Disease, fuels and potential fire behavior: Impacts of Sudden Oak Death in two coastal California forest types

Alison B. Forrestel [a,*], Benjamin S. Ramage [b], Tadashi Moody [c], Max A. Moritz [c], Scott L. Stephens [c]

[a] Golden Gate National Recreation Area, 1061 Fort Cronkhite, Sausalito, CA 94965, USA
[b] Biology Department, Randolph-Macon College, Ashland, VA 23005, USA
[c] Ecosystem Sciences Division, Department of Environmental Science, Policy, and Management, University of California, 137 Mulford Hall, Berkeley, CA 94720-3114, USA

ABSTRACT

In the Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) and redwood (*Sequoia sempervirens* (D. Don) Endl.) forests of the central California coast, Sudden Oak Death (SOD) has led to landscape-scale mortality of tanoak (*Notholithocarpus densiflorus* (Hook. and Arn.) Manos, Cannon and S.H. Oh). As tanoak mortality progresses, fuel loads and potential fire behavior in these forests are changing. We documented increases in fuel loads over time in long-term monitoring plots in infested forests at Point Reyes National Seashore. Throughout the study, we observed a significant positive relationship between dead tanoak basal area and surface fuels. We used the fire behavior modeling program BehavePlus to compare potential fire behavior between diseased and healthy stands. Model outputs indicated the potential for longer flame lengths, higher rates of spread and more intense surface fire in diseased stands. The potential for increased fire intensity in diseased redwood and Douglas-fir forests may create additional challenges for fire and natural resources managers and may affect the ecology of these forests into the future.

Published by Elsevier B.V.

1. Introduction

Losses or dramatic declines of forest species, populations, or age classes due to pests and pathogens can have major impacts on ecosystems. These impacts include changes in ecosystem structure, decreased biodiversity, changes in hydrology and nutrient cycling, and cascading impacts throughout the food web (Ellison et al., 2005; Loo, 2009). The potential for forest pests and pathogens to interact with other ecological perturbations and yield unexpected or nonlinear responses is of particular concern (Paine et al., 1998; Turner, 2010).

Forest pathogens or insect pests have the potential to interact with wildfire by changing fuel loads and thereby fire behavior (Dale et al., 2001; Lundquist, 2007; Simard et al., 2011). Increased fuel loads from disease or pest-related mortality may lead to increased fire intensity and fire effects (Lynch et al., 2006; Metz et al., 2011). Changes in fire intensity can in turn shift the trajectory of post-fire succession and potentially create opportunities for invasion by non-native plants (Sugihara et al., 2006). Additional ecological impacts of changes in fire intensity could include below-ground impacts to microbial communities or soil structure, increased erosion and sedimentation, changes in

plant community structure and composition, and cascading effects up the food chain (Brown and Smith, 2000; Neary et al., 2005). However, the relationship between pests, pathogens and fire behavior is complex, varying with the pest or pathogen in question, the temporal trajectory of the pest or pathogen outbreak, the ecosystem that is impacted, and local fire regimes and climate (Parker et al., 2006; Jenkins et al., 2008). In some cases, forest pests or pathogens may actually dampen the potential effects of wildfire by thinning canopy fuels as trees die (e.g. Simard et al., 2011).

Several studies, mostly focused on interactions between mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks and wildfire, have documented the trajectory of fuels and fire behavior over time following a pest outbreak. In some cases, fine dead fuels and potential surface fire intensity increased over the short term (2–20 years post-outbreak) and then began to return toward pre-outbreak conditions over the longer term (20+ years post-outbreak) (Hicke et al., 2012; Schoennagel et al., 2012). These same studies report coarse woody debris continuing to increase over the long term (Hicke et al., 2012; Schoennagel et al., 2012). Similarly, the potential for crown fire in areas of mountain pine beetle outbreaks changes over time, with high uncertainty about the effects of the pest outbreak in the short term and strong evidence for a decrease in crown fire potential in the longer term (Simard et al., 2011; Harvey et al., 2014). This study examines potential

interactions between Sudden Oak Death and wildfire over a five year period in a coastal California ecosystem.

Landscape-scale mortality of true oaks (*Quercus* spp.) in the black oak group as well as tanoak (*Notholithocarpus densiflorus* (Hook. and Arn.) Manos, Cannon and S.H. Oh), referred to as Sudden Oak Death, is caused by the pathogen *Phytophthora ramorum* (S. Werres, A.W.A.M. de Cock). This pathogen is likely non-native and introduced from Asia via the nursery trade; symptoms were first observed in Marin County, California in the mid-1990's (Rizzo and Garbelotto, 2003; Mascheretti et al., 2009). *P. ramorum* causes lethal bole cankers in oaks in the black oak group and tanoaks. Dozens of other species act as foliar hosts. *P. ramorum* sporulates on these species but has little or no effect on their health. Coast live oak (*Quercus agrifolia* Née), the most impacted true oak species in Marin County, has some natural resistance, with 30% mortality observed over one 8-year study (McPherson et al., 2010). Tanoak mortality was reported at 50% in the same long-term study (McPherson et al., 2010) and others have documented tanoak mortality close to 100% (Davis et al., 2010; Ramage et al., 2011b). Mortality rates are higher for tanoak in part because it is the only species that supports both sporulation and bole canker formation (Rizzo and Garbelotto, 2003; Rizzo et al., 2005). Several studies have found evidence that suggests dramatic losses of tanoaks are likely and that extirpation may be avoided only through resprouting and augmenting natural populations with plantings (Rizzo and Garbelotto, 2003; Rizzo et al., 2005; Cobb et al., 2012; Dodd et al., 2013). Genetic studies of tanoak throughout coastal California have found some resistance to *P. ramorum* and research on the feasibility of a resistance breeding program is ongoing (Hayden et al., 2011,2013).

