Potential climatic suitability for establishment of *Phytophthora ramorum* within the contiguous United States

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Abstract

Phytophthora ramorum has caused extensive mortality to tanoak and several oak species in coastal California. This pathogen has infected at least 72 plant species under natural conditions and 32 additional species in the laboratory. Many infected hosts have been distributed across the United States by the horticultural industry. We developed a simulation model using CLIMEX software to evaluate the suitability of the climate in the United States for establishment of *P. ramorum*. CLIMEX was driven by monthly climate normal data for 1971–2000 collected from >5300 weather stations in the contiguous United States. CLIMEX growth-requirement and stress-response parameters were derived from literature data. Values for the ecoclimatic index (EI), a measure of overall climatic suitability based on temperature and soil moisture, were between 0 and 53. Much of the Intermountain West and the Great Plains was climatically unsuitable for establishment of *P. ramorum* (EI = 0). Many states bordering the Great Lakes were marginal (0 < EI < 11). Areas considered climatically highly favorable (EI > 25) for establishment of *P. ramorum* were common in the Gulf States, and areas considered favorable (10 < EI < 26) extended into southern Illinois, southern Indiana, and northwards into southern Maine. Predictions derived from CLIMEX matched known occurrences of *P. ramorum* in California and Oregon. Finds of the pathogen were 3.4-times more likely in areas classified as favorable or very favorable than in areas classified as marginal or unsuitable. Model results were only modestly sensitive to changes in values assigned to temperature parameters for growth but were more sensitive to changes in values assigned to moisture parameters for growth. Additional research is needed to determine the effects of low moisture on population growth of the pathogen. Nevertheless, our model distinguishes some areas within the contiguous United States that do not have a suitable climate for the pathogen. Such information could be used to refine survey and detection programs.

1. Introduction

Significant mortality of tanoak (*Lithocarpus densiflorus*), coast live oak (*Quercus agrifolia*), California black oak (*Q. kelloggii*), and Shreve's oak (*Q. parvula* var *shrevei*) was first observed in 1994 in the western United States and attributed to the disease Sudden oak death. The causal agent of this disease was later confirmed as *Phytophthora ramorum* (S. Werres, A.W.A.M. de Cock and W.A. Man in't Veld) (Garbelotto et al., 2001; Hansen et al., 2002; Rizzo et al., 2002a; Garbelotto et al., 2003). The pathogen also causes ramorum bleeding canker,

ramorum leaf blight, and ramorum shoot dieback in more than 68 additional plant species in 28 families in the wild and another 32 species under laboratory conditions (Davidson et al., 2003; DEFRA, 2004b; Tooley et al., 2004). Foliar hosts, especially tanoak, California bay laurel (*Umbellularia californica*) and many Ericaceae, play a particularly important role in the production of infectious sporangia and the development of epidemics (Garbelotto et al., 2003; Rizzo and Garbelotto, 2003; Tooley et al., 2004). Foliar hosts also support the development of chlamydospores, the primary survival stage of the pathogen.

Although the geographic center of origin of *P. ramorum* remains unknown (Werres et al., 2001; Brasier, 2003; Martin and Tooley, 2003), the pathogen is thought to be exotic to North America (Rizzo et al., 2002a). Outside North America, the pathogen has only been reported from Europe where it is also considered exotic (Werres et al., 2001; Brasier, 2003).

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Significant genotypic and phenotypic differences exist between North American and European strains (Brasier, 2003). In Europe, infected tree and non-tree hosts have only been detected in horticultural nurseries, public gardens, and municipal woodlands, some approaching the size of forests (Davidson et al., 2003; Appiah et al., 2004). Within the United States, extensive surveys through 2004 indicated that the primary geographic distribution of affected forests remained limited to 14 counties around San Francisco, CA with Solano county being the most inland (Rizzo et al., 2002a; Kelly, 2004; Guo et al., 2005). The pathogen also has been detected as far north as Curry county, OR (Goheen et al., 2002).

Movement of nursery stock has inadvertently spread the pathogen from the western to the eastern United States. In 2004, trace-forward surveys indicated that potentially-infected plants were shipped to 39 states from contaminated, commercial nurseries on the west coast (Stokstad, 2004); 21 states (AL, AR, AZ, CA, CO, CT, FL, GA, LA, MD, NC, NJ, NM, OK, OR, PA, SC, TN, TX, VA, WA) confirmed the presence of infected nursery stock (APHIS, 2004). The majority of positive diagnoses were from nursery sites. Intensive sampling could not confirm a purported positive case of infection in the environs of New York state (NYDEC and FHP, 2005).

Future survey efforts and impact assessments might be refined if geographic areas with favorable climatic conditions for supporting the pathogen could be identified. A preliminary hazard map was developed by the US Department of Agriculture, Forest Service to help direct survey efforts in 2003 (USDA, 2004). In 2004, sampling occurred where potentially-infected nursery stock had been distributed. Forty-nine states (all but Hawaii) and Puerto Rico participated in the national survey despite the fact that only 25 (of the 48 contiguous) states had a high or moderate hazard rating (USDA, 2004).

