Introduction

This Chapter discusses the development and use of models to predict areas at risk for Phytophthora ramorum occurrence, and summarizes the literature on modeling of the spatial-temporal aspects of the disease.

Risk Models

Disease models are used to predict and describe the interaction between the environmental, host and pathogen variables that result in disease. The variables used are based on laboratory and field data regarding the host and the pathogen, as well as on disease spatial and temporal variability (http://www.ipm.ucdavis.edu/DISEASE/DATABASE/diseaseModelDatabase.html). Using climate and P. ramorum host distribution data, computer models that predict areas at risk for pathogen occurrence have been developed. These risk models are valuable tools used by researchers, managers and policy makers to assist in early detection, survey, prevention, and regulatory policy decisions.

Regional risk models: Models predicting the potential distribution of P. ramorum in California have been developed. Meentemeyer and others (2004) developed an expert knowledge-driven, rule-based GIS infection risk model (a rule-based model uses research data and expert input, rather than statistical inference, to determine the importance of predictor variables), to predict the risk of spread and establishment of P. ramorum in California based on plant host susceptibility and weather variables (precipitation, relative humidity, maximum temperature and minimum temperature). Host distribution and monthly weather conditions were analyzed in a GIS to generate risk ranks per-variable and per-month. Spread risk predictions were then generated by combining the variables over the 6 month pathogen reproductive period (December through May) and averaged to generate the risk map (Fig. 1).
Fig. 1. Six-month average (December-May) predicted spread risk map for *Phytophthora ramorum* in California (Meentemeyer and others 2004).
The model characterized the climate of coastal California—from Del Norte County in the north to San Luis Obispo County in the south—and the western slopes of the northern Sierra Nevada in Butte and Yuba counties, as moderately to highly suitable for establishment and spread of *P. ramorum* from December to May.

Guo and others (2005) used and compared one-class and two-class support vector machines (SVMs) techniques to predict the potential distribution of *P. ramorum* in California. Because the data often required by other methods to map the predicted spread of a disease may be unknown with a recently introduced pathogen such as *P. ramorum*, the authors compared one-class SVM models (using presence only data) and two-class SVM models (using both presence and pseudo-absence data). Fourteen variables (seasonality of climatic variables such as temperature, precipitation and solar radiation—which are considered key to limiting *P. ramorum*—as well as distance to main roads and distance to edges of patches of hosts) were used to predict the potential distribution of *P. ramorum* in California. The one-class SVM predicted a greater risk area (Fig. 2), including much of the foothills of the central Sierra Nevada, and along the coast in Humboldt County to the north and Los Angeles County to the south. The authors suggested that one-class SVMs are computationally more efficient (no need to generate pseudo-absence data) than two-class models, and are more applicable in the case of a new invasive species where absence data are not available.

![Fig. 2. Predicted area of sudden oak death risk in California. Mapped results from: (A) one-class SVMs; and (B) two-class SVMs (Guo and others 2005).](image)

1 Techniques for separating data points into classes. Support vector machines derive nonlinear boundaries to optimally separate clouds of points.
National risk models: The United States Department of Agriculture-Forest Service (USDA-FS) developed a national risk map for *P. ramorum* in 2002 as part of the sample design for a national sudden oak death (SOD) detection survey (Smith and others 2002, USDA FS 2004). Variables used included 1) distribution of hosts known or likely to be susceptible to the pathogen, 2) climatic conditions adequate for survival and propagation of the pathogen, and 3) pathways for introduction of the disease outside the currently infested region. The resulting map consisted of hexagons indicating three levels of risk (high, moderate, low) covering the conterminous U.S. (Fig. 3).

An updated national risk map was created (Koch and Smith 2008) by incorporating current data and approaches (recent host information, daily rather than monthly weather data, exclusion of areas where the minimum temperature was below 0°C for 150 or more days, and consideration that *P. ramorum* could escape from ornamental plantings in residential landscapes into natural forests) to better depict principal factors of *P. ramorum* risk. The resulting map (Fig. 4) showed an expansion of risk areas in the southeastern U.S. and a shifting of risk in portions of mid-Atlantic and south-Midwest states from moderate to low.
Magarey and others (2005) used The North Carolina State University/APHIS Plant Pest Forecast System (NAPPFAST [Borchert and Magarey, 2004]) to construct a climate and host risk map for \textit{P. ramorum} (Fig. 5). The map was based on an assumption that \textit{P. ramorum} occurrence would be climatically limited by temperature and moisture requirements. They used 10 year historical climatic data. The daily combination of minimum temperature, optimum temperature, maximum temperature and total leaf wetness hours per day was used to estimate the annual number of days suitable for infection. A second modeling effort examined the effects of soil temperatures less than -25°C, which reduce survival of \textit{P. ramorum} sporangia and chlamydospores in laboratory tests (Defra 2004). The cold temperature exclusion reduced the northern extent of risk from the pathogen (Fig. 6). Magarey and others (2008) incorporated understory sporulator hosts (seven Ericaceae hosts of \textit{P. ramorum}) into the model to further refine the at-risk infection areas (Fig. 7).
Fig. 5. The percent chance of at least 60 favorable days for infection by *Phytophthora ramorum* and hardwood hosts (Fowler and others 2006, Magarey and others 2005).

