



Surface fuels in recent *Phytophthora ramorum* created gaps and adjacent intact *Quercus agrifolia* forests, East Bay Regional Parks, California, USA

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ABSTRACT

Phytophthora ramorum, cause of “sudden oak death” or SOD, has had significant impacts on composition and structure in coastal forests of central and northern coastal California and southwestern Oregon. Despite the proximity of susceptible coast live oak (*Quercus agrifolia*) forests to densely populated urban areas, the impacts of SOD on their fuels have not been studied. We sampled surface fuels and vegetation structure in 16 plots in both SOD-caused gaps and intact stands (32 plots total) across two parks in the East Bay Regional Park District, east of San Francisco Bay. Plots were selected from a set of randomly placed pre-existing locations used in determining the disease distribution and intensity across the park system. Among the vegetation characteristics examined, only coast live oak basal area and live and dead tree density, canopy cover and maximum forb height differed between SOD created gap plots and adjacent intact forest plots. However, surface fuels such as vegetation cover, litter cover, wood cover, duff depth, fuels height, ladder fuels abundance, 1 h, 10 h, 100 h, and 1000 h fuels were greater in gap plots than intact forest plots. Although no fire behavior models were run, surface fuels suggest SOD created gaps may facilitate passive crown fire due to increased ladder and other fuels. This study represents a spatially explicit (gap focused) point-in-time estimate of surface fuels that will continue to change through time as disease progresses through these stands causing vegetation changes as fuels accumulate and decompose.

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1. Introduction

Invasive, non-native forest diseases are some of the most important threats to forests of the world, particularly those caused by organisms in the genus *Phytophthora* (Forest Phytophtoras of the World website: <http://forestphytophtoras.org/>, last checked November 1, 2016). *Phytophthora ramorum*, cause of sudden oak death (SOD), is the most destructive *Phytophthora* currently active in California forests, causing mortality of tanoak (*Notholithocarpus densiflorus*), coast live oak (*Quercus agrifolia*), California black oak (*Q. kelloggii*), canyon live oak (*Q. chrysolepis*) and Shreve's oak (*Q. parvula var. shrevei*). On other hosts *P. ramorum* causes mostly

non-lethal leaf and shoot blights, infections which support sporulation on many species (California Oak Mortality Task Force website <http://www.suddenOakDeath.org/> last checked November 1, 2016). Likely introduced into California in the 1990s (Rizzo et al., 2002), *P. ramorum* has led to rapid changes in forest structure and increased fuel loads. The resulting increased potential for more serious fires has become a major concern as the range of this *P. ramorum* epidemic expands and the impact intensifies, leading to mortality for millions of trees (Metz et al., 2011; Forrestel et al., 2015).

The forest types most severely impacted by SOD include the coast redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*)-mixed hardwood, and coast live oak forests and woodlands (McPherson et al., 2005, 2010; Ramage and O'Hara, 2010; Metz et al., 2011, 2012; Ramage et al., 2011, 2012; Cobb et al., 2012a, 2012b; Forrestel et al., 2015). In coast redwood and Douglas-fir forests, the high susceptibility of tanoak has led to a

Abbreviations: SOD, sudden oak death; CWD, coarse woody debris.

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shift in forest composition by favoring non-hosts or foliar hosts, e.g., coast redwood, Douglas-fir, and California bay laurel (*Umbellularia californica*) (Ramage et al., 2012; Metz et al., 2012; Cobb et al., 2012b), and removing the larger tanoaks from the landscape (Cobb et al., 2012b). Since California bay laurel has been shown to facilitate disease transmission without succumbing to SOD (Davidson et al., 2005) and spores are produced on tanoak foliage, a cycle is developing that may inhibit recovery of tanoak and susceptible oaks.

The effects of this disease on canopy (green and dead fuels in tree canopies), surface (fuels lying on or above ground) and ground fuels (combustible fuels in the ground matrix such as roots, deep duff) depend on numerous factors, but especially on stand species composition and percentage of various canopy layers occupied by susceptible hosts when the pathogen arrives (Valachovic et al., 2011; Metz et al., 2011; Cobb et al., 2012a; Forrestel et al., 2015). Disease resident time in a stand is particularly relevant because as hosts are killed a pulse of fuels occurs, and as the disease intensifies tree species composition changes (Metz et al., 2011; Cobb et al., 2012a). Canopy gaps and coarse fuels increase in the near term, with long term dynamics being very stand specific (McPherson et al., 2010; Ramage et al., 2012; Forrestel et al., 2015). Forrestel et al. (2015) found that dead tanoak basal area was positively related to surface fuel amount in coast redwood and Douglas-fir forests. Similarly, coarse woody debris (CWD) in coast redwood forests was 0.27 Mg ha⁻¹ in snags and 1.16 Mg ha⁻¹ in logs of uninfected forests, while in infected forests there was 22.4 Mg ha⁻¹ of tanoak snags, and 11.5 Mg ha⁻¹ in logs (Cobb et al., 2012b). Metz et al. (2013) have shown that redwood mortality from fire is greater in diseased stands than in those without disease due to increased surface fire severity from tanoak contributed fuels.

Despite the importance of coast live oak forests in central coastal California and their proximity to urban habitations, the influences of SOD on fuels, fire risk, and behavior are not understood, even though *P. ramorum* is established in many of these forests (McPherson et al., 2005, 2010). This forest type generally occurs below 500 m in the coastal fog belt within 100 km of the coast, often mixed in a mosaic with annual grasslands, shrublands, and riparian areas (Allen-Diaz et al., 2007). The litter layer can be deep and understory shrubs, grasses, and ferns form aggregations that create discontinuous or patchy fuels, and these may have high moisture content (Davis and Borchert, 2006). The historic fire regime of coast live oak forests and woodlands of the Central Coast Bioregion is poorly known, but is thought to include short to medium fire return intervals, with fires of variable size, complexity and magnitude, and with surface fires common (Davis and Borchert, 2006).