The objectives of this study were to identify geographic areas within the contiguous United States that are not likely to provide a climate suitable for the long-term establishment of *P. ramorum* and to measure the impact of parameter uncertainty on model predictions. The model was developed in CLIMEX (Sutherst and Maywald, 1985), a software package that has been used extensively to predict the potential geographic range of introduced species. Although the model has been used most commonly for weeds (e.g., Scott, 1991; Holt and Boose, 2000; Kriticos et al., 2003; Goolsby, 2004) and insects (e.g., Worner, 1988; Venette and Hutchison, 1999; MacLeod et al., 2002; Hoddle, 2004; Sutherst and Maywald, 2005), CLIMEX also has been used to investigate the potential distribution of several pathogens (e.g., Scherm and Yang, 1999; Pivonia and Yang, 2004; Yonow et al., 2004), including *Phytophthora cinnamomi* (Brasier and Scott, 1994; Brasier, 1996).

2. Materials and methods

2.1. Software and climate data

CLIMEX 2.0 (Sutherst et al., 2004) was used to characterize the suitability of regional climates for facilitating establishment

of *P. ramorum* within the contiguous United States. CLIMEX includes a database with monthly climate normals from 1931 to 1960 for 2218 locations worldwide of which 175 occur in the United States (Baker, 2002). For each location, the database includes monthly-mean maximum air temperature, minimum air temperature, precipitation, and relative humidity (morning and afternoon measurements). A preliminary analysis (data not shown) indicated that certain CLIMEX indices, calculated using monthly climate normals from 1971 to 2000, differed significantly from indices based on normals from 1931 to 1960. To have the most current data possible and improve the spatial resolution of the dataset, we replaced the standard database with climate information from the *US Monthly Climate Normals*: 1971–2000 (NCDC, 2000) for 5524 locations with both temperature and precipitation records in the United States, Puerto Rico, and the Virgin Islands. This dataset includes 5320 locations in the contiguous US. Relative humidity records were not available.

Within the 'compare locations' function, CLIMEX calculates an ecoclimatic index (EI) which reflects the combined potential for population growth during favorable periods and persistence during stressful periods. EI is bounded between 0 and 100. Calculation of the EI depends on the climatic requirements/tolerances of a species and climatic conditions at a given site. Relative humidity does not factor into the EI. Specifically, EI is calculated using:

$$\text{EI} = \left[\frac{100}{52} \sum_{w=1}^{52} (\text{TI}_w \times \text{MI}_w) \right] \times \left[\left(1 - \frac{\text{CS}}{100}\right) \left(1 - \frac{\text{HS}}{100}\right) \left(1 - \frac{\text{DS}}{100}\right) \left(1 - \frac{\text{WS}}{100}\right) \right],$$

where w is the week of the year; TI_w the temperature index for week w; MI_w the moisture index for week w; CS the annual cold stress, HS the annual heat stress, DS the annual drought stress, and WS the annual wet stress. Each stress index is calculated on a weekly basis and expressed as a sum over the year. Sutherst and Maywald (1985) and Sutherst et al. (2004) provide further detailed explanations of the theory and mathematics behind the calculations. As per Vera et al. (2002) and Hoddle (2004), we considered EI values of 0 unsuitable, 1–10 marginal, 11–25 favorable, and ≥ 26 very favorable for establishment. We note that an alternative interpretation suggests locations with an EI > 20 are highly favorable (Sutherst and Maywald, 2005).

2.2. CLIMEX parameters

CLIMEX parameter estimates for *P. ramorum*, derived from reports in the literature, are presented in Table 1. Temperature requirements were calculated from studies by Werres et al. (2001) and the UK Department for Environment, Food, and Rural Affairs (DEFRA, 2004a). Moisture requirements for the growth of the pathogen are poorly understood. Consequently, we used soil moisture parameters developed by Brasier and Scott (1994) and modified by Sutherst et al. (2004) to describe growth of *P. cinnamomi*. No adjustments were made for soil type. Our baseline model consisted only of temperature and soil

Table 1
Parameter values used in CLIMEX to characterize growth requirements and stress responses for *Phytophthora ramorum*

Parameter	Definition	Value
Temperature[a]		
DV0	Lower limit for growth	2
DV1	Lower optimum for growth	17
DV2	Upper optimum for growth	25
DV3	Upper limit for growth	30
Moisture[b]		
SM0	Lower limit for growth	0.4
SM1	Lower optimum for growth	0.7
SM2	Upper optimum for growth	1.3
SM3	Upper limit for growth	3.0
Cold stress[c]		
DTCS[d]	Cold stress degree day threshold	15
DHCS[e]	Cold stress degree day rate	−0.0001
Heat stress[c]		
TTHS[a]	Stress threshold	30
THHS[f]	Stress accumulation rate	0.005
Dry stress[c]		
SMDS[b]	Stress threshold	0.2
HDS[f]	Stress accumulation rate	−0.005
Wet Stress[c]		
SMWS[b]	Stress threshold	2.5
HWS[f]	Stress accumulation rate	0.002

[a] Units in °C.

[b] Expressed as a proportion of soil moisture holding capacity (=1 at saturation).

