Research Article

Foliar Consumption across a Sudden Oak Death Chronosequence in Laboratory Fires

Howard Kuljian [1†] and J. Morgan Varner [1,2*]

[1] Wildland Fire Laboratory, Department of Forestry and Wildland Resources, One Harpst Street, Humboldt State University, Arcata, California 95521, USA

[2] Current address: Department of Forestry, Forest & Wildlife Research Center, Mississippi State University, Box 9681, Mississippi State, Mississippi 39762, USA

[†] Deceased

* Corresponding author: Tel.: 001-662-325-0792; e-mail: mvarner@cfr.msstate.edu

ABSTRACT

The recent introduction and spread of sudden oak death (SOD; caused by *Phytopthora ramorum*) has caused heavy mortality in native tanoak (*Notholithocarpus densiflorus* [Hook. & Arn.] Manos *et al.* = *Lithocarpus densiflorus* [Hook. & Arn.] Rehder) forests in California and Oregon, USA. Following tree death, killed tanoaks retain their dead foliage, resulting in a 1 to 3 year period of extremely low foliar moisture and increased probability of crown ignition. We compared foliage ignition and consumption in a laboratory experiment at simulated crown heights from 0.5 m to 1.5 m across a range of representative foliar moistures (80 %, 70 %, 9 %, and 5 %) found in affected regional forests. Results revealed differences in live and dead foliage consumption. All foliage categories were consumed at the lowest crown base heights; consumption of live foliage declined quickly with increasing height, with minimal consumption occurring above 1 m. Consumption of dead foliage also declined with increasing heights, but some consumption (~25 %) still occurred up

RESUMEN

La reciente introducción y dispersión de la muerte súbita del encino (MSE; ocasionada por *Phytopthora ramorum*) ha causado una fuerte mortalidad en bosques de "tanoak" (*Notholithocarpus densiflorus* [Hook. & Arn.] Manos *et al.* = *Lithocarpus densiflorus* [Hook. & Arn.] Rehder) en California y Oregon, en los Estados Unidos. Después de la muerte del árbol, los troncos muertos en pie retienen el follaje muerto, lo que resulta en un periodo de 1 a 3 años de humedad foliar extremadamente baja e incremento en la probabilidad de ignición de copas. Comparamos la ignición y consumo del follaje en un experimento de laboratorio a alturas de copa simuladas, desde 0.5 m a 1.5 m, a lo largo de un rango de humedad foliar representativa (80 %, 70 %, 9 % y 5 %) encontrada en los bosques afectados. Los resultados mostraron diferencias en el consumo del follaje vivo y muerto. Todas las categorías de follaje fueron consumidas a la altura de copa más baja; el consumo de follaje vivo declinó rápidamente con el incremento en altura, con un consumo mínimo ocurriendo por encima de 1 m. El consumo de follaje muerto también declinó con el incremento en alturas, pero ocurrió incluso (~25 %) por encima de 1.25 m. Estos to 1.25 m. These data inform the mechanism for patterns of individual tree torching and firebrand generation reported in wildfires in SOD-infected forests and woodlands.

datos proporcionan información sobre el mecanismo de formación de antorchas en árboles individuales y generación de pavesas reportados en incendios en bosques y zonas arboladas infectadas por MSE.

Keywords: California, crown ignition, fire behavior, non-native pathogens, *Notholithocarpus densiflorus*, *Phytophthora ramorum*, tanoak

Citation: Kuljian, H., and J.M. Varner. 2013. Foliar consumption across a sudden oak death chronosequence in laboratory fires. Fire Ecology 9(3): 33–44. doi: 10.4996/fireecology0903033

INTRODUCTION

Wildland fire and forest pests and pathogens are common disturbance agents that can act simultaneously or in succession to alter the behavior and effects of fire in ecosystems (Castello *et al.* 1995, Parker *et al.* 2006, Simard *et al.* 2011, Metz *et al.* 2013). Changes in fire behavior or flammability are manifested as altered fuels, such as changes in foliar moisture, foliar chemistry, surface area-to-volume ratios, live-to-dead ratios of trees and shrubs, continuity of fuels, and bulk density (Hummel and Agee 2003, Lundquist 2007, Page and Jenkins 2007, Jenkins *et al.* 2012, Jolly *et al.* 2012*a*). Examples of this dynamic in North America include wildfire following *Phellinus weirii* (Murrill) Gilb.-caused mortality in mountain hemlock (*Tsuga mertensiana* [Bong.] Carrière) forests (Dickman and Cook 1989); western spruce budworm (*Choristoneura occidentalis* Freeman) outbreaks in mixed-conifer forests (Hummel and Agee 2003); and lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson) killed by mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Castello *et al.* 1995, Page and Jenkins 2007, Jenkins *et al.* 2012).