Coast live oak forest of the California East Bay Region dominate the environment along a soil - hydrologic transition zone between valley bottom and toe-slope redwood/Douglas-fir forests and non-forested chaparral along ridgetops. Although *P. ramorum* can occur in the forest/woodland without causing distinct mortality centers, in coast live oak it may create mortality centers with distinctive canopy gaps as mortality spreads from an initial infection area (Kelly et al., 2008). Modeling fire behavior in this forest type is extremely difficult as no data exist for canopy bulk density and other fuels parameters. The objective of this study was to characterize and compare vegetation and surface fuels associated with *P. ramorum* canopy gaps and the nearby forest with an intact canopy. We hypothesized that diseased tree fall would significantly increase surface fuels, and the height of ladder fuels with an increase in herb, shrub, and tree growth in the gaps. This approach measures the greatest possible impact of *P. ramorum* on fuels, and will provide managers some perspective on the complex fuels interaction of an emerging forest disease.

2. Materials and methods

2.1. Study area

We sampled coast live oak forests in Anthony Chabot and Redwood Regional Parks, East Bay Regional Park District, California (website: <http://www.ebparks.org/>, last checked November 1, 2016). The parks are managed for multiple uses, primarily as natural areas. Coast live oaks infected by *P. ramorum* were first confirmed in the East Bay Hills in 2001 at two sites approximately 35 km apart. The landscape consists of a complex mosaic of vegetation types within a small, highly dissected mountain range. Characteristic tree species are redwood, California bay laurel, and Douglas-fir in valley bottoms, toe slopes and north slopes, with coast live oak-dominated forests typical of the transition zone between these wetter environments to dry chaparral and grass lands on the upper slopes. California bay laurel, big leaf maple (*Acer macrophyllum*), and Pacific madrone (*Arbutus menziesii*) are common overstory associates of coast live oak. Midstory woody species include California coffeeberry (*Frangula californica*) and Christmas berry (*Heteromeles arbutifolia*). Understory vegetation rarely exceeds 1.5 to 2 m in height, and is composed of mixed grass, herb and the shrubs; poison oak (*Toxicodendron diversilobum*), sticky monkey-flower (*Mimulus aurantiacus*), California hazelnut (*Corylus cornuta*), manzanita (*Arctostaphylos* spp.), and huckleberry (*Vaccinium* sp.).

Elevation of plots varied from 212 m to 404 m. The climate is characterized as Mediterranean, with a dry summer, and wet winter. Climate data are from the Western Regional Climate Center for Oakland, California just west of the study area and near sea level (Oakland Museum: <http://www.wrcc.dri.edu/cgi-bin/cli-Main.pl?caokmu+sfo>, last checked November 1, 2016). Average annual precipitation is 57.7 cm, with mean July precipitation of 0.1 cm and a January average precipitation of 11.3 cm. Average annual temperature is 15.2 °C, with an average high of 19.4 °C and average low of 11.1 °C. The January average temperatures are a minimum of 7.0 °C and maximum of 14.2 °C, and July average temperatures are a minimum of 13.8 °C and maximum of 22.4 °C.

2.2. Field sampling procedure

2.2.1. Plot selection

Canopy gap plots were sites with distinct canopy openings associated with *P. ramorum* caused mortality and intact forest plots were sites with no significant canopy openings, i.e. there were no dead trees in the canopy and the overstory cover was >90%. Plots were selected from known locations in an existing plot network established in 2011 (O'Neill, 2014; McPherson et al., 2015). Gap plots were selected from the most severely infected (highest basal area infected) plots available, and intact plots were selected from adjacent plots with no SOD-caused coast live oak mortality, but similar structure and tree composition. A total of 32 plots were located, 8 of each type –intact, or gap plot– in both the Anthony Chabot and Redwood Regional Parks, for 16 plots in each park. Gap plots were centered in the canopy openings created by SOD mortality. Plot aspect, slope, and gap size (length x width) if relevant were recorded. Ladder fuels amount was ocularly estimated by the field crew as low = 1, moderate = 2, or high = 3, and the most abundant ladder fuel woody species were noted. Ladder fuels are typically difficult to consistently quantify (Menning and Stephens, 2007), but the same field crew estimated them for all plots.

2.2.2. Plot layout and tree measurement

Each plot consisted of a central fixed area plot (11.35 m radius; 0.04 ha) with eight transects (15 m length) radiating from the center in four cardinal (N, E, S, W) and four sub-cardinal directions (NE, SE, SW, NW). Standing live and dead trees were measured within the 0.04 ha plot; surface fuels and canopy cover were measured along each transect (methods below). At 6 m from plot center one fixed area subplot (2.5 m radius) was established at each N, E, S, and W directions, for a total of four subplots. Within the 2.5 m radius subplot we estimated vegetation attributes, including tree seedlings and sapling density (methods below). For overstory trees or snags >5 cm diameter at breast height (dbh, measured at 1.37 m on uphill side) in the 0.04 ha plot, we recorded dbh (cm), and tree height (m) for each species.

2.2.3. Vegetation cover and height measurements

Canopy cover was measured using a convex densiometer at five points in each plot (at each subplot center and the plot center). At each point we took four readings (N, E, S, W) by rotating around the point in a clockwise position. Shrub cover and height were measured for the dominant species on the 2.5 m radius subplot. Total shrub cover, total dead shrub cover, and both the average and average maximum height of shrubs in the 2.5 m radius subplot were recorded. Average height of shrubs was estimated from several measurements and the average maximum height was estimated from 2 to 3 measurements of the tallest shrubs. Seedlings were defined as being less than 1.37 m in height. Saplings were defined as >1.37 m in height but <5 cm DBH. The center of the seedling/sapling bole at the ground surface had to be in the plot to be counted. Tree seedlings and saplings were tallied by species in 5 cm height classes and their basal diameter measurement taken with small calipers as close to the ground surface as possible.

