

***Armillaria* species: Primary drivers of forest ecosystem processes and potential impacts of climate change**

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Species of the fungal genus *Armillaria* are pervasive in forest soils and are associated with widely ranging tree species of diverse forests worldwide (Baumgartner et al., 2011). As primary decay drivers of ecosystem processes, *Armillaria* species exhibit diverse ecological behaviors, ranging from virulent root and/or butt pathogens of diverse woody hosts, such as timber, fruit, nut, and ornamental trees, beneficial saprophytes, or mycorrhizal associates of orchids (Baumgartner et al., 2011). Furthermore, genets of *Armillaria* spp. are recognized as being among the oldest and longest lived organisms on earth, where a single genet (genetically identical individual) has been estimated to occupy up to 965 ha and be of 1,900 – 8,650 years of age (Ferguson et al., 2003).

Although the genus has a world-wide distribution with over 40 recognized morphological species, the northern and southern hemispheres typically do not share *Armillaria* species (Volk and Burdsall, 1995). Several *Armillaria* species appear to have circumboreal or circumaustral distributions. Based on the morphological and biological species concepts, several *Armillaria* species, such as *A. mellea*, *A. solidipes* (= *A. ostoyae*), *A. socialis* (= *A. tabescens*), *A. gallica*, *A. sinapina*, *A. cepistipes*, have been shown to occur in Eurasia and North America (Volk and Burdsall, 1995). Similarly, species, such as *A. limonea*, *A. luteobubalina*, and *A. novae-zelandiae*, occur in Australasia and South America; however, African *Armillaria* species appear to be comprised in two separate clades that are separate from other southern hemisphere clades (Coetzee et al., 2005).

Pathogenic *Armillaria* spp. have diverse ecological behaviors with regard to impacted host species and environmental tolerances that vary among regions (e.g., McDonald et al., 2003). In addition to tree mortality, *Armillaria* root disease can cause growth losses up to 58% in living trees, frequently in the absence of readily observable symptoms (Cruickshank, 2011). Symptoms of *Armillaria* root disease are generally nondescript, such as reduced growth, thinning and yellowing of foliage, or basal resinosis (conifer species); whereas, signs of *Armillaria* root disease are more definitive. These signs can be observed as white mycelial fans under the bark, rhizomorphs (reddish black, flat, shoestring-like mycelial cord) on or beneath the bark

of roots/lower stem and in surrounding soil, and/or honey-colored mushrooms, which are produced only sporadically during the favorable season (Fig. 1).

To develop management approaches for *Armillaria* root disease, a first step is to identify which *Armillaria* species are present or potentially present on sites of interest. Currently, phylogenetic analysis, based on DNA sequences, is among the most effective and cost-efficient tools to identify *Armillaria* species (e.g., Ross-Davis et al., 2012a; Fig. 2). Surveys and biological sampling (rhizomorphs, mycelial fans, rotten wood, and fruiting bodies) are also critical to understand the geographic distribution of each *Armillaria* species and the distribution of impacted host tree species. After sufficient data are collected on the geographic locations of each *Armillaria* spp. of interest, bioclimatic modeling can be used to predict geographic areas that have suitable climate space (the geographic area that is climatically **suitable** for a particular species' survival) for the root disease pathogen, and predict areas at risk for *Armillaria* root disease (Klopfenstein et al., 2009).

Although the genus *Armillaria* has a very wide host range, each *Armillaria* species exhibits varying impacts depending on host species and climate. In a general sense, pathogenic *Armillaria* spp. have a greater impact on stressed trees and trees that are maladapted to the site. For this reason, negative impacts of *Armillaria* root disease are predicted to increase under climate change as more trees become maladapted to current and future climates (e.g., Kliejunas, 2011; Sturrock et al., 2011). The suitable climate space of *Armillaria* and its host species, as well as potential impacts of *Armillaria* root disease, can be predicted under various projected climate-change scenarios. *Armillaria* root disease is expected to increase within geographic areas where climate is predicted to remain suitable for the pathogen, but less suitable for the host. For example, Fig. 3 illustrates the current and future distribution for the pathogenic *A. solidipes* and Douglas-fir (*Pseudotsuga menziesii*) in the interior northwestern forests of the USA. In this example, an increase in *Armillaria* root disease is expected in year 2060, due to decreased availability of suitable climate space for Douglas-fir (Rehfeldt et al., 2006; Fig. 3D) coupled with consistent availability of suitable climate space predicted for *A. solidipes* (Fig. 3B).

Armillaria root disease is not easily managed because pathogens are pervasive and long-term inhabitants of the forest site. A preferred management approach is to favor tree species that are more tolerant of the disease, and well adapted to the site under current and future climates. Other management methods, such as inoculum reduction and biological control, have generated mixed results, depending on the site (e.g., Fox, 2000; Vasaitis et al., 2008). Ongoing studies are examining the genome and transcriptome (expressed genes) of *Armillaria* spp. (Baumgartner et al., 2011;

Ross-Davis et al., 2012b). Such high-powered genetic tools should provide insight into the genetic interactions among hosts, pathogen, and other components for the biotic and abiotic environment. As these interactions become better understood, management techniques will become further refined to mitigate damage cause by *Armillaria* root disease.

