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The effects of sudden oak death on foliar moisture content and crown fire potential in tanoak

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ABSTRACT

The introduction of non-native pathogens can have profound effects on forest ecosystems resulting in loss of species, changes in species composition, and altered fuel structure. The introduction of *Phytophthora ramorum*, the pathogen recognized as causing Sudden Oak Death (SOD), leads to rapid decline and mortality of tanoak (*Lithocarpus densiflorus*) in forests of coastal California, USA. We tracked foliar moisture content (FMC) of uninfected tanoaks, SOD-infected tanoaks, SOD-killed (dead) tanoaks, and surface litter for 12 months. We found that FMC values differed significantly among the three categories of infection. FMC of uninfected tanoaks averaged 82.3% for the year whereas FMC of infected tanoaks had a lower average of 77.8% (ANOVA, $P = 0.04$). Dead trees had a significantly lower FMC, averaging 12.3% (ANOVA, $P < 0.01$) for the year. During fire season (June–September), dead tanoak FMC reached a low of 5.8%, with no significant difference between dead canopy fuels and surface litter (ANOVA, $P = 0.44$). Application of low FMC values to a crown ignition model results in extremely high canopy base height values to escape crown ignition. Remote estimation of dead FMC using 10-h timelag fuel moisture shows a strong correlation between remote automated weather station (RAWS) 10-h timelag fuel moisture data and the FMC of dead leaves ($R^2 = 0.78$, $P < 0.01$). Results from this study will help refine the decision support tools for fire managers in SOD-affected areas as well as conditions in other forests where diseases and insect epidemics have altered forest canopy fuels.

1. Introduction

Plant pathogens and insects are found in all forest ecosystems and are responsible for forest dynamics at both small (gap phase) and large (landscape pattern) scales (Castello et al., 1995). Often, pathogens and insect attacks manifest as recurring disturbances and, as such, are essential to maintaining forest structure (Turner, 1989; Haack and Byler, 1993; Hessburg et al., 2000). These disturbances will often work in concert with secondary disturbances that synergistically influence the larger disturbance regime (White and Pickett, 1985). In many cases diseases will alter surface fuels (Dickman and Cook, 1989; Castello et al., 1995) where the subsequent fire intensity and severity are increased.

Non-native plant pathogen introduction can have an even greater impact on the invaded ecosystems (Coblentz, 1990; Vitousek et al., 1996). Host species typically have limited or no resistance to non-native pathogens resulting in substantial population decline or elimination of a species. The introduction of chestnut blight (*Cryphonectria parasitica*) and white pine blister rust (*Cronartium ribicola*) are two well-known North American examples (Paillet, 2002; Ellison et al., 2005). As with native pathogens and insects, there is potential for secondary disturbances, especially fire. Trees weakened by pathogens may suffer greater mortality during fire than healthy trees (Agee, 1993), and trees killed can elevate fuel loads and exacerbate fire effects (Harrington and Hawksworth, 1990; Hummel and Agee, 2003).

The introduction of the non-native pathogen *Phytophthora ramorum*, recognized as causing Sudden Oak Death (SOD), has caused profound effects at the ecosystem and landscape scales in coastal forests of central and northern California, USA (Rizzo and Garbelotto, 2003; Waring and O'Hara, 2008). Since its discovery in 1995 in the San Francisco Bay area, SOD has quickly spread north and south along the coastal forests and woodlands from Monterey to Humboldt County and isolated areas of southwest Oregon infecting all dominant tree species including coast redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), coast live oak (*Quercus agrifolia*), Pacific madrone (*Arbutus menziesii*) and tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.) (Davidson et al., 2005; Rizzo et al., 2005; Murphy et al., 2008). Among these species, tanoak is most susceptible to SOD, with tree mortality exceeding 95% in some areas and over 3 million trees killed to date (Moritz et al., 2008; USDA Forest Service, 2009a). Since tanoak is common as an

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understory component, a co-dominant, or found in pure stands (Sawyer et al., 1977; Tappeiner et al., 1990), SOD infection has the potential to severely diminish or eliminate this species and change the composition and structure of forests where tanoak is a significant component (Waring and O'Hara, 2008).

In addition to changes in species composition, changes in forest fuel structure are also eminent as tanoaks succumb to SOD. These changes often follow a pattern that can be considered as four distinct phases (Fig. 1): *Phase 1*—individual trees are infected, crowns become yellow with reduced foliar density; *Phase 2*—the tree remains standing dead with leaves attached one or more years (D. Rizzo, unpublished data, 2010). Due to the characteristics of *P. ramorum* infection, the mechanism of leaf abscission is interrupted, resulting in prolonged dead leaf retention. *Phase 3*—leaf fall occurs, adding considerable litter fuel to the forest floor fuelbed, thereby elevating surface fire hazard (crown fire potential is reduced while surface fire hazard increases); *Phase 4*—branches, limbs, and entire stems begin to fail, falling to the forest floor resulting in a substantial increase in surface woody fuel loading. These phases are not necessarily sequential. For example, stem failure can occur at any point in the sequence as a result of secondary organisms such as *Hypoxylon thouarsianum* and/or ambrosia beetles (Swiecki and Bernhardt, 2005). Across this sequence, the incipient Phases 1 and 2 likely represent the most acute crown fire hazard attributable to lower foliar moisture. Crown foliar mass in these phases may remain high enough to sustain crown fire spread (Van Wagner, 1977). Beyond phase 2, surface fire intensity may increase as a result of elevated fuel loading; however, the reduction of crown fuel density makes the probability of crown ignition and/or spread unlikely.