Ground cover was classified by type (bare including stone or rock, woody fuels, tree or old snag base, litter, total vegetation) and given % cover values that summed to 100%. This included cover of items that are within 1 cm of the ground surface. Within each subplot a 2 × 2 m quadrat was used to quantify forb and grass cover, and height, and % ground cover divided into bare ground including stone or rock, woody fuels, tree or old snag base, litter, and total vegetation.

2.2.4. Surface fuels

Surface fuels were measured as described by Brown (1974). Along each 15 m transect, the number of 1, 10, 100, and 1000 h fuels (down dead woody material) were tallied, in addition to measurements of litter, duff, and fuels height. Fuel diameter classes were defined and measured as; 1 h: 0–0.64 cm – tallied from 5 to 7 m along transect, 10 h: 0.65–2.54 cm – tallied from 5 to 10 m along transect, 100 h: 2.55–7.62 cm – tallied from 5 to 15 m along transect, 1000 h: >7.62 cm – tallied and diameter measured at their transect intersection along the entire 15 m. Additionally, 1000 h fuels were identified to species when known and assigned a five factor decay class (DC-1 to DC-5) after Pyle and Brown (1998), where DC-1 is fresh and sound and DC-5 is powdery. All fuels transect data were calculate to Mg ha⁻¹ using the methods detailed in Brown (1974), totaling the smaller 1 to 100-h size classes using the non-slash average square diameter, specific gravity, and non-horizontal particle angles from Brown (1974). For calculation of 1000-h fuel we used specific gravities of 0.55 for California bay laurel, 0.59 for coast live oak, 0.52 for *Eucalyptus globulus*, 0.58 for Pacific madrone, and 0.56 as an average when species was unknown. All specific gravities used were from Miles and Smith (2009). We corrected the specific gravity for decay class using multipliers of 1.0 for DC-1, 0.78 for DC-2, 0.45 for DC-3, and 0.4 for DC-4 and DC-5 (Waddell, 2002).

Litter depth, duff depth, and fuels height were measured at 5 and 15 m along each transect. Litter is the 01 horizon or "L" layer of the floor and includes freshly fallen leaves, needles, bark flakes, fruits, dead matted grass, and a variety of miscellaneous vegetative parts. If they were more than one-half below the litter, the material was considered duff. Duff is the fermentation and humus layers beneath the litter layer. The top of the duff is where needles, leaves, and other castoff vegetative material have begun to decompose. Often the color of duff differs from the litter above. Individual particles usually will be bound by fungal mycelium. When moss is present, the top of the duff is just below the green portion of the moss. The bottom of the duff is mineral soil. Fuels height (cm) was measured at 5 and 15 m on the fuels transects by extending perpendicular lines 0.5 m to the right (facing outward from plot center) then recording the highest single point of 1, 10, or 100 h fuels.

2.2.5. *Phytophthora ramorum* documentation/California Bay laurel leaf collection

All live and standing dead coast live oaks in each tree plot (0.04 ha) were evaluated for the presence of bole bleeds, stains, *Annulohypoxylon thouarsianum* fruiting bodies, and beetle boring dust as symptoms of SOD infections in trees (Rizzo and Garbelotto, 2003). Trees killed by *P. ramorum* characteristically exhibit all these signs and may maintain dead leaves for a year or longer (McPherson et al., 2000). We did not attempt to sample oaks for cultural determination of *P. ramorum*.

At each plot we collected 8–12 California bay laurel leaves expressing "drip tip" symptoms that may be characteristic of *Phytophthora* infection (Rizzo and Garbelotto, 2003). They were collected systematically along the N, E, S, W transects out to approximately 20 m if needed to find available specimens. Leaves were stored in a cooler and transported to Corvallis, OR where one lesion per leaf was plated onto cornmeal agar-ampicillin-rifam picin-pimaricin selective media and incubated in the dark for 7–12 days at 20 °C. Species identification was based upon the presence of hyphae, sporangia, and chlamydospores characteristic of *P. ramorum* (Werres et al., 2001). Any cultures lacking one feature were incubated an additional week and reexamined.

2.3. Statistical analysis

The response variables used to achieve the objectives of this study were: fuels (duff depth, litter height, fuel height, 1 h, 10 h, 100 h, 1000 h fuels, ladder fuels, bare ground cover, woody ground cover, bole ground cover, and litter ground cover) and vegetation characteristics (coast live oak basal area (BA) ha⁻¹, California bay laurel (BA) ha⁻¹, % canopy cover, % forb cover, average maximum forb height, % graminoid cover, average graminoid height, average maximum graminoid height, % dead graminoid cover, average dead graminoid height, average maximum dead graminoid height, % shrub cover, average shrub height, average maximum shrub height, % cover dead shrubs, average dead shrub height, average maximum dead shrub height, % cover of seedling and saplings, mean seedling and sapling height, mean seedling and sapling basal diameter, and total number of saplings and seedlings/plot, as well as coast live oak seedlings/sapling ha⁻¹, and California bay laurel seedlings/saplings ha⁻¹).

Even though plots were systematically chosen based on canopy gap development, differences in the vegetation and surface fuel parameters between intact and gap plots were compared through ANOVA for mixed models using a randomized complete block design with 2 blocks (park) and 2 treatments (control/mortality). Treatment was modeled as a fixed effect, block was modeled as a random effect using the Mixed procedure in SAS 9.4 (2002–2012 SAS Institute Inc., Cary, NC, USA). During the analysis, model

assumptions of normality and equal variance of residuals were tested using normal probability plots and plots of residuals (observed versus predicted), respectively. When necessary, data transformations were used to ensure these assumptions were met, and the means and 95% confidence intervals created from the analysis subsequently back-transformed for presentation. Comparisons with a $P \leq 0.05$ were considered statistically different.

