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RESEARCH ARTICLE

TREE-RING INDICATORS OF FIRE IN TWO OLD-GROWTH COAST REDWOOD FORESTS

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ABSTRACT

Fires that burn through forests cause changes in wood anatomy and growth that can be used to reconstruct fire histories. Fire is important in *Sequoia sempervirens* (D. Don) Endl. (coast redwood) forests, but fire histories are limited due to difficulties crossdating annual rings of this species. Here we investigated three fires (1985, 1999, 2008) in two old-growth forests (Montgomery Woods State Natural Reserve and Landels-Hill Big Creek Reserve, California, USA) to quantify these responses via crossdated increment cores from lower trunks of 53 trees, including 10 that were climbed and cored at 10 m height intervals. Redwoods frequently responded to fire by producing anomalous growth during the fire year; 100 of 240 lower trunk cores recorded at least one anatomical indicator (i.e., intra-annual density fluctuation, faint latewood, resin, or scar). Following fire, radial growth decreased by 29 % to 43 % compared to the fire year. After accounting for climatic influences, radial growth was 27 % to 32 % lower than expected in the post-fire year

RESUMEN

Los incendios que queman a través de bosques, producen cambios en la anatomía de la madera y en el crecimiento que pueden ser utilizados para reconstruir historias de fuego. El fuego es importante en los bosques de *Sequoia sempervirens* (D. Don) Endl. (sequoia roja costera), pero las historias de fuego son limitadas debido a dificultades para co-fechar anillos anuales de esta especie. Nosotros investigamos tres incendios (1985, 1999, 2008) en dos bosques maduros (Reserva Natural de Montgomery Woods State y Reserva de Landels-Hill Big Creek, California, EEUU) para cuantificar estas respuestas a través del co-fechado, mediante tarugos tomados en la parte inferior del tronco de 53 árboles, incluyendo 10 árboles en los cuales se hicieron tarugos en el tronco a distintas alturas a intervalos de 10 m. Los bosques de sequoia roja respondieron frecuentemente al fuego produciendo un crecimiento anómalo durante el año del incendio; 100 de 240 datos tomados de la parte inferior de los troncos mostraron al menos un indicador anatómico (i.e., fluctuación de la densidad intra-anual, leño tardío empalidecido, resina o cicatriz). Después del incendio, el crecimiento radial decreció de 29 % a 43 % comparado con el año en que ocurrió el fuego. Luego de tener en cuenta las influencias climáticas, el crecimiento radial fue de 27 % a 32 % más bajo que lo esperado en and declined to as low as 46% after three years. Growth suppression persisted for up to seven years after fire, followed by up to 40% higher than expected radial growth. Several of the climbed trees expressed disruption of incremental growth along the height gradient following fire. The 1985 event consistently generated stronger growth and anatomical responses than the 1999 and 2008 events, and showed a co-occurrence between faint latewood during the fire year and subsequent narrow or missing rings. We used post-fire low growth relative to drought combined with anatomical indicators to detect past fires, identifying five additional events at Landels-Hill Big Creek Reserve dating back to 1634. Although other disturbances could have initiated these responses, our detection method enhances current capabilities for the spatiotemporal resolution of redwood fire histories via non-scar indicators on increment cores from living redwoods.

el año post-fuego y declinó hasta el 46% tres años después. La supresión del crecimiento persistió hasta 7 años después del fuego, seguido luego por hasta un 40% más que el crecimiento radial esperado. Varios de los árboles tarugados en altura mostraron una disrupción del incremento del crecimiento a lo largo del gradiente de altura después del fuego. El evento de 1985 generó sistemáticamente respuestas en el crecimiento y respuestas anatómicas más evidentes que en los eventos de 1999 y de 2008, y mostraron una co-ocurrencia entre la palidez del leño tardío y subsecuentemente en el crecimiento de anillos, que resultaron más angostos o ausentes. Nosotros utilizamos el crecimiento lento post-fuego en relación a la sequía, combinado con indicadores anatómicos para detectar fuegos pasados, identificando cinco eventos adicionales en la Reserva de Landels-Hill Big Creek datando hacia el pasado hasta el año 1634. Aunque otros disturbios pudieron haber iniciado estas respuestas, nuestro método de detección refuerza las capacidades actuales para la resolución espacio-temporal de historias de fuego de la sequoia roja, a través de indicadores en datos de incremento de crecimiento en sequoias vivas mediante tarugos y no mediante cicatrices.

Keywords: California, coast redwood, dendrochronology, fire indicators, fire response, *Sequoia sempervirens*

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INTRODUCTION

Tree rings provide useful information about fire in *Sequoia sempervirens* (D. Don) Endl. (hereafter, redwood) forests. Remnant charcoal on trunks is visual evidence of fire (Sawyer *et al*. 2000), and ring counts of fire scars on redwood stumps extend over 1200 years (Fritz 1931). Fire is ecologically important and redwood has fire-adapted traits (e.g., thick bark, basal and epicormic sprouting), but the temporal and spatial variability of this disturbance across the redwood region is complex. Published fire histories for these forests indicate a wide range of fire-return intervals, from >100 yr to <10 yr within sub-regions, with several factors influencing this high variability (Lorimer *et al*. 2009). The north-south and coastal-interior climate gradients (Jacobs *et al*. 1985, Stuart and Stephens 2006) shape regional-scale differences, while localized topography and fuels can contribute to landscape-level variability (e.g., Heyerdahl *et al*. 2001). Human disturbances also impact fire regimes in the redwood region and include Native American burning, Euro-American ranching and logging, and fire exclusion (Greenlee and Langheim 1990, Brown and Baxter 2003, Anderson 2005, Stuart and Stephens 2006). Fire histories for redwood forests are less articulated than many other forests in the western United States due in large part to difficulty crossdating redwoods' annual rings (Fritz 1940).