The recent introduction of *Phytophthora ramorum* Werres *et al*., the pathogen responsible for sudden oak death (SOD), has caused widespread mortality of several native tree species in California and Oregon, USA, most notably tanoak (*Notholithocarpus densiflorus* [Hook. & Arn.] Manos *et al*.) (Davidson *et al.* 2005, Rizzo *et al.* 2005). By 2005, SOD had infected 3176 ha (Meentemeyer *et al.* 2008), with predictions that by 2030 the epidemic will spread by a factor of 10, chiefly in northern California and southern Oregon (Meentemeyer 2009). In these forests, tanoak is common as an understory component, co-dominant, or dominant found in pure stands (Tappeiner *et al.* 1990), and is highly susceptible to SOD, with tree mortality exceeding 95% in some areas, with more than 3 million trees killed to date (USDA Forest Service 2009).

Sudden oak death results in several important changes in tanoak forests and fuels. Following infection, foliar moisture declines from healthy values of 83% down to 72% when yellowed, and down to 5% to 15% when the leaves brown (Kuljian and Varner 2010). Because *P. ramorum*-infected tanoaks can retain their leaves for two years post-mortem, heightened potential for crown torching and elevated local fire severity results. Managers in the region have reported an increase in crown ignitions in sudden oak death-affected forests (Valachovic *et al.* 2011) and fire severity is increasing as a result of sudden oak death (Metz *et al.* 2011, Metz *et al.* 2013). Litterfall and branch and stem senescence increase the surface woody fuel loads and inflate the fuelbed loads for a protracted period following tree death (Valachovic *et al.* 2011).

A hypothesized mechanism for the reported increases in crown ignition is the reduced foliar moisture in the crowns of declining and dead tanoaks infected with SOD (Kuljian and Varner 2010). Foliar moisture and the height of the crown fuel mass act together with surface fireline intensity to regulate crown ignition (Van Wagner 1977, Cruz *et al.* 2006, Tachajapong *et al.* 2008). Relative to fireline intensity and canopy base height, the effect of foliar moisture content on crown ignition has been considered minor (Keyes 2006). In situations where dead or declining crown foliage is retained with low foliar moisture content, as with SOD-killed tanoak, the relative importance of foliar moisture content may increase dramatically (Jolly *et al.* 2012*b*). When initially infected with SOD, tanoak foliar moisture content dips to between 72% and 83% (down from uninfected values between 80% to 91%; Raymond and Peterson 2005, Kuljian and Varner 2010), and when the trees are killed by SOD, the retained dead foliage can decline to values as low as 5% (Kuljian and Varner 2010). Additionally, because tanoak is a shade-tolerant tree in the region's forests (Tappeiner *et al.* 1990), its crown base is typically low, often intermingled within the flaming zone of surface fires. The relative degree to which these factors (extremely low foliar moisture content, low crown height) affect foliar flammability is unclear, and may have implications for other wilt-affected forests.

Some research has quantified the ignition of foliage (e.g., Stockstad 1975, Fuglem and Murphy 1979, Xanthopoulos and Wakimoto 1993, Sun *et al.* 2006, Fletcher *et al.* 2007, White and Zipperer 2010, Jolly *et al.* 2012*a*), but surprisingly limited work exists that examines patterns of foliar moisture content due to disease and mortality (Cheyette *et al.* 2008, Kuljian and Varner 2010, Simard *et al*. 2011, Jolly *et al.* 2012*a*, Page *et al.* 2013). To address these points, a laboratory burning experiment was designed to provide: 1) a better understanding of the relative differences among foliage ignition and consumption from uninfected, infected, and dead tanoaks; and 2) the role that crown base height plays in ignition across the disease sequence. This experiment is an important first step in providing data about poorly understood ignition characteristics of disease-killed foliage, with implications for other species suffering from disease and insect epidemics.

METHODS

Laboratory Burning Apparatus

To quantify the relationship between foliar moisture content and critical crown base height, we constructed a laboratory apparatus that suspended foliar samples across a foliar moisture gradient at predetermined heights over a repeatable surface fire (Figure 1). The structure incorporated a vertical column fabricated from a standard construction-grade 8.75 cm × 8.75 cm Douglas-fir beam, 2.5 m tall, attached upright to a plywood base wrapped in fire shelter material (Cleveland Laminating Corporation, Cleveland, Ohio, USA). We constructed a foliage basket from 0.64 cm metal hardware cloth and divided it into four separate 35.5 cm × 25.4 cm × 15 cm deep compartments. Compartments were divided using 0.89 cm thick sheet metal to prevent ignition crossover between compartments. The basket was supported by an adjustable 1.27 cm diameter copper pipe and positioned at one of five predetermined heights: 0.5 m, 0.75 m, 1.0 m, 1.25 m, or 1.5 m. The base of the beam was centered in a 1 m × 1 m fuel tray constructed of 2 cm × 8 cm Douglas-fir, again coated with fire shelter material. We wrapped wood in and near the fuelbed with heavy gauge aluminum foil to prevent ignition of the apparatus during burning. The structure was placed beneath a 2.75 m × 2.75 m adjustable fume hood elevated 2 m above the fuelbed. Additional fire shelter material was curtained around the hood to 50 cm above the floor to moderate inflow and restrict smoke escape to the laboratory.