The direct impacts of SOD on coastal California forests, including mortality rates and changes in stand structure and regeneration, have been well documented (Waring and O'Hara, 2008; McPherson et al., 2010; Ramage et al., 2011a, 2011b). However, the potential interactions between SOD and other disturbance agents such as wildfire are less well studied. There is some evidence that SOD infection rates are lower in areas that have recently burned (Moritz and Odion, 2005). A few studies have attempted to quantify the impacts of SOD on wildfire. Metz et al. (2011) took a retrospective approach to investigate the relationship between SOD severity and fire effects in the 2008 Basin Fire in Big Sur, California. The authors found that an overall comparison of healthy versus diseased plots in the Basin Fire showed no differences in burn severity. However, plots with recent SOD infections, where infected tanoaks were still standing with dead leaves, showed higher burn severity than both healthy plots and plots with older infections (Metz et al., 2011). However, this study did not incorporate factors such as weather and topography that would have impacted fire severity and potentially confounded their results. Valachovic et al. (2011) measured fuel loads in healthy and recently infested stands as well as stands where tanoak had been killed with herbicide (a standard forestry practice which was used in this study as a proxy for older SOD-infestations) and did prospective modeling of the potential impacts of SOD on fire behavior. They did not find a significant difference between the fuel loads of diseased versus healthy stands, but they did find differences between herbicide-treated and healthy stands as well as increases in modeled outputs of fire intensity in herbicide-treated stands. Another study looked at potential changes in crown fire ignition of tanoaks killed by *P. ramorum* (Kuljian and Varner, 2010). This study found that foliar moisture content, which is an important predictor of the ability for a surface fire to transition to crown fire, decreased from 82% in healthy tanoaks to 78% in diseased tanoaks and to 12% for dead tanoak foliage. While the change from 82% to 78% would not have a significant effect on fire behavior, the drop to 12% for standing dead tanoaks would result in much higher likelihoods of

a fire transitioning from a surface fire to a crown fire (Kuljian and Varner, 2010).

This is the first study to directly measure changes in surface fuels over time associated with Sudden Oak Death and to use those data to model potential changes in fire behavior. We combined direct field observations with fire behavior modeling to assess the impacts of SOD on potential fire behavior of Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) and redwood (*Sequoia sempervirens* (D. Don) Endl.) forests in Point Reyes National Seashore, California, USA. We tracked surface fuels over a five year period in a network of plots and used those data to populate fire behavior models. Our study tests the following hypotheses: 1. Surface fuels initially increase and then level off over time in SOD-infested Douglas-fir and redwood forests and 2. Increased surface fuels lead to increased predicted fire intensity.

2. Methods

2.1. Study area and plot selection

Fieldwork was conducted in Point Reyes National Seashore and in adjacent areas of Golden Gate National Recreation Area that are managed by Point Reyes National Seashore (referred to collectively here as PRNS). The combined area managed by PRNS is approximately 36,000 hectares and is located in Marin County, California, about 45 km northwest of San Francisco. The climate of PRNS is Mediterranean with mild, wet winters and cool, dry summers. Based on local weather station data from 1964 to 2012, the average minimum and maximum monthly temperatures during summer months ranged from lows of 6 °C to 9 °C to highs of 18 °C to 24 °C. Average winter minimum and maximum temperatures were similar with lows ranging from 2 °C to 4 °C and highs of 15 °C to 17 °C. Average annual precipitation in the study area over this same time period was approximately 100 cm per year (Bear Valley Weather Station 1964–2012). A large majority of the precipitation occurs between October and March although the summer drought is attenuated by coastal fog, which can provide substantial moisture inputs to ecosystems when intercepted by plant canopies. Fog drip has not been quantified for PRNS, but one study further north on the California coast found that fog drip added 22–45 cm of precipitation annually (Dawson, 1998). Elevations in the study area range from 170 m to 480 m. Vegetation at PRNS is characterized by coastal grassland and scrub closer to the Pacific Ocean and Douglas-fir, mixed evergreen and redwood forest along ridge lines and valleys further inland. Inventory plots were located in both redwood/tanoak and Douglas-fir forest types as defined in the PRNS vegetation classification (Fig. 1; Schirokauer et al., 2003). Historical fire regimes in redwood and coastal California Douglas-fir forests were characterized by high frequency, low and moderate severity fires many of which were likely associated with Native American management practices (Lorimer et al., 2009). The redwood and Douglas-fir forests of PRNS are second-growth stands that were logged in the late 19th and early 20th centuries. SOD was first documented in PRNS in 2004. Portions of the study area directly abut the Marin Municipal Water District, which was the likely location of SOD introduction in Marin County, California in the mid-1990s (Rizzo et al., 2002; Mascheretti et al., 2009; McPherson et al., 2010).