Most redwood fire-return intervals derive from ring counts of undated tree-ring records (Jacobs *et al*. 1985, Stephens and Fry 2005, Jones and Russell 2015), and we know of only one published fire history based on crossdated samples from pre-Euro-American-settlement trees (Brown and Swetnam 1994). Redwood exhibits frequent discontinuous or missing rings (Fritz and Averill 1924, Carroll *et al*. 2014), declining radial growth with age that can result in ring widths <0.1 mm (Sillett *et al*. 2010, Carroll *et al*. 2014), and anomalous growth near basal buttressing (Sillett *et al*. 2015). These characteristics limit crossdating, especially for older trees, which are targets for accessing tree rings to reconstruct fire histories. Centuries to millennium-scale crossdating along the latitudinal distribution has recently been achieved via intensive within-tree sampling of standing redwoods in old-growth forests, which improves crossdating confidence related to dendroclimatic variation (Carroll *et al*. 2014, 2017).

Reconstructing annually resolved fire histories in redwood forests has the added challenge of accessing evidence of past fires. Tree-ring sampling near fire scars reveals distinctive cambium damage caused by fire with subsequent events affecting the same vulnerable areas (Arno and Sneck 1977, McBride 1983). Even though partial cross-sections can be collected from living trees to study fire history (Arno and Sneck 1977), such cuts from large redwoods would be unethical, like the case enunciated for *Sequoiadendron giganteum* (Lindl.) J. Buchholz (hereafter, giant sequoia) by Swetnam *et al*. (2009), limiting sampling of fire-scarred redwoods to stumps and fallen trees. Such sampling is the foundation of multi-millennial fire histories for giant sequoia (Swetnam *et al*. 2009) due to its comparatively straightforward crossdating (Carroll *et al*. 2014). While fire-resistant bark and extremely decay-resistant heartwood promote redwood longevity and allow centuries-old dead trunks to persist in old-growth forests, fire-scarred surfaces are often poorly preserved after bark loss and sapwood decay (Brown and Baxter 2003). The best fire-scar records may occur directly above the root crown (Brown and Swetnam 1994, Norman 2009), but the exclusion of partial cross-sections from living trees and difficulty in crossdating basal samples warrants examination of higher trunk positions.

Sudden changes in ring width in response to fire are well documented in the literature (Py *et al*. 2006, Lombardo *et al*. 2009, Swetnam *et al*. 2009, Margolis *et al*. 2011). A growth release (ring-width increase) may be attributed to reduced competition from damaged or killed neighboring trees that temporarily increased a tree's resource availability (Hartesveldt 1964, Lombardo *et al*. 2009). Giant sequoia, the closest relative of redwood, has a comparatively well known fire history, including many instances of growth release after fire (Swetnam *et al*. 1991, Brown *et al*. 1992, Swetnam 1993). Fire severity mediates growth response, and some low-severity fires do not reduce competition or increase soil nutrients enough to promote radial growth, while high-severity fires can cause major foliage damage and delay growth increases (Mutch and Swetnam 1995). Fuel accumulation due to fire suppression can influence growth responses, but large post-fire releases exist in pre-Euro-settlement tree-rings for giant sequoia (Caprio *et al*. 1994, Mutch 1994) and redwood (Brown and Swetnam 1994). The most common growth response to fire that has been observed in about a dozen fire-scarred redwood stumps near Redwood National Park in northern California, USA (41°24'N, 123°59'W), is an abrupt growth increase ranging from two years to several decades (Brown and Swetnam 1994). Conversely, some redwoods produce narrow or micro rings one to two years after a fire, with this ring-width variation being unrelated to climate (Brown and Swetnam 1994, Carroll *et al*. 2014). Loss of leaf area due to foliage scorch, heat-induced cambial damage, or heavy investment in reiteration (i.e., epicormic branching, basal sprouting) and roots following fire may cause such growth suppression (Brown 1991, 2013; Swezy and Agee 1991; Brown and Swetnam 1994; Seifert *et al*. 2017).

Anatomical indicators supplement scars for dating historical fires, often in conjunction with changes in ring width (Swetnam *et al.* 1991, Holz and Veblen 2009, Swetnam *et al.* 2009, Margolis *et al*. 2011). Redwood, giant sequoia, and other members of the Cupressaceae respond to injury by producing inducible traumatic resin ducts (TRD) in the xylem (Hudgins *et al*. 2004, Krokene *et al*. 2008), and fire-associated TRD occur up to 6 m above the ground on redwood trunks (Brown and Swetnam 1994). TRD provide evidence of fire in redwoods (Jones and Russell 2015), but the mechanics and variation of fire-induced TRD are poorly understood. Other anatomical reactions to heat exposure in conifers include resin soaking, discolored wood, and callus tissue formation (Smith *et al*. 2016). Intra-annual density fluctuations (IADFs) such as false rings and double latewood correspond with fire in both redwood and giant sequoia (Brown and Swetnam 1994, Swetnam *et al*. 2009, Jones and Russell 2015). IADFs result from disruption of normal xylogenesis during the growing season and reflect variations in environmental conditions often caused by climate (Vieira *et al*. 2010, De Micco *et al*. 2016).