3. Results

3.1. Vegetation

Canopy gaps in gap plots ranged in size from 56 m^2 to 533 m^2 (Fig. 1A, Table 1) with canopy cover significantly lower at 77.1% (74.8–79.4% CI = 95% confidence interval) than in adjacent intact plots at 93.8% (91.0–96.7% CI, Table 2 and Fig. 2). Live tree basal area for coast live oak in the intact plots was significantly greater at $40.6\text{ m}^2\text{ ha}^{-1}$ (30.5 – $54.1\text{ m}^2\text{ ha}^{-1}$ CI) than $20.0\text{ m}^2\text{ ha}^{-1}$ (15.0 – $26.6\text{ m}^2\text{ ha}^{-1}$ CI) for gap plots, while live tree basal area for California bay laurel was similar between plot types (Tables 2 and 3). Corresponding live tree density of coast live oak was similarly higher for intact plots at 489 ha^{-1} (386 – 604 ha^{-1} CI) than gap plots at 311 ha^{-1} (230 – 404 ha^{-1} CI), with no differences for California bay laurel tree between plot types (Tables 2 and 3). Dead coast live oak density at 150 ha^{-1} (105 – 203 ha^{-1} CI) in gap plots were also statistically higher than the 26 ha^{-1} (10 – 50 ha^{-1} CI) for intact



(A)



(B)

Fig. 1. Photos of (A) a canopy gap plot (#32, Tables 1 and 3) and (B) an intact plot (#10, Tables 1 and 3), both in Redwood Regional Parks, East Bay Regional Parks, California.

Table 1

Characteristics of intact stand plots and gap plots sampled in Anthony Chabot and Redwood Regional Parks, East Bay Regional Parks, California. UMCA = Umbellularia californica, TODI = *Toxicodendron diversilobum*, COCO = *Corylus cornuta*, VACC = unknown *Vaccinium* spp., MIAU = *Mimulus aurantiacus*, BAPI = *Baccharis pilularis*, FRCA12 = *Rhamnus californica*, QUAG = *Quercus agrifolia*, ARME = *Arbutus menziesii*, VAOV2 = *Vaccinium ovalifolium*.

Plot	Elev (m)	Aspect	Slope (%)	Gap size (m^2)	Ladder fuels amount	Dominant ladder fuels
<i>Intact stands (Anthony Chabot plots 1–8; Redwood 9–16)</i>						
1	326	90	0	N/A	Moderate	UMCA
2	280	355	17	N/A	Moderate	UMCA, TODI
3	282	340	47	N/A	Low	UMCA
4	344	88	65	N/A	High	UMCA, TODI, COCO, VACC
5	268	21	40	N/A	Low	MIAU, BAPI, TODI
6	332	264	50	N/A	Moderate	UMCA
7	225	6	52	N/A	High	UMCA
8	235	344	55	N/A	Moderate	UMCA, COCO, FRCA12
9	245	210	65	N/A	Low	UMCA, FRCA12, TODI
10	325	225	35	N/A	Low	UMCA, FRCA12, QUAG
11	309	240	45	N/A	Low	UMCA
12	290	75	60	N/A	Moderate	QUAG, BAPI, TODI, UMCA
13	260	166	40	N/A	Low	TODI, UMCA
14	381	106	55	N/A	Low	UMCA, COCO, QUAG
15	381	135	49	N/A	Low	UMCA
16	276	282	70	N/A	Low	UMCA
<i>Gap stands (Anthony Chabot plots 17–24; Redwood 24–32)</i>						
17	347	331	50	242	Moderate	UMCA, COCO
18	198	52	47	79	High	COCO, VAOV
19	166	30	45	154	Low	COCO, QUAG
20	339	307	23	78	Moderate	UMCA, QUAG, FRCA12
21	233	125	63	139	High	UMCA, TODI, ARME, COCO
22	168	96	65	193	High	ARME, QUAG, UMCA
23	214	21	45	268	High	UMCA, COCO
24	340	355	47	60	Moderate	VAOV2, UMCA
25	229	200	43	533	High	UMCA, FRCA12, COCO
26	203	54	53	163	Low	UMCA
27	316	245	80	118	Moderate	UMCA
28	212	0	35	217	Low	UMCA, QUAG
29	280	228	44	158	High	ARME, QUAG, UMCA
30	248	235	36	82	Moderate	UMCA, ARME, QUAG, VACC
31	243	211	40	434	Moderate	ARME, FRCA12, HEAR5, UMCA
32	405	38	56	56	Moderate	COCO, VAOV

forest plots (Tables 2 and 3). There were insufficient dead California bay laurel to compare statistically (Table 3). Within gaps, forb maximum height averaging 51.3 cm (35.3 – 67.4 cm CI) was the only ground vegetation attribute (Table 2 and Fig. 3) statistically different from adjacent intact forest plots, averaging 33.1 cm (17.0 – 49.1 cm CI). There were no differences in seedling/sapling attributes (Table 2).

3.2. Fuels

Several surface fuels attributes differed between SOD created gap plots and intact coast live oak forest plots (Table 4, Fig. 4). Total vegetation cover, wood cover, fuels height, ladder fuels abundance, 1 h, 10 h, 100 h, and 1000 h fuels were all statistically greater in the SOD gaps, whereas litter cover and duff depth were lower. Bare ground, bole cover, litter depth, and live and dead shrub attributes

Table 2

Vegetation attributes of intact *Q. agrifolia* forest plots and canopy gap plots at Anthony Chabot and Redwood Regional Parks, East Bay Regional Parks, California caused by *P. ramorum* mortality. Bold indicates significant difference. QUAG = *Quercus agrifolia*, UMCA = *Umbellularia californica*.

