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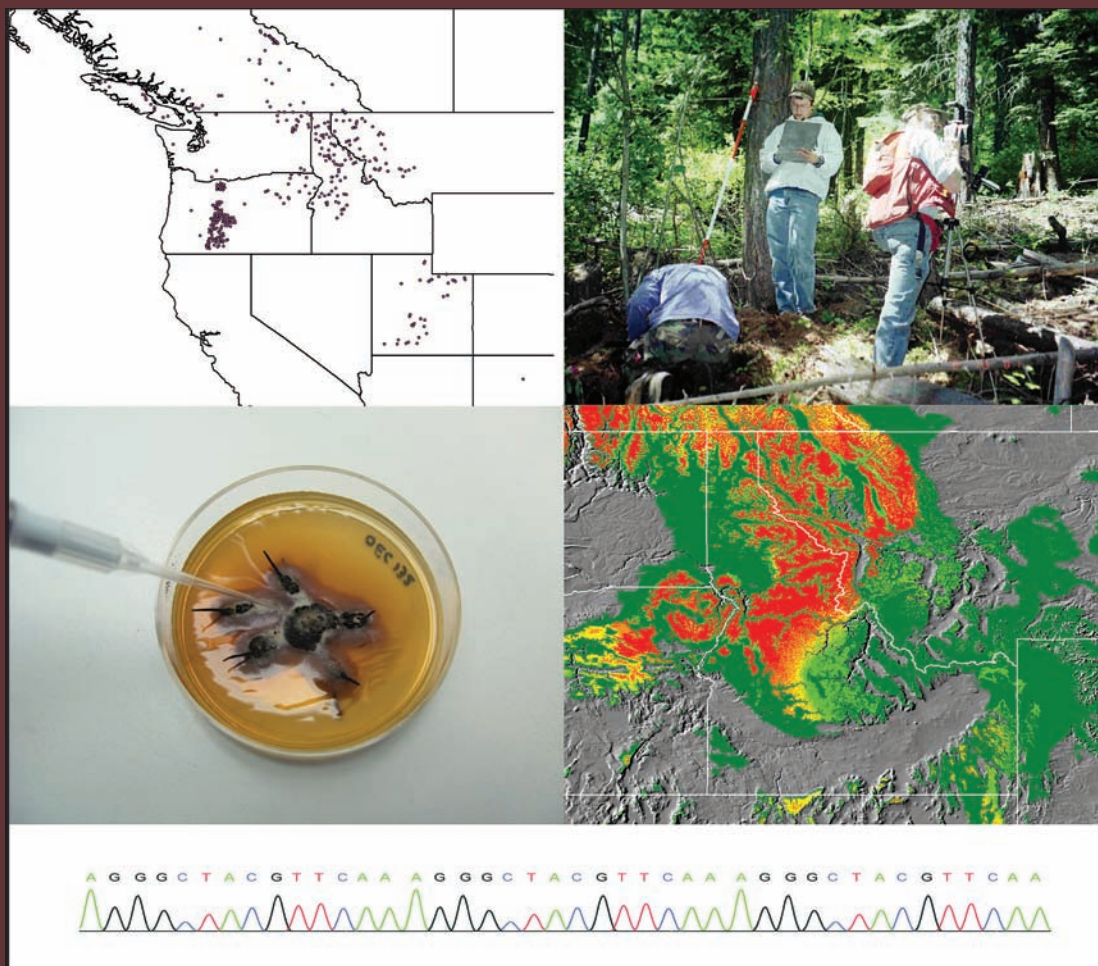
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Approaches to Predicting Potential Impacts of Climate Change on Forest Disease:

An Example With Armillaria Root Disease

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Bryce A. Richardson, and John Lundquist



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Abstract

Predicting climate change influences on forest diseases will foster forest management practices that minimize adverse impacts of diseases. Precise locations of accurately identified pathogens and hosts must be documented and spatially referenced to determine which climatic factors influence species distribution. With this information, bioclimatic models can predict the occurrence and distribution of suitable climate space for host and pathogen species under projected climate scenarios. Predictive capacity is extremely limited for forest pathogens because distribution data are usually lacking. Using *Armillaria* root disease as an example, predictive approaches using available data are presented.

Keywords: climate change, forest diseases, *Armillaria*, bioclimatic models, forest pathogens, global warming, MaxEnt

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Introduction

Climate change is expected to cause dramatic, direct impacts on the health of forests worldwide. For some areas of the world, computer models predict that many tree species will become maladapted (i.e., ill-suited to survive, grow, and reproduce in the ambient environment) to the predicted climate change over the next century (e.g., Rehfeldt and others 2006). Impact on forest health will be even greater if damage from diseases and insects is enhanced by climate change (Dukes and others 2009; Klienjunas and others 2008; McCarthy and others 2001; Sturrock 2007). Thus, it is critical to consider the impacts of disease when predicting impacts of climate change. If impacts of climate change on forest disease can be predicted, then appropriate management practices can be implemented to minimize disease impacts.

Many types of tree diseases threaten the health and sustainability of forests. In this paper, we focus on a root disease. Climate change will likely have significant influences on tree root diseases, such as Armillaria root disease (Ayres and Lombardero 2000; Kliejunas and others 2008; McCarthy and others 2001; Sturrock 2007). Climate change could alter patterns of root disease by 1) direct effects on the development, survival, reproduction, dispersal, and distribution of hosts and pathogens; 2) physiological changes in tree defenses; and/or 3) indirect effects from changes in the abundance of mutualists and competitors (Ayres and Lombardero 2000).

The goal of this paper is to discuss approaches to predict impacts of climate change on root disease; however, similar approaches could be applied to other forest diseases. Our work with Armillaria root disease is used as an example.

