrhizobium* - lupin symbiotic systems, like salinity [169,170], prolonged water logging [166,170] and increased nitrate soil content [171], which characterize many European fields. Also herbicides have been shown to negatively affect nodule structure and reduce nodule activity [172,173]. *Bradyrhizobium* strains often confer better tolerance to abiotic stresses such as herbicide and salinity tolerance than other *Rhizobium*–legume symbioses. The identification of such strains would greatly facilitate the introduction of *L. mutabilis* into sustainable crop cultivation systems in Europe.

5.2. Andean Lupin Interaction with Pollinator Species Abundant in Europe

The mating system of a species is of fundamental importance in determining the appropriate breeding strategies, the optimal genetic structure of improved varieties and the isolation requirements for seed production. Suso et al. [174] review the current knowledge of the patterns of mating systems in different *Lupinus* spp. According to the authors' review, and citing Kazimierska and Kazimierski [175], the genus is composed of many species that, depending on genetic and environmental factors, present a range of pollination modes, from strictly self-pollination and self-pollination with facultative cross-pollination to prevailing cross-pollination. Even within each species, the outcrossing rates vary depending on the genotype, the location linked to the pollinator fauna species and population. Nevertheless, most cultivated lupin species are regarded as self-pollinated, although there is a degree of outcrossing [176].

By using ISSR markers in different germplasm accessions of *L. mutabilis*, Chirinos-Arias et al. [177] observed a relatively high genetic polymorphism for an autogamous species such as the Andean lupin. According to Chirinos-Arias et al. [177], the high degree of polymorphism observed might be the result of cross-pollination or in-situ gene flow. Caligari et al. [26] examined the rate of cross-pollination

under top-cross experiments over two years, with low and high anthocyanin containing plants as markers. Outcrossing rates between 16.6% and 58.8% were obtained, which indicates that *L. mutabilis* is an entomogamous, partially allogamous crop that needs to be treated in breeding programs as a cross-pollinated crop.

Lupins are entomophilous species, attracting insects with multi-colored flowers, nutritious pollen and fragrance, which are visited by a great number of solitary and social bees. The presence of different species of pollinators can vary depending on the growing conditions and especially on the availability of bees [175]. Both self-pollination and cross-pollination can be facilitated by bees, which vary widely in behavior and frequency [175]. Bee pollinators play a key role in plant breeding, as they facilitate cross-fertilization, which is needed in order to achieve heterosis of agronomic trait exploitation. Empirical data (not published, in the frame of LIBBIO H2020 EU project) has shown that the most frequent positive floral visitors to lupins are bumblebees (*Bombus terrestris*) in Southern Spain, but solitary bees of the *Eucera*, *Andrena* and *Anthophora* genera are also visitors. *Xylocopa* was also noted as positively visiting, although at very low proportions. No negative visits, robbing nectar through holes bitten at the base of the flowers, were observed. *Xylocopa* bees were the most frequent pollinators observed on Andean lupin flowers in Athens, Greece, but *Anthophora* and *Megachile* bees, as well as *Bombus* sp., were also recorded [78,144]. Williams et al. [178] on the other hand mentioned that *Apis mellifera*, *Bombus* spp., *Andrena ovulata*, *Andrena labialis* and *Eucera* sp. have been observed to pollinate *L. albus, L. luteus* and *L. mutabilis* in France, although without identifying which pollinator species pollinates each lupin species separately. Studies on *L. mutabilis* pollinator species are still missing from the literature regarding Central and Northern Europe. Future pollinator studies could aim for the identification of the species responsible for the pollination of Andean lupin.

6. Future Uses and Investigation Prospects

Lupinus mutabilis is a legume with many uses (both as seed and biomass) that are mentioned with detail in the literature. On one hand, *L. mutabilis* has been used as a cover crop or green manure for improving soil quality [21,86,179]; on the other hand, seeds are commonly used as food for humans and animals in the Andean region [3], after debittering [180]. In addition, the seeds can also find applications in bread making [24], as cheese substitutes [181] and in other food products [24], medicine [177,182] and cosmetics [23,183,184]. A more thorough review of *L. mutabilis* uses can be found in the literature [3,21,23,24,86,177,179–184].