Since crown fuels (foliage and twigs <0.6 mm) become more available for combustion as foliar moisture declines, and managers in the region have reported an increase in crown fire ignition in SOD-affected forests (Lee and Valachovic, 2009), there is an immediate need to quantify the susceptibility of crowns to ignition. Van Wagner (1977) developed the crown fire model used in the majority of fire behavior and spread prediction software (Scott and Reinhardt, 2001; Finney, 2004). The Van Wagner model requires four parameters: (1) fireline intensity (FLI); (2) canopy base height (CBH); (3) crown bulk density (CBD); (4) and foliar moisture content (FMC) (Van Wagner, 1977). Small changes in FLI and CBH have considerable influence on the probability of crown ignition. Applying the range of normal FMC values found in healthy trees (73–150%; Keyes, 2006), to the Van Wagner model, the effect of FMC on crown ignition is minor (Scott and Reinhardt, 2001; Cruz et al., 2006). To date, no work has evaluated the effect of reduced FMC (below 70%) on crown fire ignition, an important oversight if dead foliage remains attached to standing trees for a prolonged period of time, as is the case with SOD-killed tanoak.

Substantial research has been conducted to quantify foliar moisture of conifers (Johnson, 1966; Philpot and Mutch, 1971; Agee et al., 2002; Keyes, 2006), however considerably less is known about the foliar moisture characteristics of broadleaf trees and foliar moisture patterns of evergreen hardwoods is lacking altogether. Limited research has been conducted on the diurnal FMC pattern of whiteleaf manzanita (*Arctostaphylos viscida*) foliage (Philpot, 1965), seasonal trends in sugar maple (*Acer saccharum*) and trembling aspen (*Populus tremuloides*) (Van Wagner, 1967), and understory shrubs (as a group) in Pacific Northwest forests (Agee et al., 2002). For deciduous hardwood trees, Van Wagner (1967) found FMC values that far exceeded co-occurring conifers. For tanoak, limited FMC data were collected following the Biscuit Fire in southwest Oregon during late summer (Raymond and Peterson, 2005). Clearly, current data typifying the FMC of hardwoods is lacking.

Given that SOD-killed tanoaks retain dead foliage for one or more years following death, and tanoak can typically comprise one third or more of the basal area in these coastal forests, we sought to quantify the decline in FMC and evaluate its magnitude on potential crown fire ignition. The objectives of this study were to: (1) quantify the patterns of FMC monthly over a one year period; (2) compare FMC among healthy tanoaks, tanoaks infected with SOD, and dead tanoaks across the same period; (3) compare the FMC of standing dead trees to surface litter moisture and; (4) investigate the potential of using 10-hour timelag fuel moisture data (representing woody fuels 0.63–2.53 cm in diameter) obtained from a remote automated weather station (RAWS) to predict the FMC of dead tanoak leaves. Methodology developed for this study can be applied to other ecosystems where pathogens and insects are reducing FMC and causing prolonged dead leaf retention of trees (i.e. vascular wilts, root diseases, and beetle-killed trees). Data derived from this study would be an important contribution in order to link crown ignition to spread rates via crown fire and/or spotting, a topic not considered in this study due to the complexity of the canopy fuel strata in forests where tanoak is co-dominant or an understory component. Results from this study are also critical for decision support software used to evaluate the likelihood of crown fire ignition by resource managers in tanoak forests.

2. Methods

In March 2008, we began tracking the FMC of uninfected tanoak, live SOD-infected tanoak, and dead tanoak. Individual tanoak trees were selected in an area of known SOD infection on CAL FIRE Eel River Camp and adjacent properties near Redway, CA, USA (40°08′29.12″N, 123°49′29.80″W) where SOD has been known to exist since 2004 (Y. Valachovic, personal communication, 2007). The species composition in the study area consisted of California bay, Douglas-fir, Pacific madrone, and coast redwood (occasionally) with tanoak as a dominant, co-dominant or understory component. Concerned that uninfected tanoaks in the study area could become infected during the course of the study, but not detected until after sampling had finished, a second site was selected as a control, 70 km north of the area of infection at the L.W. Schatz Demonstration Tree Farm (LWSDTF) near Maple Creek, California (40°46′07.04″N, 123°52′12.29″W). The LWSDTF site offered stand and weather conditions similar to the Eel River Camp with a comparable elevation (172 m for Eel River Camp, 245 m for LWSDTF) and distance to the ocean (23 km for Eel River Camp, 27 km for LWSDTF; Fig. 2).

At Eel River Camp a total of 25 trees were selected for monthly sampling: 8 live uninfected tanoaks, 10 live SOD-infected tanoaks, and 7 standing dead tanoaks (SOD killed with leaves on). Given that individual trees could change from uninfected to infected or infected to dead during the course of the study, less importance was given to attaining even sample sizes across infection categories. More importance was given to selecting individual trees based on their similar size and stand characteristics, and their proximity to one another allowing field sampling to occur within the narrow windows used in previous FMC research (Philpot, 1965). At the LWSDTF 12 tanoaks (uninfected) of similar size and canopy position as that of the tanoaks at Eel River Camp were chosen for sampling monthly. Samples from each tree consisted of removing approximately 30 g of >1-year old leaves, <1-year-old leaves, and twigs (0.0–0.6 mm) with a 6 m pole pruner. On each sampled tree, we collected leaves from randomly selected branches, removing foliage without regard to presence of flagging, dead margins, or entirely dead leaves. Additionally, we also collected 15 g of surface leaf litter (at the upper surface of the litter layer) beneath sampled dead tanoaks monthly. We collected surface litter to compare this commonly measured variable in surface fire rate of spread (Rothermel, 1972) to FMC patterns and to provide perspective on the magnitude of moisture dynamics in SOD-infected ecosystems.