To compare replicates and to evaluate burning treatments, a total of eight insulated iron-constantan (Type J, 30 gauge, 0.9 mm to

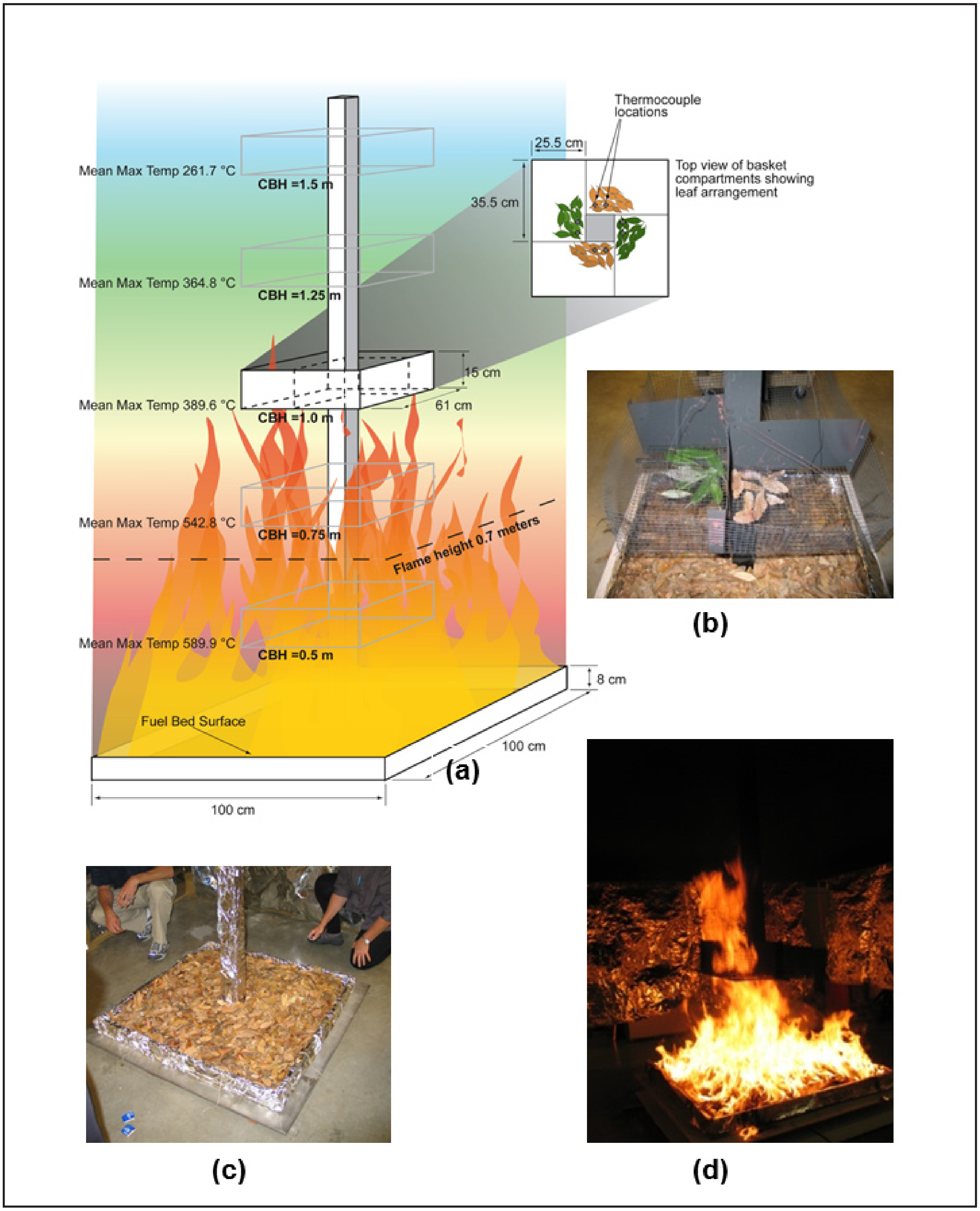

Figure 1. Laboratory design to evaluate ignition of healthy, sudden oak death-infected, and sudden oak death-killed tanoak leaves at five heights. (a) Illustration of structure showing all tested canopy base heights (CBH). (b) Layout of leaf samples. (c) 1 m × 1 m fuelbed prepared for ignition. (d) Burning trial at a crown base height of 0.75 m showing ignition of foliar samples.

1.2 mm diameter) thermocouples, attached to a CR1000 datalogger (Campbell Scientific Inc., Logan, Utah, USA), were placed at the bottom of the foliage baskets to record average temperature at 5 sec intervals during 43 of the 45 burns. Two thermocouples per basket compartment (as a check against aberrant or missing values) were placed ~8 cm away from the central post.

Leaf Samples

Prior to each burn, we randomly selected a tanoak branch containing approximately 50 to 75 one-year old or older leaves and removed it from one of three adjacent tanoak trees (dbh 28 cm to 40 cm) located near Kneeland, California, USA (40°45’01.00” N, 123°58’55.52” W). Following harvest, we transported each branch to the lab within 30 minutes. As a control, we verified foliar moisture content from branch samples by taking a random subsample (~12 leaves) from the branch and evaluated by obtaining the green weight, then oven-drying at 70 ºC (to balance volatile losses) until no further weight loss occurred (typically 48 hours). Foliar moisture content for all field samples collected throughout the experiment ranged between 80 % to 85 %, typical of values in other field studies of tanoak (Raymond and Peterson 2005, Kuljian and Varner 2010).