[c] Excluded from the baseline model.

[d] Weekly sum of degree days (above threshold of 8 °C) required to sustain the population.

[e] Weekly mortality per degree day below DTCS.

[f] wk^{-1}, defined in Sutherst et al. (2004).

moisture requirements for growth; all stress values (i.e., CS, HS, DS, and WS) were set to 0. Quantitative tests of the viability of sporangia and chlamydospores over time in response to drought, flooding, heat, or cold have yet to be reported for *P. ramorum*. Thus, we used stress parameters for *P. cinnamomi* given in Sutherst et al. (2004). Preliminary data on the effects of environmental stresses are available from DEFRA (2004a) but are not detailed enough to allow for the calculation of stress parameters. The potential effects of stress were only considered during the sensitivity analysis. Because the worldwide distribution of the pathogen is poorly characterized at this time, it was not possible to generate CLIMEX parameters using the iterative geographic fitting procedure.

2.3. Spatial interpolation

All CLIMEX results were exported to a geographic information system (ArcView 3.2 and Spatial Analyst 1.1; ESRI, Redlands, CA) to interpolate values between weather stations and measure map attributes. For interpolation, we used optimized inverse distance weighting as recommended by Collins and Bolstad (1996) for isotropic regional climatic data. Optimization was achieved by withholding 30-randomly selected points, selecting a power parameter of 1, 1.5, 2, 2.5,

3, 4, 6, or 8, interpolating a surface, and comparing the predicted and observed values at the withheld locations. The same 30 points were used to evaluate each power parameter. During optimization, interpolation was performed using a 2.5-km grid in an equidistant conical projection.

The power parameter was selected on the basis of bias, mean absolute error, and qualitative classification of sites. Chi-square analysis was used to compare the known and predicted frequency distributions of sites classified as unsuitable, marginal, or favorable. Favorable and very favorable classes were combined for this analysis because of the low number of sites classified as very favorable. There was no evidence of bias among any of the power parameters. A power parameter of 1 had the lowest mean absolute error (2.14), but the distribution of qualitative classifications differed from the known distribution ($\chi^2 = 6.6$, d.f. = 2, $P < 0.05$). A power parameter of 1.5 had a slightly greater mean absolute error (2.20), but the distribution of qualitative classifications did not differ significantly ($\chi^2 = 4.6$, d.f. = 2, $P > 0.05$). All other power parameters had larger mean absolute errors, ranging from 2.26 to 2.66, although qualitative classifications did not differ ($\chi^2 < 2.93$, d.f. = 2, $P < 0.05$). We used a power parameter of 1.5 to interpolate between all 5320 weather stations in the contiguous United States. Interpolation was performed on a 2.5-km^2 grid with the 12 nearest neighbors to each grid cell in an equidistant conical projection. Each grid cell was then classified (unsuitable to very favorable). Grid cells were converted to a shapefile. The map was changed to an Albers equal area conical projection, and the area of each polygon was measured using the recalculate-area,-length,-and-perimeter function of spatial analyst.

2.4. Model validation

To validate the baseline model, we overlaid the location of *P. ramorum* finds (diagnoses) in the field (through 24 March 2005; Sudden Oak Death Project, Center for the Assessment and Monitoring of Forestry and Environmental Resources, University of California, Berkeley) on the map of climatic suitability. We then examined the frequency of finds among suitability classes. As these locations were not used to develop the model, they provided independent validation. A Chi-square analysis was used to test the observed frequency of finds in each suitability class against the expectation (assuming a random distribution) that finds should occur in direct proportion to the area occupied by each suitability class within California. Unsuitable and marginal areas were combined for analysis, as were favorable and very favorable areas.

2.5. Sensitivity analyses

The baseline model was subjected to sensitivity analyses to evaluate impact of parameter uncertainty on results. Firstly, parameters describing the effects of temperature on population growth (Table 1) were adjusted accordingly: DV0 = −1 or 5 °C; DV1 = 14, 20 or 23 °C; DV2 = 19, 22, or 28 °C; and DV3 = 27, 33 or 36 °C, respectively. Only one parameter was adjusted at a

time, and all other parameters were held constant as in the baseline model. Temperature parameters always were subject to the constraint DV0 < DV1 < DV2 < DV3. The model was re-run after adjusting parameters describing the effects of soil moisture on population growth (Table 1). One parameter was adjusted at a time with the values: SM0 ± 25% and ±50% (i.e., SM0 = 0.2, 0.3, 0.5, or 0.6, respectively); SM1 ± 25% and +50%; SM2 ± 25% and +50%; and, SM3 ± 25% and ±50%, respectively. Moisture parameters were subject to the constraint SM0 < SM1 < SM2 < SM3. For each model, we measured the area of the contiguous United States that was classified as unsuitable, suitable, favorable, and very favorable, respectively. Secondly, we examined the change in model results as each stress factor (Table 1) was individually added to the baseline model.