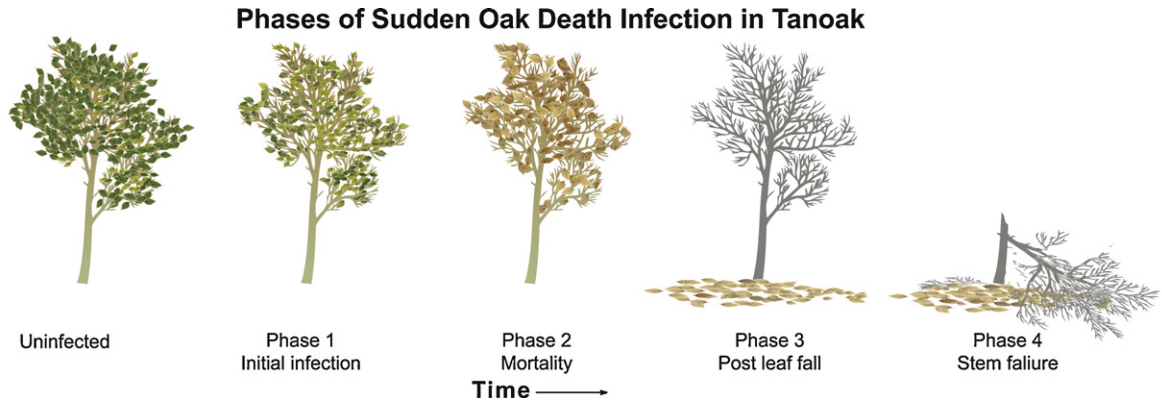

Fig. 1. Decline of tanoak caused by sudden oak death proceeds in phases until all components of the tree are recruited to the surface fuel complex. This study quantified change in crown fuels from uninfected trees through phases 1 and 2, where trees are standing dead with dead leaves attached.

At both sites all trees were sampled each month for 12 months (March 2008 to February 2009). Sampling for each site was completed on consecutive days whenever possible, never occurring more than 2 days apart. All foliar samples were removed from the lower 1/3 of the canopy on the southern aspect of each tree (Agee et al., 2002) between 1200 and 1600 h to minimize any possible variation due to residual moisture resulting from overnight or early evening dew accumulation. Samples were sealed in 15 cm × 23 cm polyethylene bags, weighed wet, then oven-dried at 70 °C until no further weight loss occurred (typically 48 h). To confirm that our sample methods were minimizing any diurnal variation, crown fuels were collected on a subset of the LWSDTF tree group ($n = 5$) every 3 h from 10:00 to 22:00 h on 11 October 2008. These tanoaks showed no difference throughout the 12 h sampling

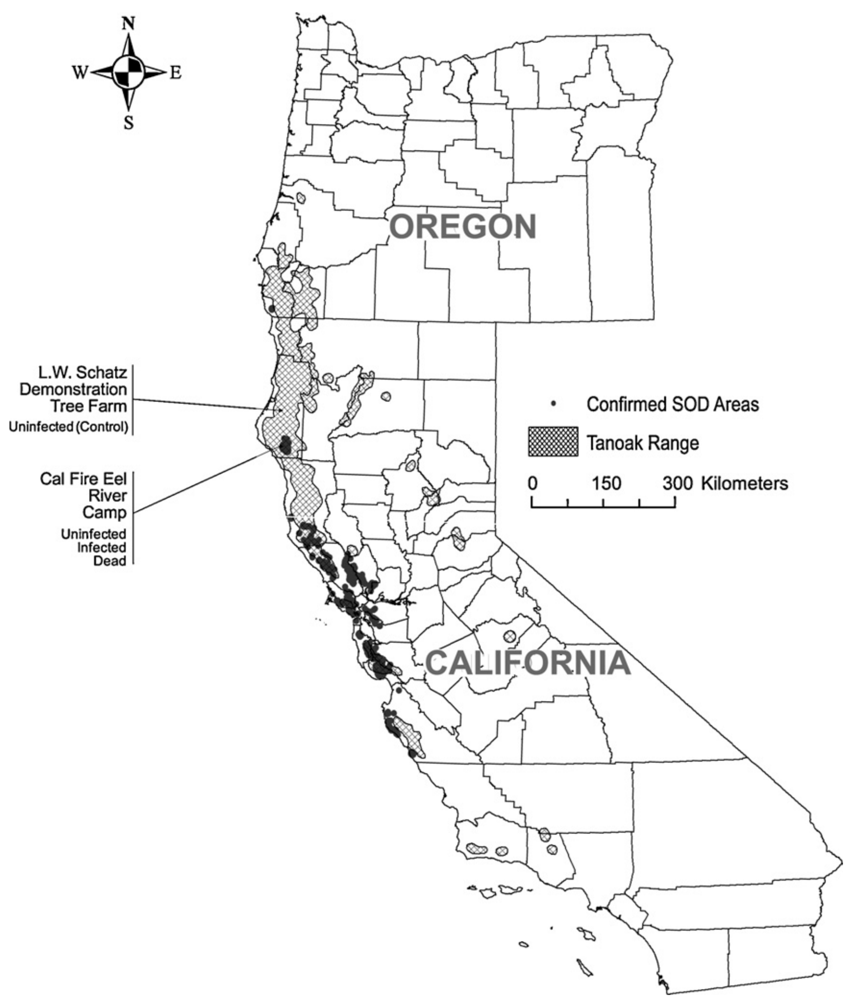

Fig. 2. Sudden oak death (SOD) is well established within the range of tanoak and is expected to spread throughout the coastal tanoak range within the next decade. Foliar moisture content of individual trees was sampled at two study sites for this study. Uninfected, SOD-infected, and SOD-killed trees were sampled at the Cal Fire Eel River Camp in southern Humboldt County. To avoid losing sample trees to infection, we selected a second uninfected tanoak site, 70 km north of the area of infection at the L.W. Schatz Demonstration Tree Farm near Maple Creek, California.

period for >1 year leaves (p = 0.95), <1 year leaves (p = 0.08), or twigs (p = 0.37).