Climate variation affects both tree growth and fire incidence on multiple time scales. Redwood inhabits a wide precipitation gradient, from rainforests in the north to drier forests in the south, although forests across the range experience dry summers with <4% annual precipitation moderated by fog, which contributes hydrologic input and reduces water stress (Dawson 1998, Burgess and Dawson 2004, Van Pelt *et al.* 2016). Warm and dry summers constrain inter-annual redwood growth with a general trend of increasing sensitivity to drought and maximum temperature from north to south (Carroll *et al*. 2014). Most fires in the redwood region occur during dry late summer to early fall, as shown by twentieth century records (Gripp 1976) and sub-annual position of fire scars (Brown and Swetnam 1994, Brown and Baxter 2003, Jones and Russell 2015). In the North Coast Ranges of California, USA, fire often occurs during dry years (Skinner *et al*. 2009), and across the western USA, climate contributes to regionally synchronous fire years while terrain, fuels, and aspect influence landscape-level variability in fire severity (Swetnam 1993, Heyerdahl *et al*. 2001, Bigio *et al*. 2016). For the redwood region, fog and low cloud cover affect surface temperature variation (Iacobellis and Cayan 2013) and may temper the relationship between drought and fire for interior forests (Norman *et al*. 2009). Given that climate influences inter-annual growth and fire incidence, climate-induced variation should be considered when assessing indicators of fire in redwood forests.

In this study, we examine tree-rings in relation to fire in two old-growth redwood forests. Increment cores collected from live trees sample growth rings following fires in 1985, 1999, and 2008. Specifically, our goals are: 1) to document fire-associated ring features, including growth metrics and anatomical indicators; 2) to compare how fire indicators are expressed at different heights of standing trees; 3) to assess the effect of fire on growth after accounting for climate influences; and 4) to use growth and wood anomalies to detect past fire events in one forest.

METHODS

Study Area

We sampled tree rings in two old-growth redwood forests—Montgomery Woods State Natural Reserve (MW) and Landels-Hill Big Creek Reserve (LH)—that were part of a 16-plot network (Figure 1; Carroll *et al*. 2014, Sillett *et al*. 2015, Van Pelt *et al.* 2016). Central within the redwood distribution, MW is located 21 km northwest of Ukiah, California, USA, and 30 km from the Pacific Ocean at 39°14’N, 123°23’W, at elevation 285 m. Forest in the 1 ha MW plot was pure redwood canopy (i.e., 100% of live trees >5 cm diameter at breast height [DBH]), including 15 trees >107 m tall, in a flat valley (slope at study trees ≤1°) with plentiful access to water amidst steep slopes covered by much shorter woodland vegetation and chaparral (Van Pelt *et al*. 2016). Near the southern extreme of the redwood distribution, LH is located 61 km south of Monterey Bay, California, USA, and 2 km from the Pacific Ocean at 36°5’N, 121°35’W, at elevation 165 m. Forest in the 1 ha LH plot was redwood dominated (i.e., 63% of live trees >5 cm DBH), including trees up to 80 m tall, but contained 13% tanoak (*Notholithocarpus densiflorus* [Hook. & Arn.] Manos) and 19% California bay (*Umbellularia californica* [Hook. & Arn.] Nutt.) (Van Pelt *et al.* 2016). LH is in a steeply incised canyon that abruptly transitions to chaparral toward ridgelines. The slopes at LH study trees ranged from 26° to 70° with a mean of 51°.

Both forests are characterized by cool, wet winters and warm, dry summers. Average annual precipitation at MW and LH was 1200 mm and 800 mm, respectively, with <2% falling during summer. Average summer maximum temperatures were higher at MW than at LH (29.3°C vs. 23.1°C), and average winter minimum temperatures were lower at MW than at LH (2.0°C vs. 3.9°C). Radial growth of redwoods at both forests is sensitive to spring precipitation, summer temperature, and growing season soil moisture, with growth at LH limited earlier in the growing season than at MW (Carroll *et al*. 2014). LH has a particularly strong sensitivity to regional drought proxies compared to other redwood locations, including MW (Carroll *et al*. 2014).

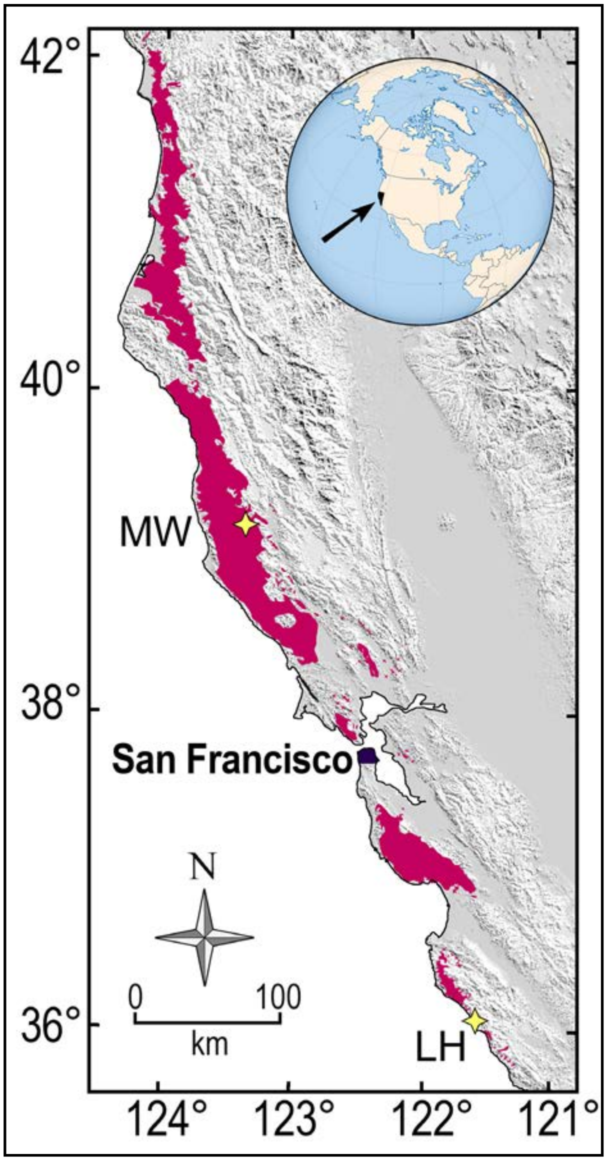

Figure 1. Geographic distribution of *Sequoia sempervirens* (shaded in pink) along the Pacific Coast of North America and study locations (yellow stars) at Montgomery Woods State Natural Reserve (MW) and Landels-Hill Big Creek Reserve (LH).