3. Results and discussion

Our baseline model predicts that large areas within the western and the northeastern United States should not be climatically suitable for the establishment of *P. ramorum* (Fig. 1). Most of the intermountain states were classified as unsuitable (EI = 0), primarily due to a lack of adequate moisture for growth of mycelia or production of sporangia. Likewise, much of southern Florida was classified as unsuitable because moisture was predicted to be inadequate. In the northeastern United States, large areas were classified as marginal (0 < EI < 11) because cold temperatures limited the potential for growth. Favorable areas (11 < EI < 26) were extensive in the southeastern United States and the middle- and north-Atlantic states. Very favorable areas (EI > 25) for *P. ramorum* establishment were most extensive in Louisiana, Mississippi, Alabama, Arkansas, and Tennessee. Smaller pockets of very suitable climate were identified in Oklahoma, Texas, Georgia, North Carolina, South Carolina, West Virginia, and New York.

The results from our model compared well with the observed geographic distribution of *P. ramorum* in California on non-tended hosts (Fig. 2). If observed locations were distributed at
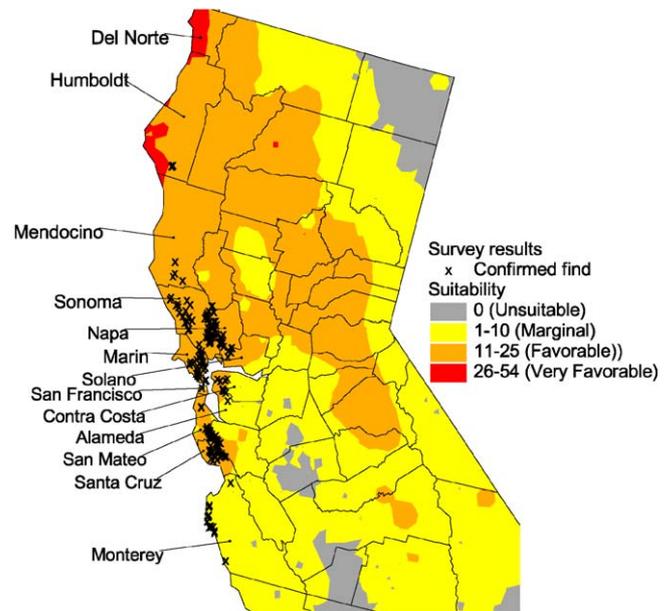
Fig. 2. Locations in California counties with *Phytophthora ramorum* diagnoses overlaid onto a map of climate suitability for establishment, based on the ecoclimatic index from CLIMEX.

random in California, we would expect 15.1% of these locations to fall in areas that our baseline model classified as unsuitable; 59.7% in marginal areas; 24.5% in favorable areas; and 0.7% in very favorable areas. In reality, 113 of 499 (22.6%) confirmed finds of *P. ramorum* in California occurred in marginal areas; *P. ramorum* was not reported from any sites classified as unsuitable. The remaining 386 confirmed finds (77.4%) occurred in areas classified as favorable. No finds were reported in areas predicted to be very favorable. *P. ramorum* was found more often in favorable and very favorable sites than would be predicted by chance alone ($\chi^2 = 717.7$, d.f. = 1, $P < 0.005$). Positive finds were 3.4-times more likely to occur in an area classified as favorable or very favorable than as unsuitable or marginal. Anecdotally, the distribution of diagnosed *P. ramorum* infections in Humboldt county, an area identified with a very suitable climate, expanded notably during 2005 to 54.4 km^2 (21 miles^2) (Palmieri and Frankel, 2005).

Our predictions were only modestly sensitive to changes in DV0, the lower temperature limit for population growth. A lower DV0 created the potential for population growth earlier in a year and more total time for growth. When DV0 was changed to −1 or 5 °C, the total area of very favorable sites increased by 63% or lowered by 63%, respectively, relative to the baseline model; areas classified as unsuitable, marginal, or favorable changed by <16% (Fig. 3A). The range of temperatures used for DV0 span the range of published temperatures required for growth. Fourteen isolates of *P. ramorum* had a minimum temperature for growth at 2 °C (Werres et al., 2001). Orlikowski and Szkuta (2002) suggested that 3 °C was needed for growth of an European isolate. In contrast, DEFRA (2004a) reported modest growth of both European and American isolates at 0 °C.

Results were also modestly sensitive to changes in DV1 and DV2 which describe the range of temperatures for optimal growth. Of all growth-temperature parameters, the model was
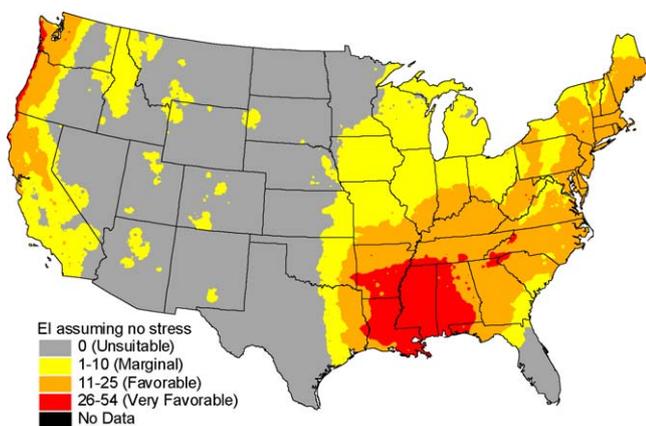

