

A glimpse at future forests: predicting the effects of *Phytophthora ramorum* on oak forests of southern Appalachia

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Received: 17 March 2010 / Accepted: 26 October 2010 / Published online: 10 November 2010
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Abstract The highly pathogenic *Phytophthora ramorum*, causal organism of sudden oak death (SOD), is established in forests of the Pacific Northwest (USA) and is threatening invasion of other regions. Given the breadth of its host range, with dozens of asymptomatic ornamental hosts and with oaks, *Quercus* spp., in the red oak (*Erythrobalanus*) subgenus particularly susceptible, we investigated the consequences of its invasion and establishment in oak-dominated deciduous forests of the eastern USA. We evaluated the nature and extent of pathogen invasion using vegetation assessments coupled with growth simulations. The woody plant community was assessed in three strata (upper, mid- and lower) and was used to characterize forest composition and structure. Using the Forest Vegetation Simulator (FVS), we then projected woody vegetation growth 50 years into the future with and without the effects of SOD. In forest simulations lacking pathogen invasion, little change in composition or structure is forecasted. Both red oaks and white oaks (subgenus *Leucobalanus*) increase slightly but significantly over the length of the simulation. In contrast, in SOD-affected forests our projections predict a significant loss of red oaks within 10 years of pathogen invasion. Basal area of white oaks and non-oaks is expected to

increase more so in the absence of red oaks. The loss of red oaks to pathogen infection will result in greater increases in red maple, *Acer rubrum*, and yellow poplar, *Liriodendron tulipifera*, than in forests free of SOD. Loss of red oak represents a significant loss of hard mast, with potentially devastating consequences for wildlife. Red oak loss will also affect decomposition rates, nutrient cycling, forest structure, and timber values, with consequences for forest health and sustainability.

Keywords Sudden oak death · *Quercus* · Invasive species · Forest vegetation simulator · Modeling

Introduction

Extensive mortality of several ecologically significant tree species in the western USA, including tanoak, *Lithocarpus densiflorus* (Hook. and Arn.) Rehder, coast live oak, *Quercus agrifolia* Née, and California black oak, *Q. kelloggii* Newberry (Fam.: Fagaceae), have been associated with the oomycete pathogen *Phytophthora ramorum* (Order: Pythiales; Fam.: Pythiaceae). *P. ramorum* causes a bark canker on susceptible hosts that girdles the stem, disrupts the vascular system and causes wilt beyond the point of infection, rapidly causing tree mortality (Garbelotto et al. 2001). Because of the rapid mortality caused by infection of susceptible hosts, the pathogen and associated symptoms have been designated ‘sudden

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oak death' (SOD). The pathogen is air-, water- and soil-borne (Davidson et al. 2002). Since its initial detection in 1995 in Marin County, CA (McPherson et al. 2000), SOD has spread south and north along the Pacific coast in the western USA (COMTF 2010), decimating susceptible species with both economic and ecological consequences. Dozens of other woody plant species serve as a reservoir and are alternate hosts; these hosts are asymptomatic or sustain nearly inconsequential leaf spots or tip dieback. These alternate hosts are often ornamental shrubs that play a critical role in disease epidemiology (Davidson et al. 2003); infected yet asymptomatic nursery stock has been shipped to numerous uninfected areas (USDA 2005). The geographic range (15 counties in 2 states) and our knowledge of the host associations (over 128 plant species) have increased dramatically since its initial discovery in the USA (Jones 2009; USDA 2010).

The southern Appalachian region is particularly at risk for *P. ramorum* establishment both climatologically (Venette and Cohen 2006) and with respect to SOD-susceptible host material (Gottschalk et al. 2003). Forests in the central hardwoods region of the southern Appalachians contain a substantial component of highly susceptible red oaks, including scarlet, *Q. coccinea* Münchh., northern red, *Q. rubra* L., black, *Q. velutina* Lamb., and pin, *Q. palustris* Münchh. Inoculation success is quite high in red oaks, leading to pathogen re-isolation from 80 to 100% of inoculated leaves in some species (Balci et al. 2008; Denman et al. 2005). Although the red oak group (subgenus: *Erythobalanus*) is most susceptible to *P. ramorum*, artificial inoculation studies suggest that white oaks (subgenus: *Leucobalanus*) are also susceptible (Balci et al. 2008; Tooley and Kyde 2007), and infestations have been found on white oaks in Europe (Brasier et al. 2004). The southern Appalachians also contain a number of white oak species, including chestnut, *Q. prinus* L., white, *Q. alba* L., and post, *Q. stellata* Wangenh.