6.1. Prospects of Using L. mutabilis as Feed and Biomass for Bioenergy

Due to their high protein content, oil content and health-promoting secondary metabolites, lupin seeds form a great feed for ruminants, pigs, poultry and fish, improving their productivity when provided in the recommended amounts [185,186]. Until now, most research has focused on Old World lupins [185–188], while the use of *L. mutabilis* seeds has only been directly evaluated in experiments as feed for fish and shrimps [189,190]. In some Northern European countries, *L. mutabilis* grows continuously due to its indeterminate growth habit; in this context, the large mass of above ground biomass can be used as forage or for bioenergy. Gulisano et al. [23] propose the use of *L. mutabilis* as green fodder or silage, particularly for Northern Europe, where high biomass yields are achieved. Literature about *L. mutabilis* as forage or silage is limited. A lower fodder yield was observed from Mikić et al. [46] in *L. mutabilis* legume–legume intercrops, in comparison to *L. albus* relative intercrops. However, in the same study, among the intercrops and sole cropping, *L. mutabilis* yielded higher fodder when intercropped with pea. Until now, there have been no data about ensiling whole plants of Andean lupin, although there are some studies regarding white lupin and lupin–grass intercrops for silage. A study conducted in Northern Italy showed that whole crop lupin ensiling was successful only if it was inoculated with ensiling inoculants, due to the high moisture content after harvesting [191]. Carruthers et al. [192] found that intercropping white lupin with corn produced less biomass than

soy–corn intercropping silage in Canada, with lupin biomass comprising only 0–6% of the whole intercrop harvest.

A new possibility for using Andean lupin biomass is to produce bioenergy from the whole plant. In Germany, the Julius Kühn-Institut and the University of Rostock tested the dry-matter yields of different Andean lupin accessions in comparison with white and blue lupins. Andean lupins had higher dry-matter yield than white or blue lupins, but not as high as silage maize [193]. In 2019, a new project was started by the Julius Kühn-Institut with a combined growing of Andean lupins and maize or white lupins and oats in the same field in order to optimize the cultivation and the adaptability for making silage.

6.2. Opportunities and Challenges for Breeding

The outcrossing rates obtained for *L. mutabilis* allow a high level of heterozygosity. The high degree of heterozygosity probably has repercussions on yield and resilience, mediated by heterosis. The variation in outcrossing rate among different cultivars, locations and years suggests that genetic and environmental conditions should be considered when selecting breeding approaches for this species. The importance of assessing cultivar-specific responses to insect pollination has been highlighted [194]. So far, breeders do not generally select for changing or even measuring traits related to pollinators [195,196].

It is therefore useful to reflect on the two basic philosophies that could be held by breeders to deal with the partial allogamy of *L. mutabilis*: (1) the development of uniform varieties/pure line cultivars through classical line-breeding methods, making crosses and selecting the most promising genotypes or (2) the development of hybrid cultivars and synthetic/open pollinated populations that demonstrate improved yield, mediated by heterosis. Synthetic varieties, produced by inter-crossing several parental lines on the basis of their general combining ability, make partial use of yield, yield stability and resistance to biotic and abiotic stresses mediated by heterosis. Based on the *L. mutabilis* partial allogamy, the development of synthetic varieties could be an objective in order to improve the sustainability of the crop by means of genetically heterogeneous cultivars. To develop synthetic varieties, breeders have to choose a method to maintain a high level of cross-pollination in the area where they have to work.

Lupinus mutabilis is a partially allogamous species, with estimates of allogamy as high as 58.8% [26], which allows the exploitation of heterosis, and F1 hybrids or synthetic populations could be used. High-yielding heterotic groups are one of the crucial determinants for the successful development of hybrid technology. Clements et al. [197], citing Hardy and Huyghe [53], reported a 46% heterosis yield increase for *L. mutabilis*.

Efforts to exploit heterosis in partially allogamous crops also require a cost-effective system for hybrid seed production as a result of an efficient pollen transfer mechanism. Stable male-sterile and female-fertile systems could be useful for increasing crossing efficiency. Male sterility is described in *L. mutabilis* by Clements et al. [197]. They identified and selected both naturally occurring and male-sterile induced plants. A naturally occurring male sterility was established to be cytoplasmic with the identification of restorer and maintainer genotypes. Once an appropriated male-sterility system is obtained, it is necessary to transfer the pollen from the male parent to the female parent. Similarly to other legumes, in *L. mutabilis*, manual cross-pollination to produce large quantities of hybrid seed for yield trials is difficult and time-consuming, and very poor rates of hybrid seed set are obtained [197]. With increasing interest in the potential of *L. mutabilis* to become a higher-value lupin grain, additional efforts to improve crossing and hybrid breeding technologies for this species are being carried out. Studies that are examining crossing methods to improve seed set without the use of sterility are underway.