Vegetation attribute ^a	Gap plots	Intact plots	<i>P</i>	<i>F</i> ^b
QUAG basal area ($m^2 ha^{-1}$)	20.0 (15.0, 26.6)	40.6 (30.5, 54.1)	<0.001	28.44
QUAG live tree density (# ha^{-1})	311 (230,404)	489 (386,604)	0.013	6.95
QUAG dead tree density (# ha^{-1})	150 (105,203)	26 (10,50)	<0.001	26.84
UMCA basal area ($m^2 ha^{-1}$)	3.8 (1.8,8.0)	2.2 (1.0,4.5)	0.272	1.25
UMCA live tree density (# ha^{-1})	209 (133,301)	148 (86,227)	0.268	1.28
Canopy cover (%)	77.1 (74.8,79.4)	93.8 (91.0,96.7)	<0.001	87.58
Forb cover (%)	11.7 (7.5,15.9)	6.6 (2.5,10.8)	0.089	3.10
Forb height (cm)	28.8 (16.6,41.1)	20.3 (8.0,32.5)	0.113	2.66
Forb max ht (cm)	51.3 (35.3,67.4)	33.1 (17.0,49.1)	0.023	5.79
Grainoid cover (%)	0.08 (0.01,1.11)	0.13 (0.01,1.81)	0.581	0.31
Graminoid ht (cm)	12.5 (2.7,22.4)	15.7 (5.9,25.6)	0.352	0.90
Graminoid max ht (cm)	19.2 (2.8,35.7)	23.3 (6.8,39.8)	0.465	0.55
Dead graminoid cover (%)	0.04 (0.01,0.36)	0.05 (0.01,0.40)	0.900	0.02
Dead graminoid ht (cm)	3.3 (1.1,6.8)	4.2 (1.6,8.1)	0.607	0.27
Dead graminoid max ht (cm)	4.6 (3.0,11.1)	6.8 (2.0,14.4)	0.416	0.68
Seedling/sapling cover (%)	0.9 (0.4,2.0)	1.2 (0.5,2.7)	0.472	0.53
Seedling/sapling ht (cm)	37.1 (28.9,45.3)	30.8 (22.6,39.0)	0.273	1.25
Seedling/sapling base dia. (cm)	6.3 (4.7,8.5)	7.1 (5.2,9.5)	0.587	0.30
Seedling/sapling stems (# ha^{-1})	26,969 (16,409,43,528)	26,938 (13,378,40,497)	0.629	0.24
QUAG seedling/sapling (# ha^{-1})	8928 (4468,14,916)	10,643 (5704,17,111)	0.653	0.21
UMCA seedling/sapling (# ha^{-1})	9839 (2758,21,278)	11,861 (3872,24,206)	0.446	0.60

^a Mean (95% confidence interval); max = maximum; ht = height; # ha^{-1} = number per hectare.

^b Degrees of freedom 1, 29.

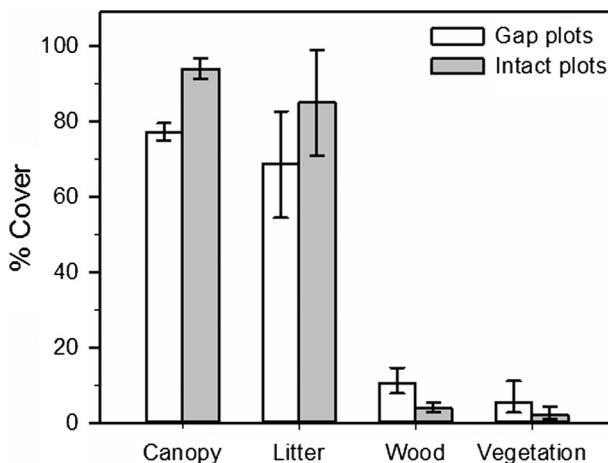


Fig. 2. Percent cover for canopy, litter, wood, and vegetation in *P. ramorum* caused gap plots, and intact forest plots in Anthony Chabot and Redwood Regional Parks, East Bay Regional Parks, California. Bars represent means and 95% confidence intervals for those cover variables statistically different between plot types. *P* values are listed in Tables 3 and 4.

were not different, consistent with no statistical differences in vegetation attributes in Table 2. The 1000 h fuels were over 19 times greater in SOD created gap plots, averaging $1199.7 \text{ Mg } ha^{-1}$ ($513.6\text{--}2172.7 \text{ Mg } ha^{-1}$ CI) compared to intact forest plots averaging $62.2 \text{ Mg } ha^{-1}$ ($15.9\text{--}390.7 \text{ Mg } ha^{-1}$ CI, Fig. 4). Eighty-one percent of gap plots had ladder fuel amounts as moderate or high, in comparison to 44% for intact forest plots (Fig. 1, Table 1). Typical woody ladder fuels included California bay laurel, poison oak, and western hazel (Table 1).

3.3. Incidence of SOD in coast live oaks and *P. ramorum* in California Bay laurels

Coast live oak in intact plots represented 24% of all live trees and 52% of all dead trees with signs and symptoms consistent with SOD, including bleeding and bark stains from older bleeds, beetle boring dust, and *A. thouarsianum* fruiting bodies. In gap plots,

24% of the live trees and 89% of the dead trees were symptomatic. The average number of live trees/plot was 20.4 for intact plots and 13.4 for gap plots, while the average number of dead trees/plot was 1.5 for intact plots and 6.7 for gaps plots. Two hundred and seventy California bay laurel leaf samples from intact plots and 287 from canopy gap plots were screened for the presence of *P. ramorum*. The pathogen was isolated from all intact plots except one in Redwood, and two in Anthony Chabot (13 of 16 sites). The proportion of positive samples within intact plots ranged between 0 and 81% (mean = 29%). *P. ramorum* was detected at all the canopy gap plots except two in Redwood (14 of 16 sites) with the proportion of positive samples ranging between 0 and 75% (mean = 32%). Eleven samples across all sites contained culturable species (probably *Phytophthora* spp. or *Pythium* spp.) not identified.