Fig. 1. Predicted climatic suitability for establishment of *Phytophthora ramorum* in the contiguous United States based on the ecoclimatic index (EI) from CLIMEX excluding environmental stresses.
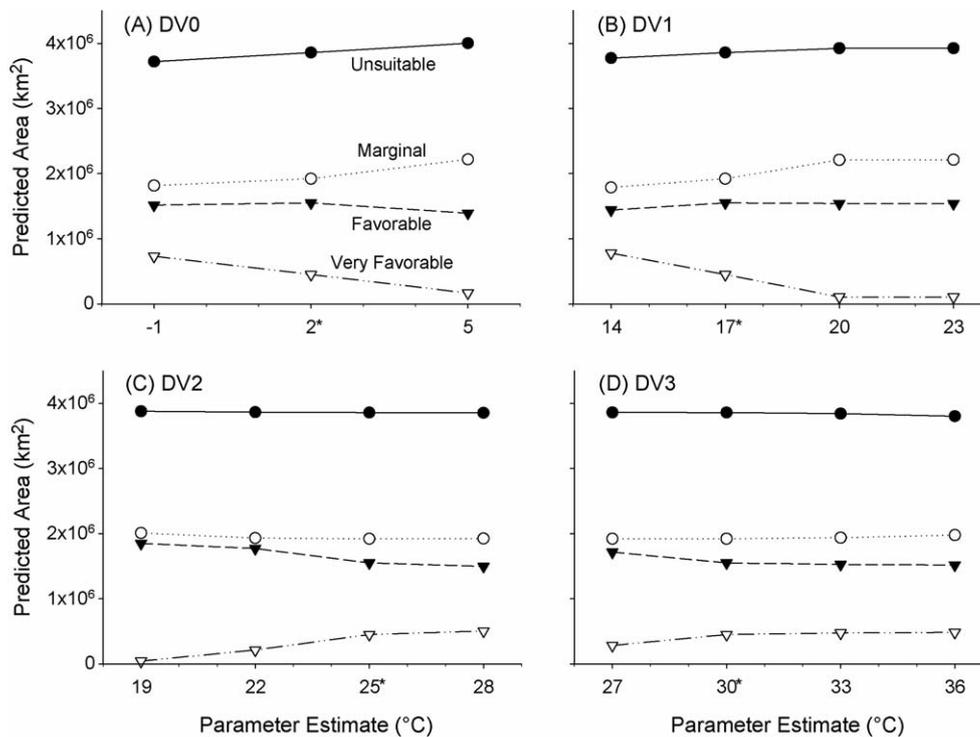
Fig. 3. Sensitivity analysis of CLIMEX parameters characterizing temperature requirements for growth and the subsequent characterization of areas within the contiguous United States as unsuitable, marginal, favorable, or very favorable for establishment of *Phytophthora ramorum*: (A) DV0, lower temperature limit; (B) DV1, lower temperature for optimal growth; (C) DV2, upper temperature for optimal growth; and (D) DV3, upper temperature limit. Asterisks mark values used in the baseline model.

most sensitive to DV1. Lowering DV1 translated to faster growth at temperatures between DV0 and DV1. Lowering DV1 to 14 °C increased the area of very favorable habitat by 74%, while raising DV1 to 20 °C lowered very favorable habitat by 77% relative to the baseline model (Fig. 3B). A further increase to 23 °C changed results by <1% compared with those obtained at 20 °C. Changes to DV1 affected the areas of habitat classified as unsuitable, marginal, or favorable by <16% (Fig. 3B). Modifications to DV2 changed the area of habitat classified as unsuitable or marginal by <5% compared with the baseline model (Fig. 2C). Lowering DV2 to 19 °C, increased the area of favorable habitat by 19% relative to the baseline model, but this was largely at the expense of very favorable habitat which declined by 90% relative to the baseline model (Fig. 3C). Raising DV2 to 28 °C increased the area of very favorable habitat by 12%, but all other habitat classifications changed by <4% compared with the baseline model. Optimal temperatures for mycelial growth of *P. ramorum* on media varied between 17 and 25 °C (mode = 20 °C, Werres et al., 2001), or 20–25 °C (mode = 20 °C, DEFRA, 2004a). Lesion development on excised bay laurel leaves was optimal at 17–22 °C (Hüberli et al., 2003).

Model results were not sensitive to changes in DV3, the upper temperature at which *P. ramorum* can grow. Over the range of temperatures considered, the area of unsuitable, marginal, and favorable habitat changed by <11% compared with the baseline model. Lowering DV3 to 27 °C resulted in a 37% reduction in the area classified as very favorable (Fig. 3D). Werres et al. (2001) reported maximal temperatures for growth between 26 and 30 °C (mode = 27 °C). Orlikowski and Szkuta (2002) reported an upper

temperature limit of 30 °C. Chlamydospores and sporangia survived less than 24 h exposure to 40 °C (DEFRA, 2004a). Temperatures >35 °C were lethal to *P. ramorum* (Garbelotto et al., 2001). In the field in California, success at isolating *P. ramorum* from infected leaf tissue declines substantially during the hot dry summer (Davidson et al., 2003), reflecting a reduction in viable inoculum.