In addition to generating substantial revenue, oaks play key roles in determining forest composition and structure, influencing nutrient dynamics and watershed characteristics, and affecting wildlife species composition and distribution patterns (Clark 1992; Abrams 2003). Oaks provide mast for a number of game and nongame animals and habitat for closely-associated avian species. The loss of this

food and shelter source due to SOD-induced oak mortality will alter wildlife distribution patterns, since no comparable mast providers are present to replace the oaks. In addition to optimal climatic conditions and abundant primary hosts, a number of abundant and widespread understory species, including mountain laurel, *Kalmia latifolia* L., *Vaccinium* spp., and other Ericaceae are ideal pathogen reservoirs (Davidson et al. 2003). Furthermore, forest disturbance could play a role in SOD invasion and establishment. An outbreak of southern pine beetle, *Dendroctonus frontalis* Zimm., in 1999–2002 decimated the shortleaf pines, *Pinus echinata* Mill., in mixed oak-pine forests throughout the southern Appalachian/Cumberland Plateau region. As these highly disturbed forests are recovering, it is likely that they will be more susceptible to invasive pathogens, including SOD, as well as non-native plants and insects. Should SOD become established in the eastern USA, replacement forests will have a drastically different composition and structure. *P. ramorum* establishment in these oak-dominated forests will devastate the oaks, potentially creating a hardwood-pine forest with considerably less value to wildlife and humans.

Our objective was to evaluate immediate and long term effects of invasion and establishment of *P. ramorum* on forest composition and structure in the central Appalachian region. We used the Forest Vegetation Simulator (FVS) to model SOD-induced red oak mortality in southern Appalachian mixed hardwood forests of eastern Kentucky, and predict likely changes in stand composition and structure. FVS is a growth and mortality model developed by the USDA Forest Service to predict the effects of forest disturbances and to guide management decisions. FVS uses vegetation data (stem diameter, height, crown height, crown class, average age, tree growth), forest landscape characteristics (elevation, aspect, slope, and slope position), and forest structure to model existing tree data, and to project future forest conditions on a 5 year cycle, up to 50 years (Dixon 2002). It's one of a number of tools available to provide natural resource managers the ability to predict the consequences of disturbance on forest composition and structure, thereby minimizing their impacts. FVS is a complex growth and yield predictor built from several regional forest growth models (Donnelly et al. 2001). The variability in species

composition, topography, climate, and growth and mortality rates necessitated generating multiple regional variants throughout North America, four of which are relevant to forests in the eastern United States. The Southern Variant is most appropriate for the central/southern Appalachian region (Keyser and Stephens 2002; Spaulding and Rieske 2010), and for sites in eastern Kentucky, growth equations are calibrated to the Daniel Boone National Forest (Donnelly et al. 2001). FVS has been used to evaluate pest outbreaks and forest disturbances, including gypsy moth, oak decline, and hemlock woolly adelgid (Crookston and Dixon 2005; Gottschalk and Courter 2007; Spaulding and Rieske 2010).

Materials and methods

Vegetation assessment

Vegetation was characterized at eighteen mixed deciduous forest sites in the Daniel Boone National Forest in the Cumberland Plateau region of Kentucky (Laurel, McCreary, Pulaski, and Whitley Counties) in 2008. At each site, three randomly selected 0.04-ha fixed-radius whole plots were established a minimum of 50 m from forest edges, and separated by a minimum of 50 m, to survey woody plant vegetation and assess stand characteristics and landscape variables. Data were collected in accordance with the protocols of the USDA Forest Service's Natural Resource Information System and its Field Sampled Vegetation Module (FSVeg) and associated Common Stand Exam procedures (Anon 2003). The height, diameter, and basal area of all woody vegetation were measured, and canopy structure, ground surface cover, slope, slope position, elevation, and aspect were assessed in each plot. Ten subplots, five 0.004-ha and five 0.0004-ha, were nested within each whole plot (0.04-ha) to enhance precision of our vegetation assessments. Whole plots (0.04-ha) were used to assess overstory and midstory vegetation, while 0.004-ha subplots were used to assess saplings and shrubs (≥ 137 cm height), and 0.0004-ha subplots were used to assess seedlings, shrubs (< 137 cm height), and vines. One of each subplot size was positioned at the whole plot center and in each cardinal direction, 7.7 m from the plot center. Thus a