Infected trees were initially selected based on visual symptoms that characterize SOD including areas of dark brown or black discoloration of bark on the lower bole, "bleeding" from cankers on the bark, the presence of small black fungus fruiting bodies (*Hypoxylon thouarsianum*), the presence of frass produced by bark or ambrosia beetles, and yellowing or thinning of foliage in the canopy (Davidson et al., 2003; Swiecki and Bernhardt, 2005). Laboratory attempts to isolate *P. ramorum* on the study trees were inconclusive; however, the presence of *P. ramorum* has been repeatedly confirmed throughout the stand (C. Lee, U.C. Cooperative Extension laboratory, Eureka, CA) using foliar samples from California bay laurel (*Umbellularia californica*) host species and bark samples from symptomatic tanoaks (Rizzo, 2002; Swiecki and Bernhardt, 2002; Garbelotto et al., 2003). Confirmation of *P. ramorum* infection within tanoak is difficult and false negatives are common (Rizzo et al., 2005). Other pathogens such as *Armillaria* can produce similar symptoms on tanoak, however none are known to lead to the large patches of mortality caused by *P. ramorum* (Baumgartner and Rizzo, 2001). Considering the heavy tanoak mortality in this area we assumed our selection of diseased tanoaks typified the conditions found in SOD-infected stands.Repeated measures ANOVA was used to compare mean FMC of >1 year leaves, <1 year leaves, and twigs across three categories of infection (uninfected, infected, and dead) for the 12 month sampling period at Eel River Camp. Also, FMC of <1 year foliage was compared between uninfected and infected tanoaks and dead canopy FMC was compared to surface leaf litter moisture using repeated measures ANOVA. Finally, categories of >1 year leaves, <1 year leaves, and twigs were compared between the uninfected trees at Eel River Camp and the same categories from the control trees at LWSDTF. If a statistically significant difference occurred among the 3 categories of infection, the 2 categories of <1 year leaves, or the 2 categories of dead leaf (canopy vs. litter), sample means for each date were compared using one-way ANOVA with Tukey-Kramer post hoc means separation (Zar, 1999). Data that did not meet assumptions of normality or equal variance were log or square-root transformed; where transformations were made, they are listed in Appendix A. If the data still failed to meet assumptions of normality or equal variance, a non-parametric Kruskal-Wallis one-way ANOVA on ranks was used. Significance for all analyses were determined using $\alpha = 0.05$.

The relationship between data from local RAWS 10-h timelag fuel moisture and dead leaf moisture (FMC_{dead}) was examined using data from the RAWS unit at the CAL FIRE Eel River Camp (NWS ID 040421), located less than 1 km from the primary study site. RAWS 10-h timelag fuel moistures were averaged for 4 different time spans: 1200–1800 h, 1200–2300 h, 1600–2300 h, and 1800–2300 h. Regression analysis was used to compare measured 10-hr moisture content at these time periods as a predictor of FMC_{dead}. The response variable (FMC_{dead}) was transformed using natural log to normalize the residuals.