The relationship between moisture and growth of *P. ramorum* is highly uncertain. Unlike many *Phytophthora* spp., *P. ramorum* does not have a clear affiliation with flooded soils or standing water (Garbelotto et al., 2001; Rizzo et al., 2002a) but during dry summer months, detection of the pathogen from symptomatic hosts can be difficult (Garbelotto et al., 2001; Davidson et al., 2003). Initial evidence suggests that infection by *P. ramorum* is more likely in moist areas where trees have a higher stem water potential than in dry sites (Swiecki and Bernhardt, 2002). Epidemics have occurred in areas where annual rainfall ranges from 85 to 200 cm, and heavy rains associated with El Niño events in particular have contributed to intense sporulation (Davidson et al., 2005) with subsequent widespread infection and mortality of oaks (Rizzo and Garbelotto, 2003; Rizzo et al., 2005). Chlamydospres and zoospores can survive >30 d under moist conditions in the laboratory, but neither spore type can survive >30 min at <30% relative humidity (Davidson et al., 2002). Similar results were obtained from the field (Fichtner et al., 2005). These observations are qualitatively similar to the characterization of moisture on growth of *P. ramorum* that we have used in our model.

Results from our model were highly sensitive to changes in SM0 and SM1, the soil moisture levels (expressed as a proportion of moisture holding capacity) needed for minimal and optimal growth, respectively. Lowering SM0 from 0.4 to 0.2 resulted in a 44% reduction in the area of the contiguous United States classified as unsuitable (Fig. 4A), while areas classified as marginal, favorable or very favorable increased by 32, 44, and 82%, respectively, relative to the baseline model. Raising SM0 to 0.6 led to a 21% increase in the area classified as unsuitable and a 59% reduction in the area classified as very favorable. Lowering SM1 from 0.7 to 0.525 caused a 45% increase in the area of very favorable habitat within the contiguous United States; all other habitat classes changed by <15%. Increasing SM1 to 1.05 (just above saturation) caused a 74% reduction in the area of the contiguous United States classified as very favorable, 22% reduction in the area classified as favorable, 21% increase in the area classified as marginal, and a 7% increase in the area classified as unsuitable. Collectively, these results suggest soil moisture, particularly dry soils, are likely to have a strong limiting effect on the growth of *P. ramorum*.

The model was relatively insensitive to changes in SM2 or SM3. The area of very favorable habitat within the contiguous United States was reduced by 50% when SM2 was lowered to 0.975 (Fig. 4C) and by 32% when SM3 was lowered to 1.5 (Fig. 4D). All other habitat classifications changed by <15% (Fig. 4C and D). Consequently, it is unlikely that high moisture limits the growth of *P. ramorum*.
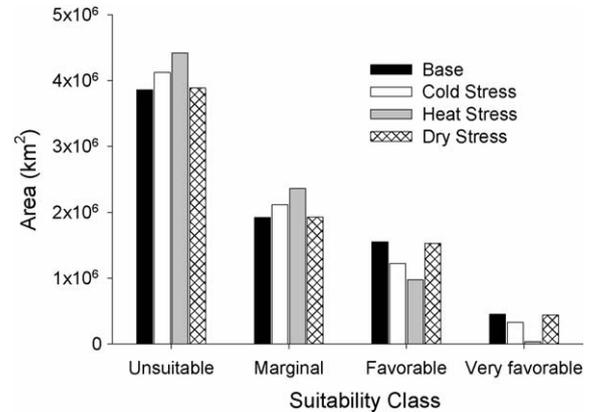

Fig. 5. Changes in the area of the contiguous United States predicted to be unsuitable, marginal, favorable, or very favorable for establishment of *Phytophthora ramorum* as affected by the inclusion of CLIMEX parameters describing population responses to climatic stresses.

