



Review

# Harnessing Legume Productivity in Tropical Farming Systems by Addressing Challenges Posed by Legume Diseases

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### **Abstract**

Legumes are among the most important crops globally, serving as a major food source for protein and oil. In tropical regions, the cultivation of legumes has expanded significantly due to the increasing demand for food, plant-based products, and sustainable agriculture practices. However, tropical environments pose unique challenges, including high temperatures, erratic rainfall, soil infertility, and a high incidence of pests and diseases. Indeed, legumes are vulnerable to infections caused by bacteria, fungi, oomycetes, viruses, and nematodes. This review highlights the importance of legumes in tropical farming and discusses major diseases affecting productivity and their impact on the economy, environment, and lives of smallholder legume farmers. We emphasize the use of legume genetic resources and breeding, and biotechnology innovations to foster resistance and address the challenges posed by pathogens in legumes. However, an integrated approach that includes other cultivation techniques (e.g., crop rotation, rational fertilization, deep plowing) remains important for the prevention and control of diseases in legume crops. Finally, we highlight the contributions of plant genetic resources to smallholder resilience and food security.

**Keywords:** *Arachis hypogaea*; food security; *Glycine max*; *Phaseolus vulgaris*; plant genetic resources; *Vigna* species



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### 1. Introduction

Legume crops play a vital role in global food security and serve as important sources of livelihood for farmers. Major grain legumes grown across tropical Africa, Asia, and Latin America include common bean (*Phaseolus vulgaris*) [1,2], cowpea (*Vigna unguiculata* (L.) Walp) [3,4], chickpea (*Cicer arietinum* L.) [5], pigeonpea (*Cajanus cajan* (L.) Millsp.) [6],

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mung bean (*V. radiata* (L.) R. Wilczek) [7,8], groundnut (peanut) (*Arachis hypogaea*) [9,10], and soybean (*Glycine max*) [11–13]. These crops are traditional protein sources and cash crops in many smallholder farming systems. Alongside the major legumes, several underutilized legume species are cultivated on a smaller scale but hold significant potential. Examples include Bambara groundnut (*V. subterranea*) [14], winged bean (*Psophocarpus tetragonolobus*) [15], horse gram (*Macrotyloma uniflorum*) [16], and African yam bean (*Sphenostylis stenocarpa*) [17]. These minor legumes often possess unique stress tolerances and nutritional profiles, yet they have historically received less attention in research and improvement programs [18].

In tropical regions, the cultivation of legumes has expanded significantly due to the increasing demand for food, plant-based products, and sustainable agriculture practices. Legumes are valued for their high nutritional content and economic importance, making them essential components of diversified and sustainable cropping systems [19]. However, tropical environments pose unique challenges, including high temperatures, erratic rainfall, soil infertility, and a high incidence of pests and diseases. Soil nutrient limitations, particularly nitrogen deficiencies (N<sub>2</sub>) and phosphorus (P), are widespread in agricultural systems globally and represent a major constraint to crop production. These deficiencies severely compromise soil fertility and the productivity of agroecosystems [20,21]. Although applying mineral fertilizers can address these shortfalls, their use is frequently associated with adverse ecological impacts. Notably, excessive or inappropriate fertilizer usage can disrupt the natural balance of soil biota, diminishing the abundance and functionality of beneficial organisms, including free-living nematodes that contribute to decomposition, nutrient cycling, and regulation of pests and pathogens [22,23]. High humidity, elevated temperatures, and prolonged rainy or dry seasons characterize tropical climates. These conditions increase the incidence of pests, diseases, and abiotic stresses such as drought and soil acidity.

This paper addresses these key questions: What are legumes' ecological and economic roles in tropical farming systems? Which major diseases affect legumes in these environments? How do plant physiological processes and soil nutrition contribute to disease development? What are the economic, environmental, and social impacts of legume diseases? Finally, what research directions and programs are needed to manage these challenges effectively? Examining these questions and proposing targeted research initiatives will enhance legume productivity in tropical agriculture.

# 2. What Is the Ecological and Economic Importance of Legumes?

Among legumes' most critical ecological roles is their unique ability to fix atmospheric nitrogen, a process that fundamentally supports sustainable agriculture. Through a symbiotic association with nitrogen-fixing bacteria, predominantly *Rhizobium* spp., which live in their root nodules, legumes convert inert atmospheric nitrogen (N<sub>2</sub>) into ammonia (NH<sub>3</sub>), a form readily available to plants [24]. This biological nitrogen fixation (BNF) reduces the need for synthetic nitrogen fertilizers, mitigating their associated costs and environmental consequences. It also enhances soil fertility and productivity in subsequent cropping cycles [25,26]. Using legumes in crop rotation systems contributes significantly to soil health by increasing soil organic matter, humus content, and microbial biomass. Moreover, their extensive and deep-rooting systems improve soil structure and porosity, thereby enhancing water infiltration and retention [27–29]. This not only stabilizes soil aggregates but also mitigates the loss of topsoil due to wind and water erosion [30], thus preventing soil erosion. Over time, legume cultivation can rejuvenate degraded soils, improving their physical, chemical, and biological properties [31] and supporting long-term agricultural productivity.

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Incorporating legumes into cropping systems helps to reduce atmospheric carbon dioxide (CO<sub>2</sub>) levels. Legumes capture CO<sub>2</sub> from the atmosphere through photosynthesis and store it in plant biomass and soil through their root systems, enabling long-term carbon sequestration [32]. Legumes mitigate carbon emissions linked to synthetic nitrogen fertilizer production through BNF, which enhances soil organic carbon storage [27]. While legumes can store 30% more soil organic carbon compared to other species, the extent of carbon sequestration depends on legume species, morphological characteristics, total biomass production, soil aggregation dynamics within the cropping system, and the nature of agronomic interactions throughout the crop growth period [33].

Leguminous plants support biodiversity by providing nectar, pollen, and seed-based food resources for pollinators, birds, and small mammals [34]. Their incorporation into intensive agricultural systems can reverse the decline in biodiversity by creating microhabitats and reducing reliance on chemical inputs [35]. Insects attracted to legume flowers promote pollination, while birds and mammals feed on protein-rich seeds. Policies such as the EU's Common Agricultural Policy have recognized the ecological benefits of legumes, facilitating their integration into environmentally friendly farming systems [36,37].

From a nutritional perspective, legumes are a cornerstone of plant-based diets and a major source of vegetable proteins, essential amino acids, and their combination of carbohydrates, dietary fiber, and minerals (particularly iron and zinc) [38]. Their high protein content makes them vital components of vegetarian and vegan diets, especially for populations with limited access to animal protein. Their protein content, ranging from 16% to 50% depending on the species, is higher than that of eggs, cereals, and meat [39–41]. They provide essential amino acids, particularly lysine, which is often lacking in cereal grains, making them ideal dietary complements. Their versatility in food formulations allows for use in meat substitutes, dairy alternatives, and functional food products due to their emulsifying, gel-forming, and foaming properties [41,42]. However, as individual legume protein profiles vary, blending them with cereals is recommended for optimal nutritional balance.

Legumes are a powerful source of dietary fiber, with content ranging from 9% to 24%, including soluble and insoluble forms. Fiber enhances gastrointestinal health, supports satiety, modulates blood sugar, and reduces the risks of cardiovascular disease and type 2 diabetes [43–45]. Regular consumption of legumes contributes to long-term health maintenance due to their low-fat content and absence of cholesterol, making them a healthy option for various food applications. Moreover, legumes are rich in B-complex vitamins, particularly folate (0.4–2.1 mg/100 g), thiamine (0.3–1.6 mg), and riboflavin (0.12–0.33 mg), which support fetal development, energy metabolism, and neurological function [19,46]. Sprouted legumes exhibit even higher vitamin content, especially vitamin C, making them particularly valuable for micronutrient enhancement. Legumes also contain significant levels of essential minerals: iron (6.23 mg), calcium (113 mg), zinc (3.5 mg), magnesium (177 mg), phosphorus (367 mg), potassium (1.244 mg), selenium (7.9 mg), and copper (0.76 mg) per 100 g [47]. These nutrients play key roles in cellular metabolism, immune function, and antioxidative defense. However, the bioavailability of these minerals can be decreased by the presence of antinutritional factors (ANF) such as trypsin, phytates, tannins, lectins, amylase inhibitors, or flavonoids [48]. These compounds bind with the minerals or interfere with nutrient absorption, thus limiting the intake, digestion, and utilization of nutrients. It is essential to emphasize that processing techniques such as soaking, fermentation, and sprouting can reduce ANF and improve nutrient absorption. Legumes also offer bioactive compounds, including oligosaccharides, polyphenols, carotenoids, and saponins, known for their antioxidant and anti-inflammatory properties. These phytochemNitrogen 2025, 6, 65 4 of 43

icals help protect against oxidative stress, support immune regulation, and are linked to a reduced incidence of chronic conditions like cancer and heart disease [49,50].

Economically, legumes play a crucial role in global food security and poverty alleviation, particularly in resource-limited areas. They provide accessible and cost-effective sources of protein and nutrients, earning them the title of "poor man's meat." Considering a growing global population and increasing food insecurity, legumes represent a sustainable and affordable food source, especially in low-income regions [51,52]. Their high nutrient density and low cost make them a dietary staple in developing countries, where access to animal-based foods is limited. Additionally, their compatibility with local agroecologies and diets enhances their acceptance and use in national food programs. In agricultural systems, legumes offer income opportunities for smallholder farmers, lower input costs through crop rotation benefits, and function as important commodities in international trade. Their industrial applications range from food processing and pharmaceuticals to biofuels and animal feed, increasing their economic relevance. Legume production provides significant income opportunities, especially for smallholder farmers in the Global South. Their cultivation requires relatively low inputs, and many species are drought-resistant and adaptable to marginal soils. High-value legumes such as soybeans, lentils, and chickpeas are also critical cash crops in global trade markets, generating export revenue for countries like Canada, India, and the United States [53,54]. Legumes present an economically viable farming option in areas with limited capital or irrigation infrastructure.

Another economic importance of legumes is their contribution to crop diversification strategies, which reduce risks associated with monoculture farming. Their inclusion in crop rotations enhances soil fertility, disrupts pest and disease cycles, and decreases the need for chemical fertilizers. These benefits result in lower input costs and improved crop yields, contributing to farm resilience and profitability. Legumes are increasingly utilized in industrial sectors, particularly soybeans, which serve as key raw materials for vegetable oils, biofuels, cosmetics, and pharmaceuticals [40,55]. As the demand for plant-based products and green technologies increases, legumes are integral to food and non-food supply chains. Their multipurpose nature boosts their market value and encourages further investment in legume-related industries. Legumes play a crucial role in sustainable agricultural practices by reducing the reliance on synthetic fertilizers, enhancing soil fertility, promoting crop diversity, and ultimately lowering greenhouse gas emissions (GHGs) [56,57]. These traits make legumes valuable to climate-resilient farming systems adapted to changing climatic conditions. Furthermore, promoting legumes as a dietary staple helps decrease the environmental impact of animal-based protein production, thereby contributing to more sustainable food systems [58,59].

Legumes are critical in ecological balance, nutritional provision, and economic sustenance. However, the tropical environment where these legumes are grown is predisposed to high temperatures, erratic rainfall, and a high incidence of biotic stress, particularly plant diseases. The frequent rains and humid conditions exacerbate the adverse effects of plant pathogens on legume yield and quality. An important aspect of effective disease management is understanding legume diseases' biology, pathology, and epidemiology.

# 3. What Are the Key Diseases Affecting Legumes in Tropical Farming Systems?

Legumes are vulnerable to various diseases caused by bacteria, fungi, oomycetes (Table 1), viruses (Table 2), and nematodes (Table 3). These pathogens reduce crop yields and negatively affect seed quality, resulting in significant economic losses [60,61]. Understanding the primary diseases caused by these organisms is essential for developing effective and sustainable disease management strategies.