Fire Events

Three recent fires provided an opportunity to examine tree-ring responses to known events. Two low-severity to moderate-severity fires reached LH after lighting ignitions on 6 July 1985 (Gorda-Rat Fire) and 13 September 1999 (Kirk Complex Fire) (USGS 2016). We were unable to distinguish external indicators of fire between 1985 and 1999 because bark scorch could have occurred during either event. Lightning strikes on 20 June 2008 ignited 129 fires, and one of those fires, low-severity Orr Fire, reached MW. Bark of several redwoods was scorched and small patches of cambium were killed on several trees, but no known major crown dieback or tree death occurred in the plot.

Tree-Ring Measurements

During two collection periods (November 2010 and 2015 at MW, October 2011 and 2016 at LH), we sampled 42 trees and 248 series at MW, and 26 trees and 201 series at LH. Replicate (2 to 3) increment cores were obtained at breast height (BH, 1.37 m) and top of buttress (TB, 3.4 m to 12.4 m above ground at MW, and 2.5 m to 8.6 m above ground at LH) from large redwoods in each plot (34 trees 94 cm *f*-DBH to 481 cm *f*-DBH up to 112 m tall at MW, 23 trees 93 cm *f*-DBH to 334 cm *f*-DBH up to 80 m tall at LH, where *f*-DBH is the functional DBH for non-round bases using footprint analysis; Van Pelt *et al*. 2016). Two cores were generally taken at each position (BH and TB) from opposite sides and away from fire scars or abnormalities as dictated by related research goals. Eleven smaller trees (8 at MW, 3 at LH) had minimal buttressing and round trunks at BH or, if standing on a steep slope, the high point of ground. These trees each received two cores at that height. We measured bark thickness as radial distance from cambium to a tape measure wrapped around the trunk, where cambium was located by inserting a probe into the core hole. We also cored a subsample of five trees of various sizes in each plot at 10 m intervals to quantify incremental growth along the height gradient. In all trees, BH and TB cores were relatively young, often <100 years, but cores from 10 m and higher captured longer time series (up to >1000 yr; Carroll *et al*. 2014). Samples and measurements inaccessible from the ground were obtained by climbers on rope (Sillett *et al*. 2015). Crossdating and excluding cores that did not reach fire years resulted in a final sample size of 31 trees at MW and 22 trees at LH.

We prepared, surfaced, measured, and crossdated all cores utilizing published methods and tree-ring chronologies for MW and LH (Carroll *et al*. 2014), combining visual crossdating techniques of listing marker years and staggered correlation analysis in COFECHA software (Holmes 1983) for ring widths measured to 0.001 mm (WINDENDRO software v.2009b, Régent Instruments Inc., Québec, Canada). Due to the inherent difficulty of crossdating redwood, we classified years based on confidence in annual resolution (Carroll *et al*. 2014) and excluded from analysis time series and trees for which at least moderate confidence was not obtainable. In addition to measuring ring width, we examined growth rings produced during fire years and five subsequent years for anatomical indicators of this disturbance, noting occurrences of IADFs, faint latewood, resin, and scars. IADFs were distinguished by a band of latewood-like cells in the earlywood or earlywood-like cells in the latewood (De Micco *et al*. 2009). Faint latewood was visually determined by the light coloration of the latewood compared to the normal appearance of surrounding rings, similar to the identification of light rings based on hardly visible or lighter latewood due to thinner cell walls (Liang and Eckstein 2006). Occurrence of resin included both TRD noted by cell structure and infused resin noted by coloration. Fire scars were identified by ring separation, darker coloration, and subsequent large rings associated with occlusion of wounds.

Computing Growth Increments

For smaller trees with round bases, we computed radial growth simply as average ring widths of replicate cores, and for the large trees with complex bases, we combined all available information between BH and TB to express growth as trunk-level ring width. Depending on the height and complexity of buttressing, we quantified functional diameters at 1 to 7 additional heights between BH and TB. Existing equations allowed prediction of bark thickness at all heights (Sillett *et al*. 2015: Appendix C), but some trees had unusually thick or thin bark for a given diameter. We used a four-step algorithm to accommodate such tree-to-tree variation before computing growth increments. First, we averaged measured and predicted values to estimate bark thickness at BH and TB. Second, we computed a correction factor at each height by dividing estimated values by predicted values. Third, we used linear interpolation to compute correction factors for intervening measurement heights. Fourth, we multiplied correction factors by predicted values to estimate bark thickness at intervening heights. We then subtracted bark thickness from total radius (i.e., half of functional diameter) to compute wood radius. After interpolating ring widths at measurement heights between BH and TB, time series of trunk wood volume and cambium area were calculated as conic frusta starting with year of measurement and continuing via subtraction of ring widths as far back as dendrochronology allowed. We computed wood volume increment by subtracting previous values from subsequent values and then expressed radial growth (mm yr^{-1}) as the specific volume increment (wood volume increment divided by average cambium area at start and end of each year).