Plot selection followed a stratified random split-plot sampling design. Paired plots, one healthy and one diseased, were established at the beginning of the study period. Random points were generated in GIS in both Douglas-fir and redwood vegetation types using the PRNS vegetation GIS layer (Schirokauer et al., 2003). In the field, an expanding radius search starting from these random points was used to locate diseased-healthy plot pairs that met
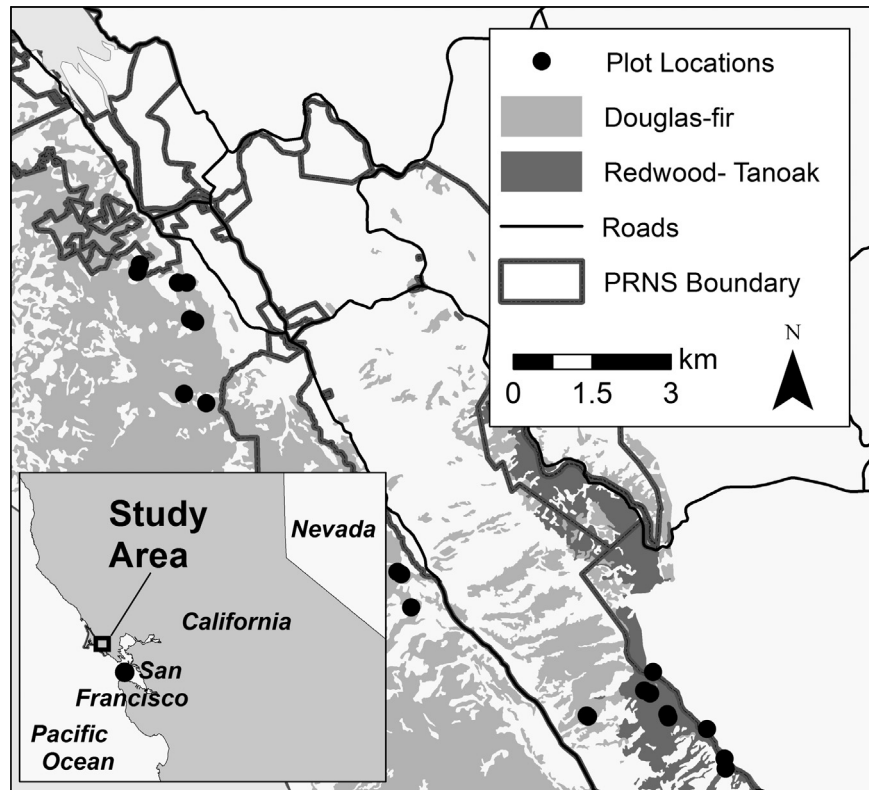
Fig. 1. Map of Point Reyes National Seashore, California, showing forest types and plot locations.

our selection criteria. Selection criteria included a minimum threshold for both canopy cover ($\geqslant$25%) and basal area ($\geqslant$0.46 m^2) of the dominant species (redwood or Douglas-fir), slopes less than 60%, and a minimum basal area of tanoak (live and/or dead) of 0.93 m^2. In a few cases, a healthy or diseased plot was established without a paired plot of the opposite condition (if both conditions were not present in close proximity). All plots were circular with a 12.62 m radius (0.05 ha). In total, 15 Douglas-fir (5 diseased, 10 healthy) and 14 redwood (7 diseased, 7 healthy) plots were established. Sample sizes between the two forest types are uneven because, based on initial data analysis in 2007, one of the redwood diseased plots was identified as an outlier due to much higher stem densities and smaller trees than other plots and was removed from future field measurements and analysis. Note that the label "healthy" refers only to the initial condition of the plot. Many healthy plots exhibited substantial SOD mortality by the end of the study period. More details about plot selection are provided in Ramage et al. (2011a).

2.2. Data collection and sampling

Plots were initially established in the summer of 2007 and were remeasured during the summers of 2009 and 2011. Within each plot, each tree $\geqslant$3 cm diameter at breast height (DBH) was mapped. The following characteristics for each tree were recorded in each sampling year: species, DBH, height, height-to-live crown and status (live versus dead). For SOD-susceptible species (tanoak and coast live oak), we also recorded detailed information on SOD symptoms (bleeding, bole cankers, Hypoxylon fungi, beetle holes and (or) frass, and canopy dieback (Swiecki and Bernhardt, 2006; McPherson et al., 2010)). Post-mortality deterioration for these species was characterized using a visual estimate of the percentage of dead leaves still clinging to dead trees as well as the height and stem diameter of bole breakage. Stems of species other than tanoak

were not recorded if broken below breast height, but to ensure that we captured the majority of SOD-induced tanoak mortality, tanoak stems that were broken below breast height were recorded if the fallen bole wood was intact at the outset of the study. Multi-stemmed trees that were split below breast height were counted as separate trees.

Fuels data were collected using 12.6 m standard planar intercept transects (Brown et al., 1982). During the initial sampling effort, in 2007, two transects (at 0° and 180° azimuths from plot center) were measured. In 2009 and 2011, this was increased to four transects per plot, one in each cardinal direction. Along each transect, surface fuels were tallied in timelag-classes. The number of 1-h fuels (<0.64 cm diameter) and 10-h fuels (0.64–2.54 cm diameter) that crossed the transect plane between 10.5 and 12.5 m were counted, and the number of 100-h fuels (2.54–7.62 cm diameter) that crossed the transect plane between 8.5 and 12.5 m were counted. Diameter was recorded for each 1000-h fuel (>7.62 cm diameter) that crossed the transect plane between 0 and 12.62 m. If no 1000-h fuels were encountered between 0 and 12.62 m, transects were extended to 20 m.

2.3. Data analysis

We used one-tailed t-tests to analyze change over time in each fuel class with the total change from 2007 to 2011 as our response variable. We used Bonferroni corrections to adjust for multiple comparisons. Fuel loads were calculated with the program FFI (Lutes et al., 2009) using standard fuel constants (Brown, 1974). Calculations were adjusted to account for the increased length of transects when transects were extended to capture more 1000-h fuels. We also tested the effects of tanoak mortality (basal area of dead tanoak) on total fuels in each sampling year using linear mixed effects models where each plot-pair was treated as a block. Because surface fuels tend to have high spatial variation and our

sample size was relatively small, we combined our data across forest type and disease status for this analysis. Two healthy Douglas-fir plots were excluded from this analysis because they contained large, fallen Douglas-fir trees which overwhelmed the fuels signature of the plot and were outliers compared to other healthy plots in this study and across the landscape. All data were tested to ensure they met assumptions of normality and homoscedasticity and 2011 data required log-transformation to meet those assumptions. However, untransformed data are shown graphically to allow for visual comparison with 2007 and 2009 data.

The surface fire modeling program BehavePlus (Heinsch and Andrews, 2010) was used to compare potential changes in fire

Table 1
Fuel characteristics for field data (gray) and standard fire behavior models TL3 and TL5.