We prepared leaf samples to simulate four stages of SOD on tanoak leaf moisture observed in a field study: Healthy (80 % to 85 % foliar moisture content [FMC]); Infected (70 % to 75 % FMC); Dead (9 % FMC); and Dry Dead (5 % FMC) as quantified in nearby forests by Kuljian and Varner (2010). We randomly selected Healthy leaf samples from the branch and placed them in the basket compartment without any further preparation; their FMC was 80 % to 85 % (as previously determined). Infected foliage was replicated by a random selection of one-year old or older leaves oven-dried for 10 minutes at 50 ºC, resulting in a foliar moisture content ranging between 70 % to 75 % (2 min to 4 min out of oven), consistent with measurements taken in the field for early phase SOD-infected tanoaks. Dead leaves used were all collected from SOD-trees killed between March 2008 and February 2009 and stored under laboratory conditions (~20 ºC and 50 % relative humidity). Foliar moisture content for these leaves averaged 8.6 ± 0.7 %, approximating summertime dead foliage in the field study. In pilot burning in the laboratory, we detected no significant differences in flammability between litter collected beneath Healthy or SOD-Infected stands (J.M. Varner, Mississippi State University, unpublished data). Dry Dead leaves were intended to replicate extreme fire conditions and were approximated by oven-drying dead leaf samples at 50 ºC for 10 minutes. At the time of burning, foliar moisture content for these samples averaged 5.1 ± 1.2 %, close to the driest fire season values observed in the field.

Immediately prior to each burn, we weighed a sample of 8 to 10 leaves from each of the four moisture categories (“wet” weight) and arranged them on each 35.5 cm × 25.4 cm wire mesh compartment to form a single layer with minimal overlap. We placed leaves as close to the center post as possible and covered with an additional piece of wire mesh to prevent convection from lifting individual leaves out of the basket during experimental fires. After each burn, we oven-dried sample leaves to calculate mass loss, accounting for their preburn moisture content.

Laboratory Burning

For each burn, we filled the 1 m × 1 m fuelbed with approximately 1600 g of oven-dry fuel collected from an uninfected tanoak fuelbed. The average fuelbed composition consisted of tanoak litter (83.5 ± 2% by mass), with minor components of Douglas-fir needles (*Pseudotsuga menziesii* [Mirb.] Franco; 5.3 ± 1.7 %), California bay leaves (*Umbellularia* *californica* [Hook. & Arn.] Nutt.); 1.4 ± 0.5 %), with woody twigs <0.6 cm in diameter comprising the remainder (9.8 ± 4 %). For all burns, fuelbed depth was maintained at 8 cm, with a corresponding fuelbed bulk density of approximately 21.0 kg m^{-3}.

Fire behavior in the laboratory experiments was characterized in several ways (Table 1). We estimated flame length (m) by assuming that flame length equaled flame height given that the uniform ignition pattern resulted in a vertical flame. Our visual estimates were recorded on all burns and video footage was recorded on 10 burns using a Canon XLS1 DV video camera (Canon Inc., Tokyo, Japan). Average maximum flame height for yellow flame tip temperature was used to estimate flame height (Saito 2001). Flame temperature was estimated via thermocouple data facilitating the development of a thermal profile from 0.5 m up to 1.5 m (Figure 1). The flame temperature profile was compared to flame height using 500 ºC as the level of flame height (Yokoi 1960). A linear regression analysis using burn data from this experiment predicted that 500 ºC was reached at the 0.8 m height (R^2 = 0.64; data not shown). To quantify mass loss rate (kg min^{-1}), the fuelbed was placed on a Champ CQ 25R33 bench scale (Ohaus Corp., Pine Brook, New Jersey, USA) to measure mass loss during three representative burns. We logged mass every second via a RS232 cable from the bench scale connected to a computer. Plume flow velocity (m sec^{-1}) was estimated by recording three representative burns using the video camera. Plume flow was estimated by tracking individual ember particle movement frame by frame (at 30 frames sec^{-1}) in relation to height markings on a vertical column placed behind the fuelbed. Fuelbed consumption (%) was measured on three representative burns by subtracting the weight of the residual particles from the total fuel weight before burning. Lastly, we recorded flaming time (sec) within the fuelbed over four representative burns.

To minimize variation in the intensity of the experimental fires, we draped four 1 m cotton strings soaked in xylene (dimethylbenzene; $C_6H_4(CH_3)_2$) 10 cm away from each edge and across the surface of the constructed fuelbeds. Each corner of the fuelbed was ignited with a lighter in quick succession. This ignition pattern was designed to allow a uniform burning pattern from each side and minimize spatial variation in fire behavior (i.e., generating equal heat flux to all sample compartments).

We conducted a total of 45 experimental burns consisting of nine burns at each height of 0.5 m, 0.75 m, 1.0 m, 1.25 m, and 1.5 m. Immediately after each burn, we assessed mass loss and ignition or non-ignition of foliar samples. Mass loss was calculated on a dry weight basis by oven drying the sample residues post-burn and comparing results to the expected dry weight for that foliar moisture category.

