Root Rot Diseases in Plants: A Review of Common Causal Agents and Management Strategies

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Introduction

Root rot pathogens cause some of the most important plant diseases worldwide impacting several crops [1,2]. Root rot symptoms are a major threat because the damage starts below the ground, where the first symptoms are not discernible. When the symptoms become apparent on the above ground part of the plant, yield is already compromised and plant survival is jeopardized.

Several pathogens can cause root rot, some are host-specific and some have a broader range of hosts. Reported root rot pathogens can belong to different groups such as bacteria [3] virus [4], oomycetes [5] and fungi [6-8]. In addition, root nematodes and other parasites play a role in facilitating root rot by wounding the plant and enabling the entrance of other pathogens. Fungi are the most abundant causal agents of root rot and they can stay dormant and overwinter in debris and infested soil for several years [9].

Some of the symptoms associated with root rot are browning and softening of root tips, root lesions that vary in size and color—from reddish to brown and black, trimming of the root and decay, yellowing and wilting of leaves, stunted plant growth, reduced yield and loss of crop [10-12].

The progression and success of infection depends on the disease triangle, which comprises the host-pathogen-environment interactions. Root rot is highly influenced by the environment and is favored by: moderate to high soil moisture, optimal temperature for pathogen growth, soil compaction, poor drainage, continuous or frequent cropping and other factors that contribute to plant stress [13,14]. This review presents a comprehensive overview of different groups of root rot agents in plants, along with alternative methods and strategies to manage and prevent root rot diseases.

Bacterial and Viral Root Rots

Bacterial root rot is not very common but it can be devastating to fruit, vegetable and ornamental plant production. Often, the bacteria gain entry into the host via a wound. Storage organs such as tubers are the preferred site of entry and the damage progresses rapidly beyond the roots. The soft rot caused by the members of Enterobacteriaceae is a good example of
generalized damage. Two genera in this group, Pectobacterium and Dickeya, with a wide range of pathogenic species, cause wilt and root diseases on monocot and dicot plant hosts worldwide. These bacterial pathogens secrete high amounts of plant-cell-wall-degrading pectinases and polygalacturonases which digest plant cell walls and cause soft rot symptoms [15].

Within the Pectobacterium genera, an economically important pathogen is P. betavasculorum which has been reported to cause bacterial vascular necrosis and root rot of sugar beet. Within the Dickeya genera, Erwinia chrysanthemi is an economically important pathogen because it causes bacterial stem and root rot of sweet potato [16]. This pathogen causes soft rot disease in a wide range of crops in mild climate regions and in greenhouse settings [17].

Bacterial stem and root rot is common in storage but may also affect plants in the field and in seedbeds. The first symptom is the partial wilting of the plant and eventually the entire plant may collapse and die. Water-soaked, sunken brown to black lesions are observed at the base of stems and on petioles. On fibrous roots, localized lesions are observed, but the entire root system can be affected, showing the characteristic black, water-soaked appearance. Dark streaking in the vascular tissue of the roots has also been reported [18].

Viral root rots are less common than bacterial root rots. Some studies have reported cassava brown streak virus as a causal agent of root necrosis. Two distinct virus species have been identified, cassava brown streak virus and Ugandan cassava brown streak virus. Both are members of the Potyviridae family and are transmitted by the whitefly vector Bemisia tabaci (Gennadius). Dissemination of the virus is through cuttings that are taken from infected parent material [19]. As detection methods evolve, information regarding the non-traditional causative agents of root rot is expected to increase.

**Oomycetes**

Oomycetes, also known as water molds, are a large group of terrestrial and aquatic eukaryotic organisms that superficially resemble fungi in mycelial growth and mode of nutrition. However, molecular studies and distinct morphological characteristics have placed them in the kingdom Chromalveolata, phylum Heterokontophyta [5]. The terrestrial oomycetes are primarily parasites of vascular plants, and include several important root pathogens such as Aphano myces spp., Pythium spp., and Phytophthora spp.