Insect-aided technology and the efficient use of local pollinators as an agent of crossing for hybrid seed production has been recommended [198]. Pollinators forage non-randomly among plants by using floral cues to recognize the available options. Effective cross-pollination largely depends on the types of pollinators visiting flowers and the manipulation of their pollinator behavior by the plant's

reproductive characteristics [199]. The characteristics of flowers may lead to a substantial difference in outcrossing. The concept of this approach is to develop a crop with floral traits that influences pollinator behavior and pollination efficiency, which in turn is linked to plant mating patterns and thus to potentially increasing or decreasing the outcrossing rate. Therefore, both pollinator behavior and pollinator interactions with floral traits should be considered in the context of developing a hybrid seed technology.

To increase the level of outcrossing and simultaneously improve crops' environmental functions (bee-pollinator conservation) in order to support better integration into a healthy agroecosystem, the crop design system (CDS) approach has been proposed. Detailed information on the CDS approach was published by Suso et al. [200]. In the CDS approach, breeders develop cultivars with enhanced heterozygosity as a result of appropriate functional floral traits (discovery, attraction and reward) within the crop for supporting the bee pollinator populations to be used as agents of crossings.

Flowers are the interface at which plants and pollinators interact, and their functional traits will influence how likely a pollinator is to visit the flower. Kazimierska and Kazimierski [175] review the biology of flowering in several *Lupinus* species. Lupin provides a rich foraging habitat for several beneficial insects, with mass flowering and substantial amounts of nutritious pollen. In addition to pollen, which provides nutritive rewards to bees, functional morphology modifies both attraction and handling efficiency [201]. Pollen transfer efficiency is mediated by the mechanical fit of pollinators to flower morphology. *Lupinus mutabilis* has a typical papilionated flower. The petals are modified into a standard, wings and keel, with the reproductive structures being enclosed by the keel. Due to the elaborate architecture of Papilionoideae flowers, the application and reception of pollen is achieved only through very specialized mechanisms [201]. The flower possesses three basic functional structures. The standard is for visual discovery and attraction. Besides its visual role as an advertisement, the standard has at least one other important role: the formation of a pollen guide. *Lupinus mutabilis* has a yellow spot that may help to highlight the design of the flower during the approach, making foraging more efficient. The wings facilitate the landing of the pollinator as well as the required active handling of the keel. The keel also has an essential function: it provides the structure that helps to release the hidden pollen and deposit it onto the visiting bee. Simple morphological mismatches appearing in the flowers could therefore be problematic (Figure 2). The manipulation of mechanisms that control various crop floral traits for the benefit of pollinators could represent a promising future direction for *L. mutabilis* crop improvement and hybrid breeding technology. This approach has been first proposed by Suso et al. [202] and Suso and Río [176], specifically for faba bean, and it has been advocated in several other crops by other researchers [192,203–209].

(**a**)	(**b**)
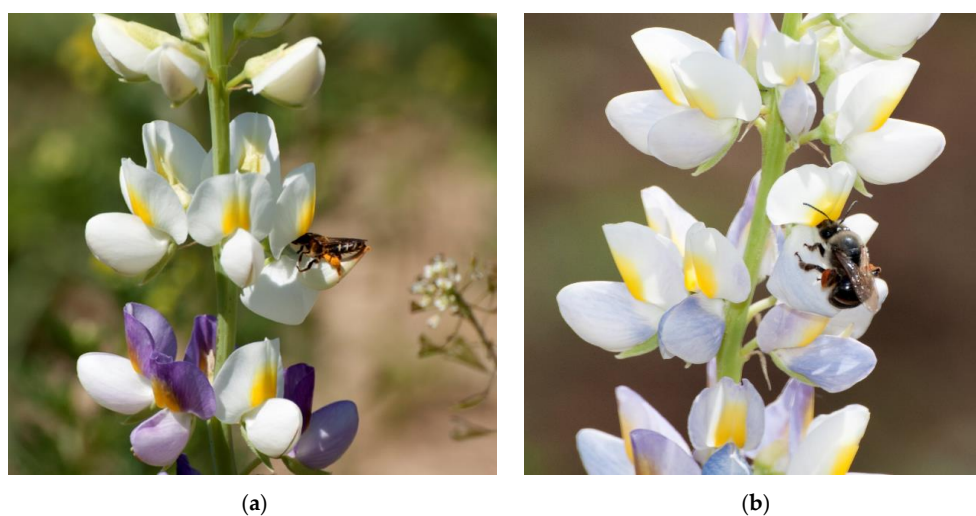
Figure 2. (**a**) Morphological match of a bee and a *L. mutabilis* flower; (**b**) Pollinator visit on a *L. mutabilis* flower, frontal view.