Fuels	Healthy	TL3	TL5	Diseased
1 h (tons/acre)	0.35	0.5	1.15	1.00
10 h (tons/acre)	1.70	2.2	2.5	4.04
100 h (tons/acre)	2.26	2.8	4.4	5.18
Fuel bed depth (ft)	0.25	0.3	0.6	0.93

Fig. 2. Disease progression, shown as proportion of total tanoak basal area that was alive, over the study period for diseased and healthy redwood (dashed line) and Douglas-fir (solid line) plots. Vertical lines show plus/minus one standard error.

behavior between diseased and healthy stands. BehavePlus provides information on modeled surface fire behavior at the stand level. BehavePlus inputs were based on a combination of field data and pre-existing datasets. We selected standard surface fuel models (Scott and Burgan, 2005) based on the average fuel characteristics of healthy and diseased plots. In assigning fuel models, we used 2007 healthy plots as our reference for fuels in healthy forests and 2011 diseased plots as our references for fuels in diseased forests since these two time points represent each end of the healthy-diseased spectrum. Fuel model TL3 (Moderate Load Conifer Litter) was selected to represent healthy plots because TL3 most closely matched field conditions, although it is a slight over-estimate of fuels and therefore the intensity of predicted fire behavior (Table 1; Scott and Burgan, 2005). For diseased plots, we selected fuel model TL5 (High Load Conifer Litter), which is a slight under-estimate of fuel conditions as measured in the field (Table 1; Scott and Burgan, 2005).

Fine dead fuel moisture and wind data were calculated using 97th percentile weather from the Barnabe RAWS station (1995–2004), which is 2.5 km north of the study area. The 97th percentile corresponds with weather during the 1995 Vision Fire which burned approximately 5000 ha of PRNS northwest of the study area. Live woody fuel moisture was based on values measured by Marin County for peak fire season (October) (Forrestel et al., 2011; Marin County Fire Department, 2012). All statistical analyses used R Statistical Software (version 2.15.0, R Development Core Team, Vienna, Austria) with the nlme package (Pinheiro et al., 2009).

3. Results

3.1. Tanoak mortality and fuel loads

Tanoak mortality progressed over the study period across both forest types in healthy and diseased plots (Fig. 2). Fuel loads increased over the same time period across all forest type, fuel size and disease status categories (Fig. 3). Changes in fuel loads were significant for 1-h fuels across both forest types and disease
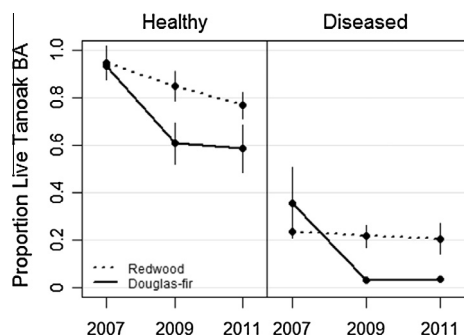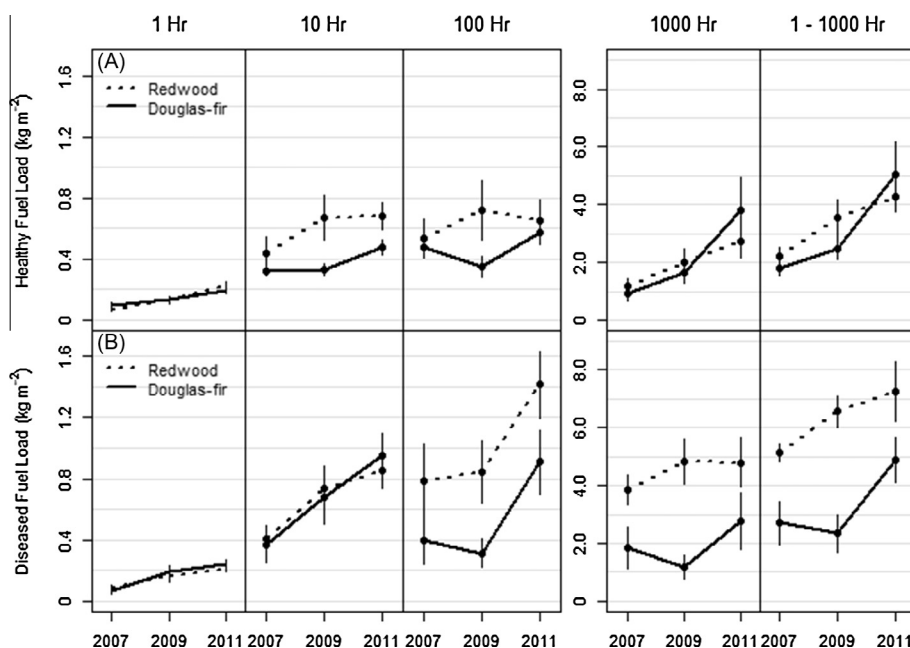

Fig. 3. Change in fuel load over time for each time-lag fuel class and for total fuels. (A) Healthy plots are shown in the top row and (B) diseased plots in the bottom row. Douglas-fir plots are depicted with a solid line and redwood plots are shown with a dashed line. Vertical lines show plus/minus one standard error.

statuses and for 10-h fuels in Douglas-fir plots ($p < 0.01$ with Bonferroni correction; Table 2). Changes in 100-h fuels were significant only in redwood diseased plots. Total fuels changes (1-through 1000-h) were significant for diseased Douglas-fir and healthy redwood plots. For all years, there was a significant relationship between fuel load and basal area of dead tanoaks (Fig. 4). However, if the outlier plots that had large, fallen Douglas-fir trees had remained in the analysis, the relationship between tanoak mortality and fuels for 2011 would not have been significant.

3.2. Fire behavior modeling

Weather and fuel moisture values used as BehavePlus inputs are shown in Table 3 along with modeled outputs for healthy and diseased stands. Modeled fire behavior in diseased stands exhibited higher rate of spread, heat per unit area, fireline intensity and flame length than in healthy stands. Rate of spread and fire line intensity, were both an order of magnitude larger for diseased versus healthy stands and predicted flame lengths were three times higher in diseased versus healthy stands.