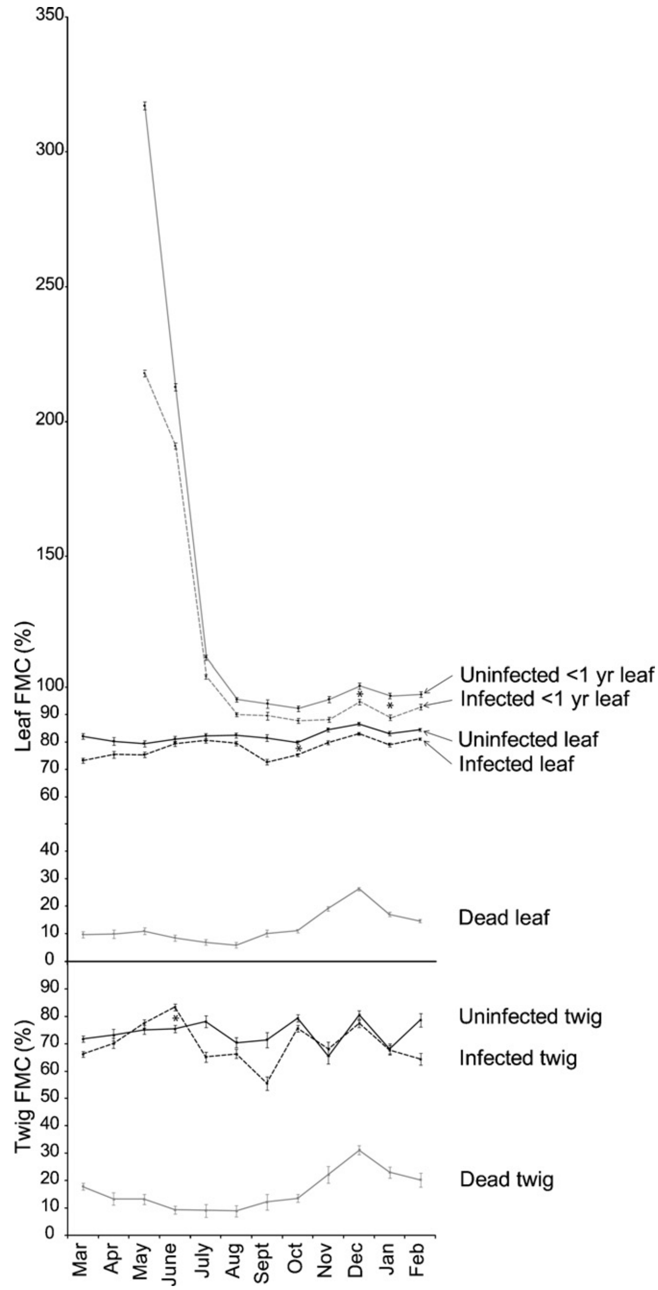

Fig. 3. Monthly leaf, <1 year leaf, and twig moisture (±SE) of Eel River Camp tanoaks across 3 categories of infection status: Uninfected, SOD-infected, and SOD-killed. Mean FMC of SOD-infected and uninfected tanoak foliage (>1 year leaf) did not differ more that 10% for the 12 month sampling period. Mean FMC of dead tanoaks was significantly lower than infected and uninfected groups for both leaves and twigs ($P < 0.01$). Asterisks indicate statistical significance between categories.

3. Results

Across the 3 infection categories (uninfected, SOD-infected, and dead trees), FMC values for dead tanoak foliage >1 year were significantly lower than uninfected or SOD-infected trees ($P < 0.01$). Mean foliar moisture for SOD-infected leaves was lower than uninfected, but only the October sampling date was statistically different. The 1 year mean FMC for uninfected tanoak leaves was 82.3% (SE ± 1.5) ranging from 79.5% in May to 86.7% in December (7% difference). The mean FMC of SOD-infected tanoaks was 77.8% (SE ± 1.3) across the sampling period with a range from 72.7% in September to 83.0% in December (10% difference). The mean FMC of dead leaves averaged 12.6% (SE ± 1.6) across the 12 month sampling period with a high of 26.4% to a low of 5.9%, observed during August 2008 (Fig. 3).[1]

The pattern in tanoak twig moisture was similar to the FMC of 1 year old leaves. Dead twig moisture was significantly lower than twig moisture of uninfected or SOD-infected tanoaks. Twig moisture of uninfected and SOD-infected tanoaks was not significantly different with the exception of the June sampling date. Mean twig moisture for uninfected tanoaks was 73.6% (SE ± 1.9%) with a range from 65.5% in November to 80.5% in December. The mean

[1] For specific FMC values across all categories and months see Appendices A–C.

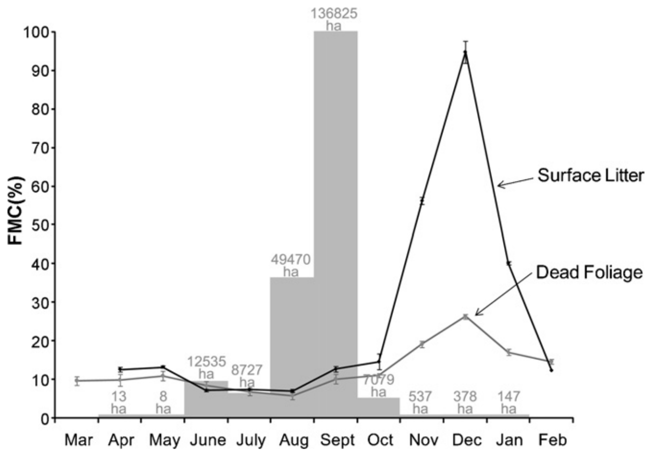

Fig. 4. Monthly dead leaf moisture (±SE) of tanoaks and surface litter moisture in Humboldt County, California. Months June through September show no significant difference in moisture content between surface litter and dead foliage, coincident with peak fire season (SE = 0.6; P = 0.44). Horizontal grey bars indicate fire season showing total area burned (hectares) by month (1944–2008) in tanoak forests of the California north coast region (source data: Cal Fire FRAP).

twig moisture of the SOD-infected tanoaks was 69.7% (SE ± 1.8%) across the sampling period with a range from 55.6% in September to 84.1% in June. Mean twig moisture of dead tanoaks was 16.0% (SE ± 2.2%) across the 12 month sampling period, peaking at 32.3% in December down to a low of 8.7% in August (Fig. 3).

Foliar moisture of new foliage (<1 year) did not differ between uninfected tanoaks and SOD-infected tanoaks for all months except for the months of December (P = 0.046) and January (P = 0.014). Foliar moisture of new leaves declined rapidly from May to July with little change occurring after August.

Surface leaf litter moisture varied significantly among months with a high of 40.3% in December to a low of 7.1% in July (P < 0.01; Fig. 4). Mean litter moisture values differed significantly from dead leaf FMC for the months of April, November, and December. For the months May through October there was no significant difference between dead leaf FMC and surface litter.

Mean FMC of uninfected 1 year leaves and of uninfected <1 year leaves at Eel River Camp did not differ significantly from leaves sampled at LWSDTF (P = 0.438 1 yr leaf, P = 0.671 new leaf). Mean FMC of twigs between sites (uninfected) were different for the year (P = 0.004); the months February, June, and September through December did not differ, while the remaining 6 months had a mean difference between sites ranging from 9 to 21% moisture content.

A strong relationship was found between RAWS 10-h timelag fuel moisture and daily FMC_{dead}. Using the time period between 1600–2300 h explained the greatest amount (78%) of variability in FMC_{dead} (P < 0.01; Fig. 5).