4. Discussion

Phytophthora ramorum was first detected relatively recently, in 2001, in the East Bay Regional Parks area (McPherson et al., 2015). Therefore, this is an emerging disease epidemic (Rizzo et al., 2005) with potential to greatly reduce proportions of large coast live oaks in the area, as documented by McPherson et al. (2010) in Marin County forests northwest of the East Bay Region. After 8 years of monitoring, they reported 5%/yr infection rates and 3.1%/yr mortality rates for coast live oak. In addition, infection rates increased as stem diameter increased in both Marin County (McPherson et al., 2010) and East Bay Parks (O'Neill, 2014). McPherson et al. (2010) estimated 90% of all coast live oaks in the Marin County sites would be infected within about 36.5 years. Given *P. ramorum* detection on California bay laurel in almost all of our plots, with about 25% of all live trees and 50% of all dead trees in intact plots showing indications of infection, we anticipate similar impact severity in the East Bay Regional Parks forests, leading to increasing numbers of large dead trees for the foreseeable future.

Canopy gaps and associated fuels are linked with the epidemiology of *P. ramorum* mortality, branch death, litterfall, and associated vegetation responses. Gap creation is then related to the dynamics of *Q. agrifolia* interactions with sporulating hosts that excludes itself because its bole cankers do not produce *P. ramorum* spores, and therefore is considered a dead-end host (Rizzo et al.,

Table 3

Basal area in m^2 and (number of trees), for live and dead (snags) > 5 cm dbh on 0.04 ha plots in Anthony Chabot and Redwood Regional Parks, East Bay Regional Parks, California. QUAG = *Quercus agrifolia*, UMCA = *Umbellularia californica*, ACMA3 = *Acer macrophyllum*, AECA = *Aesculus californica*, and ARME = *Arbutus menziesii*.

Plot	QUAG		UMCA		ACMA3 Live	AECA Live	ARME	
	Live	Dead	Live	Dead			Live	Dead
<i>Intact stand (Anthony Chabot plots 1–8; Redwood 9–16)</i>								
1	1.77 (24)	0.18 (2)	0.09 (10)	0.01 (2)	—	—	—	—
2	1.22 (14)	0.03 (2)	0.04 (1)	0.16 (1)	—	—	—	—
3	2.20 (16)	0.01 (2)	0.19 (9)	—	0.25 (1)	—	—	—
4	1.89 (22)	0.04 (2)	0.01 (4)	—	—	—	—	—
5	1.45 (32)	—	0.02 (4)	—	—	—	—	—
6	2.46 (15)	0.10 (1)	0.22 (18)	—	—	—	—	—
7	1.69 (9)	—	0.14 (13)	—	—	—	—	—
8	1.12 (12)	0.06 (1)	0.10 (3)	—	—	—	—	—
9	1.51 (18)	0.37 (3)	0.09 (6)	—	—	—	—	—
10	2.08 (37)	0.01 (1)	0.27 (4)	—	—	—	—	—
11	2.10 (29)	0.55 (3)	0.20 (11)	—	—	—	—	—
12	1.52 (20)	0.02 (1)	0.30 (4)	—	—	—	—	—
13	2.20 (33)	—	—	—	—	—	—	—
14	1.71 (14)	—	0.86 (9)	—	—	—	—	—
15	0.86 (9)	0.08 (2)	0.06 (8)	—	—	0.25 (1)	—	—
16	1.17 (23)	0.11 (3)	0.24 (7)	0.01 (1)	—	0.01 (3)	0.02 (5)	—
Ave.	1.68 (20.4)	0.1 (1.4)	0.18 (6.9)	0.01 (0.25)	0.02 (0.06)	0.02 (0.25)	0.00 (0.3)	—
<i>Gap stand (Anthony Chabot plots 17–24; Redwood 24–32)</i>								
17	1.33 (17)	0.23 (6)	0.22 (5)	—	—	—	—	—
18	0.75 (9)	0.15 (1)	0.07 (1)	—	—	—	—	—
19	1.11 (9)	0.16 (3)	0.03 (1)	—	—	—	—	—
20	1.24 (27)	0.17 (7)	1.36 (5)	0.01 (1)	—	—	—	—
21	1.18 (16)	0.72 (6)	0.44 (10)	—	—	—	—	0.01 (1)
22	0.85 (20)	0.70 (10)	0.14 (16)	—	—	—	—	0.05 (1)
23	0.60 (13)	0.32 (12)	0.12 (14)	—	—	—	0.01 (1)	—
24	1.15 (9)	0.46 (2)	0.02 (5)	—	—	—	—	—
25	0.70 (19)	1.05 (11)	0.23 (21)	—	—	—	0.02 (1)	—
26	0.53 (6)	0.28 (6)	0.11 (3)	—	—	—	0.28 (1)	—
27	0.82 (9)	1.37 (18)	0.30 (16)	—	—	—	—	—
28	1.78 (29)	0.46 (5)	0.01 (2)	—	—	—	—	—
29	0.30 (11)	0.37 (4)	0.13 (9)	—	—	—	0.06 (6)	0.03 (1)
30	0.39 (5)	0.42 (7)	0.60 (15)	—	—	—	0.38 (10)	—
31	0.74 (8)	0.71 (9)	0.33 (22)	—	—	—	—	—
32	0.62 (6)	0.08 (1)	0.40 (11)	—	—	—	—	—
Ave.	0.88 (13.4)	0.48 (6.7)	0.28 (9.8)	0.00 (0.1)	—	—	0.05 (1.2)	0.00 (0.2)

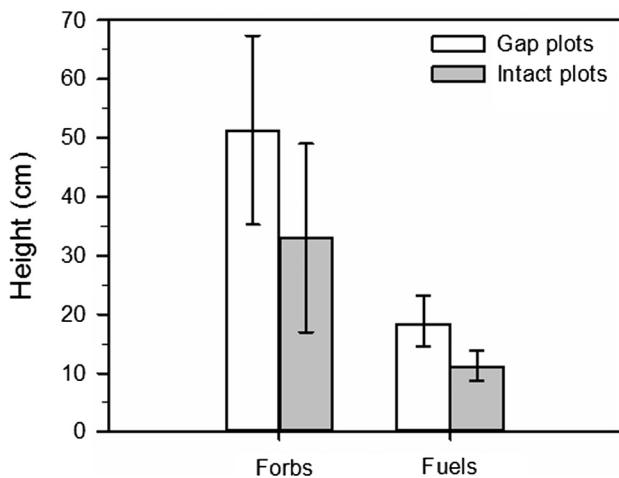


Fig. 3. Maximum forb height and fuels height in *P. ramorum* caused gap plots and intact forest plots in Anthony Chabot and Redwood Regional Parks, East Bay Regional Parks, California. Bars represent means and 95% confidence intervals. *P* values are listed in Tables 3 and 4.