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**Table 1.** List of major diseases of legumes, their causal agents, estimated yield losses, and countries affected.

Crop	Disease	Causal Agent	<b>Major Countries Affected</b>	Reported Yield Loss (%)
	Common Bacterial Blight	Xanthomonas spp.	USA, Brazil, Kenya	Up to 45%
Common Bean	Anthracnose	Colletotrichum lindemuthianum	India, USA, Brazil	20–60%
	Halo Blight	Pseudomonas syringae pv. phaseolicola	Ethiopia, East Africa	Up to 45%
	Bacterial Blight	Pseudomonas syringae pv. glycinea	USA, Argentina, China	4–40%
Soybean	Phytophthora Root Rot	Phytophthora spp.	USA, Brazil, China	Up to 50%
	Downy mildew	Peronospora spp.	USA, Central Europe, Asia, Africa	5–10%
	Ascochyta Blight	Ascochyta rabiei	India, Australia, Turkey	Up to 100%
Chickpea	Fusarium Wilt	Fusarium oxysporum f. sp. ciceris	India, Pakistan, Spain	10–90%
Field Pea	Ascochyta Blight	Ascochyta pisi, A. pinodes, A. pinodella	Canada, Australia, UK	20–50%
	Downy Mildew	Peronospora viciae	USA, UK, India	10–40%
	Bacterial Blight	Pseudomonas syringae pv. pisi	Ethiopia, Australia, UK, Canada, US	Up to 22%
	Root Rot	Aphanomyces euteiches	Ethiopia, US, Canada, France	22-80%
Cowpea	Cercospora Leaf Spot	Mycosphaerella cruenta	Nigeria, India, China	Up to 40%
	Root Rot Complex	Rhizoctonia solani, Fusarium spp., Pythium spp.	Canada, India, Nepal	10–30%
	Ascochyta blight	Ascochyta lentis	China, Italy	23–62%
Lantil	Stemphylium blight	Stemphylium botryosum	Bangladesh, Canada, Ethiopia, Morocco, Syria	Up to 100%
Lentil	Fusarium wilt	Fusarium oxysporum f.sp. lentis	India, West Asia, North Africa, East Africa, Syria, Pakistan, Czechoslovakia	40–90%
	Anthracnose	Colletotrichum truncatum	Bangladesh, Canada, Ethiopia, Morocco, Syria	23–62%
	Rust	Uromyces fabae	Bangladesh, Canada, Ethiopia, Morocco, Syria	Up to 100%
	Ascochyta blight	Ascochyta fabae	Australia	30–70%
	Chocolate spot	Botrytis fabae	China, Ethiopia, Australia	Up to 100%
Faba bean	Rust	Uromyces viciae-fabae	Bangladesh, Canada, Ethiopia, Morocco, Syria	27–80%
	Black root rot	Fusarium solani	Bangladesh, Canada, Ethiopia, Morocco, Syria	Up to 100%

**Table 2.** Major disease-causing viruses infecting primary legume hosts in the tropics.

Genus	Virus	Major Tropical Legume Hosts	Symptoms	Transmitted Through	References
Alfamovirus	Alfalfa mosaic virus	Soybean	Leaf mottling; light and dark green, yellow patches; leaf curling; deformation; stunting	Aphids (plant lice); seeds or pollen to the seed	[62]
	Bean golden mosaic virus	Common bean, Lima bean	Yellow-green mosaic patterns on leaves; distorted and stunted plant growth	Whiteflies (Bemisia tabaci)	[63]
	Bean golden yellow mosaic virus	Common bean	Yellow-green mosaic patterns on leaves; distorted and stunted plant growth	Whiteflies (Bemisia tabaci)	[64]
	Dolichos yellow mosaic virus	Lablab bean	Mosaic yellow pattern; patches of yellow alternating with green; stunting; leaf curling; reduced pod size	Whiteflies ( <i>Bemisia tabaci</i> ); seed transmission	[65]
	Horsegram yellow mosaic virus	Common bean, Mung bean, Pigeon pea	Bright yellow mosaic patterns on the leaves; reduced leaf size; rugosity; stunting of the entire plant	Whiteflies (Bemisia tabaci)	[66]
Begomovirus	Macroptilium yellow spot virus	Common bean, Lima bean	Yellowing or spotting on the leaves; bright yellow mosaic patterns on the leaves; a combination of bright yellow and green patches; stunted growth	Whiteflies (Bemisia tabaci)	[67]
	Mungbean yellow mosaic virus	Mung bean, Soybean, Common bean, Cowpea, Black gram, Pigeon pea	Yellow mosaic patterns, leaf curling, stunting	Whiteflies (Bemisia tabaci)	[68]
	Mungbean yellow mosaic India virus	Mung bean, Soybean, Common bean, Cowpea, Black gram, Lima bean, Pigeon pea, Lablab bean	Bright yellow mosaic patterns on the leaves; stunted growth; reduced leaf size; shriveled and misshapen seeds	Whiteflies (Bemisia tabaci)	[69]
	Tomato leaf curl virus	Soybean, Common bean	Stunting; reduced leaf size; upward curling of leaves; interveinal chlorosis	Whiteflies (Bemisia tabaci)	[70]
	Tomato yellow leaf curl virus	Common bean, Cowpea	Yellowing and curling of leaves; stunted growth; reduced fruit production; bushy appearance	Whiteflies (Bemisia tabaci)	[71]

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Table 2. Cont.

Genus	Virus	Major Tropical Legume Hosts	Symptoms	Transmitted Through	References
Carlavirus	Cowpea mild mottle virus	Cowpea, Soybean, Common bean, Mung bean, Lima bean, Lablab bean	Severe leaf chlorosis, mottling, and distortion; stunting	Whiteflies ( <i>Bemisia tabaci</i> ); mechanical transmission; seed transmission	[72]
Comovirus	Bean pod mottle virus	Soybean	Green to yellow mottling (blotchiness) of young leaves; distortion; stunting; reduced pod size	Bean leaf beetle (Cerotoma trifurcata)	[73]
	Cowpea severe mosaic virus	Cowpea	Mosaic patterns, leaf deformation, stunting	Bean leaf beetle (Cerotoma arcuata)	[74]
Cucumovirus	Cucumber mosaic virus	Soybean, Peanut, Common bean, Cowpea, Mung bean, Lima bean	Mosaic patterns; leaf distortion; stunting; mottling; chlorosis; necrosis	Aphids (a non-persistent, stylet-borne mechanism); seed transmission	[75]
	Peanut stunt virus	Peanut, Soybean	Mosaic patterns; vein clearing; leaf rolling; chlorosis; stunting	Aphids	[76]
Cytorhabdovirus	Soybean blotchy mosaic virus	Soybean	Stunting; reduced leaf size; mild mottling; malformed pods; shortening of petioles; leaf crinkling; chlorotic spots	Aphids ( <i>Aphis craccivora</i> , A. spiraecola, Myzus persicae)	[77]
Emaravirus	Pigeon pea sterility mosaic virus 1	Pigeon pea	Stunting; bushy growth; reduced leaf size; mosaic patterns on the leaves; excessive vegetative growth; ring spots	Eriophyid mite (Aceria cajani)	[78]
	Pigeon pea sterility mosaic virus 2	Pigeon pea	Mosaic patterns on the leaves; stunting; sterility; interveinal chlorosis	Eriophyid mite (Aceria cajani)	[78]
Gammacarmovirus	Soybean yellow mottle mosaic virus	Soybean, Mung bean, Black gram	Leaf mottling; mosaic of light and dark green areas; stunting; reduced pod numbers	Seed transmission	[79]
Ilarvirus	Tobacco streak virus	Soybean, Peanut, Mung bean, Black gram	Bud blight; necrotic streaks and rings; leaf distortion; stunting; wilting	Thrips; seed transmission	[80]
Luteovirus	Soybean dwarf virus	Soybean	Puckered leaves; interveinal chlorosis; leaf rugosity; stunting	Aphids (Acyrthosiphon solani)	[81]

 Table 2. Cont.

Genus	Virus	Major Tropical Legume Hosts	Symptoms	Transmitted Through	References
Nanovirus	Faba bean necrotic stunt virus	Common bean	Leaf yellowing; stunting; reddening of leaves; thickening of leaves; suppression of flowering; pod setting	Aphids (Acyrthosiphon pisum, Aphis craccivora, A. fabae)	[82]
	Milk vetch dwarf virus	Cowpea, Mung bean, Lablab bean	Yellowing; stunting; leaf rolling; crinkling; mosaic; dwarfism	Aphids (Aphis cracciviora)	[83]
	Capsicum chlorosis virus	Peanut	Chlorosis; mottling; ringspots; leaf deformation	Thrips (Ceratothripoides claratris, Frankliniella schultzei, Microcephalothrips abdominalis, Thrips palmi)	[84]
Orthotospovirus	Groundnut bud necrosis virus	Peanut, Cowpea, Mung bean, Black gram, Lablab bean	Chlorosis; mottling; lesions; stunted growth; necrotic rings; bud necrosis	Thrips (Thrips palmi)	[85]
Ormorospoemus	Groundnut ringspot virus	Peanut, Soybean	Bronzing; mosaic; mosaic with ringspots; yellowing; stem necrosis	Thrips (Frankliniella occidentalis, F. schultzei, F. intonsa, F. gemina)	[86]
	Soybean vein necrosis virus	Soybean	Yellowing near leaf veins, eventually turning to reddish-brown lesions	Seed transmission	[87]
	Tomato spotted wilt virus	Peanut	Bronzing; curling; necrotic streaks and spots on the leaves; stunting	Thrips (Frankliniella occidentalis); seed transmission	[88]
	Bean common mosaic necrosis virus	Common bean, Lablab bean	Mosaic patterns; necrosis (black root); leaf rolling; blistering; light and dark-green patches; chlorotic vein banding; mottling and malformation of leaves	Aphids (Acyrthosiphon pisum, Aphis fabae, Myzus persicae); seed transmission	[89]
Potyvirus	Bean common mosaic virus	Common bean, Soybean, Peanut, Cowpea, Mung bean, Black gram, Lablab bean, Bambara groundnut	Mosaic patterns; green vein banding; leaf curling and distortion; stunted growth	Aphids; seeds; pollen	[89]
	Bean yellow mosaic virus	Common bean	Mottling; mosaic appearance; leaf distortion; downward cupping; stunting; rough pods	Aphids: mechanical transmission	[90]

Table 2. Cont.