Data Analysis

The study was set up as a completely randomized design. Foliar consumption (%) was compared among foliar moisture content cate-

Table 1. Burning characteristics for laboratory crown fires of *Notholithocarpus densiflorus* foliage.

Burning variable	*n*	Mean ± SD	Maximum	Minimum
Flame height, visual estimate (m)	10	0.7 ± 0.1	0. 8	0.5
Mass loss rate (g min^{-1})	3	858.3 ± 0.1	863.0	854.0
Plume flow velocity (m sec^{-1})	12	4.3 ± 0.5	5.0	3.8
Fuel consumption (%)	3	84.2 ± 5.9	90.5	78.8
Flaming time (min)	4	5.4 ± 0.3	5.8	5.1

gories and among heights with ANOVA followed by the conservative Tukey-Kramer post-hoc means separation (Zar 1999). All data were evaluated for assumptions of normality and equal variance. Significance for all statistical analyses was determined using α = 0.05. All data analysis was performed using the statistics program NCSS (NCSS, Kaysville, Utah, USA).

RESULTS

Tanoak foliage consumption in the laboratory burns was affected strongly by the foliar moisture treatments and the height above the flames. Both dead foliage categories (Dead and Dry Dead; low FMCs) had high consumption and did not differ from another across any crown height evaluated (Figure 2). The Healthy and Infected foliage categories (higher FMCs) mimicked one another and also did not differ from each other cross any height.

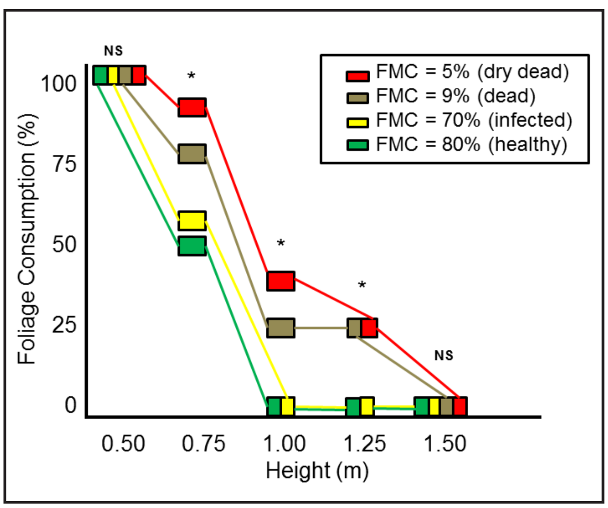

Figure 2. Percent of foliage consumed as a function of height and disease category (as represented by moisture content) for laboratory burns of tanoak (*Notholithocarpus densiflorus*) foliage. Significant differences among tree status (as represented by foliar moisture content) are denoted with *; in all cases where there were differences, Dead categories (5% and 9% foliar moisture content [FMC]) > Healthy and Infected categories (70% and 80% FMC). Significant differences among heights ($P < 0.05$) were detected among the following: 0.5 m > 0.75 m > all others using a post-hoc Tukey-Kramer HSD test.

All FMC treatments had 100% consumption at 0.5 m; the higher FMCs had intermediate consumption (49.0% to 59.4%) and the low FMCs had substantial consumption (77.9% to 92.2%) where flames were just beneath the 0.75 height treatment (flame height = 0.7 m). At 1.0 m and 1.25 m heights, significant differences were found between the two broad FMC categories: the high FMC treatments experienced <1.1% consumption while the low FMC treatments were all >20.6% consumed. At 1.5 m, only minimal consumption occurred, regardless of foliar moisture (Figure 2).

The variability in foliar consumption across FMC and crown height treatments revealed interesting patterns. As measured by standard error, consumption was uniform across the FMC treatments. In contrast, consumption varied widely across crown heights: at the low and high heights, little variability was recorded (i.e., they either all consumed, as in the 0.5 height or failed to consume very much, as in the tallest 1.5 m treatment). Just above the flaming zone, in the 0.75 m treatment, we observed high variability in consumption, decreasing with increasing FMC. These differences further illuminate the effect of the disease on foliar ignition and consumption and their marginal differences across heights above flames.

DISCUSSION

Past studies have evaluated the influence of foliar moisture on ignition (e.g., Van Wagner 1967, Quintilio 1977, Fuglem and Murphy 1979) or a time-temperature relationship to ignition (Stockstad 1975, Bunting *et al.* 1983, Xanthopoulos and Wakimoto 1993, Dimitrakopoulos and Papaioannou 2001). Clear patterns of tanoak foliage consumption were revealed by this experiment. Consumption of living foliage (foliar moisture content = 70% and 80%) declined rapidly with height, demonstrating a clear threshold at 0.75 m (near the flame height), above which only minimal consumption (~1%) was observed (Figure 2). Living foliage was often heavily scorched at this height, but the leaves failed to ignite. What minimal weight loss that did occur was likely dehydration and not dry matter consumption. Dead foliage (foliar moisture content = 5% and 9%) consumption diminished at a slower rate as height increased, showing a greater threshold at 1.25 m, above which mass loss was minimal (~3%; also likely dehydration losses). Dead foliage at the 1.5 m height did not ignite. The differences observed between living and dead foliage suggest that, as foliar moisture content drops to low values, the relative effect on crown ignition is magnified. Whether the changes wrought by disease affect only moisture and not other foliar chemistry (Jolly *et al.* 2012*a*) or physical characteristics is unknown.