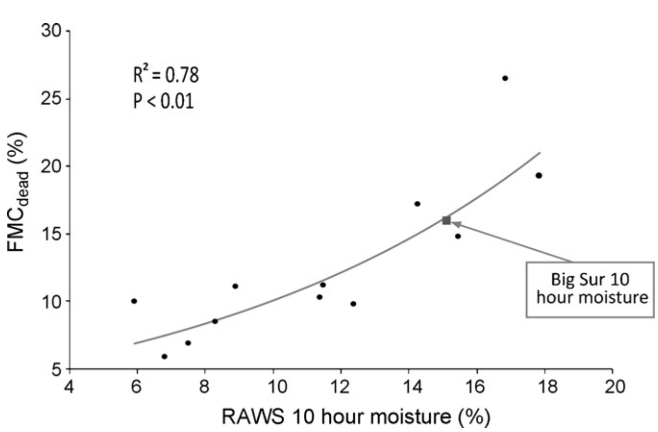

Fig. 5. Relationship between remote automated weather station 10-hour timelag fuel moisture content (average from 1600 to 2300 h) and dead leaf foliar moisture content. The equation of the line shown is: ln Dead Leaf FMC (%) = (1.3486) + (0.0955) RAWS – 10-h fuel moisture (%).

4. Discussion

The mean monthly range of FMC for healthy tanoaks in this study (80–87%) is at the low end of published FMC values for North American trees. For example, Douglas-fir, a species associated with tanoak throughout much of its range, has a range of 80–120% for >1 year old foliage. For the month of August, Raymond and Peterson (2005) found the average FMC of >1 year leaves for Douglas-fir in southwest Oregon was 147%, while their tanoak FMC for >1 year leaves averaged only 91% FMC. These low FMC values pale in comparison to deciduous hardwoods reported in Van Wagner (1967), where FMC ranged between 135 and 250%.

There was little seasonal change in the FMC of tanoak, contrary to seasonal moisture trends frequently found for conifers (Keyes, 2006) and other broadleaf deciduous trees (Van Wagner, 1967). This lack of variation is unusual considering that conifer FMC can fluctuate as much as 66% annually depending on the species (Keyes, 2006). Other broadleaf FMC data from sugar maple (*Acer saccharum*) show moisture ranging from 170% to 250%, and trembling aspen (*Populus tremuloides*) from 135% to 245% (Van Wagner, 1967). Additionally, healthy tanoaks in this study did not show any diurnal variation of foliar moisture, contrary to the diurnal patterns observed in conifers (Agee et al., 2002) and broadleaf shrubs (Philpot, 1965).

While infected tanoaks did not have a significantly lower FMC than healthy tanoaks, the results indicate there may be a tendency for some infected individual trees to exhibit lower FMC values. This may be due to the fact that samples collected from infected trees often exhibited "leaf flagging", a symptom common to SOD-infected tanoak (Davidson et al., 2003), which likely will result in lower moisture content of those individual leaves. Nevertheless, the small changes in FMC between infected and uninfected tanoaks observed in this study are inconsequential from the standpoint of crown fuel ignition. For example, a 1 m flame length in the Van Wagner (1977) model shows that a change in FMC from 85% to 75% will raise the canopy ignition height by only 0.2 m. The largest difference among the 3 infection categories was between dead tree foliage and leaves of uninfected/infected categories. Mean dead leaf FMC levels dropped as summer (fire season) progressed, resulting in a concomitant moisture content dip below 6% in August (Fig. 4). Surface litter moisture closely tracked dead leaf FMC, averaging 7% during the mid-summer months. It is interesting to note the overlap of historical fire season pattern (indicated on Fig. 4) with the FMC levels of dead leaves and litter. Generally these critically low moistures coincide with fire season during the mid-summer months. The slight rise in FMC of dead and surface litter during September is in all probability indicative of the weather pattern preceding the sample date. With the onset of winter, seasonal patterns of precipitation and high relative humidity result in the large differences seen between surface litter moisture and dead tree foliage.

The relationship between RAWS 10-h timelag fuel moisture and FMC_{dead} is encouraging in that RAWS data may be a possible indicator of FMC of dead leaves. Due to the inherent lag time of 10-h timelag fuel moisture, these values are capturing what transpired in the preceding 2–20 h (Lancaster, 1970). This technique could be applied to evaluate an overall trend in dead canopy fuel moisture patterns using accessible online RAWS data, thus giving fire managers an additional decision support tool. Admittedly, the samples used to develop this relationship were collected in the northern half of the tanoak range, however on 11 July 2008, samples collected near the warmer and dryer southern end of the range during the Basin Complex Fire (Big Sur, California) match the modeled relationship generated in our study (Fig. 5). Future work should explore this relationship further using samples and RAWS data throughout the range. Other moisture metrics may provide better surrogates for predicting FMC of dead leaves, such as the Fine Fuel Moisture Code (FFMC) component of the Canadian Fire Weather Index (Van Wagner, 1987); however, to date no work has focused directly on prediction of dead canopy fuel moisture.