To quantify wood production along the vertical gradient, we computed wood volume increment for main trunks of climbed trees in each plot. Above TB, we used linear interpolation to compute ring widths at measurement heights between core samples. Below BH, we calculated ring width as the average of ring width at BH and the ring-width:wood radius ratio at BH multiplied by wood radius at lower height. This procedure accounted for wood investment in buttress formation while maintaining a consistent rate of taper change (Sillett *et al*. 2015). To visualize vertical growth patterns, we converted ring widths to cross-sectional areas at each height by sequentially subtracting wood cross-sections (e.g., 2014 cross-section subtracted from 2015 cross-section yielded 2015 ring area). Across all measurement heights for each tree, we regressed ring area against wood radius and computed the coefficient of determination (R^2) for each year. These ring-area versus radius correlations tended to be positive and strong ($R^2 > 0.9$) most years as a consequence of geometry, but when disruptions in ring taper (e.g., missing or abnormally large rings) occurred for whatever reason, R^2 values dropped precipitously. We identified anomalous years in ring-area versus radius correlation time series (hereafter, taper anomalies) by expressing each year as the difference between preceding and subsequent 5-year means, and then standardizing values by standard deviates across the full time series for each tree.

Dendroclimatic Analysis

Because climate is a major driver of ring-width variation, we accounted for climatic influence on radial growth to isolate potential fire effects. Climate variables considered for modeling radial growth included monthly and seasonal precipitation, maximum temperature, minimum temperature, Palmer Drought Severity Index (PDSI), and streamflow. We used PRISM (Parameter-elevations Regressions on Independent Slopes Model, LT81) data at 800 m resolution for precipitation and temperature (PRISM Climate Group 2016) and PRISM-based WestWide Drought Tracker data at 4 km resolution for PDSI (Western Regional Climate Center 2017). PDSI incorporates temperature and precipitation and serves as a proxy for surface soil moisture (Dai *et al*. 2004). For streamflow information, we acquired United States Geological Survey (USGS) monthly discharge data for the Russian River near Ukiah, California (USGS site 11461000) and the Big Sur River near Big Sur, California (USGS site 1143000), located within 25 km of MW and LH, respectively. To identify the most relevant climate variables influencing lower-trunk growth, we regressed average radial growth (10-tree replication: LH 1950 to 2016 and MW 1953 to 2015) at each location with monthly and seasonal climate variables. We then examined correlations between radial growth and climate, used stepwise regression in JMP 13 (SAS Institute Inc., Cary, North Carolina, USA) to select the best climate variable or variables for predicting radial growth of lower trunks, and used residuals as a metric of non-climatic effects on growth.

Detecting Past Fires

Five trees cored at 10 m intervals, two trees partially cored above TB, as well as three remnant wood samples at LH provided hundreds of years of tree-ring history to examine for fire indicators. The strong growth sensitivity to a single climate variable with a reliable long-term proxy (PDSI) and documented post-fire narrow rings (Carroll *et al*. 2014) made LH suitable for analysis beyond the time period of historical climate records. For multi-century PDSI data representative of LH, we obtained reconstructed PDSI for grid point 36 (37°30'N, 122°30'W; Cook and Krusic 2004). At LH, we created a ring index aligned with earlier methods (Carroll *et al.* 2014) and updated with new samples. We generated tree-level chronologies using only series with high crossdating confidence and ≥50-year length, then detrended in ARSTAN (Cook 1985) with a 32-year spline. Tree-level chronologies were combined into one plot-level chronology, and the standard version was used for analysis. Crossdating the earliest years of one LH remnant sample that had no comparable redwood series before 1653 was confirmed using a blue oak (*Quercus douglasii* Hook. & Arn.) chronology composed of the four nearest locations from Stahle *et al*. (2013) with data retrieved from the International Tree Ring Data Bank (NOAA 2017). We obtained remnant wood samples cut as sections from fallen redwoods on or near the plot in the same drainage.

To identify possible post-fire years, we regressed tree-ring and PDSI indices and used residuals to isolate years with lower than expected growth. We divided the period of analysis into two series based on replication (<5 trees 1540 to 1721, ≥5 trees 1722 to 2003). Years with anomalously low radial growth (residuals <2 SD below mean) in each series were then examined for anatomical indicators of fire, including the subsequent five rings.

RESULTS

Anatomical Indicators of Fire

The three fire years were frequently associated with wood anomalies, as 100 of 240 (41.7%) crossdated lower-trunk rings recorded at least one indicator (Figure 2). At the tree-level, an indicator was present for the fire year on at least one core for 48 of 75 (64%) occurrences. The 1985 fire at LH was the most impactful with 87.5% of cores and 100% of trees recording at least one indicator (Table 1). The most frequent indicator was faint latewood in the 1985 ring (65.6% of rings, Figure 2B), but faint latewood occurred on <8% of the 1999 and 2008 rings. Mean ring width in 1986 was significantly smaller when 1985 had faint latewood (0.244 mm versus 1.315 mm; $t_{26} = 4.73$, $P < 0.001$), and of 42 cores with faint latewood in 1985, 30 had a missing (i.e., locally absent) ring in 1986. IADFs noted as latewood-like cells in the earlywood corresponded with summer fires (1985 and 2008; Figure 2C and 2D), and earlywood-like cells in the latewood occurred for all three fires