surveyed site contained a total of three 0.04-ha whole plots, 15 0.004-ha subplots, and 55 0.0004-ha subplots. In the whole plots (0.04-ha), all living overstory and midstory trees (≥ 12.7 cm DBH) were assessed by species, diameter (DBH), height, and crown height (distance to lowest continuous part of the crown). In the 0.004-ha subplots, all live saplings (≤ 12.7 cm DBH) and shrubs (≥ 137 cm height) were identified and measured following the same protocol as in the whole plots (0.04 ha). Lastly, seedlings, shrubs, and vines (< 137 cm height) were identified and plant height assessed in each of the 0.0004-ha subplots (Coleman et al. 2008). Thus there were 18 sites, each with three randomly located 0.04-ha plots, for a total of 54 plots used for woody plant censusing and subsequent modeling.

Predictive modeling

We used FVS to predict likely changes in forest composition and structure at the eighteen selected sites, in both the presence and absence of *P. ramorum*. Four scenarios with oak mortality modifiers were evaluated to predict changes in oak and non-oak basal area in the presence of SOD, including: (1) 25% SOD-induced oak mortality for both red oaks and white oaks, (2) 50% mortality for red oaks, 20% for white oaks, (3) 75% red oak mortality and 15% white oak mortality, and (4) 90% red oak mortality and 10% white oak mortality (Spaulding 2009). Mortality modifiers based on our evaluations, coupled with estimates from the literature, were then used to initiate SOD-induced oak mortality at 4 years from the beginning of the simulation. The highly SOD-susceptible species in the red oak group (*Q. rubra*, *Q. velutina*, *Q. coccinea*, and *Q. falcata* Michx.) were assigned a 90% mortality rate (O'Brien et al. 2002; Gottschalk et al. 2003; Denman et al. 2005; Tooley and Kyde 2007; Balci et al. 2008), and those in the less susceptible white oak group (*Q. alba*, *Q. prinus*, and *Q. stellata*) received a 10% mortality rate (Balci et al. 2008; Tooley and Kyde 2007). Simulations continued at 10-year intervals through 50 years. Predicted basal area (m^2/ha) of selected species were calculated from the model output. Vegetation assessments and predictive modeling were used to evaluate the likely outcome of invasion by *P. ramorum*.

Statistical analysis

For each site, oak basal area and basal area of all woody plant species was assessed. Predicted mean total basal area, basal area of both the *Erythrobalanus* (primarily *Q. velutina* and *Q. coccinea*) and the *Leucobalanus* (specifically *Q. alba*, *Q. prinus*, and *Q. stellata*), and basal area of combined non-oak species were compared at 10-year intervals and between SOD and non-SOD simulations up to 50 year using an analysis of variance (ANOVA). Thus there were six 10-year time increments and 18 censused stands, for a total of 108 observations. All analyses were performed using SAS 9.0, and individual predictions were compared using a least squares means comparison.

Results

We identified 21,817 woody plants representing 74 species in 26 different families, of which the most abundant was red maple, *Acer rubrum* L. (4,462 stems), followed by partridge berry or teaberry, *Mitchella repens* L. (3,303 stems) and lowbush blueberry, *Vaccinium pallidum* Aiton (1,489 stems). The most species-rich family was the Fagaceae, with 11, followed by the Ericaceae ($N = 9$) and the Juglandaceae ($N = 6$).