Genus	Virus	Major Tropical Legume Hosts	Symptoms	Transmitted Through	References
	Cowpea aphid-borne mosaic virus	Cowpea, Lima bean, Bambara groundnut	Mosaic; mottling; interveinal chlorosis; vein-banding; vein-clearing; vein-yellowing; blistering	Aphids (Aphis craccivora, A. gossypii, A. spiraecola, A. fabae, A. sesbaniae, Macrosiphum euphorbiae, Myzus persicae, Rhopalosiphum maidis, Acyrthosiphon pisum); seed (true seeds) transmission; mechanical transmission	[91]
Potyvirus	Peanut mottle virus	Peanut, Soybean	Dark-green mosaic or mottle; crinkled leaflet margins; leaf chlorosis and deformation	Aphids (Aphis craccivora, Aphis gossypii, Hyperomyzus lactucae, Myzus persicae, Rhopalosiphum maidis, Rhopalosiphum padi); peanut seed	[92]
	Soybean mosaic virus	Soybean	Vein clearing in the upper trifoliate leaves; downward curling of the leaf margins; raised puffes and puckering; necrosis of the petioles and stems; bud necrosis	Non-specific transmission by aphids; seed transmission	[93]
Sobemovirus	Southern bean mosaic virus	Common bean	Mosaic patterns; leaf distortion	Beetles ( <i>Cerotoma trifurcata</i> ); seed transmission	[94]
	Soybean yellow common mosaic virus	Soybean Leaf mottling	Leaf mottling, stunting, leaf distortion	Aphids	[95]
Umbravirus	Groundnut rosette virus	Peanut	Chlorotic or green rosette patterns; severe stunting; bushy appearance	Transmitted by <i>Aphis craccivora</i> in the presence of groundnut rosette assistor virus	[96]
Unassigned	Groundnut rosette assistor virus	Peanut	Mild mottle symptoms; severe rosette disease symptoms	Transmitted by <i>Aphis craccivora</i> in a persistent manner	[97]

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Crop	PPN	Pathogen(s)	Reference
Bean	Meloidogyne incognita	Fusarium oxysporum f.sp. phaseoli	[98]
	M. incognita	F. oxysporum	
	M. javanica Pratylenchus thornei	$\vdash \alpha r u c n \alpha r u m + c n \alpha r u c $	
Lentil	M issueries	F. oxysporum f.sp. lentils	[101]
Peanut	M. javanica	Rhizoctonia solani	[102]
Pea	M. incognita Rotylenchulus reniformis	F. oxysporum f.sp. pisi	[103,104]

**Table 3.** Nematode–pathogen disease complexes reported in legumes.

#### 3.1. Bacterial Diseases

Heterodera glycines

Soybean

Several bacterial pathogens present significant threats to bean production (Table 1). One of the most notable pathogens, *Xanthomonas campestris* pv. *vignicola*, causes bacterial blight disease in beans (*P. vulgaris*) [61,107]. This disease is characterized by small, water-soaked leaf lesions that later turn necrotic, resulting in leaf drop, reduced photosynthesis, and seed discoloration [107]. In severe instances, entire fields can suffer from premature defoliation and yield losses of up to 40%. Another significant bacterial pathogen is *Pseudomonas syringae* pv. *phaseolicola*, which causes halo blight. This pathogen leads to water-soaked spots surrounded by a yellow halo, primarily on leaves but occasionally extending to stems and pods. Infected seeds can act as primary inoculum, increasing the spread across growing seasons [108]. Though primarily a threat to solanaceous crops, *Ralstonia solanacearum* has increasingly been reported in beans, particularly in tropical climates. It causes bacterial wilt and root rot disease, two vascular diseases leading to rapid plant collapse. The pathogen enters through the roots and clogs the xylem vessels, ultimately leading to wilting and death [61,109].

F. solani

Phytophthora sojae

[105]

[106]

# 3.2. Fungal Diseases

Fungal pathogens are perhaps the most diverse and widespread group affecting legumes (Table 1). One of legumes' most severe fungal diseases is Fusarium wilt, caused by various species of *Fusarium*, such as *F. oxysporum* f. sp. *phaseoli* in beans. This disease leads to yellowing, wilting, and plant death, particularly under warm and moist conditions [110]. This soilborne fungus can persist in the soil for years, making crop rotation and resistant varieties essential [60]. Additionally, root rot diseases caused by *Rhizoctonia solani* significantly impact soybeans (*G. max*) and peas (*P. sativum*), often resulting in plant mortality [60]. Typical symptoms include stunted growth, dark lesions on stems near the soil line, and root necrosis. This pathogen thrives in poorly drained soils and is particularly destructive in cool, wet conditions [60].

Aspergillus flavus, while not a disease-causing agent, produces aflatoxins in legumes (A. hypogaea) that pose a significant health risk, as these toxins can contaminate food supplies and are harmful to both humans and livestock [60,111]. Other notable fungal pathogens include Ascochyta spp., Botrytis cinerea, Stemphylium botryosum, and Septoria spp., which impact chickpea, lentil, cowpea, and faba bean, contributing to foliar blight and leaf spot epidemics [60]. Pande et al. (2009) [60] reported that more than 50% of crop losses can be linked to Botrytis gray mold and Ascochyta blight in affected regions. Additionally, Colletotrichum lindemuthianum causes anthracnose disease, resulting in dark, sunken lesions

on stems, pods, and leaves. Anthracnose is seedborne and can spread rapidly in favorable conditions, particularly in dense canopies and humid environments [61].

### 3.3. *Oomycete Diseases*

Though traditionally grouped with fungi, oomycetes are now considered members of a distinct kingdom (Stramenopila). They are commonly referred to as water molds and devastating bean pathogens. One of the most well-known oomycetes is *Phytophthora infestans*, which can infect beans under favorable conditions, although it is more prominent in potatoes and tomatoes. *Pythium* species commonly cause seedling damping-off and root rot in beans, especially under wet soil conditions [60]. *Phytophthora sojae* causes root rot in soybeans, thriving in waterlogged soils and leading to root decay, wilting, and plant death under poor drainage conditions [60,112]. *Aphanomyces euteiches* is destructive in peas and other legumes such as alfalfa and clover, surviving for years in soil and lacking adequate chemical controls [113]. Additionally, *P. cactorum* causes crown and root rot in humid regions, severely limiting plant development [60]. Integrated disease management strategies that combine host resistance, agronomic practices, fungicides, and biological control agents have been emphasized as crucial in managing such diseases [60].

Downy mildew, caused by various species of *Peronospora*, further poses a significant threat to legume crops such as peas and soybeans (Table 1), particularly in cool and humid environments. The disease manifests through symptoms like leaf chlorosis, distortion, and stunted plant growth, leading to severe yield losses. In Canada, *Peronospora viciae* f. sp. *pisi* has caused yield reductions of up to 75% in field peas [114]. Similarly, in Brazil, *P. manshurica* infections in soybeans have led to yield losses ranging from 30% to 40%. In contrast, losses of up to 14% in the United States have been reported under favorable conditions [115].

#### 3.4. Viral Diseases

Legumes are highly affected by various diseases caused by viruses from more than ten genera, including Alfamovirus, Begomovirus, Carlavirus, Comovirus, Cucumovirus, Cytorhabdovirus, Emaravirus, Gammacarmovirus, Ilarvirus, Luteovirus, Nanovirus, Orthotospovirus, Potyvirus, Sobemovirus, and Umbravirus, among others (Table 2). These viruses can infect various legume hosts and cause substantial yield losses. Among these viruses, the genera Begomovirus, Potyvirus, and Orthotospovirus appear to comprise the most member species that cause legume viral diseases (Table 2).

Among the major viruses affecting legumes is the bean common mosaic virus (synonym: peanut stripe virus), the causal Potyvirus agent of bean common mosaic disease in common bean characterized by leaf yellowing, vein banding, curling, distortion, mosaic patterns, and stunting symptoms. This virus affects a wide range of legume hosts, including common bean, soybean, peanut, cowpea, mung bean, black gram, lablab bean, and Bambara groundnut [116–118] (Table 2). This virus is globally distributed and transmitted through aphids, seeds, and pollen (Table 2). In common beans, the disease is also caused by bean common mosaic necrosis virus [89,118], which similarly affects lablab beans [119] (Table 2). Another significant virus species prevalent in tropical regions is the whiteflytransmitted mungbean yellow mosaic virus, the causal agent of yellow mosaic disease in mung bean [120], characterized by yellow mosaic patterns and curling of leaves and stunting symptoms (Table 1). This *Begomovirus* infects soybeans, common beans, cowpeas, black gram, and pigeon peas [120] (Table 2). A related species, namely, mungbean yellow mosaic India virus, causes similar yellow mosaic disease in these legume crops and has also been reported to infect lima bean [121] and lablab bean [122] (Table 2). Both viruses are widely distributed in Asia, especially in countries in the Indian subcontinent and Southeast

Asia. In addition to these viruses, the horse gram yellow mosaic virus, present in India and Sri Lanka, has also been implicated in causing yellow mosaic symptoms in mung bean, common bean, and pigeon pea [66,123] (Table 2).

Another virus with worldwide distribution is the cowpea mild mottle virus, which causes severe chlorosis, mottling, and distortion of leaves and stunting symptoms in cowpea (Table 2). It is a significant virus affecting several major legumes, including cowpea, soybean, common bean, mung bean, lima bean, and lablab bean [124–126] (Table 2). Aside from whiteflies, the virus also spreads via mechanical and seed transmission (Table 2). On the other hand, the cowpea aphid-borne mosaic virus infecting cowpea [127], which induces mosaic, mottling, interveinal chlorosis, and blistering of leaves and disorders of leaf veins, is also a significant pathogen in lima bean and Bambara groundnut [125,127]. The virus is transmitted by various species of aphid vectors and through mechanical transmission and infected seeds (Table 2). It is mainly distributed in African countries and some parts of Asia, South America, and Australia. The thrip-transmitted groundnut bud necrosis virus is also a primary virus of peanut [128], which also infects tropical legume crops such as cowpea, mung bean, black gram, and lablab bean [129,130] (Table 2), causing symptoms of chlorosis, mottling, lesions, bud necrosis, and stunted plant growth. The virus is predominantly found in South Asia, especially India, but also in some parts of Southeast Asia. Another primary legume virus is the seed-borne soybean yellow mottle mosaic virus, which induces bright yellow mosaic on young soybean leaves, along with reduced growth of older leaves, mottling, and plant stunting [131] (Table 2). A distinct strain of this virus also infects mung bean and black gram, causing mild mottling and chlorotic blotching symptoms [132]. The virus is present in North America and some parts of Asia.

The aphid-transmitted cucumber mosaic virus, known for its extensive host range and worldwide distribution, is also a significant virus of legumes infecting soybean, peanut, common bean, cowpea, mung bean, and lima bean [130,133] (Table 2), where it causes mosaic, distortion, stunting, mottling, chlorosis, and necrotic symptoms in the leaves. Another primary virus, with several legume hosts and wide global distribution, is the tobacco streak virus, which affects soybean, peanut, mung bean, and black gram [134] (Table 2), leading to plant stunting and necrosis of growing leaves. The virus is transmitted via thrip vectors and infected seeds (Table 2). Originally known as major causes of leaf curl disease in solanaceous crops like tomato, the globally widespread tomato yellow leaf curl virus and tomato leaf curl virus (and their related species) transmitted by whiteflies are also capable of infecting legumes such as common bean, cowpea, and soybean [135,136] (Table 2) where they induce chlorosis, yellowing, thickening, and curling of the leaves (Table 2). Additionally, the milk vetch dwarf virus has been reported to infect cowpea, mung bean, and Lablab bean [83,137] (Table 2), causing symptoms of stunting, leaf rolling, yellowing, and curling. Thus far, this virus has been detected only in several Asian countries.

In addition to these major viruses affecting multiple legumes, various viruses significantly impact soybeans. Among them, the soybean mosaic virus is considered one of the most devastating pathogens of soybeans [138] and is prevalent in soybean-growing areas worldwide. It induces symptoms in the leaves such as vein clearing, curling, puffiness, puckering, necrosis, mottling, and distortions, and the virus is transmitted by aphid vectors but can also be spread through planting infected seeds (Table 2). Additional significant viruses include soybean blotchy mosaic virus, soybean dwarf virus, soybean vein necrosis virus, soybean yellow common mosaic virus, Alfalfa mosaic virus, and bean pod mottle virus [130] (Table 2). Meanwhile, groundnut rosette disease is a primary peanut disease in Africa, which induces chlorotic or green rosette symptoms and a bushy appearance in plants (Table 2). It is caused by a complex involving two viruses, namely, groundnut rosette assistor virus (with an unassigned genus) and groundnut rosette virus (Table 2), in

association with a satellite RNA known as groundnut rosette virus satellite RNA [139], all of which are transmitted by an aphid vector (Table 2). Peanut is also severely affected by spotted wilt disease, caused by the tomato spotted wilt virus [140], a pathogen first identified in tomato and now distributed worldwide. Additional significant peanut-infecting viruses include peanut mottle virus [141], groundnut ringspot virus [86], and peanut stunt virus [128], all of which are also capable of infecting soybean [141–143]. Another emerging virus in peanut is the capsicum chlorosis virus [105], which occurs across tropical and temperate regions. In common bean, major viruses also include bean golden mosaic virus, bean yellow mosaic virus, faba bean necrotic stunt virus, and southern bean mosaic virus [82,144,145] (Table 2). The bean golden mosaic virus also infects lima bean [146]. Both common bean and lima bean are also affected by Macroptilium yellow spot virus [147], a virus present in Brazil, which induces yellow mosaic, leaf curl, and stunting symptoms.