Forest Disease: an Interaction of Host, Pathogen, and Environment

As a first step in predicting tree diseases, the conditions that are necessary for disease to occur must be considered. For disease to occur, a virulent pathogen and susceptible host must occur together at a time when the environmental conditions are favorable for the development of disease. This concept, known as the “Plant Disease Triangle,” is a fundamental principle in basic plant pathology (fig. 1). Thus, we must consider the pathogen, host, and environment when developing approaches to predict where forest diseases will occur.

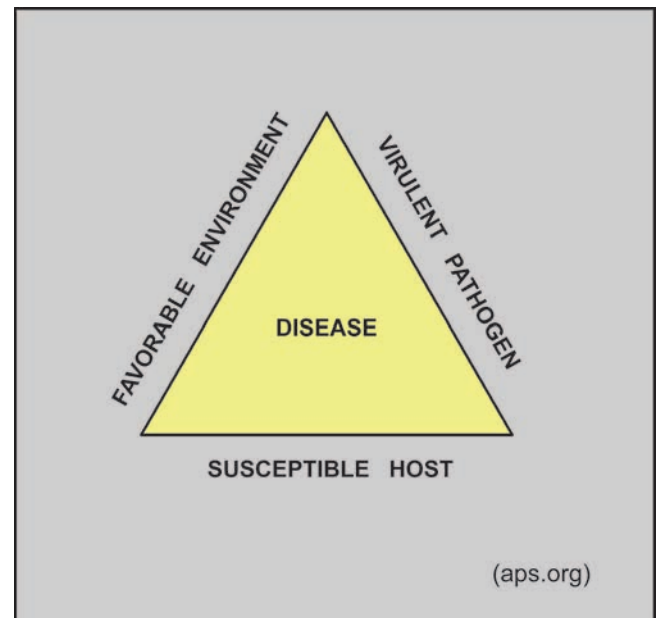


Figure 1—The plant disease triangle. Plant disease occurs when a virulent pathogen comes into contact with a susceptible host at a time when the environment is favorable for the development of disease.

Pathogens That Cause Armillaria Root Disease

The *Armillaria* genus contains many species that can cause Armillaria root disease. Because the pathogen must be accurately identified at a species or subspecies level to allow predictions of disease, we will focus on one species, *Armillaria solidipes* (a currently recognized older name for *A. ostoyae*) (Burdall and Volk 2008). This pathogen has a wide distribution across the Northern Hemisphere (fig. 2) and has a wide host range that includes most conifers and several hardwood species. *Armillaria solidipes* plays diverse ecological roles in forests, ranging from being a beneficial saprophyte to a virulent pathogen. The pathogen inhabits diverse environments and has the potential for long-term and widespread occupancy of a site. For example, one vegetative clone of *A. solidipes* is predicted to occupy 965 ha, with an age estimate of 1,900 to 8,650 years (Ferguson and others 2003). In addition, significant genetic diversity has been demonstrated within *A. solidipes* (Hanna and others 2007), and it may have the potential to hybridize with other, closely related *Armillaria* species (Kim and others 2006).

Armillaria solidipes causes tree mortality, which ranges from being extensive within a disease center to

being diffuse across a stand. Cumulative mortality from Armillaria root disease can reach 15-20% at 20 years of age (Morrison and Pellow 1994; Whitney 1988). Furthermore, root disease caused by this pathogen can also result in significant growth loss (e.g., up to 40% volume loss over 4 to 8 years in 18-year-old Douglas-fir, *Pseudotsuga menziesii*), frequently in the absence of readily observable symptoms (Cruickshank 2000; Morrison and others 2000). Although *A. solidipes* produces mushrooms in autumn under some environmental conditions, it is more consistently found 1) as rhizomorphs (root-like structures that occur on the root surface, under the bark, or in the soil); 2) as mycelial fans that occur under the bark; or 3) in decayed wood.

Hosts of Armillaria Root Disease

While *A. solidipes* has an extremely wide host range across the Northern Hemisphere, host susceptibility varies with geographic location. In western North America, *A. solidipes* can cause major growth losses in Douglas-fir or true firs (*Abies* spp.; Kile and others 1991). Because of its economic value and widespread occurrence in western North America, we focus here on Douglas-fir to predict potential impacts of Armillaria root disease.