4. Discussion and conclusions

4.1. Tanoak mortality and fuel loads

Our results show that tanoak mortality increased over the study period, particularly among plots that were healthy at the beginning

of the study. Mortality ranged from 20% of basal area to upwards of 90% of basal area by the end of the study period (Fig. 2). A detailed analysis of disease progression in these plots from 2007 to 2009 found annual mortality rates higher than had previously been reported in association with SOD (3–8% in redwood forests and 10–26% in Douglas-fir forests; Ramage et al., 2011a). The total mortality (measured as basal area) that we observed is consistent with or higher than what has been observed in other research (McPherson et al., 2010; Ramage et al., 2011a). By the end of the study period, mortality appeared to be leveling off in diseased plots, but not healthy plots. This suggests that over some time period, greater than the five-year period of this study, living tanoak basal area may stabilize at a level that is a small fraction of its initial basal area.

As tanoak mortality progressed in our study plots, surface fuels concurrently increased. The fuel loads we observed in healthy plots at the outset of the study were similar to those reported for healthy Douglas-fir and redwood forests in other studies (National Park Service, 1998; Dicus, 2003; Fonda and Binney, 2011). No one has previously quantified fuel loads in forests with well-established SOD infestations although Valachovic et al. (2011) measured fuels in a small number of diseased plots and then attempted to quantify the effects of SOD on fuel loads using herbicide-treated stands as a proxy for heavy SOD infestation. The fuel loads we observed in

Table 2
p-values for t-tests of change in fuels over time (2007 to 2011) by forest type, disease status and timelag fuel class. With Bonferroni correction for multiple comparisons, $p < 0.01$ is considered significant at the $\alpha = 0.05$ level. Significant changes are denoted with an *.

Timelag fuel class	Douglas-fir healthy	Douglas-fir diseased	Redwood healthy	Redwood diseased
1	0.0000*	0.0009*	0.0005*	0.0011*
10	0.0098*	0.0032*	0.1084	0.0223
100	0.1884	0.1175	0.2686	0.0028*
1000	0.0175	0.1050	0.0156	0.2192
All	0.0122	0.0053*	0.0063*	0.0582

Table 3
BehavePlus model inputs (above) and outputs (below). Inputs are based on 97th percentile weather from the Barnabe RAWS station (1995–2004).

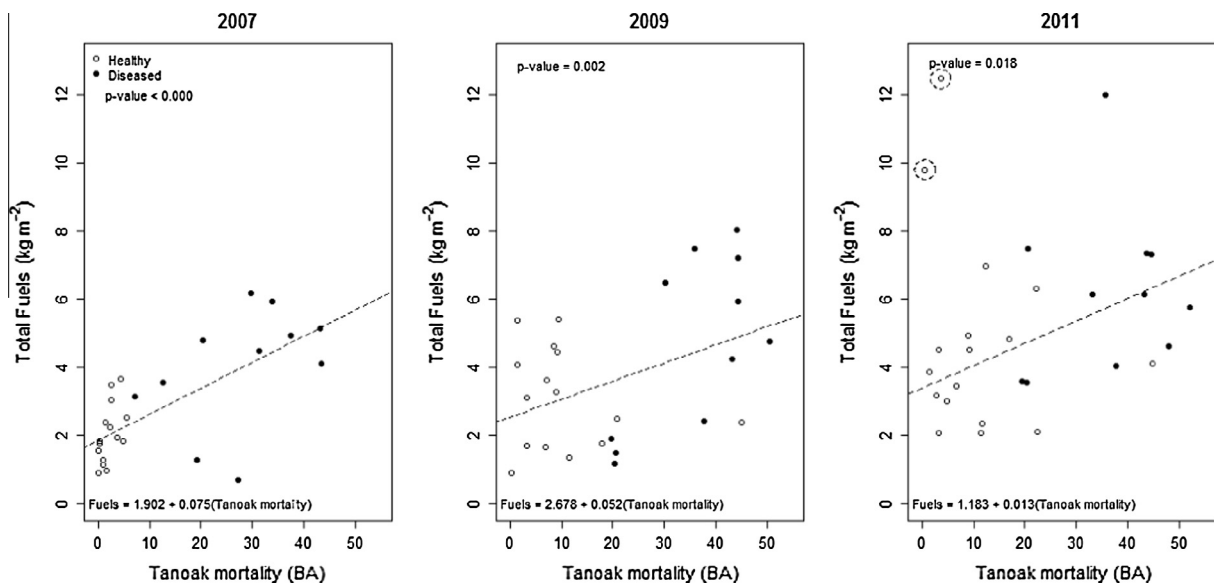|		Healthy	Diseased
Surface fuel model		TL3	TL5
Foliar moisture content (%)		80	80
Fine dead fuel moisture (%)	1 h	3	3
	10 h	4	4
	100 h	10	10
Live woody fuel moisture (%)		61	61
Wind speed (km/h)		24	24
Rate of spread (m/min)		1.6	11.8
Heat per unit area (kJ/m^2)		2.606	4.676
Fire line intensity (kW/m)		71	921
Flame length (m)		0.6	1.8

Fig. 4. Total fuels as a function of tanoak mortality for each sampling year. Tanoak mortality is expressed as basal area (BA) in meters squared per hectare. Data are combined for forest type and disease status. Healthy plots are depicted with open circles and diseased plots are depicted with closed circles. Dashed circles indicate outlier plots that were removed from statistical analysis. See text for details.

diseased stands were higher than in our healthy stands, but lower than what was reported for herbicide-treated stands in Valachovic et al. (2011). Our results for diseased stands were however similar to those Valachovic et al. (2011) reported for the few diseased stands they measured. We detected significant changes in surface fuels among the smaller fuel classes. This is important because fine fuels (litter, 1-, 10- and 100-h fuels) have the greatest impact on fire spread (Rothermel, 1972). Intuitively, this is the response we would expect as tanoaks die and leaves, branches and eventually entire trees fall to the forest floor (see Fig. 5). Fuels in the 100-h size class also increased, but changes over time were not significant except in the case of diseased redwood plots. Surface fuels are often highly variable at small scales (Fry and Stephens, 2010) and this variability may have been the reason we did not detect statistically significant changes in the 100-h size class for the other plot types.