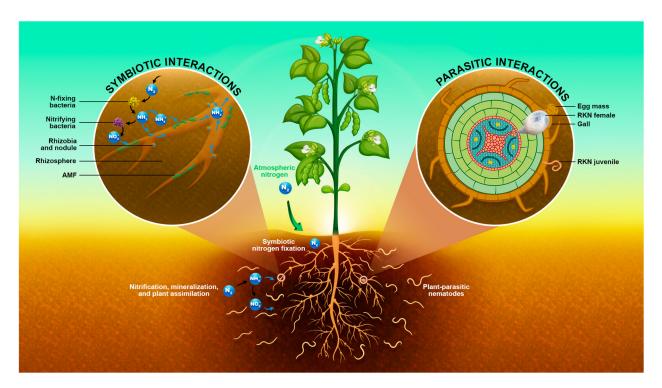
The beetle-transmitted cowpea severe mosaic virus, a member of the *Comovirus* genus, is also a major pathogen in cowpea [74] that causes mosaic, leaf deformation, and stunting symptoms (Table 2). In pigeon pea, the sterility mosaic disease is among the most damaging diseases, occurring in countries of the Indian subcontinent and parts of Southeast Asia. It is often called the "green plague," as the infected plants remain green with excessive vegetative growth but fail to flower or produce seed pods. In partially affected plants, seeds are discolored and shriveled [148]. This disease is caused by two viruses, namely, pigeon pea sterility mosaic virus 1 and pigeon pea sterility mosaic virus 2, both classified under the genus *Emaravirus* [78] and transmitted by an eriophyid mite (Table 2). In lablab bean, yellow mosaic disease is caused by Dolichos yellow mosaic virus [149], which leads to characteristic yellow mosaic patterns and curling of the leaves and can significantly reduce yield when infection occurs early in the growing season. The virus is primarily distributed in India and Bangladesh and transmitted by whiteflies or infected seeds (Table 2).

### 3.5. Nematode Diseases and Nematode-Rhizosphere Interaction

Plant-parasitic nematodes (PPN) are recognized as major yet often overlooked contributors to crop decline worldwide [150]. PPN represents a diverse group of mostly obligate parasites that feed on plant roots, leading to direct and indirect damage that severely compromises plant health and yield. While numerous PPN can cause structural and physiological alterations in the root system that can lead to stunted plant growth and reduced yield, the polyphagous nature and widespread distribution of root-knot nematodes (RKN, *Meloidogyne* spp.) make them particularly notorious to most staple crops across the globe, including most leguminous crops [151]. Furthermore, PPN can act synergistically with other soil-dwelling organisms by facilitating infections from soil-borne pathogens, either by serving as vectors, causing root wounds, or altering plant biochemistry, physiology, or the rhizosphere microbiome (=rhizomicrobiome) (Figure 1) [152,153].

Legumes can engage in two beneficial interactions within the rhizosphere. One involves a complex symbiotic molecular dialog with rhizobia, forming two specialized root structures: nodules and root galls [154–156]. The other involves mutualistic associations with arbuscular mycorrhizal fungi (AMF). Both interactions enhance nutrient uptake, thereby supporting plant development, growth, and overall health while also improving the plant's tolerance to biotic and abiotic stresses [157–160]. Although their interactions are complex and context-dependent, rhizobia and AMF may compete for resources when coexisting within a host [161]. Nevertheless, mycorrhizal colonization has been shown to enhance rhizobium efficiency in nodule formation and  $N_2$ -fixation, resulting in increased biomass and seed yield in mungbean [161].

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**Figure 1.** Conceptual illustration depicting symbiotic and parasitic interactions within the legume rhizosphere, highlighting beneficial associations with microbial symbionts such as rhizobia and arbuscular mycorrhizal fungi (AMF), alongside antagonistic relationships involving plant parasites like root-knot nematodes (RKN). Black arrows represent soil processes mediated by free-living bacteria. Blue arrows indicate readily available forms of nitrogen for plant uptake (NH<sub>3</sub> = ammonia; NH<sub>4</sub><sup>+</sup> = ammonium; NO<sub>3</sub><sup>-</sup> = nitrate).

The interactions of PPN with symbiotic microbes in legumes introduce further complexity. For instance, despite increasing the population density of the root-lesion nematode  $Pratylenchus\ thornei$ , mycorrhizal colonization conferred improved tolerance to the nematode [161]. Similar findings have been observed with  $P.\ penetrans$ , where early rhizobial nodulation is affected in a density-dependent manner, underscoring the importance of timely symbiotic establishment for optimizing  $N_2$ -fixation benefits [162].

RKN also induce root galling as they establish feeding sites that impair the plant's nutrient and water uptake capacity [163]. RKN infestations can significantly reduce nodulation and  $N_2$ -fixation efficiency, thus hampering the legume-rhizobia mutualism and contributing to broader declines in crop vigor and productivity [164,165]. Similarly, the soybean cyst nematode *Heterodera glycines* has also been shown to adversely affect rhizobial performance [166–168], although suppression of this nematode has been achieved using rhizobial strains co-inoculated with other bacterial biocontrol agents [169] or by applying rhizobial culture filtrates [170]. Interestingly, PPN has acquired several parasitism-related genes through horizontal gene transfer from bacterial taxa closely related to rhizobia [171,172], enabling RKN to adopt a similar invasion strategy to that of rhizobia [173]. This convergence has led to a substantial overlap in the genetic pathways mediating legume interactions with both mutualists and parasites, resulting in a genetic conflict within the host plant [174–176].

Beyond their direct impacts on plant growth and yield, PPN can establish interactions with pathogens within the rhizosphere, oftentimes leading to disease complexes [153,177]. PPN use a protrusible stylet to pierce plant cell walls and feed, allowing them to move intraor intercellularly within plant tissues depending on their life cycle. The wounding inflicted by nematode feeding provides entry points for opportunistic pathogens, further weakening the plant host. Likewise, secondary infections may arise from pathogens adhering to the

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cuticle of migratory endoparasitic nematodes [152]. The most notoriously reported PPNs in legume disease complexes are *Meloidogyne* spp., *H. glycines*, *P. thornei*, and *Rotylenchulus reniformis* (Table 3).

Physical and physiological alterations to the root architecture induced by PPN, combined with the manipulation or suppression of plant defense mechanisms through nematode effectors [178,179], create favorable conditions for opportunistic microbial colonization. These disruptions not only compromise the structural and functional integrity of the plant but also facilitate the establishment and proliferation of secondary pathogens. These pathogens often act synergistically or additively with nematodes, compounding plant stress and accelerating crop vigor and productivity decline. This biotic pressure usually results in non-specific symptoms that are difficult to attribute to a single causal agent. Consequently, management becomes more challenging, as targeting one pathogen may yield minimal benefits if the pathogen consortium is not simultaneously addressed [153].

3.6. How Do Rhizobia, the Plant's Physiology, and Soil Nutrition Influence Disease Development in Legumes?

Legumes form symbiotic associations with soil bacteria known as rhizobia, which are considered plant growth-promoting bacteria (PGPB). Aside from their role as nitrogen fixers, rhizobia are also involved in phosphate solubilization and phytohormone production and promote plant defense by influencing metabolite production [180]. These bacteria are housed within root nodules, which form following the initial colonization of the root hairs and develop into mature nodules. Anatomical studies of *Psoralea pinnata* (L.) root nodules revealed distinct structural layers, including lenticels, periderm, outer cortex, middle cortex, inner cortex, and a central medulla region infected by bacteroids [181]. Within the nodules, bacteroids facilitate biological nitrogen fixation by converting atmospheric N<sub>2</sub> into ammonia, which is further assimilated into ureides—specifically allantoin and allantoic acid [182]. Transporting these ureides is critical for nitrogen partitioning, as repression of ureide transporters GmUPS1-1 and GmUPS1-2 in legumes significantly reduced nitrogen allocation to roots and shoots [183]. Similar regulatory effects were observed in rice (Oryza sativa), a non-nitrogen-fixing species, where silencing of the OSUPS1 transporter impaired allantoin transport. At the same time, its overexpression led to allantoin accumulation in shoots and other sink tissues [184]. Legumes substantially enhance soil nitrogen content through nitrogen fixation and assimilation, with numerous studies reporting beneficial outcomes when legumes are employed as intercrops [185]. However, the efficiency of nitrogen enrichment is influenced by factors such as crop rotation strategies, legume genotype, and the specificity and effectiveness of the associated rhizobia strains [186]. Despite these benefits, increasing soil nitrogen levels, whether through biological fixation or fertilization, may have unintended consequences, as excessive nitrogen availability can predispose plants to greater disease susceptibility. This recognition has led to extensive studies on improving nitrogen use efficiency (NUE) in legumes and other economically important crops. NUE aims to maximize yield per unit of nitrogen supplied, reduce environmental impacts associated with excessive chemical fertilizer use, lower production costs for farmers, and, more importantly, minimize disease risks linked to overfertilization [187–190].

Plants exposed to excessive amounts of nitrogen develop dark green foliage [191], reduced grain yield [192], altered water use efficiency [193], and disrupted cellular processes [194]. Collectively, these changes ultimately affect the morpho-physiological condition of plants, leading to increased vulnerability to disease [195]. In legumes such as soybean, however, the effects of nitrogen extend beyond the plant itself and influence their bacterial symbionts. Nodulation in roots is suppressed when the nitrogen supply exceeds 50 mg/L and is promoted when the nitrogen concentration is lower than 50 mg/L [196].

Similarly, nodulation in *V. faba, P. vulgaris*, and *V. sinensis* is significantly reduced after combined ammonium nitrate is applied [197]. Comparable results were observed in soybeans when supplied with 5 mM nitrate [198]. Additionally, in faba bean, ample nitrogen supplies reduced nodulation and altered the profile of flavonoids produced by root exudates [199]. Flavonoids are particularly important in legumes, as they act as initial signaling molecules indicating the presence of appropriate rhizobia and AMF partners necessary for symbiosis, and they also function as defense compounds against pathogens and insects [200–202]. For example, inoculation of rhizobia and AMF reduced the severity and incidence of soybean red crown rot [203]. While rhizobia establish symbiotic associations with legumes primarily to facilitate nitrogen acquisition, they also contribute to disease suppression in various crops by promoting overall plant growth and vigor [204,205]. However, mismanagement of nitrogen, particularly through oversupply, can disrupt these beneficial interactions and increase disease susceptibility in legumes. This shows that the effects of nitrogen oversupply are more pronounced on rhizobia, which exacerbates the negative impacts on plants.

