

Review

# *Armillaria* Pathogenesis under Climate Changes

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**Abstract:** Climate changes influencing forest ecosystems include increased air temperatures and CO<sub>2</sub> concentrations as well as droughts and decreased water availability. These changes in turn effect changes in species composition of both host plants and pathogens. In the case of *Armillaria*, climate changes cause an increase in the activity of individual species and modify the growth of rhizomorphs, increasing the susceptibility of trees. The relationship between climate changes and the biotic elements of *Armillaria* disease are discussed in overview.

**Keywords:** *Armillaria*; rhizomorphs; climate changes

## 1. Introduction

The total CO<sub>2</sub> amount together with other greenhouse gases in the atmosphere has led to increasing global temperatures [1,2]. Many authors have suggested that concentrations of CO<sub>2</sub> will increase to as much as 550 ppm by 2050 and 1250 ppm by the end of the twenty-first century [3–5]. Pearson and Dawson [6] reviewed models of climate change impacts on biodiversity and on the distribution of vegetation, and they point out the role of other important factors such as “biotic interactions, evolutionary change and dispersal ability.” Global warming will change the special diversity and functional activity of forests—affecting, for example, factors such as photosynthetic rate, tree dieback and wood production, as well as the activity of pests and pathogens—in Central Europe [3,7]. Wargo [8,9] found that defoliation of trees can substantially decrease the starch content in the root wood and the sucrose levels in both bark and cambial tissues of sugar maple roots, which should decrease the attractiveness of these tissues for root pathogens. However, defoliation may also reduce the nutrition available to mycorrhizae and reduce their ability to contribute to water and nutrient uptake for the tree [10].

Taking into consideration that conifers will probably suffer the impacts of global warming in South and Central Europe, including shifting climate zones, one can logically expect changes in the geographic distribution of boreal species. This may include an expansion of deciduous species in the north-east direction, and a decrease in conifer abundance, mainly Norway spruce [11]. “Increased temperatures and subsequent drying due to climate change will increase the presence of “new” hosts on “new” sites.” These biotic shifts may favor the initiation of new disease phenomena and increases in invasive species (e.g., those on the European and Mediterranean Plant Protection Organization Alert List), affecting the life of the “new” forest ecosystems [12]. As the coniferous habitats retreat, however, the potential increase in the range of deciduous forests (especially oak, beech, and alder) is unlikely to be fully realized, if only because of the trees dying due to active phytophthorosis and simultaneous *Armillaria* rot in these species.

Atmospheric CO<sub>2</sub> concentrations, warming, and altered precipitation regimes can limit both ecosystem productivity and activity, and change community composition and function [13–15], favoring organisms better adapted to higher temperatures and faster growth rates [16–18]. However, unfavorable relationships between fungi and CO<sub>2</sub> in the forests have also been detected. With the damage to 80- to 100-year-old Scots pine stands by root pathogens reaching 20% of the trees per ha, and up to 80% for Norway spruce, the degradation of roots and stumps could amount to 15.3 m<sup>3</sup>/ha of pine and 100.7 m<sup>3</sup>/ha of spruce [19]. Assuming that the proportion of the cellulose and lignin together average 70% of wood pulp, one can easily calculate how much CO<sub>2</sub> is released as a result of fungal enzymatic degradation. Sierota [19] estimates that from one hectare of 80-year-old pine stand, 60 tons of CO<sub>2</sub> is released in this way per year, or 3.3 Mt for all Polish forests. However, root pathogens are not the only organisms decaying wood in the forest—one should also take into account saprotrophs colonizing the so-called “dead wood”.

Climate change will increase the frequency of extreme climatic conditions, such as droughts, floods, and hurricanes. Forest damage by wind and snow are projected to increase. Some insect species will profit from increasing temperatures, especially at their northern limits. The risk of outbreaks will probably be increased by milder winters that ease the survival of insect and pathogen species during hibernation [20]. In such conditions, there is a high probability that forests will be subject to increased frequency and intensity of fungal diseases. The effects may become more disastrous because of drought and flooding, which are known as factors that predispose trees to several pathogens [21]. Changes in temperature and humidity affect pathogen sporulation and dispersal, and so changes in climatic conditions may favor certain pathogens [22]. Sudden weather changes may increase the incidence of dispersal of pathogens, thereby changing the geographic extent of diseases. Pathogens can meet new hosts and new vectors which may lead to the emergence of new risks due to changes in the species composition of trees or because of invasive species [21].