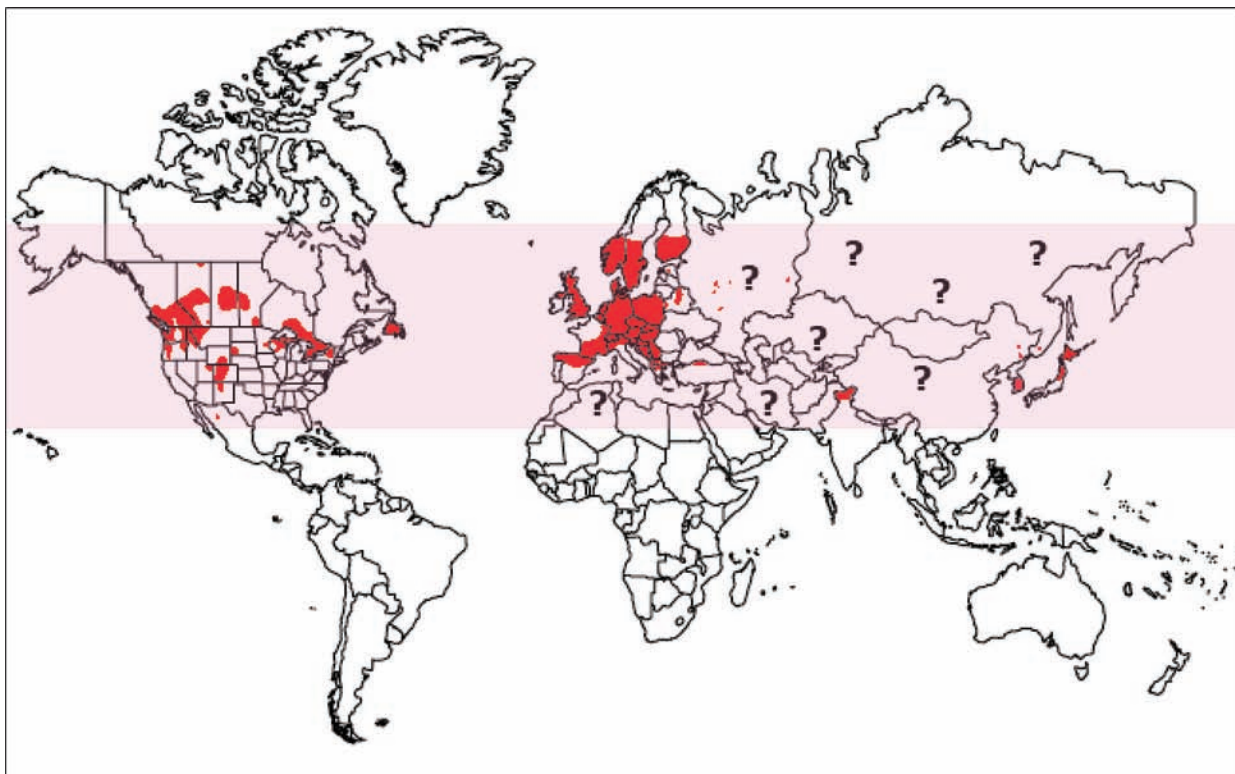


Figure 2—Distribution of *Armillaria solidipes* (depicted in red) (Hanna 2005).

Determining the Potential Distribution of the Pathogen

Accurate baseline information on pathogen occurrence is needed to develop predictions of the pathogen's current distribution. Survey plots, scattered across ranging geographic areas and diverse climates, represent a reliable method for obtaining baseline information on pathogen distribution (fig. 3). For a chronic root pathogen such as *A. solidipes*, which is not readily detected on a site based on above-ground symptoms, surveys of all host species on plots must be quite thorough and include excavation of tree roots. Samples collected from fruiting bodies, rhizomorphs, mycelial fans, or decayed wood are all acceptable for establishing fungal cultures (fig. 3). Detailed plot information, such as precise location (e.g., GPS coordinates at ± 30 -m resolution or better), elevation, slope, aspect, soil type, habitat type, and other environmental data, is

also needed. Because pathogen samples must be accurately characterized using DNA-based methods, it is recommended that pathogens be placed into culture to facilitate further study.

Accurate identification of the pathogen species, subspecies, or population is critical to establishing a data set on pathogen distribution. Because it is difficult to identify many forest pathogens, such as *Armillaria* spp., based on vegetative morphology, DNA-based diagnostic methods are particularly useful to help validate taxonomic identification (fig. 4). For this example, cultures of *A. solidipes* were identified using PCR and DNA sequencing of the intergenic spacer-1 (IGS-1) region of the ribosomal DNA (rDNA) (Kim and others 2006).

This approach establishes a data set from plots with confirmed presence or absence of accurately identified *A. solidipes*. A large data set is preferred — the larger the data set the more accurate will be the predictions of distribution.

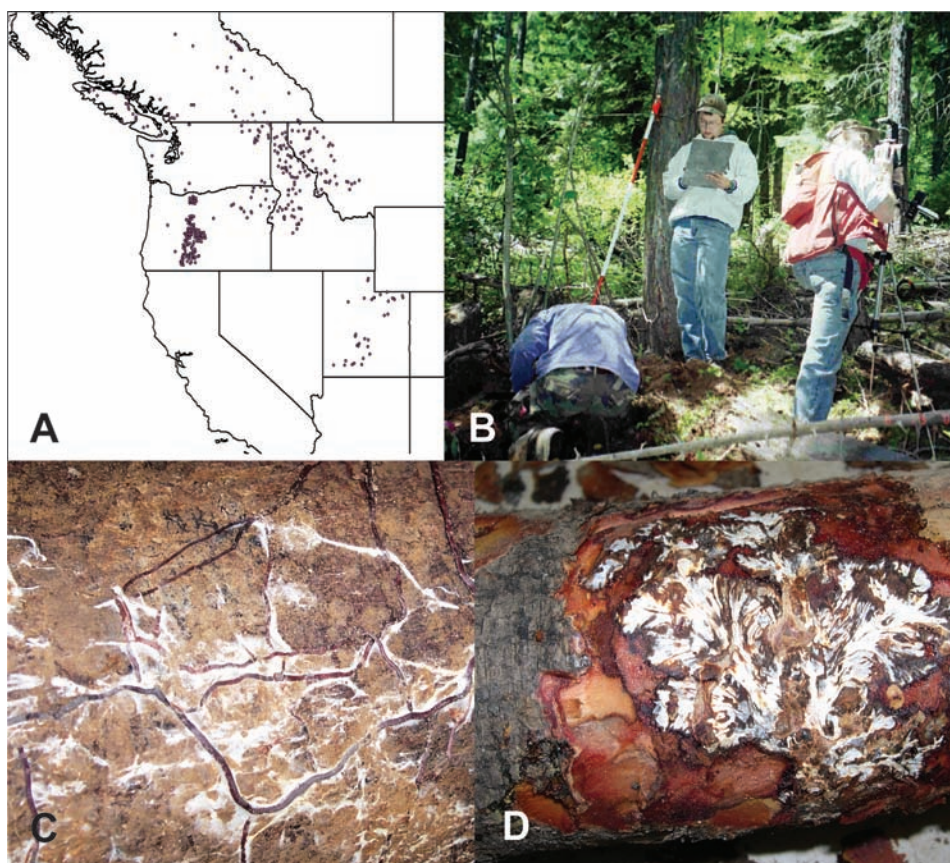


Figure 3—Survey plots of *Armillaria* root disease. A. Available presence/absence data for *Armillaria* spp. in western North America, including approximately 400 0.04-ha plots were established in western North America; B. Roots of each tree species were thoroughly inspected for the pathogen. Precise location and associated collection data were recorded; C. Rhizomorphs of *Armillaria* spp. were collected (photo courtesy of the Intermountain Forest Tree Nutrition Cooperative); D. Mycelial fans of *Armillaria* spp. were also collected (photo courtesy of the Intermountain Forest Tree Nutrition Cooperative).