Since nitrogen levels influence the association between rhizobia and plants, excessive nitrogen can reduce plants' capacity to defend against pathogens. Rhizobial activity has been demonstrated to protect against several biotic agents [206-208]. They are well known for reducing disease incidence by antagonizing soilborne pathogens such as Fusarium, Rhizoctonia, Sclerotium, and Macrophomina through the production of antibiotics, siderophores, and mycolytic enzymes [204]. They also induce systemic resistance by activating plant defense-related genes and key enzymes in the phenylpropanoid and isoflavonoid pathways. For example, Bradyrhizobium sp. inhibited the growth of fungal pathogens Macrophomina phaseolina, R. solani, F. solani, and F. oxysporum, and also suppressed RKN in soybean roots [209,210] and in vitro against F. solani, M. phasolina, and R. solani [211] as well as in chickpeas [212-214]. In addition, Tamiru and Muleta [179] reported that rhizobial inoculation in faba bean suppressed the radial growth of F. solani in vitro, with disease reduction averaging 45.1% for combined isolates compared to 29.2% for individual strains; the highest suppression (73.3%) was observed when a combination of isolates was applied before pathogen exposure. Legumes colonized by rhizobia exhibited elevated jasmonic acid (JA) induction and supported greater soybean podworm growth, although actual feeding damage was minimal [215,216]. Rhizobial symbiosis in lima bean enhanced plant growth and resistance to herbivores, likely through nitrogen allocation to cyanogenic defense compounds [217]. The biocontrol potential of rhizobia stems from their ability to produce antimicrobial compounds, notably antibiotics and hydrogen cyanide (HCN) [218]. These findings underscore that nitrogen oversupply disrupts nodulation and symbiosis and compromises systemic plant defense by interfering with metabolite signaling and microbial interactions, particularly those involving rhizobia.

The multifaceted role of rhizobia in legumes extends far beyond nitrogen fixation, encompassing critical functions in plant growth promotion, metabolite regulation, and disease suppression. However, the effectiveness of these symbiotic benefits is highly sensitive to nitrogen availability, with excessive nitrogen impairing nodulation and rhizobial activity, weakening plant defenses, and increasing disease susceptibility. To fully harness the agronomic and protective benefits of legume–rhizobia associations, careful regulation of nitrogen availability is essential, especially in the context of sustainable tropical farming systems.

# 4. What Are the Economic, Environmental, and Social Consequences of Legume Diseases?

# 4.1. Economic Consequences

Legume diseases pose severe economic challenges to tropical farming systems, primarily through direct yield losses, reduced crop quality, and escalating production costs. In tropical Asia, Africa, and Latin America, legume diseases often wipe out large portions of the crops. Fungal pathogens like soybean rust can decimate infected fields, with documented yield losses ranging from 10% to complete crop failure [219]. Similarly, Fusarium wilt in mungbean has been shown to reduce yields by as much as 96% in trials [220]. Collar and root rot caused by *Sclerotium rolfsii* results in significant quality and yield losses have also been recorded in lentils [221] and have caused as much as 80% loss in peanut production [222]. Chocolate spot disease, caused predominantly by *Botrytis fabae*, results in severe annual yield losses of 60–80% in Ethiopian faba beans under favorable conditions, impacting all growth stages and posing significant economic threats [223].

Viral diseases are equally devastating. For example, *Mungbean yellow mosaic virus* incidences in South and Southeast Asia can cause 100% yield loss under congenial conditions [224,225]. While common mosaic viruses in cowpea or groundnut often cause losses well above 50% [225]. In fact, over 160 viruses from 16 families infect food legumes globally, including bean common mosaic virus, bean yellow mosaic virus, chickpea stunt viruses, cucumber mosaic virus, tomato spotted wilt virus, etc., each with a significant economic impact [225,226]. Even minor bacterial infections like the common bacterial blight of beans can be costly, causing 30–70% yield reduction in susceptible cultivars worldwide [227,228] and up to 50% loss in Africa [229]. Furthermore, these biotic pressures often interact, as in multiple infections on one crop, which undeniably leads to yield declines in many smallholder and commercial bean, cowpea, peanut, and other legume farms across the tropics.

Aside from decreasing yield or outright loss, diseases often degrade grain quality and marketability. Infected seeds and pods tend to be discolored, shriveled, or malformed, resulting in lower prices. For example, the soybean mosaic virus cuts yield and causes mottling and other defects in soybean seeds, significantly lowering seed quality [230]. Cucumber mosaic virus (CMV) likewise induces chlorosis and reduced seed weight in chickpea, with studies showing ~45% yield loss and poorer seed appearance at high CMV incidence [231]. Fungal foliar diseases similarly reduce quality. Ascochyta blight in chickpea and lentils can lead to total crop failure and sharply reduced grain size and quality under conducive conditions [232]. Bangladesh, Ethiopia, India, and Pakistan have suffered significant yield losses due to the macrocyclic rust fungus *Uromyces viciae-fabae*, a pathogen that severely affects peas, faba beans, and lentils [233,234]. This disease is considered one of the most economically devastating under humid and warm conditions [235], and it imposes a heavy financial burden on farmers. Although specific monetary estimates of crop damage remain unreported, the ability of the pathogen to spread rapidly via rust spores from infected leaves to healthy plant parts and neighboring fields triggers a cascade of damage. Severe infections lead to premature plant death while surviving plants often fail to develop seeds or produce only wrinkled, low-quality grains [233,235]. In lentils and chickpeas infected with B. cinerea, seed quality is degraded by altering color and shape, and the infected seeds used for sowing exacerbate farm production costs because of seedling rot [236]. Infected seeds may also carry toxins, such as Aspergillus-induced aflatoxins in groundnut and cashew nuts, rendering them unsafe and unsalable [237]. These diseasedamaged legumes generally fall into lower market grades and have a shorter shelf life, diminishing farm income and food nutrition from the harvest.

Unfortunately, managing these diseases drives up the expenses of farm operations. Smallholder farmers frequently must purchase expensive certified seeds, fungicides, insecticides, or seed treatments to limit outbreaks. For instance, controlling soybean rust in Asia and Africa typically requires multiple fungicide applications per cropping season, an added cost that can erase profit margins [219]. In bean crops, farmers often spray costly chemicals against bacterial blight or anthracnose and invest in seed disinfection or rotation, which are measures that can be expensive and inaccessible for resource-poor farmers [238,239]. These extra inputs and labor to apply them inflate per-unit production costs. Moreover, repeated planting failures due to disease mean fertilizer, land, and labor investments are wasted. Furthermore, although a specific familiar figure has not been reported, these failed attempts would significantly reduce the return on investment, putting further financial strains on the farmers.

### 4.2. Environmental Impact

Legumes provide critical environmental benefits by improving soil fertility through nitrogen fixation, lowering reliance on synthetic fertilizers, enhancing agricultural productivity, and enabling sustainable disease control via intercropping as shield crops or crop rotation, all while remaining a cost-effective solution [240]. However, outbreaks of diseases in tropical legumes can erode these environmental values and, consequently, compel heavy agrochemical use. Chemical treatments, particularly fungicides, are currently the predominant and most effective approach for managing pathogens infecting legume crops [241,242].

Legume crops in the humid tropics often require pesticide use to control fungal, bacterial, and vectors of viruses, leading to documented environmental damage. Farmers in Southeast Asia, Africa, and Latin America frequently resort to repeated fungicide and insecticide sprays on beans, cowpeas, and soybeans to avoid disease losses. For example, West African cowpea studies note that reliance on synthetic pesticides negatively affects public health, animal welfare, and environmental sustainability [4]. Such overuse drives pesticide runoff and spray drift into soils and waterways, causing broad ecological harm. In modeled studies of Brazilian soy fields, spray drift of common fungicides (e.g., chlorothalonil, trifluralin, and chlorpyrifos) generated very high-risk indices for aquatic organisms. At the same time, bees and other non-targets were similarly imperiled [243]. Likewise, pesticide residues are routinely found in tropical surface waters [244] and even remote sediments, with researchers warning of contamination that threatens pollinators, fish, and soil animals [245].

Importantly, chronic fungicide applications select resistant pathogens. In Brazil and elsewhere, the emergence of fungicide-resistant strains forces more frequent spraying, creating positive chemical loading feedback and diminishing effectiveness [246,247]. Equally troubling, fungicides can undermine the beneficial microbes of legumes. Laboratory and field studies show that seed and foliar fungicides damage legume nodulation and symbiotic nitrogen fixation. For example, tebuconazole sprays cut nodule number and shoot/root biomass by 30–67% in crops like pea, mungbean, and lentil [248].

Additionally, chemical control methods for legume diseases have become increasingly problematic regarding consumer health, particularly due to toxic residues contaminating food systems. Notably, legumes are known to have some of the highest levels of pesticide residues among various types of produce [249]. This is concerning, especially with systemic pesticides, which are absorbed through the roots and transported throughout the plant rather than through direct contact with the pathogens [242]. These environmental challenges now present serious obstacles to the continued reliance on chemical treatments. As intensive pesticide use causes widespread ecological damage, it increasingly undermines

the long-term sustainability of agricultural systems, particularly in efforts to safeguard both environmental integrity and public health standards.

### 4.3. Social Implications: Livelihoods of Smallholder Farmers, Food Security Concerns

The social implications of legume diseases in tropical farming systems are profound, particularly for smallholder farmers who rely on these crops for nutrition and income. Over 500 million people in the tropics depend on legumes as a primary protein source, particularly in drought-prone areas where other crops fail [250–252]. As such, when staple legume crops fail, smallholders lose food and income, which worsens local hunger and poverty.

In principle, integrated disease management tools for legumes exist, such as resistant varieties, effective fungicides, and biocontrol agents [223]. However, resource-poor smallholder farmers in the tropics encounter significant barriers to adopting these solutions. These farmers often lack access to these tools due to financial and institutional challenges [253]. These challenges include delays in obtaining sufficient seeds from official distribution systems, high seed costs, and inadequate access to information about the characteristics and advantages of new varieties [219]. Organic or low-input systems are also particularly vulnerable since they offer limited options for chemical control, leaving farmers with virtually no defense when epidemics strike [254]. This situation forces them to adopt ineffective cultural practices, such as delayed sowing, which often fail under increasingly erratic rainfall patterns [223]. A perception survey of vegetable and legume farmers in India, Thailand, and Vietnam revealed that only a minority knew about viral disease symptoms, leading them to rely heavily on synthetic pesticides for disease control [255,256]. Consequently, training in recognizing disease symptoms, awareness of new varieties, and alternative disease management strategies is crucial for these farmers.

The burden of deprivation and debt experienced by legume growers due to recurring disease outbreaks and crop failures is disproportionately shouldered by women and youth [254,257]. In countries like Burundi and Kenya, gender roles within the bean value chain are clearly defined: men typically control land and agricultural inputs, while women are primarily responsible for labor-intensive tasks such as land preparation, weeding, harvesting, and post-harvest processing. Women also have limited decision-making power despite their central role in production, hindering their ability to benefit from their labor fully and restricting their adoption of improved technologies [258,259]. Young farmers face similar challenges. A study in Ghana and Cameroon revealed that without land titles, savings, or technical knowledge, youth could not invest in better seeds or equipment, nor even engage in bean production [260]. Addressing these issues necessitates supportive policies. For example, strengthening legume seed systems, rural credit and extension services, and gender-sensitive training can help farmers of all genders and ages access resistant varieties and learn disease management strategies [261]. Ultimately, scaling up legume sustainability through accessible and equitable integrated disease management systems relies on enabling policy frameworks and technical support.

# 5. Tackling the Challenges Associated with Legume Diseases: The Way Forward

Plant diseases present significant challenges to leguminous crop production globally. Effective management of these diseases relies on integrated approaches. Using certified disease-free seeds, crop rotation, and sanitation practices are essential to manage plant diseases. Ongoing research into disease-resistant varieties and alternative control measures will be crucial in fending off plant pests and pathogens and ensuring the sustainability of legume agriculture. For example, breeding for resistance has shown promising results,

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particularly against halo blight and bacterial blight. Fungal diseases are often managed through fungicidal seed treatments, crop rotation, and resistant cultivars. Biological control agents such as *Trichoderma* spp. have also shown efficacy against soilborne fungi like *Rhizoctonia* and *Fusarium* [60]. For oomycete pathogens, drainage improvement, seed treatment with oomycete-specific fungicides like metalaxyl, and avoidance of planting in infected fields are common strategies. Despite these efforts, the persistence of many pathogens in soil underscores the importance of host plant resistance as a cornerstone of sustainable disease control [61].