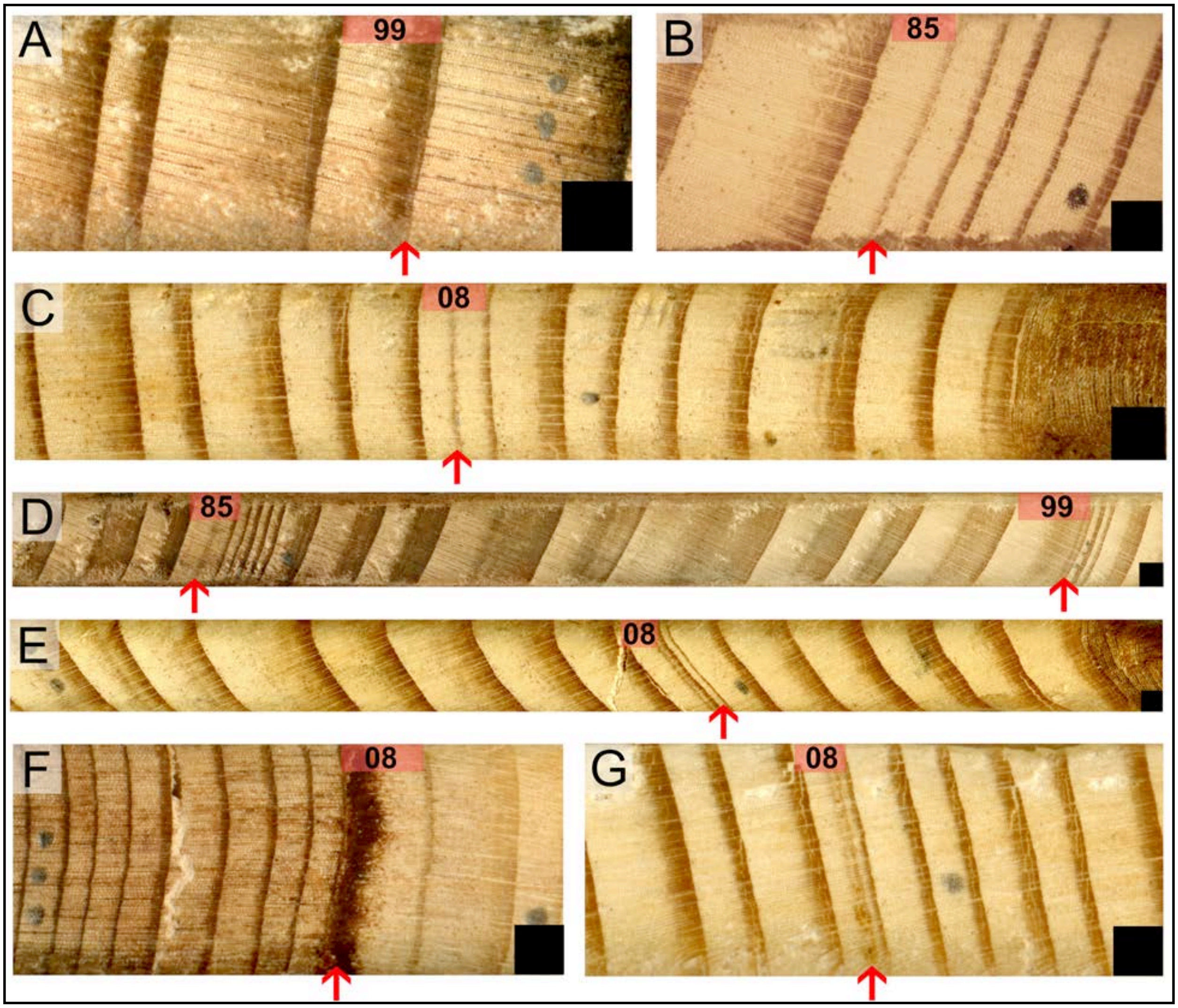

Figure 2. Anatomical indicators associated with fire years for redwoods in two old-growth forests at Montgomery Woods State Natural Reserve and Landels-Hill Big Creek Reserve. All samples from cross-dated lower-trunk cores. Growth proceeds from left to right. Red boxes span annual ring of fire years abbreviated in black text (85 = 1985, 99 = 1999, 08 = 2008). Black boxes in lower right corners cover 1 mm^2. Red arrows indicate: A) intra-annual density fluctuation (IADF) in latewood of 1999, B) faint latewood in 1985 with subsequent missing ring for 1986, C) IADF in earlywood of 2008 for June fire, D) IADF in earlywood of 1985 for July fire with reduced growth 1986 to 1989, IADF in latewood of 1999 with subsequent smaller rings for 2000 and 2001, E) post-fire narrow ring after 2008, F) infused resin in 2008, and G) traumatic resin ducts and IADF in 2008.

(Figure 2A, 2D, and 2G). Only two of 240 rings showed fire scars because our sampling avoided "catfaces." Resin occurred on ≤3.1% of lower-trunk cores for fire years (Table 1) but was the most common indicator over the subsequent five years with a maximum of eight occurrences after the 1999 fire. Growth anomalies occurred intermittently regardless of fire, with 1.2% and 2.4% of cores showing an indicator for a randomly generated year at MW and LH, respectively.

Anatomical indicators on the fire year were observed at various heights on trunks of nine climbed trees (Figure 3). Among eight trees with indicators for the fire year at or below TB, five also had indicators higher above the

Table 1. Anatomical indicators present (%) on annual ring of fire years for redwoods in two old-growth forests at Montgomery Woods State Natural Reserve (MW) and Landels-Hill Big Creek Reserve (LH). Analysis includes lower-trunk cores with crossdated fire years. Indicator tallied for trees if present on at least one core. If at least one indicator is present, it is tallied for "any indicator" category. IADF means intra-annual density fluctuation.