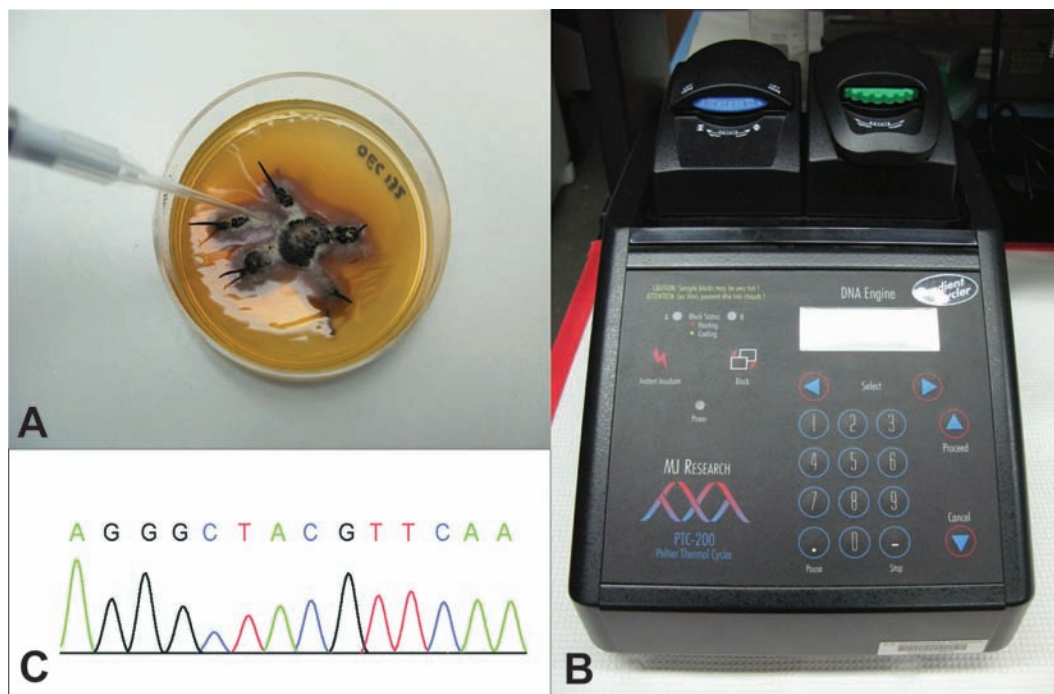


Figure 4—Identification of *Armillaria* species. A. Samples of *Armillaria* spp. were established in culture; B. Polymerase Chain Reaction (PCR) was used to amplify the intergenic spacer-1 (IGS-1) region of ribosomal DNA (rDNA); C. DNA sequences of IGS-1 were used to confirm the identification of *A. solidipes* or other species.

Determining the Potential Distribution of the Host

As with the pathogens, it is also necessary to have baseline information on the distribution of the host-tree species. Although general range information is available for many tree species, more accurate predictions of distributions must rely on survey plot data that records species presence or absence at precise geographic locations (e.g., GPS coordinates) and elevations. Fortunately, survey plot data are available for several tree species. For example, the U.S. Forest Service, Forest Inventory and Analysis (FIA) National Program maintains numerous permanent plots on forest and nonforest lands that have associated plot data for tree species and other plant species (Alerich and others 2004; Bechtold and Patterson 2005). Data sets from such survey plots are critical to developing models to predict the present distribution of forest species.

Climate Surfaces

Understanding how climatic factors vary across the global landscape is necessary to determine the influence of climatic factors on plant disease. Based on information

from numerous weather stations, various methods are available that create a climate surface, which is spatially interpolated climate data on a landscape grid (Hijmans and others 2005). Climate data are available from several sources, such as WorldClim (<http://www.worldclim.org/>; Hijmans and others 2005), Daymet (<http://www.daymet.org/>), Rehfeldt and others (2006; <http://forest.moscowfsl.wsu.edu/climate/index.html>), and others. The climate surfaces from these sources allow estimations of multiple climatic factors, such as monthly temperatures, monthly moisture, and complex interactions among multiple factors, for a specific geographic location and elevation. For example, the climate surface for Degree Days >5 °C, a measure of warmth, is shown across western North America (fig. 5A).

Models to Predict Present Distribution of the Host and Pathogen

Models to predict species distribution are based on the data set of precise locations where the species is known to be present or absent. Climate surfaces are used to estimate values for climate variables for each location. The analysis determines which climatic factors or