Most of the farmers rely on the application of commercially available synthetic pesticides and sometimes the combination of different pesticides to mitigate pests and diseases. However, the misuse of crop protection products results in pesticide resistance [262]. Integrating disease management strategies is crucial in mitigating pre- and post-harvest diseases [263] and reducing pesticide application [264]. Most plant diseases can be effectively managed by integrating disease management strategies [262,265]. Even the mycotoxin-producing plant pathogens that are carcinogenic and their byproducts in human food and livestock feeds can potentially be mitigated by integrated management strategies [262,266]. There are combinations of practices to manage important diseases in tropical legumes. These include the use of biological control agents combined with chemicals and physical control [263], biological + chemical [266–268], cultural practices, cultural + chemical + genetic [264,265,269], cultural + biological + chemicals [262,270], genetic + chemical [271–273], genetic + cultural [274]; and genetic + biological [275].

The A. flavus infection in peanuts demonstrated the lowest infection rate (2 and 2.9%), highest pod yield (2245.6 and 2233.5 kg/ha), reduced pathogen populations (3.56 and  $3 \times 10^3$  CFU/g) in normal and drought-imposed fields, respectively, after application of T. viride and Bacillus subtilis during pre-harvest, and the drying of harvest produce (with moisture content below 9%), application of extracts of Andrographis paniculata before storage in jute bag for post-harvest [263]. In addition, the application of Monarda citriodora essential oil with phytochemicals (Cuminaldehyde, Thymol, Linalool, and Terpinen-4-ol) and atoxigenic A. flavus can also be an eco-friendly alternative for storage conditions [231]. The study by Sheeba & Raja [262] revealed that seed and soil treated with B. subtilis and T. asperellum combined with need-based application of Azadirachtin 1% had only 10.5% tikka leaf spot disease incidence in peanuts compared to farmers' practices of about 24.7%. The use of resistant cultivars as components of integrated disease management systems under strip tillage can also reduce at most six fungicide applications even under severe leaf spot disease pressure [262]. Nevertheless, susceptible cultivars reduced leaf spot pressure and TSWV incidence when applied with fungicide and insecticide for vectors, respectively [272,273].

The combined application of *T. harzianum*, Provax 200 WP fungicide (75 ppm), and 3% mustard oil improved soybean performance. It was most effective in minimizing seedling mortality, disease incidence, and disease diversity in charcoal rot diseases, Fusarium root rot, and wilt of soybean [267,270]. Meanwhile, resistant cultivars C-11-2-39 and Tifrunner (for Tomato spotted wilt virus), DP-1 and GA-01R, and line C-28-305 (for early leaf spot), combined with strip tillage and minimal fungicide application, were found effective in controlling these diseases in peanut [265]. The combination of genetic and cultural practices is also a good integrated disease management (IDM) option, such as the use of resistant cultivars Georgia-06G, Florida-07, and Tifguard combined with a lower seeding rate of 9.8 seed/m of the row, which had a comparable disease reduction rate of TSWV with 19.7 seed/m of row planted susceptible variety [274]. These resistant varieties can also be coupled with in-furrow application of phorate insecticide to reduce the population of thrips as TSWV vectors [272]. While the fungicide application at low doses reduces biotic stress

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and disease severity, the use of plant growth-promoting microbes such as *T. harzianum* has the potential to minimize the negative impact on plant physiology and light-harvesting efficiency of stressed plants due to higher doses of chemical treatments for root rot disease on soybean caused by *Macrophomina phaseolina* [267].

There are also attempts to integrate management strategies that were not successful. The aphid population varied across soybean lines, where NE 3001, IA 2021, H2494, and Colfax were significantly lower. However, the time application of insecticide does not eliminate the potential impact of aphid species population emigrating, which reinforces SMV transmission [271]. The effectiveness and consistency of integrated management strategies can also vary from location due to contributing factors such as differences in crop characteristics, sites, environment, and growing seasons [269]. Nevertheless, IDM offers a comparable or higher economic return compared to conventional farmers' practices [265,266,269,272] and maximizes profit by minimizing production costs [264,273–276].

Effective management of plant viruses involves IDM strategies combining various cultural and control practices. These include using resistant cultivars, early sowing to avoid peak vector populations, and cultural and crop management techniques such as intercropping with non-host species and crop rotation. Additional practices include good sanitation, planting barrier crops, and managing vector populations (e.g., aphids, thrips, mites, whiteflies, etc.) through chemical or biological control. Using clean, virus-free certified seeds or planting materials, removing weeds and alternate hosts, and promptly eradicating infected plants are also crucial. Furthermore, avoiding planting near infected fields (especially with susceptible crops) and ensuring early disease detection is essential to minimize virus incidence and spread.

### 5.1. Harnessing Utilization of Legume Genetic Resources for Disease Resistance

The genetic diversity encompassed by major and minor tropical legumes is vast, reflecting centuries of cultivation across varied climates and cultural contexts. Harnessing this diversity through conservation and breeding is key to sustainable agriculture in the tropics. Major legume genebanks conserve vast collections of landraces and wild relatives, which harbor genetic traits to resist many plant pathogens. Domestication and modern breeding narrowed the genetic base of crops, often losing alleles for disease resistance that persisted in ancestral gene pools [277]. Crop wild relatives and traditional landraces thus serve as reservoirs of novel resistance genes for biotic stresses. For example, the wild lentil Lens ervoides provides alleles that confer strong resistance to anthracnose and Stemphylium blight, diseases that devastate cultivated lentils [278]. Similarly, wild peanut (A. stenosperma) accessions possess durable resistance to RKN, a trait absent in most cultivated peanut varieties [279]. The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) genebank alone conserves over 129,000 accessions (≈81% landraces, 2.4% wild species) across crops like chickpea, pigeon pea, and groundnut, explicitly to safeguard such diversity for traits including disease and pest tolerance. These conserved legume genetic resources form the foundation for discovering resistance genes and traits to combat evolving diseases in tropical farming systems.

Over decades, pathologists and breeders have screened thousands of accessions to find "diamond in the rough" resistances [280]. A classic example is a peanut landrace (USDA accession PI 203396) collected from a Brazilian market in 1952, which was long maintained in the genebank with no special traits noted [281]. When Tomato Spotted Wilt Virus (TSWV) emerged as a devastating disease in peanut farms in the 1980s [100], breeders tested exotic lines. They discovered PI 203396 carried gene(s) for TSWV resistance, the only accession that saved the industry. Once introgressed, its resistance alleles are present in most peanut cultivars, yielding an estimated economic benefit of over \$200 million annually.

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This dramatic case underscores how valuable resistances may lie hidden in genebanks until a crisis drives their discovery. More routine screening has likewise paid off. ICRISAT distributed over 300,000 legume samples globally, and at least 15 chickpeas, 10 pigeonpea, and 11 groundnut landraces from its genebank were so agronomically superior that national programs directly released them as new varieties [282]. These varieties often owed their success to innate disease or pest tolerance, and farmers quickly adopted them, leading to increased productivity. In common bean (P. vulgaris), the international core collection (~1440 accessions) was evaluated against destructive foliar pathogens; only ~2% showed broad resistance to all races of angular leaf spot, and <1% resisted multiple virulent anthracnose races [283]. Those few resistant landraces (mostly from pathogen hotspot regions in Latin America) became critical parents in breeding programs. Such efforts illustrate that extensive phenotyping of germplasm can reveal rare disease-resistance traits, which serve as donors for crop improvement. In India, large-scale legume germplasm screening has led to >200 accessions being registered as unique donors for key traits [284], including sources of resistance to Fusarium wilts, rusts, mildews, and viral diseases in chickpea, pigeonpea, and mungbean. These examples demonstrate the immense value of genebank accessions in identifying genes and quantitative trait loci (QTLs) for disease resistance.

The genomic era has dramatically enhanced the exploitation of legume plant genetic resources (PGR) for disease resistance. High-throughput sequencing and molecular marker platforms allow researchers to dissect the genetic architecture of resistance in diverse germplasm collections. For instance, genome-wide association studies (GWAS) and linkage mapping in biparental populations have mapped numerous resistance QTLs by leveraging exotic alleles. In lentil, a recombinant inbred population derived entirely from wild Lens ervoides accessions enabled the mapping of five QTLs for anthracnose and three for Stemphylium blight resistance, validating the contribution of both wild parents' alleles to disease defense [278]. In soybean, comparative transcriptome analyses between cultivated G. max and its wild progenitor G. soja identified defense pathways and secondary metabolites present in wild genotypes that could be introgressed to enhance disease resistance in the crop [279]. Pangenomic analyses are compelling for capturing novel resistance genes absent from reference genomes. A recent chickpea pan-genome constructed from 3171 cultivated and 195 wild Cicer accessions uncovered ~1582 previously unreported genes, some associated with stress responses [285]. These include genes for abiotic tolerances and potentially disease resistance lost during domestication, highlighting how pangenomes help "re-introduce" genetic diversity for resilience [277]. Likewise, assembling a *Phaseolus* super-pangenome (integrating common bean with wild relatives like tepary bean) reveals structural variants in disease-resistance gene clusters that breeding programs can exploit. Researchers have also begun cloning specific resistance (R) genes from unadapted germplasm. For example, the Rag1 and Rag2 genes for aphid resistance in soybean and the *Er1* powdery mildew resistance gene in pea were traced to exotic donor lines. While few cloned R-genes from legumes are commercially used, the knowledge of their sequence and allelic variants in germplasm collections facilitates marker-assisted breeding and even transgenic or gene-editing strategies. Modern "genomics-assisted breeding" now routinely uses genebank diversity: Varshney et al. [285] demonstrated that sequencing thousands of chickpea accessions can guide optimal crosses to assemble superior haplotypes for yield and disease resistance while minimizing deleterious alleles. Furthermore, the ability to "resurrect" plant immunity genes has been reported by Contreras et al. [286].

Because many wild legumes are cross-incompatible or agroecologically distant from crops, pre-breeding programs are vital in mobilizing their resistance genes. Pre-breeding involves developing bridging lines or introgression populations to transfer traits from unadapted germplasm (often wild species or landraces) into a usable form. Global legume

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initiatives have made significant progress here. In peanuts, wild Arachis species (e.g., A. cardenasii, A. stenosperma) have been crossed with cultivated peanuts to introgress resistance to late leaf spot, rust, and RKN, which have produced pre-breeding lines now used as parents in Brazil, Africa, and the USA [244]. Many of ICRISAT's groundnut breeding lines carry wild-derived resistance gene segments. In common bean, researchers at CIAT and Embrapa exploited the secondary gene pool by crossing *P. vulgaris* with its wild relatives *P. coccineus* (runner bean) and *P. acutifolius* (tepary bean). These wide crosses contributed genes for resistance to angular leaf spot, common bacterial blight, and bruchid pests, previously scarce in the common bean gene pool [283]. Notably, 62% of tested accessions from *Phaseolus* secondary gene pool showed high resistance to angular leaf spot, compared to only ~4% of wild *P. vulgaris* and ~2% of cultivated lines. This emphasizes the value of related species for broad-spectrum disease resistance. Through persistent effort, breeders have recovered fertile bean progenies with disease resistance from these interspecific crosses, some of which (e.g., lines with P. acutifolius ancestry) are now in cultivar development. In chickpea and pigeonpea, pre-breeding with wild Cicer and Cajanus species has yielded sources resistant to devastating diseases like sterility mosaic virus and Fusarium wilt that cannot be found in the cultivated gene pool [282]. For example, ICC 4958 (a drought-tolerant landrace) and a wild Cicer reticulatum donor were used to develop high-yielding chickpea lines with combined resistance to Fusarium wilt and Ascochyta blight in India. Such pre-breeding products are funneled into mainstream breeding programs. These cases show that concerted germplasm enhancement bridges the gap between exotic gene sources and elite cultivars, expanding the genetic base for disease resistance. As a result, today's improved legume varieties increasingly carry "hidden" genes from landraces and wild relatives [284].