Fig. 6. The percent chance of occurrence based upon at least 60 favorable days for infection by *Phytophthora ramorum*, hardwood hosts and -25°C soil temperature exclusion (DEFRA 2005, Fowler and Magarey 2005, Magarey and others 2005; Magarey and others 2007).

Fig. 7. The percent chance of occurrence based upon at least 60 favorable days for infection by *Phytophthora ramorum*, hardwood hosts, understory sporulator hosts and -25°C lethal soil temperature exclusion (DEFRA 2005, Fowler and Magarey 2005, Magarey and others 2005; Magarey and others 2007, Magarey and others 2008).
Kelly and others (2007) compared and evaluated the performance of five spatial risk models (Rule-based Expert-driven GIS overlay; Logistic regression [LR]; Classification and Regression Trees [CART]; Genetic Algorithms [GA]; Support Vector Machines [SVM]) generated from common input parameters to map risk from *P. ramorum* across the conterminous U.S. (Fig. 8). All models were consistent in their prediction of some SOD risk in coastal California, Oregon, and Washington; in the northern foothills of the Sierra Nevada in California; in an east-west oriented band including eastern Oklahoma, central Arkansas, Tennessee, Kentucky, northern Mississippi, Alabama, Georgia, and South Carolina, parts of central North Carolina, eastern Virginia, Delaware, and Maryland.

Fig. 8. Risk for Sudden Oak Death in the conterminous United States from five spatially referenced models: (a) Rule-based, (b) Logistic Regression, (c) Classification Tree, (d) Genetic Algorithm, and (e) Support Vector Machine. (Kelly and others 2006, Kelly and others 2007). http://faculty.ucmerced.edu/qguo/publications/CEUS_SOD.pdf
The results from the five models were combined together to create a final map based on model agreement (Fig. 9) (Kelly and others 2007).

A national rule-based and expert knowledge model to characterize suitable habitat for *P. ramorum* across the United States was developed by Venette and Cohen (2006). With the assumption that adequate inoculum and susceptible hosts are uniformly present across the contiguous United States and the use of CLIMEX software, the model focused on climate as the limiting factor in establishment of the disease. Model outputs (Fig. 10) identified many areas within the United States that do not have a climate suitable for the establishment of *P. ramorum*, including most of the Great-Lakes, Plains, or Intermountain states. Beyond the Pacific Coast, climate is relatively more suitable for establishment in southeastern, northeastern, and Mid-Atlantic States.
The risk map produced by Venette and Cohen (2006) was consistent and in general agreement with other national risk models for *P. ramorum*, providing a degree of confidence in the conclusions from the models.

In 2005, USDA APHIS requested researchers and modelers to compare eight national scale risk models for *P. ramorum*. A summary of the comparisons is presented at [http://nature.berkeley.edu/comtf/pdf/P%20ramorum%20v5%20BRS%20rev.pdf](http://nature.berkeley.edu/comtf/pdf/P%20ramorum%20v5%20BRS%20rev.pdf). The models were sub-divided into two groups: those that used *P. ramorum* observations and those that do not. In general, models that used *P. ramorum* observations predicted a more restricted distribution than those that do not. The models were generally consistent in showing a national pattern of high risk in the coastal Northwest and the central Appalachian Mountains, and a low risk in the Great Plains. The models differed in predicting the degree of risk in the Northeast, coastal California, parts of the Southeast and the northern Midwest. The greatest uncertainties among the models were the extent of the northern boundary of risk east of the Rocky Mountains; and the degree of risk in the Southeast. The review paper recommends comparing the output from several models rather than using a single model for decision-making.

Fig. 10. Predicted climatic suitability for establishment of *Phytophthora ramorum* in the contiguous United States based on the ecoclimatic index (EI) from CLIMEX excluding environmental stresses (Venette and Cohen 2006).
North American temperature model: McKenney and others (http://nature.berkeley.edu/comtf/pdf/sod_biomap_results_05%20V2.pdf) presented a map based on North American continent-wide extreme minimum temperature models (Fig. 11). Because a Department for Environment, Food and Rural Affairs (Defra) report indicated that all *P. ramorum* spores are killed after 4 hours exposure to minus 25°C (DEFRA 2005), the map may be useful in indicating climate limitations on potential distribution of the pathogen. Although useful in identifying possible environmental limits, a map based on minimum temperature only does not take into account other host-pathogen-environment interactions involved in disease introduction (McKenney and others 2003).