We observed marginally significant increases of 1000-h fuels in plots that were healthy at the start of the study, but not in heavily diseased plots. This may be because there were already substantial amounts of 1000-h fuels present on the forest floor of diseased plots at the outset of our study and suggests that fuel loads, like tanoak mortality, may level off over time. Large fuels are not the primary carriers of fire spread, but they can increase fire effects, particularly on soils. These fuels tend to smolder for long periods following the passage of the flaming front and have the potential to significantly alter soils, below-ground communities and regeneration potential (Neary et al., 1999). On the positive side, increases in large fuels could improve habitat and cover for ground-dwelling species such as the dusky-footed woodrat (*Neotoma fuscipes* Baird) (Hamm, 1995; Fehring, 2003; Tempel and Tietje, 2005).

Throughout the study period, there was a strong relationship between tanoak mortality and fuel loads at the plot level with total fuels increasing across all plots and the distinction between diseased and healthy plots breaking down over time (Fig. 4). The general pattern we observed of increasing surface fuels over the study period is consistent with what has been found in other studies of fuels trajectories over time following a pest or pathogen outbreak (Hicke et al., 2012; Schoennagel et al., 2012). We did not detect surface fuels beginning to decrease and return to pre-outbreak conditions as decomposition begins to catch up with fuels accumulation rates. There is some indication that fuels might be leveling off in the diseased plots by 2011. Based on the literature from mountain pine beetle outbreaks, it will likely be one to several decades before there is a detectable return toward pre-pathogen

outbreak fuels conditions (Hicke et al., 2012; Schoennagel et al., 2012; Harvey et al., 2014).

4.2. Fire behavior modeling

Fuel models TL3 and TL5 (Scott and Burgan, 2005) were selected for healthy and diseased plots, respectively. Using these fuel models, BehavePlus model outputs for surface fire behavior predict higher spread rate, flame length, heat per unit area and fireline intensity for diseased versus healthy plots. With all other factors equal, higher flame lengths increase the probability that a surface fire will lead to torching or passive crown fire. For example, during two prescribed fires in mixed redwood/Douglas-fir forest at nearby Muir Woods National Monument, when flame lengths increased from 0.5 m to 1 m, fire behavior became much more active and small trees began to torch (National Park Service, 1998). The combination of higher flame lengths predicted here with the lower canopy moisture rates observed by Kuljian and Varner (2010) in infected trees would make transition to crown fire much more likely and require much higher canopy base heights to resist ignition in the canopy. These increases in surface fire intensity and the increased possibility of torching or crown fire could make fires in SOD-affected Douglas-fir and redwood forests harder to suppress than in healthy forests. This was qualitatively observed by fire fighters in the 2008 Basin Fire, who reported 25% increases in fire intensity in SOD-impacted forests (Lee et al., 2009). More intense fire behavior is likely to lead to more severe fire effects. If diseased forests burn more intensely, we might expect to see decreased seedling recruitment, different species recruiting post-fire, increased canopy mortality and the potential for increased impacts to soils and soil communities. In one study, Ramage et al. (2010) found strong evidence that as fire severity increases in redwood-tanoak forests, redwoods have increasingly higher probabilities of survival as compared to tanoak. However, Metz et al. (2013) also documented up to fourfold increases in redwood mortality in areas affected by SOD. This suggests that in this forest type, the combination of SOD and fire could act synergistically to dramatically reduce these two keystone species and possibly tip the ecosystem into a novel state.

Although our results indicate the potential for increased fire intensity and probability of torching in SOD-impacted stands, these fire behavior modeling outputs should be interpreted cautiously. Our results are largely dependent on the choice of surface fuel model which is, by definition, somewhat subjective (Collins et al., 2010). In addition, the fuel and fire behavior models used in this assessment are simplified representatives of real fuel conditions (Scott and Burgan, 2005) and fire behavior (Pastor et al., 2003) and some model parameters, such as surface area to volume ratio, have not been field validated because of the difficulty of doing so (Scott and Reinhardt, 2001). Further, we expect that over some time period, likely on the order of one to several decades, potential fire intensity will return to pre-SOD conditions. However, the overall picture of substantial increases in fire intensity during the window of increased fuels from SOD is compelling.

5. Conclusions

This research documents clear patterns of increased fuel loads associated with increased SOD severity in Douglas-fir and redwood forests. In addition, our work suggests that fires in recently SOD-affected forests could burn with greater intensity. These results are consistent with the work of Valachovic et al. (2011) and Metz et al. (2011), although our results suggest more potential for increased fire intensity and severity than those reported by Metz et al. (2011).

Fig. 5. Fuel accumulation associated with fallen tanoaks in a redwood forest at Point Reyes National Seashore, California, USA.

Redwood and coastal California Douglas-fir forests have evolved with primarily low and moderate severity fire since pre-EuroAmerican settlement times (Lorimer et al., 2009). However, our work suggests that as these forests are impacted by *P. ramorum*, the potential for uncharacteristically intense fire behavior may be increasing, at least for some window of time until decomposition catches up with fuel inputs from this disease. These increases could present challenges to fire managers and make fire suppression efforts in SOD-impacted forests more difficult. In addition, there may be undesirable ecological impacts associated with more intense fires in these forests. Such impacts could include reduced diversity of below-ground communities, changes to soil or increased erosion, decreased plant regeneration, shifts in species composition and negative impacts on wildlife species such as the northern spotted owl (*Strix occidentalis* ssp. *caurina* Merriam). Although redwood and Douglas-fir forests are undoubtedly under-going substantial changes due to SOD, we are hopeful about the ability of these forests to persist even if the tanoak understory is lost and some forests experience uncharacteristically severe wildfire.