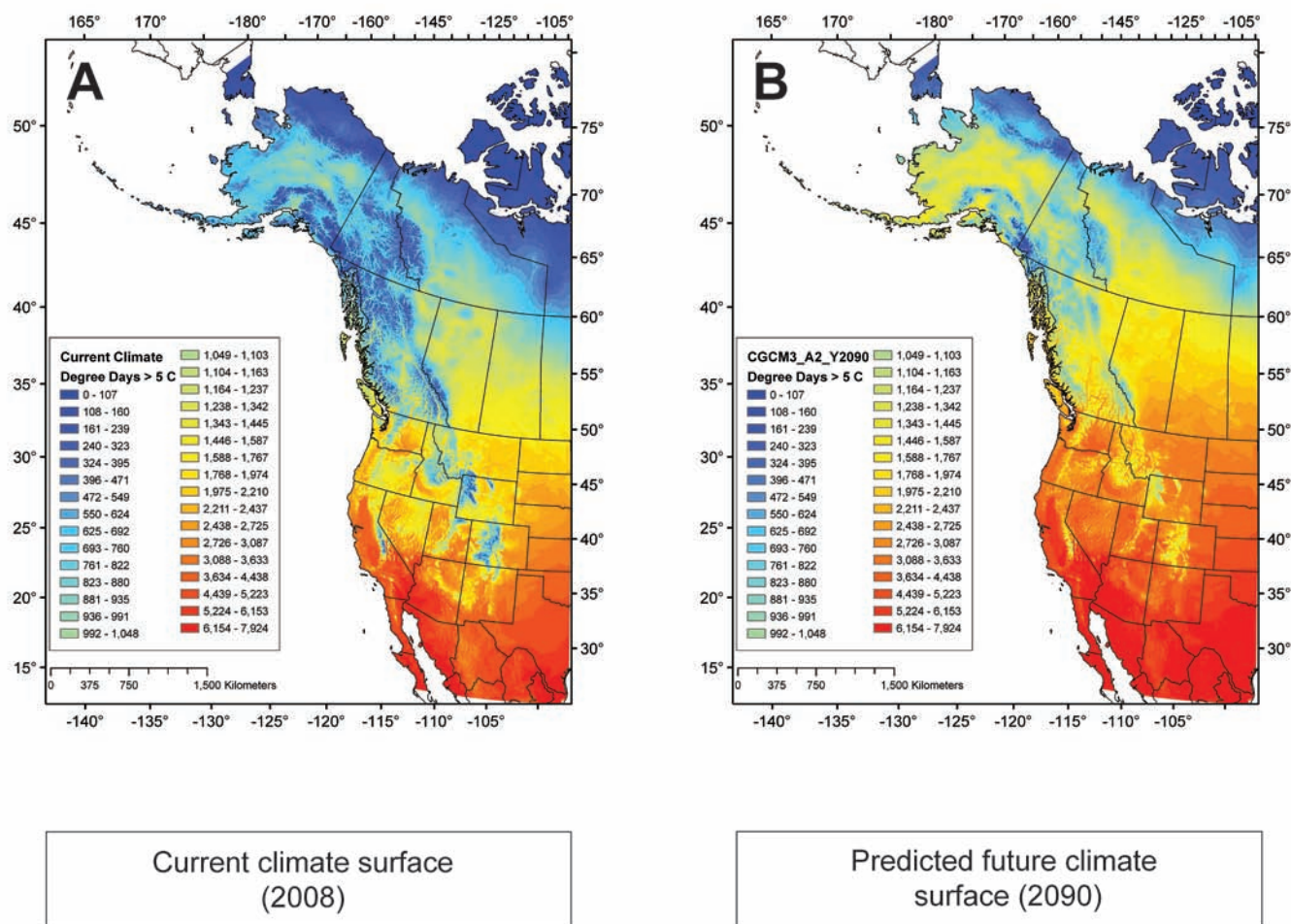


Figure 5—Example of current and future climate surface for one climatic factor (Degree Days >5 °C) using the CGCM3 model and the A2 “worst-case” greenhouse-gas scenario provided by The Intergovernmental Panel on Climate Change (IPCC) (Rehfeldt and others 2006). A. Current climate surface; B. Projected future climate surface for the year 2090.

interactions predict the presence and absence of the host species. The critical climate variables are incorporated into a bioclimatic model that predicts the probability of suitable climate space (i.e., the geographic area that possesses a climate suitable for species survival) for the species across the landscape within the area that is being analyzed. For example, Rehfeldt and others (2006) used a Random Forest classification tree algorithm to model suitable climate space for Douglas-fir across the landscape (fig. 6B). This prediction was based on ca. 120,000 plots (20,171 plots with Douglas-fir present) that were available from FIA (U.S. Forest Service) and resulted in an error of omission approaching 0 and an error of commission of less than 9%. Lower sample numbers can be used for predictive models, but the user must determine the acceptable level of accuracy for their purposes.

It is difficult to predict pathogen distribution with high accuracy because data sets confirming pathogen occurrence are usually quite limited in comparison with host data sets. For predicting the potential current distribution of *A. solidipes*, we based our prediction on ca. 400 survey plots of which *A. solidipes* was found on 202 plots. Several different bioclimatic models can be used to predict *A. solidipes* distribution. Figure 6A shows a probability distribution for suitable climate space generated using Maximum Entropy modeling (MaxEnt; Phillips and others 2006; Phillips and Dudik 2008) that is based on presence-only data. This spatial model could correspond to the present distribution of *A. solidipes* if this species has expanded to its ecological breadth and climate is the primary factor that influences its distribution.