Inoculum levels will decline at a specified rate when environmental conditions exceed pre-defined thresholds. Requisite data are not yet available to define thresholds and rates of stress accumulation for *P. ramorum*, which is why stress terms are excluded from the baseline model. Inclusion of cold stress resulted in modest reductions in the areas classified as favorable or very favorable and increases in unsuitable or marginal areas (Fig. 5). A heat stress term caused the greatest reduction in very favorable and favorable habitat. The addition of a drought stress term resulted in little change of the habitat
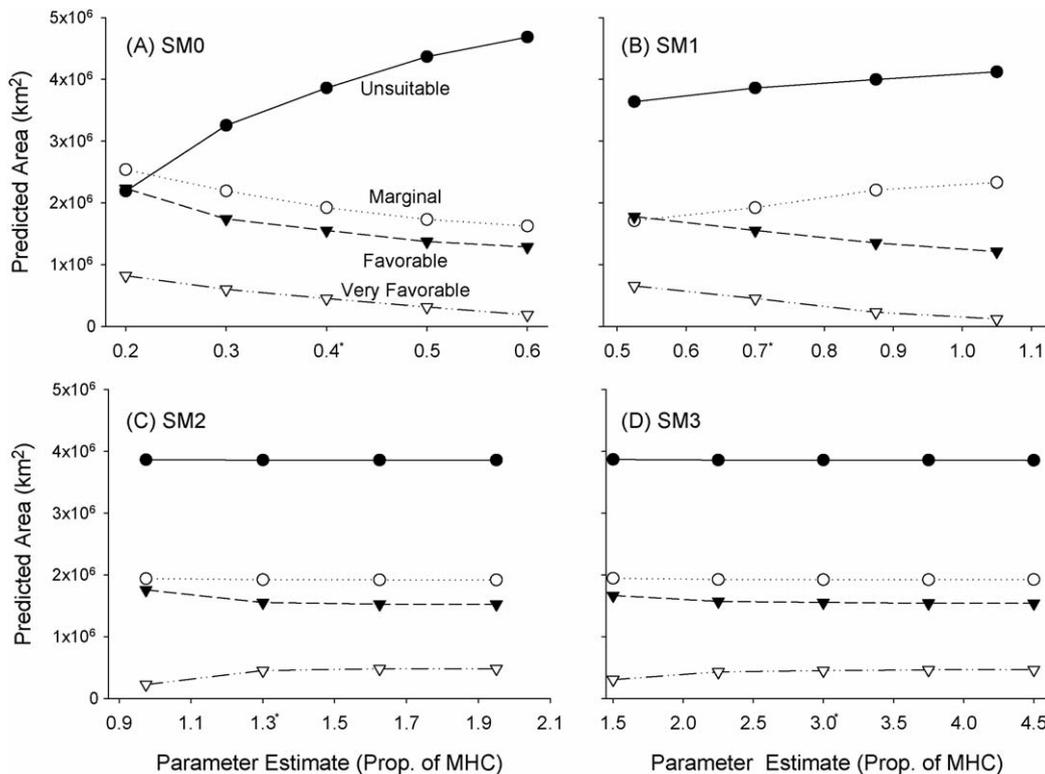

Fig. 4. Sensitivity analysis of CLIMEX parameters (expressed as a proportion of soil moisture holding capacity [MHC]) describing moisture requirements for growth and the subsequent characterization of areas within the contiguous United States as unsuitable, marginal, favorable, or very favorable for establishment of *Phytophthora ramorum*: (A) SM0, lower moisture limit; (B) SM1, lower moisture for optimal growth; (C) SM2, upper moisture for optimal growth; and (D) SM3, upper moisture limit. Asterisks mark values used in the baseline model.

characterization. These results reflect the integration of the innate sensitivity of *P. ramorum* to environmental extremes and the extent to which these conditions might be more regularly encountered in nature. Because CLIMEX uses climatic averages, infrequent extreme conditions will not be represented. Nevertheless, if populations of *P. ramorum* respond to extreme cold, heat, or drought as does *P. cinnamomi*, the results suggest that viable inoculum levels would be reduced most by excessive heat, cold, and drought.

The application of our model is most pertinent to establishment of *P. ramorum* in the different regions of the United States. Establishment occurs when a population repeatedly grows during favorable periods and persists through stressful periods over multiple years. Furthermore, exogenous inoculum is not needed for maintenance of the population. Establishment does not imply that new hosts will be infected (an outcome of local or regional population spread), nor does it assume any degree of host mortality. Establishment is a necessary precondition before spread or mortality is likely to occur. Despite the known arrival of *P. ramorum* in the eastern United States, no evidence currently indicates that the pathogen has established on resident, wild hosts in the region.

Our model assumes that adequate inoculum and susceptible hosts are present uniformly across the contiguous United States. These assumptions allow us to focus on climate as the limiting element of *P. ramorum* disease progression and to overcome current knowledge gaps about the susceptibility of eastern forest species to *P. ramorum*. Although knowledge is incomplete, some susceptible plant species do occur in the eastern US. Under glasshouse conditions, seedlings of northern red oak (*Q. rubra*) and pin oak (*Q. palustris*), both eastern species, are susceptible to infection (Rizzo et al., 2002b; Rizzo and Garbelotto, 2003). *Quercus rubra* was naturally infected by *P. ramorum* in the Netherlands (Brasier et al., 2004). *Rhododendron catawbiense*, native to the eastern United States, is also a known host (Werres et al., 2001; Rizzo and Garbelotto, 2003; Tooley et al., 2004). Several other Ericaceous hosts that are native to the eastern United States, but are widely grown as ornamentals, are susceptible (Tooley et al., 2004). Nevertheless, until the host status for more plants can be determined, it would be presumptuous to conclude that areas within the eastern United States are at low risk simply because known hosts are rare or absent. In reality, adequate inoculum will only arrive with infected host material. Thus, our map should be useful to refine strategies that prevent the spread of the fungus by highlighting areas where establishment is comparatively more likely.