Acknowledgements

References

Brown, J., 1974. Handbook for Inventorying Downed Woody Material USFS GTR-INT-16. USDA Forest Service.

Brown, J., Smith, J., 2000. Wildland fire in ecosystems: effects of fire on flora Gen. Tech. Rep. RMRS-GTR-42-vol. 2. USDA Forest Service, Rocky Mountain Research Station, Ogden, UT.

Brown, J., Oberheu, R., Johnston, C., 1982. Handbook for Inventorying Surface Fuels and Biomass in the Interior West. GTR-INT-129, USDA Forest Service, Intermountain Forest and Range Exp. Stn., Ogden, UT.

Cobb, R., Filipe, J., Meentemeyer, R., Gilligan, C., Rizzo, D., 2012. Ecosystem transformation by emerging infectious disease: loss of large tanoak from California forests. J. Ecol. 100, 712–722.

Collins, B.M., Stephens, S.L., Moghaddas, J.J., Battles, J.J., 2010. Challenges and approaches in planning fuel treatments across fire-excluded forested landscapes. J. Forest. 108, 24–31.

Dale, L.A., Joyce, L.A., McNulty, S., Neilson, R., Ayres, M., Flannigan, M., Hanson, P., Irland, L., Lugo, A.E., Peterson, C., Simberloff, D., Swanson, F., Stocks, B., Wotton, B., 2001. Climate change and forest disturbances. Bioscience 51, 723–734.

Davis, F.W., Borchert, M., Meentemeyer, R., Flint, A., Rizzo, D., 2010. Pre-impact forest composition and ongoing tree mortality associated with sudden oak death in the Big Sur region; California. For. Ecol. Manage. 259, 2342–2354.

Dawson, T., 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117, 476–485.

Dicus, C., 2003. Fuel loading and potential fire behavior after selective harvest in coast redwood stands. In: Second International Wildland Fire Ecology and Fire Management Congress, Orlando, FL.

Dodd, R., Nettel, A., Wright, J., Afzal-Rafii, Z., 2013. Genetic structure of *Notholithocarpus densiflorus* (Fagaceae) from the species to the local scale: a review of our knowledge for conservation and replanting. Madrono 60, 130–138.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D., Kloeppel, B., Knoepp, J.D., Lovett, G., Mohan, J., Orwig, D., Rodenhouse, N., Sobczak, W., Stinson, K., Stone, J., Swan, C., Thompson, J., Von Holle, B., Webster, J., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3, 479–486.

Fehring, K., 2003. Dusky-footed woodrat monitoring in Point Reyes National Seashore Final Report. In: Point Reyes Bird Observatory. Point Reyes Station, CA.

Fonda, R., Binney, E., 2011. Vegetation response to prescribed fire in Douglas-fir forests, Olympic National Park. Northwest Sci. 85, 30–40.

Forrestel, A.B., Moritz, M.A., Stephens, S.L., 2011. Landscape-scale vegetation change following fire in Point Reyes, California, USA. Fire Ecol. 7, 114–128.

Fry, D., Stephens, S.L., 2010. Stand-level spatial dependence in an old-growth Jeffrey pine - mixed conifer forest, Sierra San Pedro Martir, Mexico. Can. J. For. Res. 40, 1803–1814.

Hamm, K., 1995. Abundance of Dusky-Footed Woodrats in Managed Forests of North Coastal California. Humboldt State University, Arcata, CA.

Harvey, B.J., Donato, D., Romme, W.H., Turner, M., 2014. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecol. Appl. 24, 1608–1625.

Hayden, K., Nettel, A., Dodd, R., Garbelotto, M., 2011. Will all the trees fall? Variable resistance to an introduced forest disease in a highly susceptible host. For. Ecol. Manage. 261, 1781–1791.

Hayden, K., Garbelotto, M., Dodd, R., Wright, J., 2013. Scaling up from greenhouse resistance to fitness in the field for a host of an emerging forest disease. Evol. Appl., 1–13.

Heinsch, F., Andrews, P., 2010. BehavePlus fire modeling system, version 5.0: Design and Feature. General Technical Report RMRS-GTR-249., Department of Agriculture, Forest Service. Rocky Mountain Research Station, Fort Collins CO.

Hicke, J., Johnson, M., Hayes, J., Preisler, H., 2012. Effects of bark beetle-caused mortality on wildfire. For. Ecol. Manage. 271, 81–90.

Jenkins, M., Herbertson, J., Page, W., Jorgensen, C., 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain Wes. For. Ecol. Manage. 254, 16–34.

Kuljian, H., Varner, J., 2010. The effects of sudden oak death on foliar moisture content and crown fire potential in tanoak. For. Ecol. Manage. 259, 2103–2110.

Lee, C., Valachovic, Y., Frankel, S., Palmieri, K., 2009, Sudden Oak Death Mortality and Fire: Lessons from the Basin Complex. In: Fourth Sudden Oak Death Science Symposium. USDA Forest Service, Pacific Southwest Research Station, Santa Cruz, CA, Page 67.

Loo, J.A., 2009. Ecological impacts of non-indigenous invasive fungi as forest pathogens. Biol. Invasions 11, 81–96.

Lorimer, C., Porter, D., Madej, M., Stuart, J., Veirs, S., Norman, S., O'Hara, K., Libby, W., 2009. Presettlement and modern disturbance regimes in coast redwood forests: Implications for the conservation of old-growth stands. For. Ecol. Manage. 258, 1038–1054.

Lundquist, J., 2007. The relative influence of diseases and other small-scale disturbances on fuel loading in the black hills. Plant Dis. 91, 147–152.

Lutes, D.C., Benson, N.C., Keifer, M., Caratti, J.F., Streetman, A.S., 2009. FFI: A software tool for ecological monitoring. Int. J. Wildland Fire 18.

Lynch, H., Renkin, R.A., Crabtree, R., Moorcroft, P., 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. Ecosystems 9, 1318–1327.

Marin County Fire Department, 2012. Marin County Fire Department Fire Weather Information.