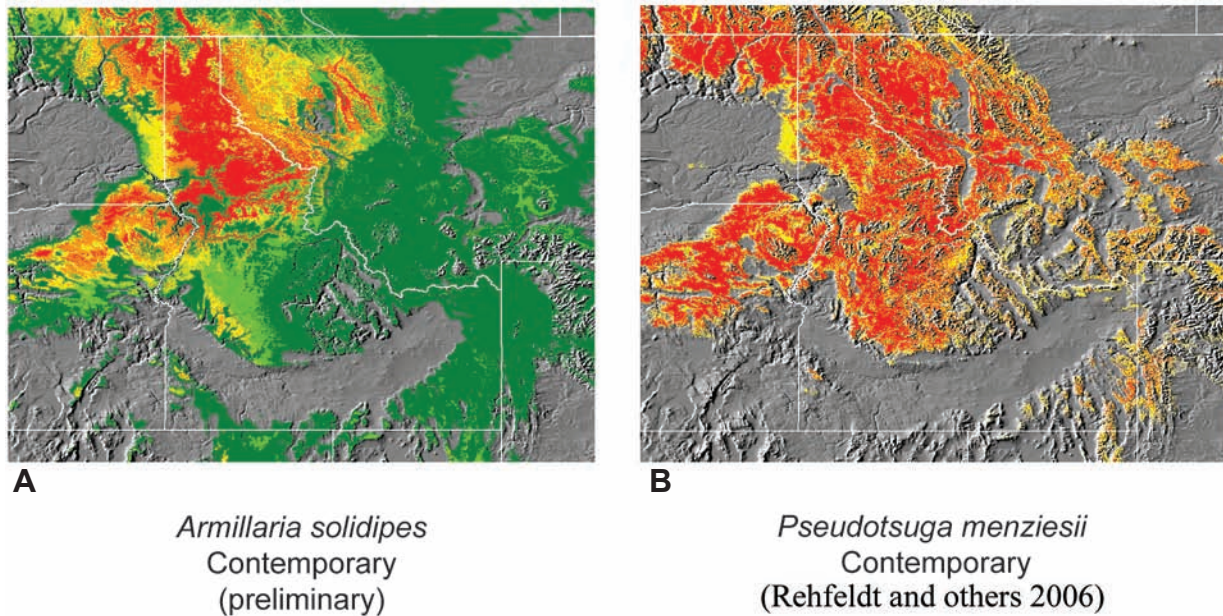


Figure 6—Examples of approaches to predict current suitable climate space for *Armillaria solidipes* and a susceptible host, Douglas-fir (*Pseudotsuga menziesii*), in the interior northwestern United States. A. Preliminary example of an approach to predict suitable climate space for *A. solidipes* using MaxEnt and the climate data and variables of Rehfeldt and others (2006); B. Predicted suitable climate space for Douglas-fir using Random Forest classification (Rehfeldt and others 2006). Colors represent the number of tree votes cast, analogous to the probability of occurrence. Yellow = 50 to 75, Red 76 to 100 votes.

Models to Predict Future Climate Surfaces

General Circulation Models (GCMs) are a class of computer models that forecast weather and climate change. GCMs can be used with various greenhouse gas emission scenarios, such as those proposed by the Special Report on Emissions Scenarios (SRES), an intergovernmental panel on climate change (IPCC), to predict the future global climate surface (McCarthy and others 2001). Examples of GCMs include 1) CGCM3 — Canadian Centre for Climate Modeling and Analysis (Flato and Boer 2001); 2) HadCM3 — Hadley Center (Gordon and others 2000); and 3) GFDL CM2.1 — Geophysical Fluid Dynamics Laboratory (Delworth and others 2006). SRES scenarios are based on different assumptions of population growth, economic development, and technological development. Three common SRES scenarios that represent low, moderate, and high estimations of future atmospheric CO₂ concentrations include the SRES B1 (atmospheric CO₂ concentration stabilizing at just below 550ppm by 2100), SRES A1B (CO₂ rate still rising but at a slower rate to 700ppm by 2100), and the “worst case” SRES A2 (increasing CO₂ shows no sign of slowing down with 800ppm by 2100) (Peterson and others 2008). Figure 5

shows an example of current and future projections of the climate surface for one climatic factor (Degree Days >5 °C) produced by the CGCM3 model and the A2 “worse case” SRES scenario. However, according to the Global Carbon Project (2008), the most recent records of the annual mean growth rate of atmospheric CO₂ show levels have increased faster than projected. The suitable climate space for host and pathogen species across the landscape can then be projected onto the future climate surfaces showing potential changes in species distributions based on the climate change scenario.

Models to Predict Future Suitable Climate Space for Hosts and Pathogens Under Changing Climate Scenarios

Future climate surfaces produced by a GCM and specified scenario for greenhouse-gas emissions serve as the basis for bioclimatic modeling of suitable climate space for hosts and pathogens across future landscapes. Different models and greenhouse gas emission scenarios produce different future climate surfaces, and projections of climate change are variable. Further comparisons

among the GCMs and discussion of their reliability are beyond the scope of this paper. However, predictions of climate change impacts on forest disease are dependent on an accurate GCM projection.

Figure 7 shows examples of approaches to predict suitable climate space for *A. solidipes* and Douglas-fir within the interior northwestern United States. In these examples for the decade 2060, minor shifts in the probability of suitable climate space for *A. solidipes* are apparent in this region. In contrast, the probability of suitable climate space for Douglas-fir is markedly decreased. If this projection holds true, it is reasonable to assume that many Douglas-fir stands in this region may become stressed due to climate maladaptation. Such stress could render trees more susceptible to Armillaria root disease.

For such prediction models, it must be noted that predicted suitable climate space for a species does not necessarily correspond to the future distribution of that species. Future species distribution will depend on many factors such as population structure, migration, regeneration, competition, susceptibility to insect attack and diseases, and other interacting factors. The realized distribution of a species will be determined by the interactions among diverse biological, climatic, and environmental factors.

Toward Determining When and Where Disease Will Occur

Predictions of potential distribution of forest pathogens and hosts under current and changing climate will provide valuable insights about where hosts and pathogens might co-occur and thus, where diseases might occur. It is important to note, however, that the co-occurrence of suitable climate space for the pathogens and their host(s) does not necessarily result in disease. The establishment and severity of disease depends on many interacting factors, including: seasonal or annual weather, micro-climatic factors, age and vigor of host plants, pathogen inoculum potential, host tree density, stand history, past management practices, host species composition and age, localized populations of hosts and pathogens, occurrence of pathogen vectors, biological control agents, and several other factors. One aspect of changing climate is the increased variability in weather and a greater likelihood of extreme weather (e.g., high temperatures, low temperatures, drought, excessive rain events) (IPCC 2001). Weather events could increase or decrease the level of forest disease depending on the weather event and the pathosystem. Predictions of