*A. mellea* (Vahl. Fr) Kummer and *A. ostoyae* (Romagnesi) Herink are already known to be strong pathogens present in Europe, but they will further benefit from a situation where trees become more stressed due to climatic effects [23] or risks posed to storm-damaged stands [21,24]. *Armillaria* spp. grow at temperatures between 10 and 31 °C, with an optimum between 20 and 22 °C [25,26]. According to Rind and Losel, the mycelial growth of *A. mellea* and *A. gallica* appears to be greater at higher temperatures [21,27]. This may mean that in a warming climate, low soil temperatures probably will not restrict the growth of rhizomorphs during winter as it usually happens in most northern temperate zones [21]. *A. gallica* will probably prefer to attack trees weakened more by changing climatic factors, both because this species of fungus is quite thermophilic (*A. Mellea*), and because it acts like a weak parasite that attacks and sometimes kills weakened trees. *Armillaria gallica* is a likely candidate for an opportunistic pathogen that may become problematic due to climate change, due to increased stress of “host” trees caused by increased temperatures and drought [21,28].

The global rising temperature of the atmosphere and the soils can accelerate the mycelial growth of root pathogens and therefore increase wood decay and CO<sub>2</sub> release. Pastor and Post [29] indicated an important role for temperature, water availability, and nitrogen uptake in the vitality of forest ecosystems. Schwarze et al. [30] found that the temperature range for mycelial growth and wood decay is 5–30 °C, although many fungi can grow at higher temperatures, even +55 °C. However, Witomski [31] found that the optimal temperature range for wood decay is 18–27 °C and below or above this range the decay of wood tissues is decreased.

Pathogens and saprotrophs decomposing timber (mostly polypore basidiomycetes) showed better growth with higher temperatures of growth medium. These fungi benefited from the water formed during enzymatic decomposition, as the humidity of the substrate increases with the degree of decomposition of the timber tissue [32,33]. The development of hyphae of wood decay fungi also occurs in winter, when it is supported by high osmotic pressure and thermal energy emitted during the decomposition of cellulose and lignin. The low concentration of CO<sub>2</sub> in the rhizosphere, on the root surface and inside the wood, has a significant beneficial effect on the development of

the spores and mycelia of many different fungi promoting their colonization of the dead wood on the forest floor [34–37]. Wells and Boddy [37] found that increased temperatures had a positive effect on soil phosphorus uptake by the mycelia of some basidiomycetes. Because temperature is the main factor affecting organic matter decomposition, taxa that regulate decomposition, such as fungi and macro-arthropods, may shift their activity or community composition in response to warming [38,39]. According to Austin [38], wood decomposition increases with temperature, but the impact of temperature might vary at sites with different climatic regimes and decomposer communities. The author predicted that warming would have larger impacts on fungal community composition at sites already under heat stress [38].

The direct and indirect impacts of climatic changes affect the health of forests in part by influencing the development of fungal diseases and insect pests [40–42]. Increases in root diseases, particularly those caused by *Armillaria* pathogens [41–43], contribute notably to these impacts. Diseases caused by this fungus can increase under drought conditions and temperature increases [41], which can lead to the reduced tree growth and attacks by secondary pests [44]. Ayres and Lombardero [45] indicated that climate change affects fungal diseases by (i) direct impact on the growth of hosts and pathogens; (ii) changes in tree defense mechanisms; and/or (iii) an indirect effect on the mutualist and competitive organisms and others in the environment, manifesting in changes in abundance and frequency. Klopfenstein et al. [40] proposed a mathematical model to predict the impact of climate change on the pathogen *A. ostoyae* attacking Douglas fir in the northwestern USA. He emphasized that the integration of a variety of tools and data is necessary to improve forecasts for the influence of climate on forest diseases.