Among the Aphano myces spp. A. cochlioides creates a major constraint in cultivation of sugar beet, causing damping off and chronic root rot [13,20]. Another economically important root pathogen in this group is A. euteiches infecting a variety of field crops worldwide, especially legumes. This pathogen can drastically reduce yield in beans [21], alfalfa [22], fava beans [23], clover, lentils and peas [24,25].

For instance, A. euteiches Drech., is responsible for one of the most damaging soil-borne root diseases in peas worldwide [26]. It can affect the plant at any developmental stage, causing rotting of the roots and epicotyls that result in stunt ed seedlings, yellow leaves and even dead plants [27]. The development of cultivars with tolerance or partial resistance to Aphanomyces root rot is generally considered to be one of the best options to reduce yield loss [25]. Resistance is limited in commercial cultivars [27]. Cultural practices for Aphanomyces root rot are highly dependent on environmental conditions, mainly because proliferation is through water-motile zoospores that thrive in poorly drained soil conditions [28].

**Pythium**, with over two hundred described species, can cause a variety of diseases including root rot in numerous plant hosts [29]. At least ten Pythium spp. cause Pythium damping off and root rot in various legumes and monocots. A rapid black rot of the entire primary root that can move up to the stem is typical of this pathogen. P. ultimum and P. irregular have been reported as the most ubiquitous pathogens in this group [30].

Root rot caused by Pythium spp. is one of the most damaging diseases restricting production of common bean [31]. This disease in corn was reported to be caused by P. graminicola in Japan. Tobacco seedlings in floating systems were also infected by P. diclinum [32]. Ornaments under different irrigation regimes were reported to be infected by P. aphanidermatum and P. ultimum [33]. These same two species were shown to infest greenhouse cucumber production [34]. Some other specialty crops such as parsnip and parsley have up to 80 % and 100 % yield losses in Australia which is attributed to Pythium [35]. P. arrhenomanes is considered to be the most important cause of sugar-cane root rot [36]. Pythium root rot is also a relevant disease for wheat [37] and common bean.

**Phytophthora spp.** belong to the family Pythiaceae along with Pythium spp. and together they attack a wide range of woody ornamentals as well as annual crops. Symptoms include wilting, yellow or sparse foliage and branch dieback. Phytophthora spp. cause late blight of potato and tomato, foliar blights on peppers and cucurbits, and root or stem rots of many plant species. Taiwan cherry was reported to be infected by P. cambivora. Root rot of pea and fava bean in Southern Sweden were found to be caused by P. pisi sp. nov. [38]. The P. citricola complex has been found associated with mortality of Aucuba japonica in the UK [39]. P. palmivora is a common causal agent in papaya root rot [40]. Phytophthora root rot is also a threat to red raspberries [41], chickpeas [42,43], pepper [44], soybean [45], ash trees [46], kiwi fruit [47], avocado [48], and innumerable other crops.

**Fungal Root Rots**

There are several fungal root rot pathogens that compromise root health. For conifers, Heterobasidion annosum sensulato, Armillaria ostoyae, and Phellinus sulphurascens are important fungal pathogens causing annosum, armillaria and laminated
root rot, respectively. These pathogens are found in temperate forests of the northern hemisphere causing decay, growth reduction and tree mortality [6].

Annosum root rot caused by *Heterobasidion* spp is common in plantation-grown conifers [49]. The *H. annosum* species complex consists of five species. Three of the species *H. annosum*, *H. parviporum* and *H. abietinum*, occur in Europe, and the other two *H. irregulare* and *H. occidentale* occur in North America, [13]. *H. parviporum* can increase drought stress while infecting the roots in Norway spruce in the Alps [50]. Infected trees often show no above ground symptoms until survival is compromised. Infected roots have lesions that can spread to other organs [51].

Armillaria root rot is caused by *Armillaria* spp. infecting oaks and other woody ornamental and crop trees and shrubs [52]. Root rot caused by *A. cepistipes* correlates positively with dieback severity and plays a role in tree decline. It was observed that even four years after tree falling, root rot was found to have a negative impact on sprouting efficiency [53]. *A. mellea* is an important phytopathological problem in the wine sector [54]. In the vineyard it reduces plant vigor, causes chlorotic leaves to develop, and hastens phylloptosis in autumn [55]. Armillaria root rot is also a threat to apple, walnut and kiwi production [56].