Our simulations demonstrate that forests free from SOD-induced mortality (Fig. 1a) show steady incremental increases in total basal area of both oak and non-oak >12.7 cm DBH. The oak component remains relative constant, changing minimally from an initial (2008) value of ~40 to ~38% after 50 years. In current SOD-free forests, black oak dominates both the red oak and the total oak component, followed by scarlet oak (85 and 12%, respectively). Free of pathogen introduction, black oak is predicted to demonstrate a slight but steady increase in total basal area, but scarlet oak remains unchanged (Table 1a). Northern and southern red oaks comprise the remaining red oak component (<3%), and remain relatively constant over the course of our 50 year simulation (Table 1a). In present day SOD-free forests, chestnut oak dominates the white oak component (59%), followed by white oak (34%) and post oak (7%). Both chestnut and white oaks increase very slightly but significantly in basal area

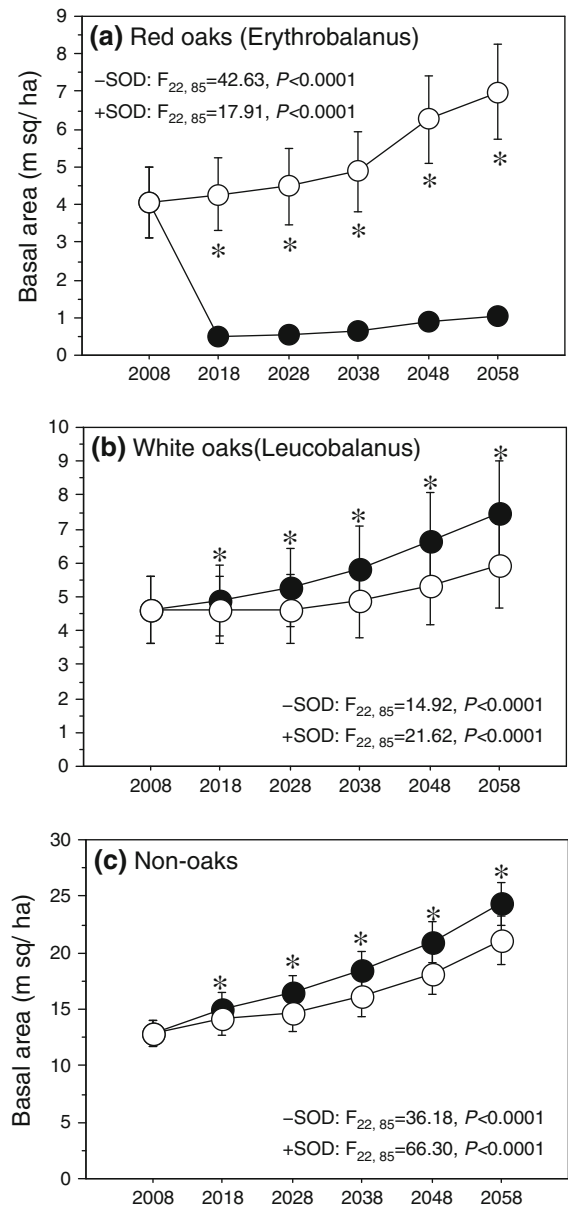


Fig. 1 Basal area (mean (s.e.)) of woody plants (oaks and non-oaks over 12.7 cm DBH), generated from FVS simulations 50 years into the future, **a** red oaks (Subgenus *Erythrobalanus*, primarily *Q. velutina* and *Q. coccinea*), **b** white oaks (Subgenus *Leucobalanus*, primarily *Q. prinus*, *Q. alba*, and *Q. stellata*), **c** non-oaks, with (filled circle) and without (open circle) SOD-induced mortality. Asterisks indicate significant differences ($P < 0.05$) between + SOD and - SOD simulations

over the course of the 50 year simulation, whereas post oak demonstrates a moderately significant decline (Table 1b).

Table 1 Current and predicted basal area (mean (se) m²/ha) of (a) red oaks (subgenus *Erythrobalanus*), and (b) white oaks (subgenus *Leucobalanus*) >12.7 cm DBH in forests un-invaded (–) and invaded (+) by *Phytophthora ramorum*