Keywords

Root disease; climate change; forest disease; bioclimatic modelling; phylogenetics

Figures and Tables



Fig. 1 Symptoms and signs of *Armillaria* root disease. (A) Mortality and growth loss of Douglas-fir (*Pseudotsuga menziesii*) within an *Armillaria*-root-disease center. (B) Basal resinosis of Douglas-fir with *Armillaria* root disease. (C) Mycelial fan of *Armillaria solidipes* located under the bark of an infected host tree. (D) Fruiting bodies (basidiomata or mushrooms) of *A. solidipes*. (E) Rhizomorphs (reddish black, flat, shoestring-like mycelial cord) of *A. solidipes* found on or beneath the bark of roots/lower stem and in surrounding soil.

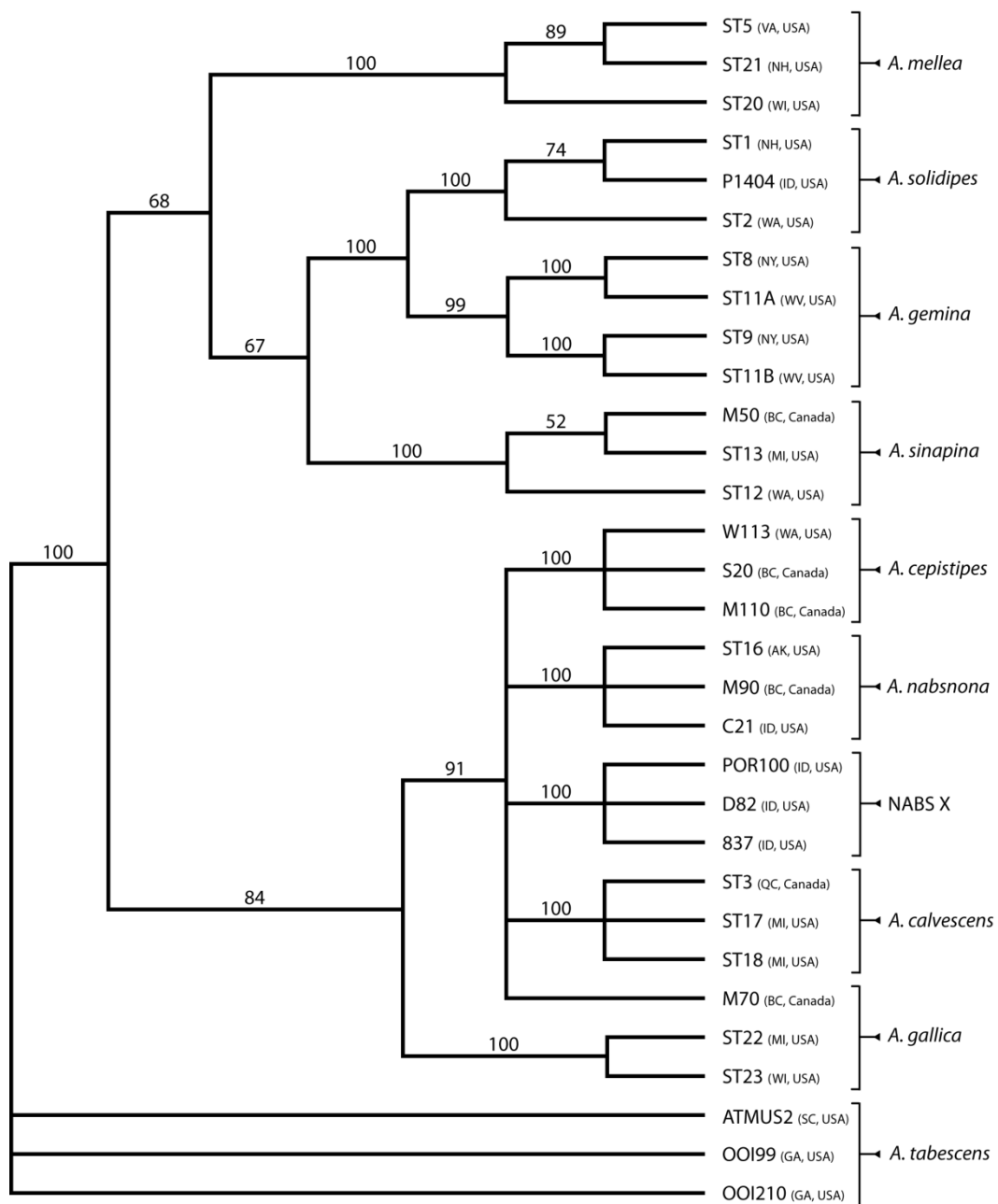


Fig. 2 Example of a phylogenetic tree of North American *Armillaria* spp. that is useful for species identification; a 50% majority-rule from Bayesian analysis of the translation elongation factor 1-alpha gene (Ross-Davis et al. 2012a).