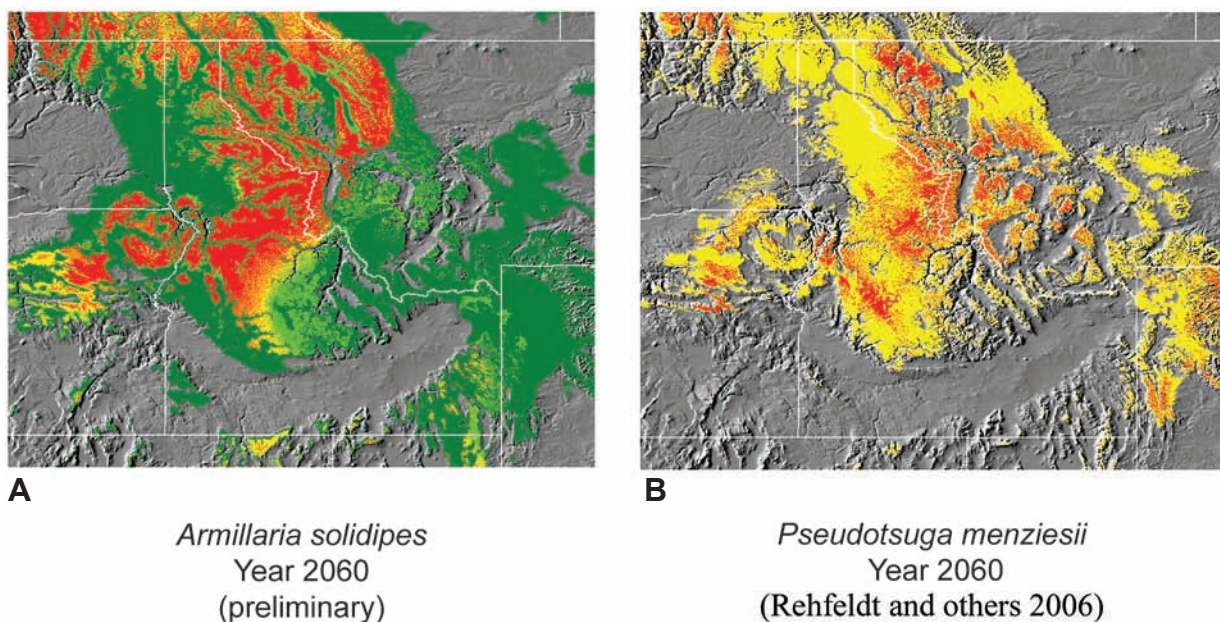


Figure 7—Examples of approaches to predict future suitable climate space for *Armillaria solidipes* and a susceptible host, Douglas-fir (*Pseudotsuga menziesii*), in the interior northwestern United States. A. Preliminary example of an approach to predict future suitable climate space for *A. solidipes* in the year 2060 using MaxEnt, CGCM3 GCM (Canadian Centre for Climate Modeling and Analysis, SRES A1B), and climate data from Rehfeldt and others (2006); B. Predicted suitable climate space for Douglas-fir using Random Forest classification (Rehfeldt and others 2006). Colors represent the number of tree votes cast, analogous to the probability of occurrence. Yellow = 50 to 75, Red 76 to 100 votes.

forest disease occurrence will likely improve when other contributing factors are incorporated into classification models. Because of lacking prerequisite information, it will likely be challenging to develop approaches to accurately predict the spatial distribution of some forest diseases. For this reason, many assessments of forest disease must still rely on information obtained at the stand level.

Regarding our *Armillaria* root disease example, it appears that *A. solidipes* and Douglas-fir are both broadly well adapted to the existing climate in the interior northwestern U.S. (fig. 6). However, *Armillaria* root disease is currently quite severe on Douglas-fir in this region. Because *Armillaria* root disease is generally more severe on trees predisposed by stress, it seems reasonable that this disease could become even more severe in the future if Douglas-fir is subjected to climate stress, such as is projected for the interior northwestern U.S. (Rehfeldt and others 2006: fig. 6B). Thus, we might expect increased likelihood of disease if 1) host trees are maladapted to climate or subjected to other stress agents such as seasonal weather (e.g., moisture or temperature extremes), insect attack, wounding, etc. or 2) past stand history or management has contributed to increased inoculum potential (McDonald and others 1987) such as by leaving colonized stumps or selectively removing tolerant tree species. Forest management decisions can be based on predictions of host and pathogen distribution coupled with other stand information.

Forest Management Applications

Predictions of forest disease incidence and severity under current and changing climate scenarios are useful to managers for strategic and management planning. Several management coping strategies have been proposed, including 1) favoring forest species and populations that are adapted to future climatic conditions; 2) altering species composition and diversity to favor resistant/tolerant hosts in areas where disease presence is predicted; 3) changing forest structure and age patterns at landscape scales; and 4) other strategies, such as reducing inoculum potential by removing its source, avoiding wounding or stressing trees, and increasing biological control activity. These suggestions are largely based on historical information; however, managers may face environmental conditions that have no historical precedent. For this reason, it is difficult to base proposed management actions on scientifically rigorous research. Managers must recognize that a changing climate will likely create novel conditions for which previous experience is unavailable.

Thus, an increased emphasis is needed on strategies that consider ecosystem adaptability.

Regarding the *Armillaria* root disease example, a number of management options are available depending on the situation and management objectives. These options could include 1) selectively removing species that are maladapted or predicted to become maladapted; 2) planting with seed-sources that are well-adapted to the predicted climate during the tree's lifespan; 3) selectively favoring seral species (e.g., *Pinus* spp. or *Larix* spp.) that are more tolerant of *Armillaria* root disease and adapted to the predicted climate; 4) avoiding wounding of trees, which may facilitate pathogen infection; 5) employing treatments that reduce or do not exacerbate tree stress; 6) applying treatments that minimize woody substrates that can serve to build up the inoculum potential; or 7) other less developed practices, such as fostering biological control. As with most forest management, management practices must be selected for the specific stand and objectives.