Parks. California bay laurel in particular is a key driver of *P. ramorum* distribution and infection in coastal forests of California because their leaves serve to produce large numbers of sporangia (Rizzo et al., 2005). This tree was present on all our plots. Gap creation is related also to landscape settings, climate and weather with potential for some years causing enhanced infections. Although spread during wet weather is probable anytime, there may be optimum conditions for major wave years of *P. ramorum* infection in N. California. In addition, some variation in resistance to *P. ramorum* is known in *Q. agrifolia* that is correlated with variation in phloem chemistry (McPherson et al., 2014). Canopy gaps and fuels dynamics will change with time-since-arrival of *P. ramorum*.

Interactions of *P. ramorum* epidemiology, fuels dynamics, and potential fire behavior are illustrated in tanoak forests where high host mortality rates and the ability of *P. ramorum* to persist have a huge influence on potential fire behavior (Metz et al., 2011; Cobb et al., 2012a; Johnstone et al., 2016). For example, Metz et al. (2011) investigated the relationship of SOD and fire behavior in the Big Sur area with a tanoak/redwood/Douglas-fir forest type burned by the 2008 Basin Complex fire. They found the amount of SOD caused mortality contributed to overstory burn severity only in recently invaded stands, while increasing accumulations of coarse fuels led to greater substrate burn severity. Johnstone et al. (2016) synthesized the feedbacks and interactions occurring between pathogen, species composition, disease transmission and fire in tanoak/redwood/Douglas-fir forests, suggesting that as bay laurel increases in abundance, fire hazard and disease transmission

2005). Coast live oak, California bay laurel, madrone, huckleberry, California buckeye (*Aesculus californica*) and big leaf maple, (*Acer macrophyllum*) are known hosts on our plots that may contribute to *P. ramorum*'s widespread occurrence that our sampling documented across forests in Anthony Chabot and Redwood Regional

Table 4

Surface fuel attributes of canopy gap plots caused by SOD mortality compared with intact *Q. agrifolia* forest plots in Anthony Chabot and Redwood Regional Parks, East Bay Regional Parks, California caused by *P. ramorum* mortality. Bold indicates significant difference.

Fuel attribute	Gap plots	Intact plots	P	F ^b
Bare ground (%)	4.0 (2.2, 7.4)	2.6 (1.4, 4.7)	0.289	1.17
Vegetation cover (%)	5.4 (2.7, 11.1)	2.1 (1.0, 4.3)	0.005	9.10
Litter cover (%)	68.4 (54.3, 82.5)	84.8 (70.7, 98.9)	0.005	9.17
Bole cover (%)	0.13 (0.0, 5.1)	0.9 (0.0, 3.2)	0.697	0.15
Wood cover (%)	10.5 (7.7, 14.5)	3.9 (2.8, 5.3)	<0.001	21.83
Duff depth (cm)	0.1 (0.0, 0.2)	0.3 (0.1, 1.1)	0.007	8.34
Litter depth (cm)	4.4 (3.5, 5.5)	4.4 (3.5, 5.5)	1.000	0.00
Fuels height (cm)	18.4 (14.5, 23.2)	11.0 (8.7, 13.9)	0.003	11.00
Ladder fuel rating (1–3)	2.2 (1.5, 2.9)	1.6 (0.9, 2.2)	0.014	6.84
Live shrub cover (%)	4.7 (2.1, 10.7)	4.6 (2.0, 10.5)	0.969	0.00
Live shrub ht (cm) ^a	39.2 (28.8, 53.3)	31.4 (23.1, 42.7)	0.305	1.09
Live shrub max ht (cm) ^a	102.1 (71.7, 132.4)	94.0 (63.7, 124.3)	0.703	0.15
Dead shrub cover (%)	0.2 (0.0, 0.9)	0.2 (0.0, 0.9)	0.999	0.00
Dead shrub ht (cm)	28.4 (13.4, 49.0)	29.3 (14.0, 50.2)	0.926	0.01
Dead shrub max ht (cm)	41.2 (16.8, 76.3)	41.5 (17.0, 76.8)	0.979	0.00
1 h fuels (Mg ha⁻¹)	1.4 (1.1, 1.6)	0.9 (0.7, 1.1)	0.002	11.02
10 h fuels (Mg ha⁻¹)	5.2 (3.8, 6.9)	2.6 (2.0, 3.6)	<0.001	24.28
100 h fuels (Mg ha⁻¹)	7.2 (5.1, 10.2)	3.2 (2.3, 4.5)	<0.001	16.16
1000 h fuels (Mg ha⁻¹)	1199.7 (513.6, 2172.7)	62.2 (15.9, 390.7)	<0.001	42.77

^a Mean (95% confidence interval); max = maximum; ht = height.

^b Degrees of freedom 1, 29.