	<i>Q. velutina</i>		<i>Q. coccinea</i>		<i>Q. rubra</i>	
	–	+	–	+	–	+
a. Red oak group						
2008	3.42 (0.82)d	3.42 (0.82)a	0.52 (0.49)	0.52 (0.49)	0.01 (0.01)c	0.01 (0.01)
2018	3.63 (0.84)d	0.41 (0.10)b*	0.52 (0.48)	0.07 (0.06)	0.01 (0.01)c	0.00 (0.00)
2028	3.84 (0.89)cd	0.46 (0.11)b*	0.53 (0.49)	0.08 (0.07)	0.01 (0.01)c	0.00 (0.00)
2038	4.21 (0.94)c	0.53 (0.12)b*	0.55 (0.52)	0.09 (0.08)	0.02 (0.01)bc	0.00 (0.00)
2048	5.54 (1.03)b	0.78 (0.15)b*	0.60 (0.55)	0.10 (0.09)	0.04 (0.02)ab	0.01 (0.00)
2058	6.21 (1.13)a	0.89 (0.17)b*	0.62 (0.58)	0.11 (0.10)	0.04 (0.02)a	0.01 (0.00)
F _{22,85}	39.76	16.83	1.23	1.13	5.34	0.82
P	<0.0001	<0.0001	0.30	0.35	0.0003	0.54
	<i>Q. prinus</i>		<i>Q. alba</i>		<i>Q. stellata</i>	
	–	+	–	+	–	+
b. White oak group						
2008	2.71 (0.83)b	2.71 (0.83)d	1.57 (0.48)c	1.57 (0.48)d	0.32 (0.13)a	0.32 (0.13)a
2018	2.71 (0.82)b	2.92 (0.89)d	1.62 (0.51)c	1.66 (0.50)cd	0.26 (0.12)ab	0.29 (0.12)ab
2028	2.74 (0.82)b	3.29 (0.99)cd	1.65 (0.54)c	1.75 (0.53)cd	0.22 (0.11)b	0.26 (0.12)b
2038	2.92 (0.87)b	3.65 (1.08)bc*	1.75 (0.57)bc	1.91 (0.57)c*	0.21 (0.12)b	0.24 (0.12)b
2048	3.20 (0.94)a	4.19 (1.23)ab*	1.94 (0.59)b	2.22 (0.59)b*	0.21 (0.12)b	0.24 (0.12)b
2058	3.44 (1.00)a	4.60 (1.34)a*	2.27 (0.66)a	2.63 (0.66)a*	0.21 (0.12)b	0.24 (0.12)b
F _{22,85}	9.29	12.19	12.25	18.02	2.30	2.65
P	0.0001	<0.0001	0.0001	<0.0001	0.052	0.028

Means followed by the same letter in each column do not differ. For each species, asterisks indicate significant within-year differences between + SOD and – SOD predictions ($P < 0.05$)

Simulations incorporating SOD-induced mortality show a rapid and significant decline in the red oak group (Table 1a and Fig. 1a). Basal area declines from ~40 to ~26% of the total in the first 10 years, a nearly 38% decrease in basal area for the red oak group. Black oak demonstrates a significant decline of >85% within 10 years, and remains at that level for the duration of the simulation (Table 1a). Scarlet oak basal area also declines, although this trend is not significant. Coupled with this mortality in the red oak group, chestnut and white oaks demonstrate a slight but steady increase in basal area in the absence of their congeners. With SOD infection, the white oaks represent a substantial component of the remaining mast-producing species, and within 30 years chestnut and white oaks are projected to have significantly greater basal area than in SOD-free forests (Table 1b and Fig. 1b). Similar to simulations

free of SOD, post oak demonstrates a moderately significant decline in SOD-infected forests (Table 1b).

Regardless of SOD infection, red maple shows a steady and significant incremental increase in basal area throughout the simulation period; this increase is significantly greater in SOD infected forests within 20 years (Fig. 2a). Similarly, yellow poplar, *Liriodendron tulipifera* L., is predicted to increase slowly over the course of the 50 year simulation; again this increase is significantly greater in SOD-infected forests within 10 years (Fig. 2b). Hickories, *Carya* spp., show no significant change in basal area over 50 years, and show no differences in basal area between SOD-free and SOD-infected forests (Fig. 2c). Shortleaf pine declines steadily and incrementally over the 50 year simulation (Fig. 2d), regardless of SOD-induced oak mortality.