Mascheretti, S., Croucher, P.J.P., Kozanitas, M., Baker, L., Garbelotto, M., 2009. Genetic epidemiology of the Sudden Oak Death pathogen *Phytophthora ramorum*in California. Mol. Ecol. 18, 4577–4590.

McPherson, B., Mori, S., Wood, D., Kelly, M., Storer, A., Svihra, P., Standiford, R., 2010. Responses of oaks and tanoaks to the sudden oak death pathogen after 8 y of monitoring in two coastal California forests. For. Ecol. Manage. 259, 2248–2255.

Metz, M., Frangioso, K., Meentemeyer, R., Rizzo, D., 2011. Interacting disturbances: Wildfire severity affected by stage of forest disease invasion. Ecol. Appl. 21, 313–320.

Metz, M., Varner, J.M., Frangioso, K., Meentemeyer, R., Rizzo, D., 2013. Unexpected redwood mortality from synergies between wildfire and an emerging infectious disease. Ecology 94, 2152–2159.

Moritz, M.A., Odion, D.C., 2005. Examining the strength and possible causes of the relationship between fire history and Sudden Oak Death. Oecologia 144, 106–114.

National Park Service, 1998. Ben Johnson and Deer Park 2 Prescribed Burn Reports.

Neary, D.G., Klopatek, C.C., DeBano, L.F., Ffolliott, P.F., 1999. Fire effects on belowground sustainability: a review and synthesis. For. Ecol. Manage. 122, 51–71.

Neary, D., Ryan, K., DeBano, L., 2005. Wildland fire in ecosystems: effects of fire on soils and water. RMRS-GTR-42vol4, USDA Forest Service, Rocky Mountain Research Station, Ogden, UT.

Paine, R., Tegner, M., Johnson, E., 1998. Compounded perturbations yield ecological surprises. Ecosystems 1, 535–545.

Parker, T., Clancy, K., Mathiason, R., 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agric. For. Entomol. 8, 167–189.

Pastor, E., Zarate, L., Planas, E., Arnaldos, J., 2003. Mathematical models and calculations systems for the study of wildland fire behavior. Prog. Energy Combust. Sci. 29, 139–153.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team., 2009. nlme: Linear and nonlinear mixed effects models. R package version 3.1-96.

Ramage, B., O'Hara, K., Caldwell, B., 2010. The role of fire in the competitive dynamics of coast redwood forests. Ecosphere 1.

Ramage, B., Forrestel, A., Moritz, M., O'Hara, K., 2011a. Sudden oak death disease progression across two forest types and spatial scales. J. Veg. Sci. 23, 151–163.

Ramage, B.S., O'Hara, K.L., Forrestel, A.B., 2011b. Forest transformation resulting from an exotic pathogen: regeneration and tanoak mortality in coast redwood stands affected by sudden oak death. Can. J. For. Res. 41, 763–772.

Rizzo, D., Garbelotto, M., 2003. Sudden Oak Death: endangering California and Oregon forest ecosystems. Front. Ecol. Environ. 1, 197–204.

Rizzo, D., Garbelotto, M., Davidson, J., Slaughter, G., Koike, S., 2002. *Phytophthora ramorum* as the cause of extensive mortality of *Quercus* spp. and *Lithocarpus densiflorus* in California. Plant Dis. 86, 205–214.

Rizzo, D., Garbelotto, M., Hansen, E., 2005. *Phytophthora ramorum*: Integrative research and management of an emerging pathogen in California and Oregon forests. Annu. Rev. Phytopathol. 43, 309–335.

Rothermel, R.C., 1972. A mathematical model for predicting fire spread in wildland fuels. USDA For. Serv. Res. Pap. INT-115, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.

Schirokauer, D., Keeler-Wolf, T., Meinke, J., van der Leeden, P., 2003. Plant Community Classification and Mapping Project Final Report: Point Reyes National Seashore, Golden Gate National Recreation Area, San Francisco Water Department Watershed Lands, Mount Tamalpais, Tomales Bay, and Samuel P. Taylor State Parks. National Park Service, Point Reyes Station, CA.

Schoennagel, T., Veblen, T.T., Negron, J., Smith, J., 2012. Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. PLoS ONE 7, 1–14.

Scott, J., Burgan, R.E., 2005. Standard Fire Behavior Fuel Models: A Comprehensive Set for Use with Rothermel's Surface Fire Spread Model. General Technical Report RMRS-GTR-153. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins CO.

Scott, J., Reinhardt, E.D., 2001. Assessing crown fire potential by linking models of surface and crown fire behavior. RMRS-RP-29, USDA Forest Service Rocky Mountain Research Station, Fort Collins CO.

Simard, M., Romme, W.H., Griffin, J., Turner, M.G., 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecol. Monogr. 81, 3–24.

Sugihara, N.G., van Wagtendonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A.E., 2006. Fire in California's Ecosystems. University of California Press, Berkeley.

Swiecki, T., Bernhardt, E.A., 2006. A field guide to insects and diseases of California oaks USDA USFS Gen. Tech. Rep. PSW-GTR-197.

Tempel, D., Tietje, W., 2005. Potential Effects of Sudden Oak Death on Small Mammals and Herpetofauna in Coast Live Oak (*Quercus agrifolia*) Woodlands. In: Proceedings of the sudden oak death second science symposium: the state of our knowledge. USFS, Monterey, CA, pp. 233–236.

Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. Ecology 91, 2833–2849.

Valachovic, Y.S., Lee, C.A., Scanlon, H., Varner, J.M., Glebocki, R., Graham, B.D., Rizzo, D.M., 2011. Sudden oak death-caused changes to surface fuel loading and potential fire behavior in Douglas-fir-tanoak forests. For. Ecol. Manage. 261, 1973–1986.

Waring, K.M., O'Hara, K., 2008. Redwood/tanoak stand development and response to tanoak mortality caused by *Phytophthora ramorum*. For. Ecol. Manage. 255, 2650–2658.