Given the low values of FMC obtained in this study (relative to the higher FMCs found in conifers), a greater probability of crown ignition may be assumed based on Van Wagner's (1977) equation. If this pattern holds, tanoaks would require a relatively high CBH to escape crown ignition. As FMC declines for SOD-infected and killed tanoaks, CBH would need to be even higher to escape ignition. For example, using FMC values for tanoaks during the month of August and a flame length of 1 m, CBH would need to be 1.56 m or greater to resist ignition for uninfected leaves (FMC = 83%) and 1.61 m for the infected leaves (FMC = 79.5%). For dead leaves (FMC = 5.8%), CBH would need to be 6.65 m or greater to escape ignition. While it is tempting to use data compiled in this study to model crown fire ignition potential based on FMC and CBH, more information is needed about ignition of ultra-low FMCs and the burning characteristics of broadleaf trees. Using FMC values below 70% to model crown fire exceeds the range of data used to generate the Van Wagner (1977) model, and this model was developed using empirical data from experimental crown fires in red pine (*Pinus resinosa*). The physical properties of tanoak leave contrast sharply with conifer needles, especially considering the surface area to volume ratio (SAVR) between the two. Average SAVR of tanoak is 113.2 cm^{-1} (Engber et al., unpublished data) while SAVR for western *Pinus* species ranges from 57.6 to 90.5 cm^{-1} (Brown, 1970). Future work will need to consider the ignition properties specific to foliage with a greater diversity of physical and chemical characteristics, and examine the effect of extremely low foliar moisture on crown ignition. This proposed research would also assist those working in insect and pathogen-killed forests that suffer similar post-mortality leaf retention phenomena (e.g. spruce budworm (*Choristoneura fumiferana*), mountain pine beetle (*Dendroctonus ponderosae*), western gall rust (*Endocronartium harknessii*), or comandra rust (*Cronartium comandrae*).

As the onset of SOD changes the fuel dynamics of tanoak forests, an assumption can be made that crown fire ignition and/or individual tree torching will become more probable, especially considering that canopy base heights found in these stands range widely (in our study stands and region-wide varying from 0.25 to 9 m). The early infection phase does not lower FMC appreciably and therefore probably will not affect the likelihood of crown fire ignition. However, the ultra-low moistures reported here in the crowns of standing dead trees seem assured to, especially considering their concurrence with the height of fire season (Fig. 4). The question arises: at what point will SOD reduce the foliar moisture of tanoaks to where crown fire becomes likely? In other words, as FMC lowers, what is the critical CBH that will allow surface fire of a given flame length to transition into the crown? To answer this question, future work should quantify the ignition thresholds (height) above a given flame length or fireline intensity (FLI) using the range of FMCs obtained in this study, and compare these results to the Van Wagner (1977) model. These data will be useful for aiding the decision support tools used by fire managers in SOD-affected forests and potentially other forests affected by pathogens.

As tanoaks of the northern California forests decline and die, dramatic changes in stand structure, species composition, and ecosystem processes are taking place. Depending on the size of the resulting canopy gaps left by the loss of tanoak, co-dominant species such as redwood or Douglas-fir expand into the smaller gaps, while other tree or shrub species will fill in the larger gaps (Waring and O'Hara, 2008). In addition, the standing dead (Phase 2) tanoaks in the canopy can affect surrounding trees due to the possibility of increased scorch and/or canopy ignition and spread. While the historical fire regime for these coastal forests was highly variable, fires in ecosystems where tanoak was prominent were dominated by low to moderate severity surface fire transitioning to moderate to mixed severity surface fire in the southern and inland areas (Wills and Stuart, 1994; Stuart and Stephens, 2006). Consequences are unknown as to how SOD-caused changes will affect future fire regimes of these forests. As this conversion takes place it may be prudent to consider measures to limit the probability of crown fire ignition by pruning, canopy thinning, and/or whole tree removal of the infected or dead tanoaks, or seeking operational landscape-level treatments, work that should be prioritized.

Predictions are that by 2030, *P. ramorum* epidemic will spread in California by a scale of 10 times or more, with the highest frequency along the north coast of California to Oregon (Meentemeyer, 2009). Implications for the spread of *P. ramorum* and subsequent tree mortality exist for other oak species across this region, especially coast live oak (*Quercus agrifolia*) and California black oak (*Q. kelloggii*), among others. Current disease risk models show large areas of high risk for *P. ramorum* infection not only on the California coast, but in the coastal Northwest forests of Oregon and Washington, as well as forests of the southern and eastern USA (Kelly et al., 2005). Species in these regions should be evaluated for changes in canopy fuel characteristics in a similar manner, as the potential for elevated fire hazard is an increasing concern for resource managers.

The frequency of introductions of non-endemic forest pathogens and insects into the United States is increasing (Pimentel et al., 2005). While our results are restricted to SOD-killed forests in northwestern California, other non-native pathogens may parallel these effects. White pine blister rust, Dutch elm disease (*Ophiostoma ulmi* and *O. novo-ulmi*), Asian longhorned beetle (*Anoplophora glabripennis*), emerald ash borer (*Aarrilus planipennis*), and hemlock woolly adelgid (*Adelges tsugae*) are all causing widespread mortality in North American forests and woodlands (Liebhold et al., 1995; Moser et al., 2009; USDA Forest Service, 2009b). Also, extensive outbreaks of endemic pathogens and insects continue to occur across North America, including black stain root disease (*Leptographium wageneri*), mountain pine beetle, western balsam bark beetle (*Dryocoetes confuses*), fir engraver (*Scolytus ventralis*), spruce beetle (*Dendroctonus rufipennis*), and Douglas-fir beetle (*Dendroctonus pseudotsugae*) (Castello et al., 1995; Ayres and Lombardero, 2000; USDA Forest Service, 2009b). As a result, conditions similar to those created by SOD (i.e. lowered FMC with concurrent dead leaf retention) are occurring in many forested ecosystems. It is hoped that the methodology developed in this study to quantify FMC of SOD-diseased and SOD-killed tanoaks can be applied to other ecosystems where changing disease and insect disturbance patterns are altering the fuel dynamics and setting these ecosystems at risk for abnormally elevated fire behavior.

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Appendix A.

Crown foliar moisture content of uninfected, Sudden Oak Death infected, and killed tanoaks near Redway, CA, USA.