![Extreme Minimum Temperature Models for North America](http://nature.berkeley.edu/comtf/pdf/sod_biomap_results_05%20V2.pdf)

**Fig. 11.** Extreme minimum temperature models for North America (McKenney and others undated, http://nature.berkeley.edu/comtf/pdf/sod_biomap_results_05%20V2.pdf).

International risk model: An international risk model for *P. ramorum* was created using NAP-PFAST (Magarey and other 2006, Magarey and others 2008) (Fig. 12). They used the International Panel on Climate Change (IPCC) data set (historical climate data for the last 10 years). The data set contains variables describing average temperature, precipitation, humidity and cloud cover. The model was based on a favorable month requiring average maximum monthly temperature to be less than 28°C, average minimum temperature to be greater than 3°C and at least 10 days with precipitation. In a later model, the authors (Fowler and Margarey unpublished) masked areas where the monthly average minimum temperature was less than -25.44°C (Fig. 13).
Fig. 12. NAPPFAST IPCC model for Phytophthora ramorum assuming at least two favorable months. (http://www.nappfast.org/casestudies_files/SOD.pdf)

Fig. 13. NAPPFAST IPCC model for Phytophthora ramorum assuming at least two favorable months; areas where the monthly average minimum temperature is less than -25.44°C are masked.
Although the authors point out that the model overestimates potential areas of pathogen occurrence because minimum precipitation data are not included, they suggest that the model may be of use in searching for the origin of the pathogen.

Refinement of the regional, national and international risk models developed for *P. ramorum* will occur as information on host range, environmental factors favoring spread and establishment, and the effects of spatial and temporal variables affecting the pathogen is better understood (Rizzo 2006). The differences that exist among the risk models point out uncertainties and the need for additional information on suitable environmental niches for the pathogen.

**Modeling Spatial-Temporal Patterns of Disease Distribution and Spread**

Kelly and Meentemeyer (2002) and Liu and others (2007) used remote sensing and spatial analysis to quantify the clustering of overstory mortality associated with SOD across large scales. High resolution imagery in combination with GIS and spatial modeling was used by Kelly and Meentemeyer (2002) to determine the presence and scale of oak mortality clustering over a 2 year period (2000 and 2001) at a location in Marin County (China Camp State Park), California. They found clustering patterns between 100 and 300 meters. They also developed a classification tree model to predict spatial patterns of risk for oak mortality based on landscape variables. Factors correlated with oak mortality included proximity to forest edge, topographic moisture index, proximity to trails, abundance of California bay laurel (*Umbellularia californica*), and potential summer solar radiation. Their results suggested that forest structure was an important risk factor in spatial pattern and spread of the disease.

Liu and others (2007) analyzed the spatial–temporal patterns of overstory oak tree mortality at the same Marin County location (China Camp State Park) over a four year period using point patterns mapped from high spatial resolution remotely sensed imagery. Univariate spatial point pattern analyses showed that the point patterns of dead oak trees are significantly clustered at different scales and spatial extents through time; and that both the extent and the scale of the clustering patterns decrease with time. Multivariate spatial point pattern analyses showed that new dead oak trees tend to be located within 300 m of dead oak trees, and that a strong spatial association exists between oak tree mortality and California bay trees within 150 m.

Because remote sensing used by Kelly and Meentemeyer (2002) and Liu and others (2007), does not capture understory or tree-specific symptomology, Kelly and others (2008) used two dimensional transect data to cover large areas and capture vegetation detail and spatial location. Kelly
and others (2008) investigated the spatial-temporal patterns of symptoms associated with SOD across landscape scales (hundreds of meters) at China Camp State Park. Using two-dimensional spatial analysis tools with data gathered in point-centered-quarter format in 2001 and 2004 at the park, they quantified the clustering of dead trees across the landscape and then investigated the relationship between disease symptoms and dead trees through space and time. The work provided an estimate of the density of symptomatic trees at different levels of disease across a forest landscape affected by *P. ramorum*. Dead trees were strongly clustered at smaller scales (about 300 m) in 2001, but after three years (2004) the clustering was less pronounced despite an increase in dead crowns. These patterns supported those found using remotely sensed data across the park (Kelly and Meentemeyer 2002, Kelly and others 2004, Liu and others 2006, Guo and others 2007), where clusters of overstory tree mortality of 200 to 400 m in size were found. Results showed that bleeding trees occur early in clusters and separate from existing dead trees, suggesting a new cohort of infected trees; that beetle-attacked trees exist throughout the forest and are not well-correlated with overstory mortality; and that the saprophytic sap rotting fungus *Hypoxylon thouasianum* is strongly related to tree mortality through time (Kelly and others 2008).