The multifunctional interactions between plants and soil communities influenced the selective pressures of pathogens, including *Armillaria* spp., on the functional features of the plants [46,47]. Because the responses of soil microorganisms to *Armillaria* pathogenesis are not well-known, it is still of great importance to investigate how the climatic parameters could influence not only the *Armillaria* pathosystem and host-tree susceptibility, but also soil community composition and microbial activity.

## 2. The Pathogen

For many decades, root and butt rot caused by *Armillaria mellea* (*sensu lato*) has been a significant threat to the boreal forests of Europe and North America. Currently, it seems to have become the most important phytopathological problem in weakened managed forests [48]. Expansion of the pathogen in colonized tissues is rather fast, depending on the tree species and health status of the host as well as on the vigor of the mycelium (which in turn is affected by the species and clone of *Armillaria* acting as the pathogen) [49,50]. The pathogenesis of *Armillaria* is described in many papers and books; however, the role of the environment in this process is rather neglected [51,52]. The intensity of losses caused by the pathogen is directly connected with changes in the climate and with weather anomalies. Long and frequent drought periods, increases in global and local CO<sub>2</sub>, summer reduction of soil moisture, and escape of available water are all relatively strong factors [53]. The deep impact of soil drought on *Armillaria* rot disease has been described by previous authors [40,54–57]. Żóćciak et al. [58] found that after drought in Poland in 2000, the disease was noted in an area of 150 thousand hectares in Norway spruce stands as late as 2005. The interactions between air and soil CO<sub>2</sub> and *Armillaria* behavior have been the subject of current and past investigations [19,36,53].

The life cycle of *Armillaria* spp. is very complicated, and is characterized by: different gametogenesis cycles (mono-, di-, eu-karyotic), different phases in ecological status (pathogenic, saprotrophic, orchid-like symbiotic), different methods of infection (basidiospores, mycelium, rhizomorphs), and different host reactions (tissue compartmentalization, resin outflow, host dying, wood decay) [59]. This sophisticated behavior can be additionally modified by site conditions, weather anomalies, and human activity, as it was described in Canadian boreal forests [60]. While *Armillaria ostoyae* favors fertile mountain forests and either pure Norway spruce or mixed spruce-beech stands in Poland [36], other *Armillaria* species can inhabit various forest stands in many

sites [61]. There is lack of publications about different species of *Armillaria* in different habitats within the context of climate changes.

The pathogenicity of the known *Armillaria* species depends on the individual virulence, host species, age of the tree, and influence of the environment [62–66]. In Europe, Sicoli et al. [67] found that *A. mellea* (Vahl: Fr.) P. Kummer and *A. gallica* Marxmüller & Romagnesi were the most pathogenic species for some *Quercus* spp. seedlings, whereas other authors showed *A. ostoyae* (Romagnesi) Herink as being the most dangerous for conifer species [21,63]. *Armillaria borealis* Marxmüller & Korhonen, *A. cepistipes* Velenovsky, and *A. gallica* are generally described as weakly pathogenic species or pathogens of weak trees [28,68], while *A. tabescens* (Scop.: Fr.) Emel. is regarded as a typical saprotroph. Nevertheless, some of the opportunistic parasite species such as *A. ectypa* can infect some stressed trees [69]. *Armillaria ectypa* (Fr.) Lamoure plays a rather minor role as a disease perpetrator [70]. The number of *Armillaria* species worldwide is still uncertain; recently some isolated species were identified as *A. nigrifulva* Orton or renamed *A. altimontana* Brazeo, B. Ortiz, Banik & D.L. Lindner (previously described as NABS X) [71–73].

*Armillaria* rhizomorphs are described as the main source of threat to roots in the pathogenesis of infection. They may also be considered to be an example of a special morphological adaptation of this fungus to different environmental conditions [74,75].