# 5.2. Innovative Breeding and Biotechnology Advancements in Legumes in the Tropics

Traditional breeding methods alone have shown limited success in immediately addressing these complex challenges. Hence, there is a growing reliance on advanced breeding and biotechnological approaches to develop cultivars that thrive in tropical conditions. Traditional breeding techniques, such as mass selection, pedigree breeding, and back-crossing, remain foundational in legume improvement. However, the efficiency of these techniques has been significantly enhanced by modern innovations such as marker-assisted selection (MAS), mutation breeding, gene pyramiding, QTL seq, omics- and *R* gene-based analysis, genome-wide association studies (GWAS), genomic selection (GS), genomic prediction (GP), and speed breeding. Biotechnological advancements and genetic engineering tools, such as *Agrobacterium*- or biolistic-mediated genetic transformation, genetic modification, RNA sprays, and the CRISPR genome editing system, have also been employed for legume improvement. These breeding innovations and biotechnology advancements have contributed to the emergence of precision breeding. This modern approach integrates biotechnology and data analytics to improve selection accuracy and predict crop performance more effectively.

MAS has enabled legume breeders to select plants carrying genes for desirable traits (e.g., resistance to pests and diseases, tolerance to abiotic stresses such as drought and salinity, increased yield and nutritional quality, etc.), which could speed up the breeding process without relying solely on phenotypic evaluation. Using MAS, the *VrPGIP2* gene—derived from a mung bean landrace and strongly associated with resistance to bruchids, a primary storage pest causing significant post-harvest losses—has been incorporated into a popular mung bean cultivar to enhance bruchid resistance [287]. MAS-based gene pyramiding has also been implemented in legumes to combine multiple resistance genes into a single genotype to enhance and prolong resistance against diseases or pests. Through MAS,

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Kiryowa et al. [288] evaluated the effectiveness of single and pyramided anthracnose resistance genes (Co-42, Co-43, Co-5, and Co-9) in common bean against four Co-letotrichum lindemuthianum races in Uganda. Co-42 and Co-5 conferred broad resistance, with pyramids Co-42 + Co-5 and Co-42 + Co-5 + Co-9 showing the lowest disease severity. Co-9 showed antagonistic effects in combinations, making it less effective for pyramiding. These findings support gene pyramiding, particularly involving Co-42 and Co-5, for durable anthracnose resistance in common bean and, potentially, in other legumes.

In crop breeding, the quantitative trait loci (QTL) analysis remains a foundational approach for identifying genomic regions associated with important agronomic traits. Since QTL mapping alone may not fully reveal candidate genes, integrating modern biotechnological tools is advantageous. QTL sequencing and RNA sequencing performed by Lv et al. [289] identified regions and genes linked to pod length, a yield-related trait in peanut. A 0.77 Mb region on chromosome 07 was associated with pod length, wherein RNA sequencing revealed four differentially expressed genes with *Arahy.PF2L6F* (*AhCDC48*) and *Arahy.P4LK2T* (*AhTAA1*) were proposed as pod-length candidate genes. In another recent study, a novel, stable, and major QTL for oil content (*qOCB09.1*) in peanut was identified on chromosome B09, spanning a 1.99 Mb region with 153 putative genes, including the oleic acid gene *FAD2B*, potentially influencing oil content [255]. These results offer key insights for the map-based cloning of beneficial oil content alleles.

In legumes, GP and GS have emerged as powerful tools to accelerate breeding progress by leveraging genome-wide DNA markers. GP estimates the genetic potential of plants for complex traits (and overall crop performance) by analyzing thousands to millions of markers across the entire genome, enabling accurate predictions without relying on extensive plant phenotyping. GS builds on these predictions to identify and select superior lines, significantly shortening breeding cycles. These approaches are efficient for plant traits controlled by multiple genes, thus revolutionizing legume breeding by enhancing selection efficiency, precision, and genetic gain. For instance, Ravelombola et al. [290,291] conducted a GWAS and GS study on maturity, plant height, seed weight, and soybean yield by genotyping 250 accessions using 10,259 SNPs. They identified more than 20 SNPs from known and novel genetic loci associated with each agronomic trait, including a newly discovered plant height locus on chromosome 20 and a region on chromosome 10 associated with yield and seed weight. These findings achieved high GS accuracy, indicating that these crop traits can be effectively selected in molecular breeding through GS. In cowpea, a GWAS of 161 accessions exhibiting a wide range of seed protein contents (21.8–28.9%) and 110,155 genome-wide SNPs identified seven significant SNPs on chromosome 8 associated with seed protein content linked to the Vigun08g039200 gene from the thioredoxin superfamily [292]. Using multiple models, GP achieved accuracies ranging from 42.9% to 52.1%, highlighting the potential of integrating GWAS and GP to fast-track cowpea breeding for improved protein content and nutritional quality. In a study by Keller et al. [293], the effectiveness of GP models in common bean breeding was demonstrated using 481 elite lines genotyped with 5820 SNPs across field trials under various environmental stresses (such as drought and low Phosphorus conditions). Prediction abilities for major agronomic traits reached 50–80% of the maximum accuracies and improved by up to 20% when genotypeby-environment interactions ( $G \times E$ ) were included in the model. Thus, incorporating  $G \times E$  and more phenotypic data enhances prediction accuracy, enabling better selection of stress-adapted varieties and accelerating genetic gain in common bean breeding. These benefits can also be extended to other legume crops.

One emerging innovation is speed breeding, which speeds up plant growth by optimizing light, temperature, and other environmental and plant conditions. This allows more annual breeding cycles, expediting the development of improved crop varieties. Taku

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et al. [294] performed a modified speed breeding method for vegetable soybean using controlled light, temperature, and  $CO_2$ , along with early pod harvest. This reduced soybean breeding time and enabled up to 4.5 generations per year without sacrificing seed germinability. Thus, speed breeding offers a valuable scheme for faster crop improvement in soybean and legume crops.

Another breeding technique that continues to be widely used in legume improvement is mutation breeding, although it is generally considered a conventional approach. When integrated with modern tools, it complements emerging advancements in biotechnology and breeding innovations by providing effective means to develop varieties with desirable traits and to increase genetic variation, particularly in legume crops, where genetic variations are often limited. In black gram, to generate novel genetic variability and broaden the narrow genetic base, Habde et al. [295] performed electron beam (EB) irradiation on the genotype 'Pant U-31', followed by genome-wide mutation characterization using combined Illumina and Nanopore sequencing technologies. They identified 728,161 variants, predominantly single base substitutions and small InDels. High-impact mutations were detected in 1271 genes, with mutation hotspots observed on chromosomes Vm1 and Vm3. Such findings demonstrate the efficacy of EB irradiation in inducing widespread genome mutations, providing valuable insights and approaches for accelerating and modernizing mutation breeding in black gram and other legume crops. Omics-based analysis offers comprehensive insights into the biological mechanisms underlying important traits and the identification of numerous genes and regulatory elements involved in, e.g., (a)biotic stress responses and crop productivity. Using combined multi-omics (transcriptomics and metabolomics) analysis of soybean against soybean cyst nematode (SCN), differentially expressed genes and metabolites were identified, leading to the identification of GmUGT88A1 as the candidate gene from the novel SCN resistance locus Rscn-16, which was fine-mapped to an 8.4 kb region on chromosome 16 [296]. Overexpression of GmUGT88A1, a UDP-glucosyltransferase encoding gene, enhanced SCN resistance, isoflavone glycoside accumulation, and seed size, while knockdown lines showed the opposite effects. These results provide valuable insights into regulating SCN resistance and highlight potential strategies for soybean and legume breeding.

Resistance (*R*) gene analysis using modern tools is a valuable approach to fast-track the identification and characterization of candidate genes that can be used in plant breeding programs to enhance disease resistance. For example, resistance gene enrichment sequencing (RenSeq) performed by Hodge et al. [297] identified novel nucleotide-binding leucine-rich repeat (NLR) *R* genes associated with *P. sojae* resistance in 20 soybean genotypes and known *Rps* differentials. More variants were found in the NLR-encoding genes within *Rps* loci on chromosomes 3, 7, 13, and 18, along with new alleles and a unique NLR discovered on chromosome 8. These results highlight RenSeq as an efficient tool for uncovering novel *R* genes and developing gene-specific markers for breeding disease-resistant soybean cultivars.

Over the past few decades, genetic transformation has emerged as a pivotal biotechnological tool for improving plant traits and revolutionizing crop production. Advancements in genetic transformation, such as *Agrobacterium*-mediated and biolistic (gene gun) methods, improved tissue culture techniques, and high-throughput phenotyping, have significantly enhanced legume genetic modification efforts. However, transformation and regeneration remain technically challenging in legumes [298], highlighting the need for continued innovation. Among tropical legumes, soybean has achieved the most successful genetic transformations, with several genetic modifications addressing challenges such as pest and disease resistance, abiotic stress resilience, herbicide tolerance, and improved nutritional content [299]. Aside from soybeans and genetically modified (GM) crops, events have

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also been recorded in cowpea and common beans, particularly insect and virus resistance traits [300]. Unlike these crops, genetic transformation in mungbean remains relatively underdeveloped. However, recent advances have focused on establishing efficient transformation systems to support functional genomics and the development of improved mung bean varieties. Tripathi et al. [301] successfully used biolistic transformation in mung bean, achieving a higher efficiency than *Agrobacterium*-mediated methods using a one-step regeneration protocol. In addition, stable transgene inheritance was confirmed, and transgenic lines expressing *AtDREB1a* (a gene derived from *Arabidopsis thaliana*) showed enhanced drought tolerance under polyethylene glycol (PEG)-induced stress. These findings offer a promising approach to improving stress resilience in mungbeans. Genome editing technologies, especially CRISPR/Cas9, have opened a new era of precise editing in legume genomes. These tools enable targeted disruption or insertion of genes or regulatory systems involved in trait improvement, such as abiotic stress tolerance, disease resistance, flowering time, seed composition, etc.

For example, CRISPR/Cas9 has been used in legume crops such as soybean for genome editing to generate multiple mutations in the *GmAITR* genes [302]. These genes belong to the family of abscisic acid (ABA)-induced transcription repressors (*AITRs*), which, when edited in *Arabidopsis*, were found to impose no fitness cost and increase abiotic stress tolerance. Editing these genes enhanced salinity tolerance and improved soybean performance under saline field conditions. In peanuts, the *AhFAD2B* gene (which converts oleic acid to linoleic acid) in the Indian cultivar GG20 was successfully edited using CRISPR/Cas9 to reduce linoleic acid synthesis. This increased the oleic-to-linoleic acid (O/L) ratio from 3.1 to 7.3, indicating improved peanut oil stability and shelf life [303]. Another innovative use of CRISPR explored in soybean involved developing an immune system based on the CRISPR/CasRx system to target soybean mosaic virus (SMV), one of the most devastating viruses in soybean [304]. Incorporating this engineered system into the plant conferred efficient resistance against SMV, which has been successfully passed on to the second generation of offspring. This provides an alternative and promising approach for developing resistant soybean plants, which can also be harnessed for other legume crops.