CLIMEX does not utilize relative humidity in the calculation of EI. Some researchers consider this a weakness, particularly for pathogens that require leaf wetness for infection (e.g., Pivonia and Yang, 2004). However, satisfactory models have been developed in CLIMEX for foliar pathogens (e.g., Yonow et al., 2004). Leaves can be wetted by rain or dew, which forms under high (>90%) relative humidity (e.g., Wallin, 1963). At coarser temporal and spatial scales, sufficient to describe the general climatic suitability for establishment of a pathogen, humidity and precipitation are correlated (Chtioui et al., 1999; Thornton et al., 2000). As a result, CLIMEX may implicitly account for leaf wetness through soil moisture parameters. Because soil moisture is dictated by precipitation in the model, pathogens with higher moisture requirements for growth will experience a greater number of days with leaves wetted by precipitation or dew than pathogens with lower moisture requirements for growth.

The results of our baseline analysis are consistent with previously published models. Using a rule-based model, Meentemeyer et al. (2004) characterized the climate of coastal California, the northern San Joaquin Valley, and the western slopes of the Sierra Nevada mountains as moderately to highly suitable for establishment and spread of *P. ramorum* from December to May. Our model suggested a similar pattern, even though we considered climate over an entire year. Differences between our results and those of Meentemeyer et al. (2004), especially in coastal, southern California are largely attributable to different seasons and climatic periods examined (1961–1990 versus 1971–2000). Our results suggest that on an annual basis, limited moisture lowers the potential for establishment in portions of coastal California. Guo et al. (2005) analyzed the current distribution of *P. ramorum* in the western US and consistently concluded that coastal California (primarily from Humboldt to San Louis Obispo county) were at risk for infection; small pockets within Santa Barbara, Ventura, and Los Angeles counties were also considered likely to support the pathogen. One modeling approach also suggested that limited areas within the northern Sierra Nevada mountains might be at risk (Guo et al., 2005). Similarly, we identified small areas in these counties and San Bernadino, Riverside and San Diego counties that were predicted to be favorable for establishment. The models by Meentemeyer et al. (2004) and Guo et al. (2005) were restricted to California.

Few models have been applied to the eastern United States to forecast where the pathogen might become established. The ''Preliminary SOD Risk/Hazard Map'' (USDA, 2004) considered the susceptibility of resident plants, existence of pathways for inoculum introduction, and suitability of the climate for infection in different regions of the contiguous US. For areas east of the Mississippi River, it was concluded from the model that much of the Appalachians were at high risk, as was a small area from Biloxi, MS to Pensacola, FL; several Mid-Atlantic States were at moderate to high risk (USDA, 2004). Again, our model is generally consistent with these results. Fowler and Magarey (2005) modeled the frequency of weather conditions suitable for infection by *P. ramorum* across the US and found that east of the Mississippi River, 8 or more of the past 10 y had conditions suitable for infection. Our model and Fowler and Magarey (2005) predict substantially higher risk in the Gulf States and New England than suggested by the Preliminary Risk Map, but the influence of non-climatic factors on results from the Preliminary Risk Map complicates comparisons of the models.

Similar characterizations of the suitability of a geographic region using different modeling techniques provide a higher degree of confidence in the conclusions from the models. Where models disagree, great uncertainty exists about any final characterization. The mechanics of our model differ from the previous models mentioned because we have developed a

simulation based upon what is known about the biology of *P. ramorum* or related taxa from laboratory studies. Consequently, field observations provide a completely independent validation of the model. Other models attempt to infer habitat requirements through statistical or qualitative analyses of the known distribution of *P. ramorum*. These are valid modeling techniques, but the same data cannot be used to develop and validate the model.

The newness of the infestations in Europe and the United States prevented estimation of CLIMEX parameters using iterative geographic fitting. This common process for the development of CLIMEX models recursively adjusts parameter values until the predicted distribution qualitatively matches the known distribution in an area outside the region of intended application of the model (Sutherst and Maywald, 1985). However, several available models including ours suggest the geographic distribution of *P. ramorum* has probably not yet reached its climatic limits in Europe or the US. Thus, a model based on preliminary, incomplete information would produce parameter estimates that would underestimate the potential distribution of *P. ramorum*.

In summary, our model shows that many areas within the United States do not have a climate that is suitable for the establishment of *P. ramorum*. Climate is likely to preclude establishment in 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. However, these results must be interpreted with caution. Establishment is not assured in areas predicted to have a favorable or very favorable climate, even if adequate inoculum were introduced to susceptible host plants. Momentary periods of unsuitable weather, not reflected in the climatic averages used by CLIMEX, have the potential to interrupt disease progression. Such a detailed analysis of the dynamics of the infection process over time is beyond the scope of our analysis. Clearly, much remains to be learned about the growth of the pathogen and reductions in inoculum during climatically stressful periods. Our model suggests understanding the impacts of soil moisture on pathogen growth and high temperatures on inoculum decline could have particularly substantial impacts on predictions of potential establishment. Nevertheless, the current results could be used to refine detection protocols and sampling efforts for the pathogen. Establishment of *P. ramorum* is unlikely in areas classified as unsuitable and is relatively more likely in areas classified as favorable or very favorable. Narrowing or stratifying the search area using this model increases the probability of finding infected plants in the eastern United States for the same allocation of resources.

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