### 3. The Rhizomorphs

*Armillaria* commonly occur as rootlike rhizomorphs growing on plant debris or epiphytically attached to the root system of dead, diseased, or healthy host plants [74–79]. Rhizomorphs look like roots or cords that are a dark brown color when old and a reddish brown color when young. Hence, sometimes rhizomorphs have been referred to as mature (black) and immature (red or brown) [80,81] or as maternal (old) and regenerated (young) because of their regenerative abilities [82]. Rhizomorphs grow towards the soil surface, possibly due to the oxygen gradient in soil [83]; however, the seasonal humidity in this layer is what probably adjusts its vertical distribution (e.g., black rhizomorphs were mostly found deeper in dry sites) [25,83]. Rykowski [82] described black rhizomorphs in the soil of rich deciduous stands as persistent organs without infection ability, whereas young, red rhizomorphs were formed mostly in plantations, infecting pines after the removal of stands.

Different species of *Armillaria* produce rhizomorphs with either a monopodial or dichotomous branching pattern [84–86]. Rhizomorphs typically grow in the soil, but they can also occur on dead trees, stumps, and even on the surfaces of living roots. Where the hosts have physical defects, *Armillaria* form apical meristems which can produce a large number of new rhizomorphs [82,87–89]. Rhizomorphs and their growing-tip hyphae are a main source of inoculum, initiating the infection processes and host reactions [82,90].

In the initiation and development of rhizomorphs, environmental factors such as moisture, soil temperature, pH, nutrients, and pollution play an important role [25,51,91–93]. These factors determine the proper functioning of apical meristems and the rhizomorphs' growth [78,82]. Redfern [81] and Kessler and Möser [94] found that low soil moisture and temperature inhibit this growth and branching. A temperature higher than 22 °C is preferred [95]; however, 30 °C limited the growth of the fungus due to enzyme inactivation [96]. Rhizomorphs can grow in different types of forest and farmland soils. Sandy soils, on the other hand, inhibit their production not only because of low nutrients but also due to a high day-night temperature amplitude [25,50,97]. Peat soils are conducive to the development of rhizomorphs, which tend to be concentrated mostly in the humus layer of the soil due to the oxygen concentration gradient. This may be related to increased susceptibility to infections around the root collars of trees [90,97,98]. In addition, *Armillaria* habitats have moist layers of substrate and low levels of oxygen and organic matter, the latter of which is digested by the soil acidic reaction products of decomposers [99]. Mallett and Meynard [100] indicated an increase in the severity of fungus root rot when increasing the content of sand in the mineral substrate layer and decreasing the content of NH<sup>4+</sup>

in the organic layer of the soil, and Singh [95] found that plants in good condition produce a callus, which initiates an effective barrier against *Armillaria* infection [95].

Lech and Żółciak [101] observed stimulation of *A. ostoyae* rhizomorph production by elevated air CO<sub>2</sub> concentration in a chamber experiment. Hintikka [34] noted the stimulation of rhizomorph growth on a medium under high CO<sub>2</sub> concentrations. Schinner and Concin [102] showed the ability of some wood rotting fungi, including *Armillaria* spp., to assimilate CO<sub>2</sub> from the air. The rate of this assimilation was low, however, reaching only 1.3 nCi/g of dry mass in the case of *Armillaria* spp., which means that 1 g of fungus tissue contained just 0.017 mg of carbon coming from atmospheric CO<sub>2</sub>. Unfortunately, studies devoted primarily to the relationship between forest tree species (hosts) and *Armillaria* spp. (pathogens) in a CO<sub>2</sub>-enriched atmosphere and/or under increased temperatures are lacking, which makes it extremely difficult to predict the future behavior and functioning of this fungal genus in forest ecosystems under climate change.

#### 4. The Hosts

There is yet another aspect of climate change effects on trees. According to the growth-differentiation balance hypothesis (GDBH) [103], the elevation of air CO<sub>2</sub> may cause a decrease in trees susceptibility towards herbivores as the augmented availability of carbon resources due to intensified photosynthesis is allocated to secondary metabolites rather than to growth. It was found that plants grown in high air CO<sub>2</sub> concentrations were characterized by a higher C:N ratio, and increased lignification and phenolic compound content in the tissues compared to plants from ambient air CO<sub>2</sub> conditions [104,105]. However, Fleischman et al. [106] found atmospheric CO<sub>2</sub> elevation up to ca. 700–800 ppm to cause an increase in beech seedlings' susceptibility to infection by root pathogen *Phytophthora citricola*. Similarly, Tkaczyk et al. [107] reported a decrease of fine root biomass of beech seedlings grown under 800 ppm air CO<sub>2</sub> and exposed to *Phytophthora plurivora* and *Ph. cactorum* artificial inoculation. Oszako et al. [108] had similar results with oak seedlings and *Ph. quercina*.