In an exploratory investigation, an RNA spray that enhances mung bean resistance against one of its major viruses, the mungbean yellow mosaic India virus (MYMIV), through an RNA interference (RNAi) mechanism, has been in development [305]. Designed for topical application, it demonstrates stability against nuclease degradation and can enter leaf cells to form small interfering RNAs (siRNAs) that combat viral infection. Thus, the application of RNA spray for enhancing resistance is considered a promising approach for controlling MYMIV in mung beans.

### 5.3. PGR Contributions to Smallholder Resilience and Food Security

Disease-resistant legume varieties derived from plant genetic resources (PGR) have a tangible impact on food security in tropical smallholder systems (Table 4). Legumes like common bean, cowpea, chickpea, pigeonpea, and groundnut are staple protein sources for millions of low-income families in Asia, Africa, and Latin America [306–308]. However, smallholder yields are often severely constrained by endemic diseases. Resource-poor farmers typically cannot afford costly fungicides or seed treatments, so genetic resistance is the most sustainable defense. Improved legume cultivars bred with genebank-sourced resistance genes have markedly reduced crop losses and stabilized yields under disease pressure. For instance, in Ethiopia, the adoption of new chickpea varieties (developed with multidisease resistance to Fusarium wilt and root rots) rose from 30% to 80% of farmers within a decade, contributing to a doubling of chickpea area and significant welfare gains [309].

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**Table 4.** Leading international and national genebanks holding legume plant genetic resources (PGR), the scale of their collections, and notable disease-resistance contributions.

Genebank (Location)	Legume Accessions Conserved	Notable Disease-Resistance Contributions
ICRISAT Genebank (India)—CGIAR <i>Crops:</i> Chickpea, Pigeonpea, Groundnut, etc.	~20,600 chickpea; ~13,500 pigeonpea; ~15,400 groundnut accessions. (Total ex situ collection > 129,000 accessions across 11 crops)	Germplasm is used worldwide for disease-resistance breeding. For example, ICRISAT provided Fusarium wilt-resistant chickpeas and rust/late leaf spot-resistant groundnuts to national programs. At least 15 chickpea, 10 pigeonpea, and 11 groundnut landraces from this collection were released directly as improved varieties, benefiting farmers with higher yields and disease tolerance. ICRISAT's mini-core collections have identified multiple resistant sources (e.g., pigeonpea lines resistant to sterility mosaic virus and chickpea to Ascochyta blight).
CIAT "Alliance" Bean Collection (Colombia)—CGIAR Crops: Common bean ( <i>Phaseolus</i> ) and wild relatives	Phaseolus collection ~40,000 accessions (incl. ~36,000 <i>P. vulgaris</i> landraces, plus <i>P. coccineus</i> , <i>P. lunatus</i> , <i>P. acutifolius</i> ). Largest global bean collection.	A key source of genetic resistance for bean diseases. CIAT identified rare landraces with broad resistance to angular leaf spot and anthracnose, guiding the breeding of multi-disease-resistant beans. Wild relatives in the collection (e.g., <i>P. coccineus</i> , <i>P. acutifolius</i> ) contributed genes for common bacterial blight and bruchid resistance, now incorporated into cultivated bean lines. CIAT-bred "biofortified" high-iron beans also carry stacked resistance to pests and diseases from genebank materials released to small farmers in Africa and Latin America.
IITA Genebank (Nigeria)—CGIAR <i>Crops:</i> Cowpea, Soybean, Bambara groundnut, others	>15,000 cowpea (Vigna unguiculata) accessions (world's largest cowpea collection); also holds >2000 soybean, ~2100 Bambara groundnut, and African yambean, among. Total > 36,000 legume samples.	Enabled the development of multiple disease-resistant cowpea varieties for sub-Saharan Africa. IITA germplasm provided sources for resistance to major cowpea viruses (e.g., CABMV), bacterial blight, and parasitic weed Striga—traits now in improved cultivars grown across West Africa. For instance, the landrace TVu 11986 from IITA's collection confers broad resistance to Striga and is used in breeding Striga-proof cowpeas. IITA's pre-breeding with wild <i>Vigna</i> species (like <i>V. vexillata</i> ) has yielded lines resistant to cowpea pod borer and fungal diseases, strengthening the crop's resilience for resource-poor farmers.

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Table 4. Cont.

Genebank (Location)	Legume Accessions Conserved	Notable Disease-Resistance Contributions
ICARDA Genebank (Lebanon & Morocco)—CGIAR Crops: Lentil, Chickpea, Faba bean, Pea, Grasspea	~15,300 chickpea; ~14,370 lentil; ~10,000 faba bean; plus ~4000 grasspea ( <i>Lathyrus</i> ) and various vetches. It holds ~48% of global faba bean and ~51% of global lentil diversity. Total collection: ~144,000 (including cereals).	Wild relatives and landraces from ICARDA have been pivotal in disease-resistance breeding for cool-season food legumes. Example: lentil accession IG 72815 (a wild Lens ervoides from the ICARDA collection) carries high-level resistance to two races of anthracnose, which has been introduced into cultivated lentil breeding lines. ICARDA's chickpea landraces from the Mediterranean region provided genes for Ascochyta blight resistance, which is now used in varieties in India and Ethiopia. Faba bean germplasm from ICARDA (e.g., Ethiopian landraces) contributed novel genes for resistance to chocolate spot and faba bean rust in breeding programs. These contributions underscore ICARDA's role in exploiting West Asian and North African legume diversity for global disease resistance improvement.
USDA National Plant Germplasm System (USA) <i>Crops:</i> Soybean, Peanut, Common bean, Pea, etc.	Major US collections: Soybean ( <i>Glycine max</i> ) ~22,900 accessions; Peanut ( <i>Arachis hypogaea</i> ) ~9000 accessions; Common bean ( <i>Phaseolus vulgaris</i> ) ~18,000; Pea ( <i>Pisum sativum</i> ) ~5500; and thousands of others (lentil, chickpea, forage legumes, wild relatives in genus <i>Glycine</i> , <i>Phaseolus</i> , <i>Arachis</i> , etc).	U.S. collections have yielded critical resistance genes for crop protection. The USDA peanut collection's PI 203396 (origin: Brazil) famously provided TSWV virus resistance, now widespread in U.S. peanut cultivars. The soybean collection preserves wild <i>Glycine soja</i> and perennial <i>Glycine</i> spp.; from these, genes for soybean rust ( <i>Phakopsora</i> ) resistance and soybean cyst nematode resistance (e.g., PI 88788 for SCN) have been identified and bred into commercial soybean lines. The common bean collection has contributed sources for BCMV virus resistance and anthracnose (e.g., landrace 'Jalo' for rust resistance). Ongoing USDA breeding programs routinely tap these germplasm resources. For example, novel alleles for Fusarium root rot resistance in bean and frog eye leaf spot resistance in soybean have been introgressed from exotic accessions, underscoring the NPGS's role in safeguarding U.S. crop health.

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Table 4. Cont.

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Genebank (Location)	Legume Accessions Conserved	Notable Disease-Resistance Contributions
ICAR–NBPGR National Genebank (India) Crops: Diverse grain legumes (pigeonpea, chickpea, mungbean, urd bean, lentils, etc.)	>63,000 legume accessions from 61 species, one of the largest national legume collections. Key holdings: pigeonpea (~12,000), chickpea (~15,000), mungbean ( <i>Vigna radiata</i> ~7000), urd bean ( <i>V. mungo</i> ~6500), lentil (~3000), lathyrus and others.	Indian legume germplasm has been extensively characterized for disease resistance. NBPGR's collection underpins breeding fusarium wilt–resistant pulses in India—for example, the pigeonpea variety 'ICP 8863' (Maruti) with wilt resistance was derived from a landrace in this genebank. Through multi-institutional evaluation, over 200 Indian germplasm accessions have been registered as donors for important traits, many for biotic stress resistance (e.g., bruchid beetle resistance in rice bean, powdery mildew resistance in pea). NBPGR also facilitated the reintroduction of lost landraces (e.g., a mungbean line with yellow mosaic virus resistance) back into cultivation. This genebank's trait-diverse collections continue to enhance legume breeding for disease-prone tropical environments.
EMBRAPA Genebank Network (Brazil) <i>Crops:</i> Common bean, Soybean, Forages, others	~18,000 soybean accessions and ~16,000 Phaseolus beans (held at Embrapa Soybean and Embrapa Rice and Beans, respectively). It also conserves Brazil's cowpea, peanut, and extensive tropical forage legume collections (stylosanthes, brachiaria, etc.).	Embrapa has leveraged its rich germplasm to breed disease-resistant cultivars suited to Brazilian and tropical agriculture. Using the Embrapa collection, the Brazilian common bean program developed the widely grown 'Carioca' and 'Pérola' bean varieties with multi-disease resistance (to angular leaf spot, anthracnose, rust) derived from landrace crosses. Embrapa's soybean collection and wild <i>Glycine tomentella</i> accessions enabled the breeding of varieties with improved Asian soybean rust resistance (e.g., the rust-tolerant line BRS 511). Embrapa collaborated with ICRISAT to use wild <i>Arachis</i> introgressions for peanut smut and early leaf spot resistance in peanut. These achievements highlight how Brazil's national PGR conservation has contributed to more resilient legume crops (and pastures) in the tropics.

Farmers valued these varieties not only for yield potential but also for their reliability. This example typifies how disease-resilient germplasm empowers smallholders to mitigate risks and improve incomes. In West and Central Africa, cowpea lines incorporating resistance to diseases from IITA's genebank have enabled more secure production of this protein-rich crop under subsistence conditions. Likewise, bean farmers in Latin America have benefited from CIAT-bred bean cultivars carrying pyramided resistance to anthracnose, angular leaf spot, bean golden mosaic virus, and rust, which were sourced from

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diverse Latin American landraces and wild *Phaseolus*. By averting major epidemics and reducing the need for chemical control, these improved legume varieties directly enhance on-farm productivity and are often faster to be adopted by smallholders. Beyond yield, the stability and resilience conferred by disease resistance help ensure a more consistent food supply and better return on labor for farming families.

#### 6. Conclusions

The contribution of legumes to ecological balance, nutritional enhancement, and economic sustainability is significant. Their capacity to improve soil health, bolster food security, and support livelihoods makes them essential in addressing the challenges of a growing population, land degradation, and climate change. However, legume production is constantly challenged by issues that negatively affect yield and harvest quality. Among major concerns are diseases caused by fungi, bacteria, oomycetes, viruses, and nematodes. Accurate and timely identification of causative agents of the disease is critical. Such diagnostics enable the implementation of targeted and integrated management strategies to reduce inoculum pressure and mitigate disease impacts below economically damaging thresholds, while mitigating the risk of secondary infections and preserving long-term legume and soil health.

Legume crops are at the forefront of innovative crop breeding and biotechnological advancements. Integrating conventional breeding programs with modern biotechnological tools offers promising prospects for sustainable legume production in tropical regions. Alongside breeding innovations and biotechnological advancements aimed at developing superior varieties, digital agriculture tools, such as remote sensing, geographic information systems (GIS), and machine learning, are increasingly being utilized [310]. These technologies enable real-time monitoring of crop status and environmental conditions, allowing optimized management practices tailored toward legume production in tropical environments. As climate change and a growing population continue to challenge global agriculture, legume breeding and biotechnology innovations will remain imperative to ensuring food security and environmental sustainability. However, an integrated approach that includes other cultivation techniques (e.g., crop rotation, rational fertilization, deep plowing) remains important for the prevention and control of diseases in legume crops.

Furthermore, using plant genetic resources for disease resistance is a cornerstone of legume improvement strategies for food security in the tropics. The continued conservation and utilization of legume genetic resources through global genebanks and breeding networks will be vital to confronting emerging plant diseases under climate change and safeguarding the livelihoods of smallholder legume farmers.

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