7. Crop Modeling for Yield Production Enhancement

Indirect introduction of a crop or a variety aiming to build up new industries, e.g., lupin oil, might be time consuming as the crop is not well adapted to the new environment. Andean lupin in its domestication area grows under the rainy season, from October to May, with annual average temperatures ranging from 11 to 18 °C [10]. In Europe, especially in southern countries, different edaphoclimatic conditions and cultivation practices are applied. Choosing appropriate genotypes, which are adapted to each region, is therefore essential [22]. In this context, plant traits like growth habit (indeterminate or determinate) and time interval between growth developmental stages were found to play a key role in the ability of *L. mutabilis* plants to grow and be productive [22]. A high genetic variability was also observed within the species [56] available for selection and breeding purposes.

After years of experimentation, determinate growth types were found to be more appropriate for Northern European countries, which are characterized by a shorter growth cycle and therefore are able to be productive under the short spring/summer period of cultivation, while indeterminate growth types were found to be more productive in Southern Europe [22,56,64]. In Southern European conditions, an early sowing from October to November [22,64] is also recommended, in parallel to appropriate genotype selection, since life cycle reduction and yield losses are observed due to the impact of high temperatures during the late crop season [64].

The number of days from sowing to flowering of an accession was recorded as varying among experimental years, and this was therefore not considered to be the most accurate method for predicting Andean lupin growth stages and production [64]. Regarding *L. mutabilis*, low temperatures during the vegetative phase do not seem to play an important role in the time of flowering [59], with the exception of late-maturing genotypes, where vernalization can decrease their flowering time by three weeks [65]. Furthermore, Andean lupin has been reported to be either neutral to photoperiod or affected and complete its biological cycle earlier during short days [27]. The number of days from sowing to the initiation of the different developmental stages of *L. mutabilis* has also been shown to vary among accessions, while day length and temperature effects were possibly responsible for this variation [64], as in other lupin species [210,211]. Determination of thermal and/or photoperiod requirements of selected *L. mutabilis* accessions would probably be a more helpful method in selecting Andean lupin accessions, as in other legume crops [212–214] and lupin species [61,70,215,216] under Mediterranean climate conditions.

8. Conclusions and Perspectives

Andean lupin is one of the "lost crops of the Incas" [217]. Worldwide, there has been an increased interest in this crop. This review demonstrates the possibilities of Andean lupin in the "Old World". Andean lupin has many benefits for the farmer, the environment and processing industries, as well the consumer. Andean lupin is high in protein and oil, has beneficial effects on its environment and can serve as raw material for the development of added value products in the biobased economy. Since its first systematic research in Europe, Andean lupin is now becoming a promising new crop. Decades of breeding and agronomical research have eventually resulted in a few accessions which are (partly) adapted to European agro-ecological conditions. The EU funded project LIBBIO has created a few accessions and agronomical practices which provide perspectives for arable farming in Europe. As for every crop, Andean lupin needs to be improved and continuously adapted to the changing conditions imposed upon us by the consequences of climate change.

More research is necessary to further understand and improve the crop and its agronomical practices. Especially, the crop's advantages relative to other crops, with respect to drought tolerance, pest and disease resistance and the effects of soil conditions like alkaline and calcareous soil on *L. mutabilis* growth and production, have not yet been studied extensively. Anthracnose is an important fungal disease and threat for lupin species worldwide. Breeding for anthracnose resistance and developing agronomical practices, e.g., seed disinfection, for reducing the probability of anthracnose infections is of the utmost importance. Anthracnose resistance appears to be available in gene

bank collections and seems to be correlated with the anthocyanin pigmentation of *L. mutabilis* seeds. Cropping management practices for optimal weed control and the study of pollinators are other themes which need additional research. Future studies on *L. mutabilis* should aim to fill these knowledge gaps. Andean lupin, with its versatile applications, provided by valuable ingredients and its untapped genetic variability, is a promising crop and treasure that can fit into sustainable and resilient cropping systems and contribute to the biobased economy in Europe and the rest of the world.

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