	Gorda-Rat Fire Jul 1985 - LH		**Kirk Complex Fire Sep 1999 - LH**		**Orr Fire Jun 2008 - MW**	
Anatomical indicators	**Cores**	**Trees**	**Cores**	**Trees**	**Cores**	**Trees**
Any indicator (%)	87.5	100	22.9	50.0	26.4	48.4
IADF (%)	37.5	59.1	15.7	31.8	17.9	35.5
Faint latewood (%)	65.6	81.8	7.1	18.2	7.5	16.1
Resin (%)	3.1	9.1	0.0	0.0	2.8	9.7
Scar (%)	0.0	0.0	1.4	4.5	0.9	3.2
	n = 64 cores, 22 trees		*n* = 70 cores, 22 trees		*n* = 106 cores, 31 trees	

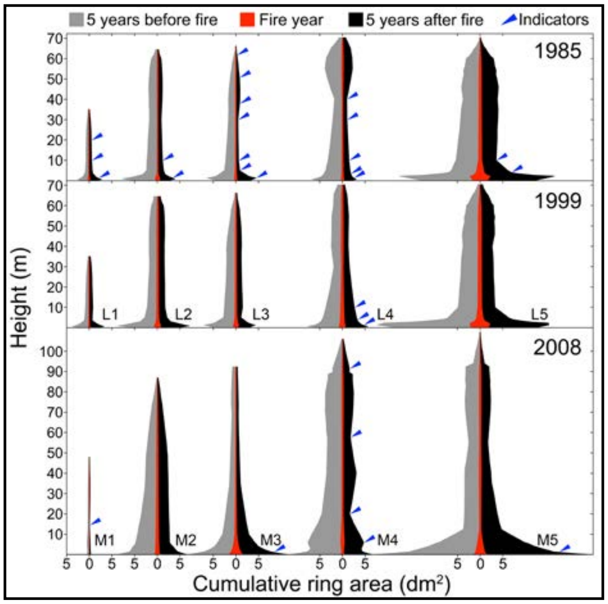

Figure 3. Ring area profiles for ten climbed trees in two locations with respect to three fires (1985 and 1999 at Landels-Hill Big Creek Reserve, 2008 at Montgomery Woods State Natural Reserve). Cumulative ring areas indicated by colors are directly proportional to trunk wood volume increments over 11 years, centered on fire year. Blue arrows show observed heights of tree-ring indicators (i.e., intra-annual density fluctuations, faint latewood, resin) during fire year. Tree name on lower right, only crossdated trees included.

ground. At LH, all five trees had indicators on the 1985 ring at or above 10 m. Tree 3 at LH had indicators on the 1985 ring at seven heights up to 61.8 m, most of which were faint latewood. Among indicators on the five rings following the 1985 fire, 31 of 43 were resin. Only one climbed tree at LH had indicators on the 1999 ring, all at or below 10 m, but all five had resin within the subsequent five years, especially 2001 (14 of 81 cores). Tree 4 at MW had indicators on the 2008 fire year at four heights up to 91.5 m, but no indicators in subsequent years.

Growth Increments

Lower-trunk radial growth decreased in the years following each fire, with trees producing some of the smallest rings since 1900 (Figure 4). At LH, radial growth plummeted after 1985 and did not recover for several years. Post-fire years 1986 to 1988 produced the smallest rings (0.60 mm to 0.70 mm) of the series, and 1986 had the largest decrease (43.2 %) in growth compared to the previous year. Post-fire year 2000 produced the seventeenth smallest ring but had the third largest decrease (37.7 %) in growth. At MW, the 2009 ring (0.83 mm) was the second smallest of the

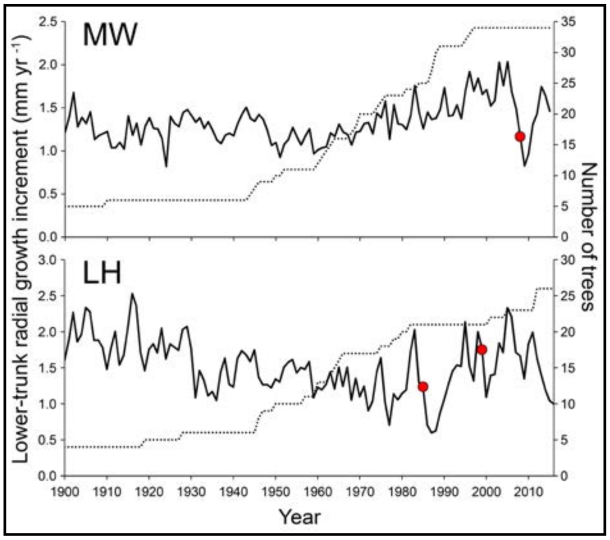

Figure 4. Lower-trunk radial growth increment and sample depth for redwoods at Montgomery Woods State Natural Reserve (MW; 1900 to 2015) and Landels-Hill Big Creek Reserve (LH; 1900 to 2016) using all crossdated cores at or below buttress. Red circles mark fires at 2008 for MW, and 1985 and 1999 for LH.

time series, behind only 1924 (0.82 mm), which had the lowest average growing season (March to October) PDSI. The year 2009 ranked twenty-sixth for PDSI, but it had the largest decrease in ring width (29.0%) compared to the previous year. These post-fire low growth rings were distinctive and easily noted during visual crossdating (Figure 2D and 2E).

As was evident with lower-trunk radial growth, whole-trunk wood volume increment of climbed trees was 26% to 35% lower for the five years after fire compared to the five years before fire (1985, $T_4 = 3.19$, $P = 0.018$; 1999, $T_4 = 3.19$, $P = 0.017$; 2008, $T_4 = 2.15$, $P = 0.049$). While the vertical pattern of wood production was similar in some trees before and after fires, other trees exhibited disruptions in ring taper. These taper anomalies were ≥2 standard deviations in trees 1 and 4 at MW, and trees 3, 4, and 5 at LH after the 1985 fire. The 1999 fire at LH caused the least disruption with only one tree (tree 3) having a taper anomaly >1 standard deviation.