Laboratory burning is subject to several shortcomings (Fernandes and Cruz 2012), although strong evidence supports its utility in understanding the underlying mechanisms of fire behavior and effects (Engber and Varner 2012, Pausas and Moreira 2012). Our fuelbeds and resulting fires were small and of somewhat moderate intensity (0.7 m to 0.8 m flame heights), well below reconstructed fire intensity in SOD-affected forests (Metz *et al.* 2013). Because they were conducted in the lab, these fires lacked proximate radiative (surrounding flames beyond the 1 m^2 fuelbed) and convective (resulting surrounding convection and the "pull" of the larger fire) heating effects that complicate scaling. An important next step for this and other laboratory-based flammability studies should be scaling to burning experiments in wildland settings. In larger fires, true radiative and convective heat flux conditions could be attained and applied to a range of crown heights and foliar moistures (as induced by disease or experimentally altered via girdling or herbicide injection surrogates).

Sudden oak death-killed trees eventually drop their attached dead leaves, reducing crown bulk density of individual trees below a threshold capable of propagating fire. Methods exist that permit the direct estimation of crown mass and bulk density (e.g., Snell 1979); however, given the heterogeneous pattern of tanoak cover, density, and the lags in infection across the landscape, application of resulting values may not be representative. Indirect methods (e.g., Andersen *et al.* 2005, Keane *et al.* 2005) to address the patchiness of crown and canopy bulk density hold promise for tanoak and other disease-killed forests.

These findings add to the growing body of understanding fire and disease interactions. Sudden oak death affects individual trees in a patchy spatial and temporal pattern (Meentenmeyer 2009). This matrix of dead, infected, and living trees complicates simplistic models for canopy spread. On the other hand, the presence of standing dead trees with attached dead leaves provides a somewhat stable source of torching trees, thereby affecting other nearby tanoaks and other intermingled species in these ecologically important forests (Metz *et al.* 2013). In addition, single tree torches can also substantially affect surface fire rate of spread via lofting dead branches and foliage to cause long-distance spotting beyond the flaming front, as was observed in several 2008 northern California fires in which dead tanoaks were present (Valachovic *et al.* 2011).

This phenomenon of diseases causing trees to retain foliage with very low moisture contents is an increasingly common one in North America (e.g., Jenkins 2007, Fraedrich *et al.* 2008, Page and Simard *et al.* 2011, Jenkins *et al.* 2012, Page *et al.* 2013). As has been argued about in other fire and pathogen interactions (see comments and replies in Jolly *et al.* 2012*b*, Moran and Cochrane 2012, and Simard *et al.* 2012), these problems often lack attention to the underlying mechanisms that lead to important landscape patterns in fire behavior and effects. As non-native forest diseases continue to expand and invade into fire-prone ecosystems (Aukema *et al.* 2010), these problems will necessitate greater research attention.

ACKNOWLEDGEMENTS

This project was funded by the L.W. Schatz Demonstration Tree Farm Trust and the USDA Forest Service Pacific Southwest Research Station. Advice on study design was provided by C. Edgar, J. Stuart, and Y. Valachovic. M. Cruz and M. Alexander provided thoughtful criticisms of laboratory methods. Laboratory assistance was provided by M. Scott-Kuljian, O. Kuljian, G. Kuljian, E. Engber, M. Cocking, and E. Banwell. The comments and suggestions made by two anonymous reviewers and the editor improved the clarity of the manuscript.

Howard Kuljian died tragically in November 2012. Many fire scientists and land managers were touched by his gentle demeanor and kindness. Howard's passion for and dedication to understanding the effects of sudden oak death on the native forests of northern California will endure in the growing body of research focusing on these changes. Photo credit: Humboldt State University.

LITERATURE CITED

Andersen, H.E., R.J. McGaughey, and S.E. Reutebuch. 2005. Estimating forest canopy fuel parameters using LiDAR data. Remote Sensing of Environment 94: 441–449. doi: 10.1016/j.rse.2004.10.013

Aukema, J.E., McCullough, D.G., Von Holle, B., Liebhold, A.M., Britton, K. and S.J. Frankel. 2010. Historical accumulation of nonindigenous forest pests in the continental United States. BioScience 60: 886–897. doi: 10.1525/bio.2010.60.11.5

Bunting, S.C., H.A. Wright, and W.H. Wallace. 1983. Seasonal variation in the ignition time of redberry juniper in west Texas. Journal of Range Management 36: 169–171. doi: 10.2307/3898155

Castello, J.D., D.J. Leopold, and P.J. Smallidge. 1995. Pathogens, patterns, and processes in forest ecosystems. Bioscience 45: 16–24. doi: org/10.2307/1312531

Cheyette, D., T.S. Rupp, and S. Rodman. 2008. Developing fire behavior fuel models for the wildland-urban interface in Anchorage, Alaska. Western Journal of Applied Forestry 23: 149–155.