Laminated root rot is the most damaging disease of young-growth Douglas-fir and other conifers in the Pacific Northwest region of the U.S. This disease is caused by the fungus *Phellinus weirii*, which survives for 50 years or more in roots after trees are harvested [57]. *Phellinus sulphurascens* is also a major naturally occurring pathogenic fungus. The disease spreads below ground at root contact regions and often occurs in combination to Armillaria root rot [6]. Laminated root rot also been reported to be caused by *Phellinus qilianense* in *qilian juniper* [7].

Another important tree root disease is the white root rot caused by the ascomycete *Rosellinia necatrix*, attacking a wide range of perennial plants [58]. White root rot is the major threat to apple in Kashmir valley. The moist conditions of the orchards and deficient irrigation system create the right conditions for this disease [59]. This pathogen is also a serious problem for avocado production in the Mediterranean [60]. Symptoms include root and collar rot of trees leading to a decline in vigor. A distinct margin is usually visible between the infected and healthy bark with a thin layer of white fungal growth found under the diseased bark. A white cottony mycelium and mycelia strands, either white or black, appear on and surrounding infected roots or inside the bark [61].

Rhizoctonia root rot is a frequent disease of many crops such as bean [62], apple [63], tobacco, blueberry [64], tomato [65], pea [66], and canola [67]. This pathogen generally attacks its hosts in the juvenile stages of development. Rhizoctonia root and crown rot, caused by *R. solani*, is the most widespread and damaging sugar beet disease in Nebraska [68]. Rhizoctonia root rot and bare-patch are diseases that limit the yield of direct-seeded cereals, especially wheat and barley [69]. *R. bataticola* is another serious threat mainly in cotton production [70].

Fusarium root rot is a common disease in several crops. Symptoms include round or irregular light brown lesions that progress to dark black lesions on below ground roots and stems, stunting and death [71]. In legumes, the major root rot causing agents are *F. solani* and *F.avenaceum* [72]. Thus, production of bean [73], soybean [74], pea [75], lentil [76], and peanut [77] is highly compromised by this type of pathogen. *F. solani* can cause severe rot in sweet potato roots [78] and cassava [79]. Fusarium spp. also cause other rots such as Fusarium crown rot in cereals and Fusarium stalk (stem) rot in corn. These species differ from those responsible for disease in dicots and include: *F.graminearum*, *F. culmorum*, *F.avenaceum*, *F.verticillioides*, and *F. Pseudograminearum*. *F. culmorum* causes foot and root rot and Fusarium head blight on different small-grain cereals, particularly wheat and barley [80]. *F.graminearum* plays a role in crown and root diseases of wheat. *F. chlamydosporum* infects coleus and other ornamentals. *F. oxysporum* is more frequently associated to wilt but it causes root rot on members of the Cactaceae family such as Schlumbergera truncate [81]. *F. oxysporum* also causes stem and root rot in melons [82].

Phoma root rot is caused by many species. *P. betae* is known to cause leaf spot and rosetting of beets during storage. *P. terrestris* has been reported to cause pink root rot of onion [83]. Red root rot of corn is also attributed to *P. terrestris* [84]. Roots and basal stalk tissue infected with red root rot have a reddish pink discoloration that becomes a deeper red color as the disease progresses [85]. *P.sclerotiorum* causes brown root rot of alfalfa and other perennial forage legumes [86].

Black root rot is primarily caused by *Thielaviopsisbasicola*. It infects a wide range of hosts, causing root disease in over 200 plant species. Symptoms include stem rot and damping off in some hosts in addition to rotten roots. Economically important hosts are tobacco [87], carrot [88], cotton [89], and soybean [90].