Additional Information Needed to Refine Disease Predictions

Approaches that are currently available for predicting climate influences on forest disease provide a solid foundation for forest planning. However, further refinements will improve accuracy and utility of these approaches. Of critical need is more information on the current distribution of accurately identified pathogens. Prediction models can be further improved by including additional information, such as more precise climate data, other geographic information (e.g., slope, aspect, topography), and other environmental data (e.g., soil type, habitat type). Improved precision will be achieved by understanding the population structure of hosts and pathogens and the adaptation of these populations to climatic factors. Other interacting biotic factors, such as the distribution and activities of biological control agents or vectors, also influence the occurrence of forest disease and should be considered where they are relevant. Once climatic influences on host and pathogen distribution are better understood, information is frequently needed to determine the climatic conditions, seasonal/annual weather, and microclimates that are suitable for the development of disease. Many forest diseases may also be influenced by inoculum potential, stand history, stand vigor, stand age, stand structure, stand density, and many other interacting factors that may require assessment at the stand level. Thus, continued surveys and research can provide necessary information for refining predictions of climate influence on diverse forest diseases.

Methods and information are available to continue refining predictions of climatic influences on forest disease. Geographic data (e.g., slope, aspect, and topography) can be obtained from various landscape modeling software (e.g., Google™ Earth, DeLorme Xmap®, ESRI's ArcGIS and ArcMap) and websites (e.g., USGS). Similarly, soils data are available for many regions from diverse sources, such as government agencies (e.g., Natural Resource Conservation Service) or commercial sources. Populations and phylogenetic relationships of hosts and pathogens can be determined by the application of genetic markers (Hamelin 2006; Kim and others 2005; Richardson and others 2005). Predicting the distribution of biological control agents or vectors can be accomplished in a manner similar to predictions for the hosts and pathogens. Furthermore, insights on the role of host maladaptation and disease development can be gained from disease surveys that include hosts growing on the margin of their range. If warranted, remote sensing tools (e.g., light detection and ranging — LIDAR, satellite imagery, spectral analysis) can be used to obtain stand-level information such as stand vigor, age, structure, and density. Other factors that contribute to disease incidence, such as stand history and inoculum potential, could be determined for the individual stands of interest.

An integration of diverse tools and data is necessary to improve predictions for climatic influence on forest disease. Reliable predictions are especially critical to address and mitigate future impacts of climate change on forest disease, which will likely be quite severe in many regions if this issue is neglected. Fortunately, approaches are currently available to develop models for predicting the potential impacts of climate change on forest disease. The health of our future forests is dependent upon continued efforts to develop and refine these models in conjunction with other predictive tools.

Acknowledgments

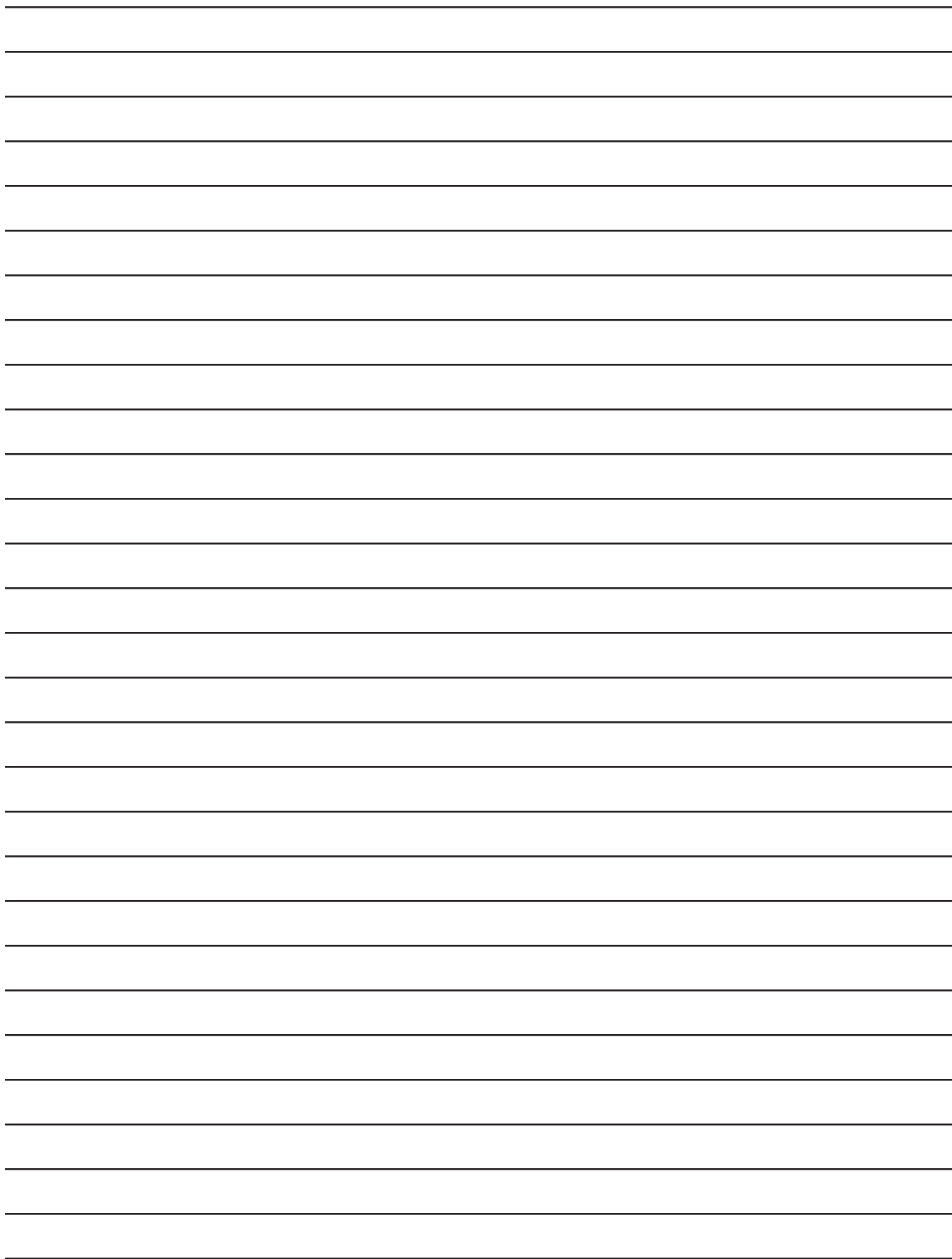
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