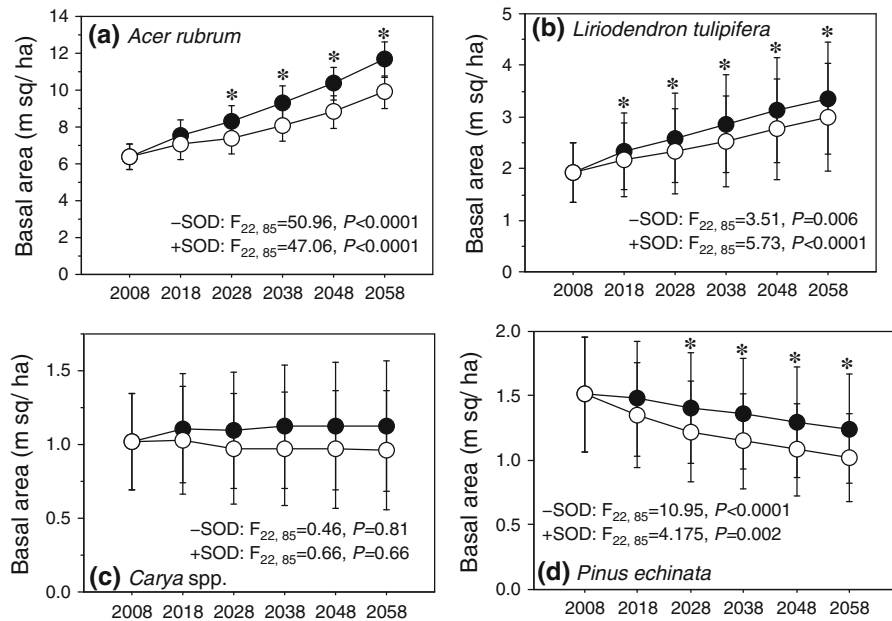


Fig. 2 Basal area of numerically dominant non-oak species, including **a** red maple, **b** yellow poplar, **c** hickory species, and **d** shortleaf pine, over 12.7 cm DBH generated from FVS simulations 50 years into the future with (filled circle) and

without (open circle) SOD-induced mortality. Asterisks depict differences in predicted basal area each year ($P < 0.05$) between + SOD and – SOD simulations

Discussion

Our simulations demonstrate significant changes in eastern North American deciduous forest composition following invasion and establishment of *P. ramorum*. In forests free of *P. ramorum*, the oak (~40%) and non-oak (~60%) components remains somewhat constant over the next 50 years. In *P. ramorum* infected forests, the total oak component is projected to decline from 40 to 26% over 50 years, led by mortality in red oaks, as the non-oak component increases to 74%. Oaks are a diverse group, and not all of them are equally susceptible to *P. ramorum* infection. We found species-specific differences in susceptibility even within the highly susceptible Erythrobalanus group, with the numerically dominant *Q. velutina* experiencing the greatest mortality. Nevertheless, these changes in the oak and non-oak components will have ramifications that include alterations in decomposition rates and nutrient cycling, altered light penetration to the forest floor that affects both woody and herbaceous plant establishment and growth, and importantly, changes in masting rates and patterns that affect wildlife distribution patterns.

Although a considerable white oak component is predicted to remain after red oak mortality, the two groups are not ecologically or economically equivalent. White oaks tend to be slower growing, long lived, shade tolerant trees that are more prominent on well-drained ridges and upland sites, whereas red oaks are more common on more mesic sites (Rogers 1990; McQuilkin 1990). Because extensive mortality of the red oak species will undoubtedly create canopy gaps that will alter the light regime to the forest floor, the suitability of remaining forests for extensive white oak proliferation, as suggested by our simulations, is questionable. White oaks are shade tolerant, but appear to be at a physiological disadvantage with regard to biomass accumulation under enhanced light regimes (Dillaway et al. 2007), and regenerate poorly under most conditions (Abrams 2003).

Wildlife abundance and distribution patterns will also be affected by the shift away from red oak mast and replacement of mast-producing red oaks with less valuable non-oak species, such as red maple or yellow poplar (McShea et al. 2007). Because they produce acorns less frequently and less predictably than red oaks (Rogers 1990; McQuilkin 1990), the shift to white oak dominance will likely affect

population dynamics of animals that rely on hard mast. Hickories also differ from oaks in their mast production patterns and in the nutritional qualities of their seeds (Smith 1990; Havera and Smith 1979); they are not expected to change significantly with respect to abundance or basal area during the next 50 years regardless of the presence of *P. ramorum*.