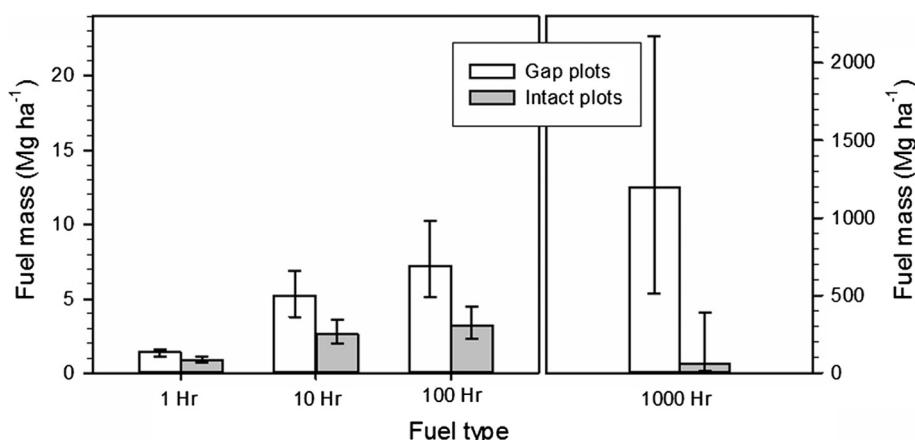


Fig. 4. One hr, 10 h, 100 and 1000 h fuels (Mg ha^{-1}) in *P. ramorum* caused gap plots and intact forest plots in Anthony Chabot and Redwood Regional Parks, California. Bars represent means and 95% confidence intervals. P values listed in Table 4.

increase. In coast live oak forests of the East Bay region, we do not yet have data on species compositional changes that may occur longer term.

In recently created SOD canopy gaps (last 10 years), the vegetation structure is not particularly different from adjacent intact forests (Table 2), but fuels characteristics are very different (Table 4), with significant increases in vegetation cover, wood cover, fuels height, ladder fuel abundance, and 1, 10, 100 and 1000 h fuels. This implies surface fires may behave differently in these canopy gaps, with the potential for increased transitions from ground to canopy fires, increased flame length, and increased substrate burn severity. Research from forests with a significant tanoak component supports these conclusions (Metz et al., 2012, 2013; Cobb et al., 2012a; Forrestel et al., 2015). For example, Metz et al. (2013) have shown coast redwood mortality was elevated in fires that occurred in SOD impacted forests, likely due to increased residence time of burning at the base of large trees. This could potentially be an issue in the East Bay Regional Parks for large trees in gaps.

Forrestel et al. (2015), using the Behave plus modeling program, predicted longer flame lengths, increased rates of spread, and increased intensity of surface fires associated with tanoak mortality in coast redwood and Douglas-fir stands. Gaps in infected

stands averaged $2.9 \times$ more 1 h fuels, $2.4 \times$ more 10 h fuels, $2.3 \times$ more 100 h fuels, and fuel bed depth $2.3 \times$ deeper in *P. ramorum* infected stands due to tanoak mortality. In the present study, SOD-created gaps averaged $1.6 \times$ greater 1 h fuels, $2.0 \times$ greater 10 h fuels, and $2.3 \times$ greater 100 h fuels, with fuels height being about $1.7 \times$ higher than in intact forest plots. However, in this study, the 1000 h fuels were $19.3 \times$ greater in canopy gap plots than in intact forest plots. In tanoak forests studied by Cobb et al. (2012a), the total CWD mass of logs was $13.3 \times$ greater in infected stands than uninfected stands.

Valacovic et al. (2011) sampled *P. ramorum* and herbicide treated stands to investigate the potential influence of *P. ramorum* on surface fuel loading. They found total fuel loadings (1-, 10-, 100-, and 1000-h fuels) doubled, averaging 58.1 Mg ha^{-1} in control stands and 106.3 Mg ha^{-1} in *P. ramorum*/herbicide stands. At East Bay Regional Parks, intact plots averaged 68.9 Mg ha^{-1} , while gap plots averaged $1213.5 \text{ Mg ha}^{-1}$ total fuel loading. The amount of 1000-h surface fuels (> 7.62 cm diameter), also considered CWD or logs, is much greater in coast live oak forests, than in tanoak forests described by Cobb et al. (2012b). Cobb et al., reported 1.16 Mg ha^{-1} in uninfected tanoak forests, while we report 62.2 Mg ha^{-1} of coarse wood for intact coast live oak forest plots. Although our intact plots had

P. ramorum present. In coast live oak gap plots, we report 1199.7 Mg ha⁻¹ of 1000 fuels while Cobb et al. (2012b) cite 11.5 Mg ha⁻¹ of logs in infected stands of tanoak. These differences between coast live oak and tanoak impacted stands probably relate to structure and composition of the stands, with growth form of coast live oak vs tanoak likely very influential. But perhaps the focus on a gap in our study reflects the extreme accumulation of recent fallen mortality, and therefore our numbers represent a spatially distinct measure, while Valacovic et al. (2011) and Cobb et al. (2012b) represent a stand level number.

The progression and intensification of SOD in the coast live oak forests of East Bay Regional Parks will determine future fuels dynamics. Significant new coast live oak mortality is likely to continue for at least several more decades leading to fresh inputs of coarse fuels and enlargement of canopy gaps. Concomitant decomposition of CWD will have unknown effects on fuels availability. Historical fire behavior in coast live oak stands is not particularly well understood but likely included variable fire complexity with surface fires common. Less common are passive, high severity crown fires which can kill most trees (Davis and Borchert, 2006). Passive crown fires may also be facilitated by increased surface fuel height and increased ladder fuels. Mature coast live oaks are thought to be very tolerant of surface fires (Davis and Borchert, 2006; Allen-Diaz et al., 2007). However, greater mortality might occur in response to increased SOD related fuel loads and the potential for enhanced substrate burn severity, such as that described by Metz et al. (2013) for coast redwood, also a very fire tolerant species. Canopy gap creation in *Q. agrifolia* forests is a complicated process. The information presented here using gaps to estimate fuels changes associated with *P. ramorum* invasion should be considered an early step toward understanding the impacts this pathogen may have on fuels and fire behavior in these forests, that will ultimately require a long-term, comprehensive approach to fully comprehend.

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