Cruz, M.G., B.W. Butler, and M.E. Alexander. 2006. Predicting the ignition of crown fuels above a spreading surface fire. Part II: model evaluation. International Journal of Wildland Fire 15: 61–72. doi: 10.1071/WF05045

Davidson, J.M., A.C. Wickland, H.A. Patterson, K.R. Falk, and D.M. Rizzo. 2005. Transmission of *Phytophthora ramorum* in mixed-evergreen forest in California. Phytopathology 5: 587–596. doi: 10.1094/PHYTO-95-0587

Dickman, A., and S. Cook. 1989. Fire and fungus in a mountain hemlock forest. Canadian Journal of Botany 67: 2005–2016. doi: 10.1139/b89-254

Dimitrakopoulos, A., and K. Papaioannou. 2001. Flammability assessment of Mediterranean forest fuels. Fire Technology 37: 143–152. doi: 10.1023/A:1011641601076

Engber, E.A., and J.M. Varner. 2012. Patterns of flammability of the California oaks: the role of leaf traits. Canadian Journal of Forest Research 42: 1965–1975. doi: 10.1139/x2012-138

Fernandes, P.M., and M.G. Cruz. 2012. Plant flammability experiments offer limited insight into vegetation-fire dynamics interactions. New Phytologist 194: 606–609. doi: 10.1111/j.1469-8137.2012.04065.x

Fletcher, T.H., B.M. Pickett, S.G. Smith, G.S. Spittle, M.M. Woodhouse, E. Haake, and D.R. Weise. 2007. Effects of moisture on ignition behavior of moist California chaparral and Utah leaves. Combustion Science and Technology 179: 1183–1203. doi: 10.1080/00102200601015574

Fraedrich, S.W., T.C. Harrington, R.J. Rabaglia, M.D. Ulyshen, A.E. Mayfield, J.L. Hanula, J.M. Eickwort, and D.R. Miller. 2008. A fungal symbiont of the redbay ambrosia beetle causes a lethal wilt in redbay and other Lauraceae in the southeastern United States. Plant Disease 92: 215–224. doi: 10.1094/PDIS-92-2-0215

Fuglem, P.L., and P.J. Murphy. 1979. Flammability of jack pine crown foliage during spring. Department of Forest Science, University of Alberta, Edmonton, Canada.

Hummel, S., and J.K. Agee. 2003. Western spruce budworm defoliation effects on forest structure and potential fire behavior. Northwest Science 77: 159–169.

Jenkins, M.J., W.G. Page, E.G. Hebertson, and M.E. Alexander. 2012. Fuels and fire behavior dynamics in bark beetle-attacked forests in western North America and implications for fire management. Forest Ecology and Management 275: 23–34. doi: 10.1016/j.foreco.2012.02.036

Jolly, W.M., R.A. Parsons, A.M. Hadlow, G.M. Cohn, S.S. McAllister, J.B. Popp, R.M. Hubbard, and J.F. Negron. 2012*a*. Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. Forest Ecology and Management 269: 52–59. doi: 10.1016/j.foreco.2011.12.022

Jolly, W.M., R. Parsons, J.M. Varner, B.W. Butler, K.C. Ryan, and C.L. Gucker. 2012*b*. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Comment. Ecology 93: 941–946.

Keane, R.E., E.D. Reinhardt, J. Scott, K. Gray, and J. Reardon. 2005. Estimating forest canopy bulk density using six indirect methods. Canadian Journal of Forest Research 35: 724–739. doi: 10.1139/x04-213

Keyes, C.R. 2006. Role of foliar moisture content in the silvicultural management of forest fuels. Western Journal of Applied Forestry 21: 228–231.

Kuljian, H., and J.M. Varner. 2010. The effects of sudden oak death of foliar moisture content and crown fire potential in tanoak. Forest Ecology and Management 259: 2103–2110. doi: 10.1016/j.foreco.2010.02.022

Lundquist, J.E. 2007. The relative influence of diseases and other small-scale disturbances on fuel loading in the Black Hills. Plant Disease 91: 147–152. doi: 10.1094/PDIS-91-2-0147

Meentemeyer, R.K. 2009. Landscape epidemiology of *Phytopthora ramorum:* measuring, mapping, and modeling spread. Phytopathology 99: S163.

Meentemeyer, R.K., B.L. Anacker, W. Mark, and D.M. Rizzo. 2008. Early detection of emerging forest disease using dispersal estimation and ecological niche modeling. Ecological Applications 18: 377–390. doi: 10.1890/07-1150.1

Metz, M.R., K.M. Frangioso, R.K. Meentemeyer, and D.R. Rizzo. 2011. Interacting disturbances: wildfire severity affected by stage of forest disease invasion. Ecological Applications 21: 313–320. doi: 10.1890/10-0419.1

Metz, M.R., J.M. Varner, K.M. Frangioso, R.K. Meentemeyer, and D.M. Rizzo. 2013. Unexpected redwood mortality from synergies between wildfire and an emerging infectious disease. Ecology 94: in press. doi: 10.1890/13-0915.1

Moran, C.J., and M.A. Cochrane. 2012. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Comment. Ecology 93: 939–941.