FVS does have limitations that must be considered in our predictions of future forest composition and structure. FVS lacks the ability to model shrubs, vines, and herbaceous vegetation, so any influence of prevalent understory shrubs such as mountain laurel, *Kalmia latifolia* L., or great laurel, *Rhododendron maximum* L., for example, is not included in our long term projections. *P. ramorum* has an extremely broad host range (USDA 2010), and Ericaceous plants appear to serve as ideal reservoirs, playing a critical role in disease epidemiology. In addition to its potential role as a pathogen reservoir, laurel has invasive tendencies and forms dense monocultures by reducing shade and monopolizing nutrients (Nilsen et al. 2001), and perhaps through allelopathic properties (Nilsen et al. 1999).

FVS is also unable to handle microclimatic variation that likely plays a critical role in pathogen sporulation. Furthermore, *P. ramorum* infection rates depend on the method of inoculation (Davidson et al. 2002, 2003), so oak mortality rates may vary locally based on proximity to suitable reservoirs, inoculation method, and on microclimatic factors favoring fungal sporulation. Susceptible oaks may remain uninfected and/or asymptomatic in areas lacking an understory with reservoir species (Brasier et al. 2004). Thus the broad mortality modifiers utilized in our predictions may not adequately operate over wide-ranging spatial and temporal scales.

Regeneration predictions are also lacking in the Southern Variant of FVS, which includes only a partial regeneration and establishment model (Donnelly et al. 2001). Any regeneration parameters will likely be of use only for a limited number of years because of the stochastic nature of regeneration and gap dynamics.

The FVS model also includes extensions and component files for predicting the likelihood and severity of pest outbreaks and other disturbances, most notably gypsy moth and oak decline (Donnelly et al. 2001; Gottschalk and Courter 2007), both of which will clearly affect the oak component.

However, because SOD-induced oak mortality occurs so much more rapidly than these mortality agents, these extensions were deemed inappropriate for use in simulating SOD infection (Spaulding and Rieske 2010).

Long-term effects of SOD-induced oak mortality will be exacerbated by interactions with other stressors. Oak decline has been a pervasive problem in temperate forests of North America and Europe in recent decades (Starkey and Oak 1989), disproportionately affecting red oaks (Kabrick et al. 2008). This pattern has been partly attributed to root fungi and other pathogens, including other *Phytophthora* species (Brasier et al. 1993), which are prevalent in forests of eastern North America (Balci et al. 2007). However, the decline in oaks and corresponding increase in other hardwood species is further complicated by additional species-specific pests and pathogens. The proliferation of beech bark disease, caused by interactions between the scale insect *Cryptococcus fagisuga* Lindinger and *Nectria* spp. fungi, ash mortality due to invasion by the emerald ash borer, *Agrilus planipennis* Fairmaire, and persistent defoliation by the gypsy moth, *Lymantria dispar* L., will continue to affect forest composition and structure. The proliferation of invasive plant species is a constant concern, particularly in forests newly disturbed by invasive pests, catastrophic weather events, and/or salvage operations.

Climate change, forest fragmentation and urbanization, management practices such as fire suppression, and native and non-native pests have contributed to substantial declines in oak basal area and dominance in eastern North America in recent years (Starkey and Oak 1989; Johnson et al. 2002; Abrams 2003). Nevertheless, the introduction of *P. ramorum* poses a greater, more focused threat that will have substantial repercussions for our oak resources and for future forest structure and composition.

Acknowledgments We would like to thank Melanie Antonik, Tom Coleman, W. Rodney Cooper, and Aerin Land for assistance, Robert Paratley for help with plant identifications, and Angela Schoergendorfer for statistical advice. Jeffrey Stringer and John Obrycki reviewed an earlier version of this manuscript, and the comments of two anonymous reviewers greatly strengthened this work. This research was supported by funds from the USDA Forest Service Southern Research Station and McIntire Stennis funds from the Kentucky Agricultural Experiment Station, and is published as Experiment Station Project 10-08-046.

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