	Foliar moisture content			*P*-value
	Uninfected	Infected	Dead	
1 Year Foliage				
March 2008*	82.3 (2.0)^{a}	73.3 (1.8)^{a}	9.7 (2.2)^{b}	<0.001
April 2008	80.4 (2.8)^{a}	75.5 (2.4)^{a}	9.9 (3.0)^{b}	<0.001
May 2008*	79.5 (2.3)^{a}	75.4 (2.0)^{a}	11.0 (2.5)^{b}	<0.001
June 2008	81.1 (2.1)^{a}	79.5 (1.8)^{a}	8.4 (2.2)^{b}	<0.001
July 2008	82.3 (1.9)^{a}	80.6 (1.7)^{a}	6.8 (2.1)^{b}	<0.001
August 2008*	82.6 (1.9)^{a}	79.5 (1.7)^{a}	5.8 (2.0)^{b}	<0.001
September 2008	81.6 (2.4)^{a}	72.7 (2.1)^{a}	10.2 (2.6)^{b}	<0.001
October 2008*	80.0 (1.1)^{a}	75.3 (1.0)^{c}	11.1 (1.2)^{b}	<0.001
November 2008	84.6 (1.5)^{a}	79.8 (1.4)^{a}	19.2 (1.7)^{b}	<0.001
December 2008	86.7 (1.2)^{a}	83.0 (1.0)^{a}	26.4 (1.3)^{b}	<0.001
January 2009	83.2 (1.6)^{a}	79.1 (1.4)^{a}	17.1 (1.7)^{b}	<0.001
February 2009	84.6 (1.1)^{a}	81.2 (0.9)^{a}	14.7 (1.2)^{b}	<0.001
Twig				
March 2008	71.7 (2.3)^{a}	66.2 (2.0)^{a}	17.8 (2.5)^{b}	<0.001
April 2008*	73.2 (4.2)^{a}	70.2 (3.7)^{a}	13.3 (4.5)^{b}	<0.001
May 2008	75.1 (3.4)^{a}	77.4 (3.0)^{a}	13.2 (3.6)^{b}	<0.001
June 2008†	75.4 (2.7)^{a}	83.3 (2.4)^{c}	9.3 (2.9)^{b}	<0.001
July 2008*	78.0 (4.3)^{a}	65.2 (3.8)^{a}	9.1 (4.7)^{b}	<0.001
August 2008*	70.4 (3.7)^{a}	66.3 (3.3)^{a}	8.9 (4.0)^{b}	<0.001
September 2008	71.4 (5.5)^{a}	55.6 (4.9)^{a}	12.1 (5.9)^{b}	<0.001
October 2008	79.3 (2.6)^{a}	75.6 (2.4)^{a}	13.5 (2.9)^{b}	<0.001
November 2008	65.5 (5.7)^{a}	68.0 (5.1)^{a}	22.2 (6.2)^{b}	<0.001
December 2008	80.5 (3.0)^{a}	77.4 (2.7)^{a}	31.1 (3.3)^{b}	<0.001
January 2009	68.2 (3.8)^{a}	67.6 (3.4)^{a}	23.0 (4.1)^{b}	<0.001
February 2009	78.6 (4.8)^{a}	64.4 (4.3)^{a}	20.2 (5.2)^{b}	<0.001

Values are sample means for each group of trees with standard errors in parentheses. Comparisons between values for each sample date were done using Tukey-Kramer post hoc means separation tests. Within study group significant differences are indicated by different superscripted letters. Data form months that did not meet assumptions of normality or equal variance were log (*) or square-root (†) transformed as indicated.

Appendix B.

Differences in FMC of new foliage (<1 year) for SOD-infected tanoaks versus uninfected tanoaks.

	Foliar moisture content <1 year Foliage		*P*-value
	Uninfected	Infected	
May 2008	317.1 (48.5)	217.9 (29.7)	0.1145
June 2008	212.8 (13.8)	190.9 (12.0)	0.1146
July 2008	112.6 (2.9)	105.6 (2.5)	0.0603
August 2008	97.0 (2.6)	91.5 (2.3)	0.2665
September 2008	95.5 (1.9)	91.0 (1.7)	0.0962
October 2008	93.8 (1.7)	89.2 (1.5)	0.064
November 2008	97.1 (3.2)	89.6 (2.9)	0.0891
December 2008	102.1 (2.1)	96.1 (1.9)	0.0464
January 2009	98.4 (2.2)	90.1 (2.0)	0.0143
February 2009	98.9 (2.4)	94.3 (2.1)	0.1771

Values are sample means for each group of trees for that month with standard errors in parentheses. Significantly different values between groups are emphasized in bold.

Appendix C.

Differences in moisture content of litter versus attached dead canopy foliage.

	Foliar moisture content		*P*-value
	Dead canopy leaf	Litter	
April 2008	9.92 (0.8)	12.69 (0.9)	0.033
May 2008	10.97 (0.2)	13.31 (1.3)	0.122
June 2008	8.41 (1.1)	7.26 (0.7)	0.313
July 2008	6.85 (0.3)	7.42 (0.7)	0.471
August 2008	5.84 (0.4)	7.10 (0.4)	0.054
September 2008	10.16 (0.6)	12.77 (0.8)	0.051
October 2008	11.09 (0.8)	14.69 (1.4)	0.054
November 2008	19.21 (1.6)	56.33 (4.0)	<0.001
December 2008	26.40 (1.0)	94.94 (2.0)	<0.001
January 2009	17.10 (1.7)	40.27 (5.8)	0.003
February 2009	14.66 (0.8)	12.42 (0.7)	0.037

Significantly different values between groups are emphasized in bold. Standard errors are shown in parentheses.

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