There are several other root rot pathogens that are less frequently reported. Some examples of such pathogens include *Aspergillus spp.*, *Alternaria spp.*, *Curvularia spp.*, *Rhizopus spp.* and *Penicillium spp.*, isolated from soil, root, stem and foliar samples of plants showing root rot symptoms [91]. Fungi *Rigidoporus lignosus* and *Phellinus noxius* are root rot pathogens reported in rubber trees. Dry root rot of chickepa caused by *Macrophomina phaseolina* is another significant fungal root disease that impacts chickepa production areas in India [92].

Overall, root rots are generally referred to as a complex, for example, black root rot of strawberry is attributed to *Pythium*, *Fusarium*, and *Rhizoctonia* pathogens [93]. Another example is the pea root rot complex where the disease is caused by a single pathogen or a combination of pathogens, including *Alternaria alternata*, *A. euteiches*, *F. oxysporum*, *Ksolani*, *F. avenaceum*, *Mycosphaerella pinodes*, *Pythium spp.*, *R. solani*, *P. betae*, and *P. terrestris*.
Sclerotinia sclerotiorum and Phytophthora spp. [94,95]. Other fungi that can be associated with pea root rots include T. basicola and Ascochyta pinodella. Phoma spp. can also be referred as part of the pea root rot complex [96].

Management Strategies for Root Rot

Effective management of root rot can be achieved by adopting resistant and tolerant varieties. Cultural practices, chemical treatments and biological control agents are also extremely important. Cultural practices can directly or indirectly affect populations of soil borne pathogens and the severity of their resultant root diseases [97].

Draining wet soils, crop rotation, soil preparation by tillage, fertilization, and weed control before planting have been reported as tools to manage root rot diseases. Planting within the recommended seed rate to avoid overcrowding can also decrease disease pressure. Crop rotation can break the disease cycle and affect soil chemistry. Many species within the Brassicaceae family contain glucosinolates that liberate products such as the volatile isothiocyanates, shown to suppress A. euteiches through hydrolysis. In this sense, Brassicaceae seed meal applications can also be used for its fungicidal benefits.

Reducing the green bridge by killing weeds or volunteer plants that allow the fungus to survive between crops is another important cultural practice. This control can be achieved by using herbicides such as glyphosate to control Rhizoctonia root rot in wheat [98]. However, fungal pathogens can survive for many years in soil as mycelium and by producing sclerotia. This increases the complexity of management, potentially mandating the application of bio control agents. Chemical treatment after planting is not a common option to treat root rots due to the advanced state of the disease by the time above ground damage is evident.

Other options for preventing root rot can include the use of chemical fungicides, inoculation or bio control agents. For instance, the population density of R. solani was reduced significantly in the rhizosphere of pea seedlings obtained from seeds pretreated with Trichoderma and/or Topsin-M. Treatment with Apron XL+Maxim4 FS+Cruiser with or without Rhizobium inoculant increased emergence and reduced root rot severity and the number of Pythium colonies compared to the untreated control.

Integrated pest management is more applicable, including timely fungicide applications, crop rotation and attention to soil moisture levels, along with developments in bio control. Plant growth-promoting rhizobacteria such as Bacillus pumilus and Pseudomonas putida, along with antagonistic fungi such as Aspergillus awamori, Aspergillus niger and Trichoderma harzianum have been used to control Fusarium root rot of pea [99]. Integration of soil application and seed treatment formulations of Trichoderma spp. for management of wet root rot of mungbean caused by R. solani has also been reported [100].

Strains of Pseudomonas spp. have been shown to reduced disease symptoms of both R. solani AG-8 and P. ultimum, and the latter four also suppressed R. oryzae and P. irregular [101]. Studies on cultures of P. cinnamomi exposed to different Ca2+ fertilizers in vitro showed significant inhibition of sporangial, chlamydospore and zoospore production at millimolar concentrations while mycelial growth was mainly unaffected [102]. Trichoderma viride and Pseudomonas fluorescens were successfully used when combined as biocontrol agents for dry root rot of chickpeas.

Other alternative treatments are recently being considered, including soil type studies. Sandy soil covered with consortium of Zea mays and Vignaunguiculata was efficient in suppressiveness against disease caused by F. solani in cassava root rot. Vermicomposting for organic production was effective to reduce root rot in a complex disease of Coleus forskohlii involving Fusarium chlamydomsporum and Ralstonia solanacearum, in terms of 73% percent less wilt incidence and 82% less severity of root rot.