Page, W., and M.J. Jenkins. 2007. Predicted fire behavior in selected mountain pine beetle-infested lodgepole pine. Forest Science 53: 662–674.

Page, W.G., M.J. Jenkins, and M.E. Alexander. 2013. Foliar moisture content variations in lodgepole pine over the diurnal cycle during the red stage of mountain pine beetle attack. Environmental Modeling and Software 49: 98–102. doi: 10.1016/j.envsoft.2013.08.001

Parker, T.J., K.M. Clancy, and R.L. Mathiasen. 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agricultural and Forest Entomology 8: 167–189. doi: 10.1111/j.1461-9563.2006.00305.x

Pausas, J.G., and B. Moreira. 2012. Flammability as a biological concept. New Phytologist 194: 610–613. doi: 10.1111/j.1469-8137.2012.04132.x

Quintilio, D. 1977. Lodgepole pine flammability. Canadian Forestry Service Report 5(2): 7.

Raymond, C.L., and D.L. Peterson. 2005. Fuel treatments alter the effects of wildfire in a mixed-evergreen forest, Oregon, USA. Canadian Journal of Forest Research 35: 2981–2995. doi: 10.1139/x05-206

Rizzo, D.M., M. Garbelotto, and E.M. Hansen. 2005. *Phytophthora ramorum:* integrative research and management of an emerging pathogen in California and Oregon forests. Annual Review of Phytopathology 43: 309–335. doi: 10.1146/annurev.phyto.42.040803.140418

Saito, K. 2001. Flames. Pages 11–54 in: E.A. Johnson and K. Miyanishi, editors. Forest fires: behavior and ecological effects. Academic Press, San Diego, California, USA. doi: 10.1016/B978-012386660-8/50004-0

Simard, M., W.H. Romme, J.M. Griffin, and M.G. Turner. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecological Monographs 81: 3–24. doi: 10.1890/10-1176.1

Simard, M., W.H. Romme, J.M. Griffin, and M.G. Turner. 2012. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Reply. Ecology 93: 946–950.

Snell, J.A.K. 1979. Preliminary crown weight estimates for tanoak, black oak, and Pacific madrone. USDA Forest Service Research Note PNW-RN-340, Pacific Northwest Research Station, Portland, Oregon, USA.

Stockstad, D.S. 1975. Spontaneous and piloted ignition of pine needles. USDA Forest Service Research Note INT-RN-194, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.

Sun, L., X. Zhou, S. Mahalingam, and D.R. Weise. 2006. Comparison of burning characteristics of live and dead chaparral fuels. Combustion and Flame 144: 349–359. doi: 10.1016/j.combustflame.2005.08.008

Tachajapong, W., J. Lozano, S. Mahalingam, X. Zhou, and D.R. Weise. 2008. An investigation of crown fuel bulk density effects on the dynamics of crown fire initiation in shrublands. Combustion Science and Technology 180: 593–615. doi: 10.1080/00102200701838800

Tappeiner, J.C., P.M. McDonald, and D.F. Roy. 1990. *Lithocarpus densiflorus* (Hook. & Arn.) Rehd. Tanoak. Pages 417–425 in: R.M. Burns and B. Honkala, technical coordinators. Silvics of North America. Volume 2, Hardwoods. USDA Agriculture Handbook 654, Washington, D.C., USA.

USDA Forest Service. 2009. America's forests: 2009 health update. US Department of Agriculture, Washington, D.C., USA.

Valachovic, Y.S., C.A. Lee, H. Scanlon, J.M. Varner, R. Glebocki, B.D. Graham, and D.M. Rizzo. 2011. Sudden oak death-caused changes to surface fuel loading and potential fire behavior in Douglas-fir–tanoak forests. Forest Ecology and Management 261: 1973–1986. doi: 10.1016/j.foreco.2011.02.024

Van Wagner, C.E. 1967. Flammability of Christmas trees. Publication 551. Canadian Department of Forestry, Forest Research Branch, Chalk River, Ontario, Canada.

Van Wagner, C.E. 1977. Conditions for the start and spread of crown fire. Canadian Journal of Forest Research 7: 23–34. doi: 10.1139/x77-004

White, R.H., and W.C. Zipperer. 2010. Testing and classification of individual plants for fire behaviour: plant selection for the wildland–urban interface. International Journal of Wildland Fire 19: 213–227. doi: 10.1071/WF07128

Xanthopoulos, G., and R.H. Wakimoto. 1993. A time to ignition-temperature-moisture relationship for branches of western conifers. Canadian Journal of Forest Research 23: 253–258. doi: 10.1139/x93-034

Yokoi, S. 1960. Study of the prevention of fire-spread caused by upward current. Japanese Ministry of Construction, Building Research Report 34, Tokyo, Japan.

Zar, J.H. 1999. Biostatistical analysis. Third edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.