Pollutants may affect the severity of *Armillaria* root disease on host plants. Impacts associated with SO<sub>2</sub> and other pollutants have been described in the past by many authors [109–113]. Domański [113] found that *Armillaria* root disease was extremely rare in polluted zones but was quite common in plots uninjured by pollution, while Horak and Tesche [114] described an increased mortality of trees both infected by *A. ostoyae* and fumigated with SO<sub>2</sub>. According to Wargo et al. [115], lead and other heavy metals present in the soils of spruce-fir sites at high elevations inhibit both mycelial and rhizomorph growth in culture.

Human land-use practices can also influence the host-parasite relationship. Sicoli et al. [116] reported that *A. mellea* attacks on *Cedrus atlantica* were predisposed by the specific soil previously used for pasture causing an iron deficiency (as indicated by reduced growth and chlorotic leaves). Silvicultural treatments such as thinning may result in the spread of *A. ostoyae* via root contacts, mainly in juvenile stands [117]. It should be remembered that the *Armillaria*-decayed roots and rhizomorphs remain as inoculum in the soil for many years. The impact of *Armillaria* inoculum from coniferous stands on the roots of entering deciduous trees (for example, in reconstruction after conifer monocultures) is not fully understood [118]. On the other hand, the higher temperatures and humidity of soil in cleared sites can indirectly protect roots by the mycoparasitism phenomenon, as occurs in the parasitism of *A. gallica* by mycelia of *Trichoderma* species [119]. Note, however, that the reverse relationship can occur: Oomycetes seem to be indicated as the primary pathogens predisposing deciduous trees for *Armillaria* attack [120]. In other biotic interactions of note, Riffle [121] and Cayrol et al. [122] found that nematodes (*Aphelenchus avenae* Bastian, *A. cibolensis* Riffle, and *A. composticola* Franklin) can actively destroy the mycelium of *Armillaria*. The qualitative and quantitative composition of compounds secreted by the roots often determines the development of the antagonistic microorganisms in the soil [123]. For example, *A. mellea* can be inhibited by gastrodianin



(an anti-fungal protein from the parasitic plant *Gastrodia* which is affected by *Trichoderma viride* present in the soil [124,125]).

In areas transitioning from coniferous to deciduous trees, seasonal changes in oxygen and CO<sub>2</sub> production due to photosynthesis and respiration are inevitable. Therefore, the additional supply of CO<sub>2</sub>. As the result of the decomposition of wood by pathogens and saprotrophs can tip the local and global carbon balance [19].

## 5. The Microbial Soil Community

Soil microbial communities are responsible for mineralization, decomposition, and nutrient cycling. These communities could be affected by abiotic factors in the climate such as temperature, moisture, and soil nutrient availability, or by biotic factors, particularly interactions with other microorganisms [126]. Certain interactions between antagonists and pathogens are initiated when the antagonistic fungi are under stress, especially nutrient stress, which has a direct impact on the growth, morphogenesis, and organogenesis of the antagonists [127]. The antagonistic fungi can receive nitrogen in the form of ammonium at high doses and they metabolize this form of nitrogen more intensively than do the pathogens. However, the pathogens have a relative advantage over antagonists when ammonium has been used up or the available nitrogen is in another form [127]. It is also known that many of the fungal isolates increase the formation of spores and chlamydospores when the concentration of nitrogen increases [128]. *Armillaria* species probably create rhizomorphs in similar situations.

Many authors report that global warming directly affects the metabolism and respiration of soil communities and the ratio of Gram-positive vs. Gram-negative bacteria [129], because these are sensitive to temperature [17,130–133] both in short-term and long-term scales [134]. The changes in temperature combined with the concomitant changes in soil moisture potentially affect many groups of fungal and bacterial communities [135]. Soil fungal communities shift from one dominant member to another while less-plastic bacterial communities remain more constant [136,137].