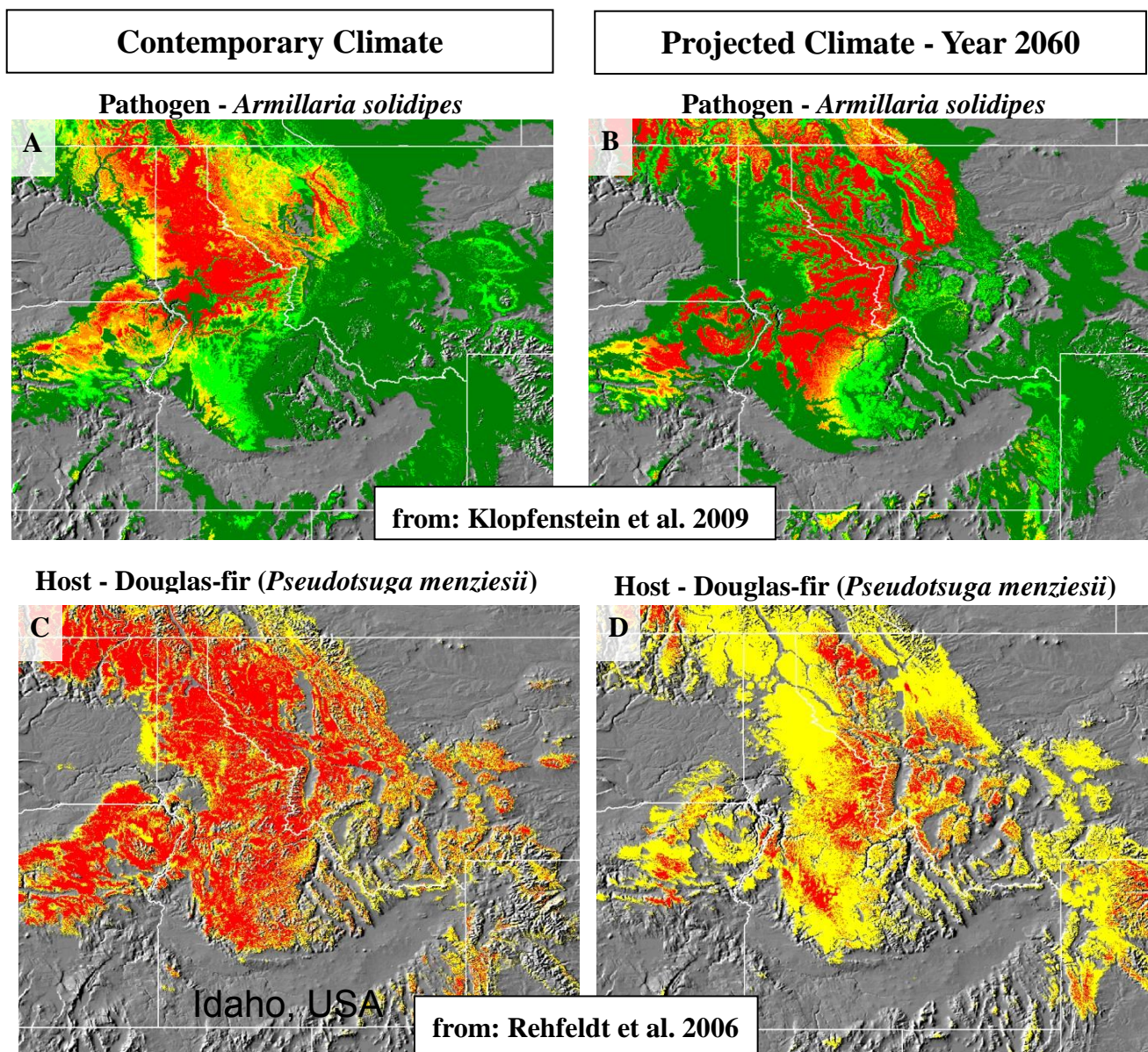


Fig. 3 Example of bioclimatic modeling of suitable climate space for pathogen (*Armillaria solidipes*) and host (Douglas-fir, *Pseudotsuga menziesii*). On left: predicted suitable climate space of (A) pathogen and (C) host under the current climate. On right: predicted suitable climate space for (B) pathogen and (D) host under modest future climate-change scenario for year 2060 (CGCM3 GCM (Canadian Centre for Climate Modeling and Analysis, SRES A1B)). Red color = geographic areas with the highest probability of having suitable climate space; other colors = lower probability of suitable climate space; and no color = low probability of suitable climate space. Under future climate change scenarios, *Armillaria* root disease is expected to increase in areas where the pathogen is well adapted and the host is maladapted.

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