In a study at Sonoma Mountain, Sonoma County, California, Condeso and Meentemeyer (2007) showed that disease severity (derived by counting the number of symptomatic leaves on each California bay laurel stem greater than 2 cm in diameter at 1.4 m for 90 stems), was greater in forests with high connectivity and with high abundance of host species. More connected forests had more disease than smaller and more isolated forests, suggesting to the authors that forest fragmentation may keep inoculum levels low and reduce spread of the pathogen. They also demonstrated that, in the system they used, optimum microclimatic conditions for *P. ramorum* reproduction and growth are influenced more by elevation than by landscape pattern.

In a follow-up study, Meentemeyer and others (2008b) reported that altered forest structure and composition, probably largely due to fire suppression, facilitated spread of *P. ramorum*. Using detailed aerial photography records between 1942 and 2000 within a 150 m radius around 102 plots within a 275 km2 area of northern California, they found that oak woodlands increased in area by 25 percent over the 58-year period, while grasslands and chaparral (non-host vegetation types) had both significantly decreased. Path analysis showed that the woodland expansion resulted in larger forests with higher densities of the primary host trees (*U. californica, Quercus agrifolia, Quercus kelloggii*) and cooler understory conditions. The authors concluded that enlargement of woodlands and closure of canopy gaps facilitated the establishment of *P. ramorum* by increasing contagion of hosts and enhancing forest microclimate conditions.

Although Meentemeyer and others (2004), Guo and others (2005), and Venette and Cohen (2006) mapped the potential spread risk of *P. ramorum*, Meentemeyer and others (2008a) provided a
quantitative estimate of the pathogen’s realized spatial distribution. Meentemeyer and others (2008a) used niche modeling and dispersal estimation to examine the degree to which local habitat conditions vs. force of infection predict invasion by \textit{P. ramorum}. Linear modeling indicated that the probability of invasion is limited by both niche constraints and dispersal. Probability of invasion was positively related to precipitation and temperature in the wet season and the presence of the inoculum-producing foliar host \textit{U. californica}, and decreased exponentially with distance to inoculum sources. Model predictions suggested that future early detection sampling should concentrate on distances within 33 km (the maximum distance an infection was detected) from a known source of inoculum.

In a preliminary abstract, Hunter and others (2008) described the development of a spatially-explicit epidemic model that predicts susceptible-infectious (SI) transitions at discrete time steps using a geographic cellular automata approach. They developed a mathematical model that simulated spatial and temporal patterns of \textit{P. ramorum} spread at large spatial scales. Using data (daily rainfall and temperature, host abundance and susceptibility, human population density, and pathogen dispersal characteristics) from field and laboratory studies, they parameterized the variables to develop a model that was implemented in GIS to simulate disease spread across California. The model predicted about 80 percent of the spatial variability in current patterns of spread of \textit{P. ramorum}, and identified numerous forest ecosystems at high risk of infestation.

Meentemeyer and others (2008c) quantified host mortality caused by \textit{P. ramorum} across the Big Sur ecoregion using remote sensing (high resolution aircraft imagery) in combination with regression models and field observations. Application of the regression models in a GIS estimated 235,678 standing dead trees in 2005 and 12,650 m$^2$ of tree basal area removed from the ecoregion (79,366 ha study area), with 64 percent of mortality occurring in redwood-tanoak forests and 37 percent in mixed oak woodlands.

The spread of \textit{P. ramorum} in the nursery trade has been modeled using the concept of networks (a set of nodes connected by links). Nodes are the nurseries trading susceptible species, and links are shipments of those plants between nurseries. If nodes are connected to other nodes randomly (with a certain probability \(p\)), then the network is random. Scale-free networks are characterized by the presence of hubs, or super-connected individuals. Modeling of \textit{P. ramorum} spread through nursery networks in England and Wales has demonstrated pathogen movement on a scale-free (compared with random) network, indicating that action at places of production (critical nodes) will help limit future spread (Jeger and others 2007, Pautasso and others 2008).

A model framework useful to those concerned with the accidental introduction of \textit{P. ramorum} into the eastern U.S. from infected nursery plants was presented by McKelvey and others (2008). They are developing a spatial network model framework, utilizing potential interstate nursery
stock movements on a bipartite network. A Bayesian approach is used to model probabilities of transmission of *P. ramorum* from entry to destination nodes within the network. Probabilities of transmission of *P. ramorum* from source to destination nodes within the network are based on nursery stock flow volumes along the links connecting each origin/destination pair. The objective is to identify locations throughout the U.S. that are most likely to receive nursery stock infected with *P. ramorum*. Such information would increase the efficiency of on-going national survey programs for the pathogen.
References


Meentemeyer, Ross K.; Rank, Nathan E.; Anacker, Brian L.; Rizzo, David M.; Cushman, J. Hall. 2008b. Influence of land-cover change on the spread of an invasive forest pathogen. Ecological Applications. 18: 159–171.