One pathogen may also inhibit another pathogen. For example, in a study conducted with alfalfa, co-inoculation with both A. euteiches and Phytophthora medicaginis resulted in significantly reduced amounts of P. medicaginis DNA detected when compared with amounts detected from inoculations with P. medicaginis alone [103].

Resistance for root rot diseases is generally imparted by more than one gene and is referred to as quantitative resistance. This type of resistance provides partial and durable resistance to a range of pathogen species in different crops [104]. Root rot resistance is often quantitative. Most of the genes underlying this trait are difficult to introgress in modern-type cultivars while maintaining field and market desirable agronomic and quality traits.

Applying genetics to improve resistance

Identification of quantitative trait loci (QTL) in carefully designed genetic studies has been a major approach to study quantitative resistance. QTL studies are used to understand: epistatic and environmental interactions, race-specificity of partial resistance loci, interactions between pathogen biology, plant development and biochemistry, and the relationship between qualitative and quantitative loci. QTL mapping also opens up the possibility of positional cloning of partial resistance genes and its subsequent use in marker-assisted selection (MAS) of complex disease resistance characters [105]. MAS is the process of using morphological, biochemical, or DNA markers as indirect criteria for selecting agriculturally important traits in crop breeding [106].

Conventional plant breeding and genetic engineering are known to have introgressed diseases resistance into several crops. Conventional breeding demands significant time and effort in field trials. Recent advances in manipulating resistance include protein and RNA-mediated resistance. RNA silencing
is a process that can induce mRNA degradation or translation inhibition at the post-transcriptional level. It can also induce epigenetic modification at the transcriptional level [107].

Regardless of the method, informed deployment of major resistance traits will enable the production of crop varieties with effective resistance [108]. However, the development of resistant cultivars needs content evaluation as pathogens evolve. For example, the use of cultivars with different resistance genotypes _Leptosphaeriamaculans_ was suggested to lead to a different spectrum of virulent isolates in oilseed rape production [109-111].

**Conclusion**

This work presented a review on root rot diseases that are a great threat to many crop systems around the world. Bacteria, virus, oomycetes and fungi are the main causal agents that can act as a primary pathogens or in combination with other pathogens in both field and greenhouse space. Bacterial stem and root rot also affects many crops and is common in storage, field and seedbeds. Viral root rots are even less common and were reported to be a problem in cassava production. Oomycetes and fungi are the most frequent yield reducers. Reported oomycetes are _Aphanomyces_ spp., _Pythium_ spp., and _Phytophthora_ spp. Several fungi cause root rot, including _H. annosum_, _A. ostoyae_ and _P. sulphurascens_ that have been reported as a problem for tree crops, as well as the broader host range pathogens _Rhizoctonia_ spp., _Fusarium_ spp.

Beneficial interactions such as legume-rhizobial and plant-mycorrhizal relationships can improve the ability of a root system to withstand stress as well as provide a boost to the plant immune system. Some microbes can also inhibit other pathogens such as _A. euteiches_ that is known to be suppressed by a vesicular-arbuscular mycorrhizal fungus. Knowledge of plant-microbe and microbe-microbe interactions can also be the basis of biocontrol research.

Due to the high environmental influence, broad range of hosts, hidden underground symptoms and overwinter structures of many root rot pathogens, root rot disease control and management is complex and hard to achieve. Chemical treatment is generally only available as preventive seed treatment for some root rots or as a way to kill the green bridge between crops.

Therefore, the adoption of resistant or tolerant varieties is still the most promising tool to control root rot. As there is no complete resistance for major diseases such as _Aphanomyces_ and _Fusarium_ root rots due to the quantitative nature of this trait, breeding for this trait is very complex. Greenhouse assays and field screenings can be expensive and the use of markers becomes a great tool to identify sources of resistance. Reliable markers such as SNPs are still lacking to develop a research foundation that will provide an understanding of the genetic mechanisms underlying resistance as well as to be used in MAS.

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