Greater or less active protection of plants against pathogens in the soil can result from the lack of ectomycorrhizal fungi as a result of climate changes (mainly drought) [138,139]. The insufficiency of mycorrhizas may stop or slow the adaptation of trees to new sites [140] and affect the ecosystem functioning [137], which could increase the susceptibility of trees to pathogens because trees are stressed. Symbiotic bacteria belonging to the *Rhizobium* genus [141] and mycorrhizal fungi [142] affect plant productivity by providing nutrients to plants. Mycorrhizal fungi can influence free-living bacterial communities to increase the transfer of nitrogen via mycorrhiza to the host plant [143]. However, interactions between mycorrhizal fungi and the host plant are not always mutualistic and can change due to environmental factors or even under plant stress [144]. Rising temperatures will lead to an increase in the allocation of carbon to mycorrhizal hyphae, which, depending on external conditions, can act as symbionts or parasites [145–148].

## 6. The Interactions with Insect Pests

Pfeffer [149] noted that after 1947, which was a “dry year,” over 90% of trees colonized by bark beetle were attacked by *Armillaria* spp. Madziara-Borusiewicz and Strzelecka [150] reported from the Carpathian region that bark beetle first attack trees previously infected by *Armillaria*. James and Goheen [151] found that over 99% of dead or dying trees were affected by root diseases and 80% of them were simultaneously colonized by secondary pests. Capecki [152] has confirmed that stands attacked by *Armillaria* spp. are most strongly threatened by bark beetle in forests of the western Carpathians and that the occurrence of secondary pests is the natural result of greater susceptibility to disease and the poor sanitary state of the stands. In contrast, Christiansen and Husek [153] did not find any significant difference in rot occurrence between dead trees previously attacked by bark beetles and those not attacked by insects. Similarly, Jankovsky et al. [154] found a lack of relationship

between the presence of the bark beetle *Ips typographu* and *Armillaria* spp. infection in spruce stands of the Szumawa Mountains (Czech Republic).

Twery et al. [155] reported the distribution of rhizomorphs of *Armillaria* spp. in uninjured mixed oak stands and in stands which were defoliated 1 and 5 years earlier by insects. Trees weakened by biotic stress were infested by *Armillaria*, with an increased abundance of rhizomorphs observed, especially on plots defoliated 5 years before sampling. The authors consider that trees' predisposal to pest invasions was a result of previous attack by *Armillaria* and deep water stress in the whole root system.

Okland et al. [156] supposed that a warmer climate would influence bark beetle populations, which may move north. The north European spruce forest, so far free from bark beetle outbreaks, showed strongly increased susceptibility to *Ips* spp. in climate change models [157–159]. Similarly, Langvall [160] connected the impact of global warming to the conditions of regeneration of Norway spruce towards the northern and higher elevations in Europe, and significant regional differences in the *I. typographus* behavior, such as voltinism. The negative impacts of drought and *I. typographus* populations in the southern range of the Norway spruce have been described by many authors [161–163]. Infection of spruce roots by *Armillaria* spp can cause production and release of specific compounds, for example, limonene,  $\beta$ -phellandrene, camphene, and bornyl acetate by needles and probably the phloem of weakened trees which are secondary pest attractants [164]. These signals can be specific to infection by *Armillaria*, and can encourage *Ips* spp. beetles to respond to these signals by choosing such trees for settlement [165].

## 7. Conclusions

*Armillaria's* life cycle, host susceptibility, and interactions with the soil and climate have been summarized in many papers. However, several gaps in research have been identified and further work could help us to predict climate change impacts on the pathogen and the forests. We hypothesize that climatic changes and global warming are not the only factors predisposing the roots of weakened trees to *Armillaria* infections, but that the bacteria and fungi, as well as macro-, meso-, and micro-organisms growing in the soil environment around root systems can also directly or indirectly enhance the proliferation of the pathogen and decrease the immune barriers in roots. The rhizomorphs are probably also colonized by endogenous bacteria and fungi that stimulate the growth of *Armillaria* hyphae and aid in the destruction of cell walls by the secretion of enzymes. This speculation requires further research.

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