Dendroclimatic Analysis

Accounting for climatic influences on lower-trunk radial growth helped to quantify fire effects. At MW, three climate variables (i.e., May PDSI, September streamflow, October precipitation) together explained 40.5% of radial growth variation, and at LH, the single predictor of mean April to August PDSI explained 42.2% of the variation (Table 2). Residual differences between measured and predicted growth were greatest in years following fire at both locations (Figure 5). At MW, radial growth was 30.4% lower than expected in 2009, and residual differences were negative until 2013. At LH, radial growth was 27.4% lower than expected in 1986, decreasing to 45.8% in 1988, and residual differences were negative until 1992, when radial growth was 40.4% higher than expected. The 1999 event showed a similar pattern with negative post-

Table 2. Equations to predict lower-trunk growth increment based on monthly climate parameters for redwoods in two old-growth forests at Montgomery Woods State Natural Reserve (MW) and Landels-Hill Big Creek Reserve (LH). Predictors (V1 to V3) followed by regression coefficients (*a* to *d*), sample size (*n*), goodness of fit (R^2), and form of equation. PDSI = Palmer Drought Severity Index, str = mean streamflow discharge, pcp = total precipitation.

Plot	V1	V2	V3	*a*	*b*	*c*	*d*	*n*	R^2	Form
MW	May PDSI	Sep str	Oct pcp	0.022	0.104	–0.001	1.234	63	0.405	$a\text{V1} + b\text{V2} + c\text{V3} + d$
LH	Apr to Aug PDSI			0.063	1.344			67	0.422	$a\text{V1} + b$

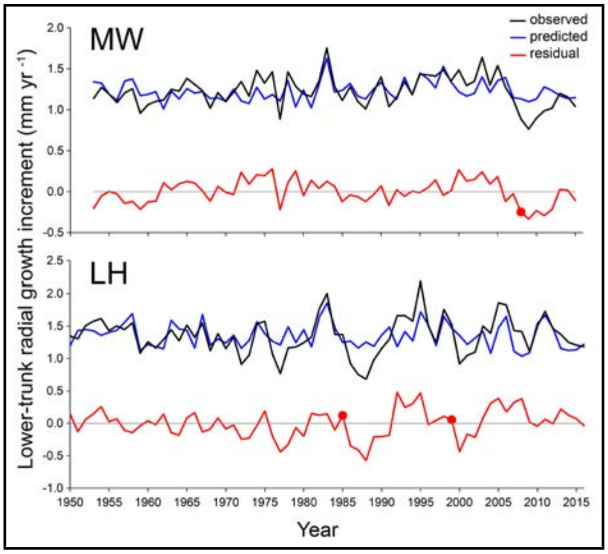

Figure 5. Lower-trunk radial growth increment for ten redwoods at Montgomery Woods State Natural Reserve (MW; 1953 to 2015) and Landels-Hill Big Creek Reserve (LH; 1950 to 2016). Black lines represent calculated growth increment using crossdated cores at or below buttress. Blue lines represent the predicted growth increment based on the strongest climate drivers. Red lines represent the residuals centered on zero. Red circles mark fires at 2008 for MW, and 1985 and 1999 for LH.

fire residual differences (i.e., radial growth 32.2% lower than expected in 2000) lasting until 2003 and followed by up to 36.7% higher than expected radial growth until 2010.

Detecting Past Fires

Linear regression of the LH ring-width index against reconstructed PDSI generated a multi-century time series of residual values to examine for evidence of fire (Figure 6). The LH ring index dated from 1540 to 2016, extending the previous LH chronology (Carroll *et al*. 2014) by 113 years. Crossdating remnant wood samples was supported by significant correlations between standardized LH and blue oak chronologies (r = 0.28, $P < 0.001$ for 1653 to 1999; r = 0.27, $P = 0.004$ for 1540 to 1652). The PDSI reconstruction explained 23.2% of ring width variation, highlighting 14 years in which radial growth was at least 2 standard deviations (SD) below the mean (Figure 6). At LH, the 1985 and 1999 fires were both identified, and 1986 had the largest residual difference between measured ring width and predicted ring width (−3.7 SD), followed by 2000 (−3.0 SD). We refined the list to eight events after combining sequential years with unusually small ring widths (e.g., 1986 and 1987). Low-growth years 1634 and 1977 were categorized as potential fire years rather than the previous year due to associated anatomical indicators. While growth releases were not used to detect past fires, the highest ring-width indices occurred in post-event windows for 1647 (3.3 SD above the mean) and 1869 (4.1 SD above the mean) (Figure 6).

In addition to the known fires, at least one anatomical indicator was observed in five of the six newly identified years and their subsequent rings (Figures 7, 8, and 9). Potential fire year 1841 and subsequent years had indicators on nine of ten trees (Figures 7 and 9D), and of the 23 indicators on subsequent rings, 17 were resin (Figure 8). Resin was the only indicator on potential fire year 1864 (4 of 40 cores on 3 trees) with resin also documented several years after the event (Figures 7, 8, and 9C). Indicators for potential fire years 1900 and 1977 were less frequent but included resin and abnormal growth for the fire year and resin for subsequent years (Figures 7 and 8). One remnant sample from outside the plot had TRD (Figure 9E) and faint latewood in the 1977 ring, and a strong band of TRD was observed in the 1634 ring of another (Figure 9F).

DISCUSSION

Redwoods growing in two old-growth forests show responses to fires in 1985, 1999, and 2008, with anomalous ring structures and changes in radial growth. While several of these features are documented in redwoods ancillary to stump-level fire scars (Brown and Swetnam 1994), we quantified indicators in

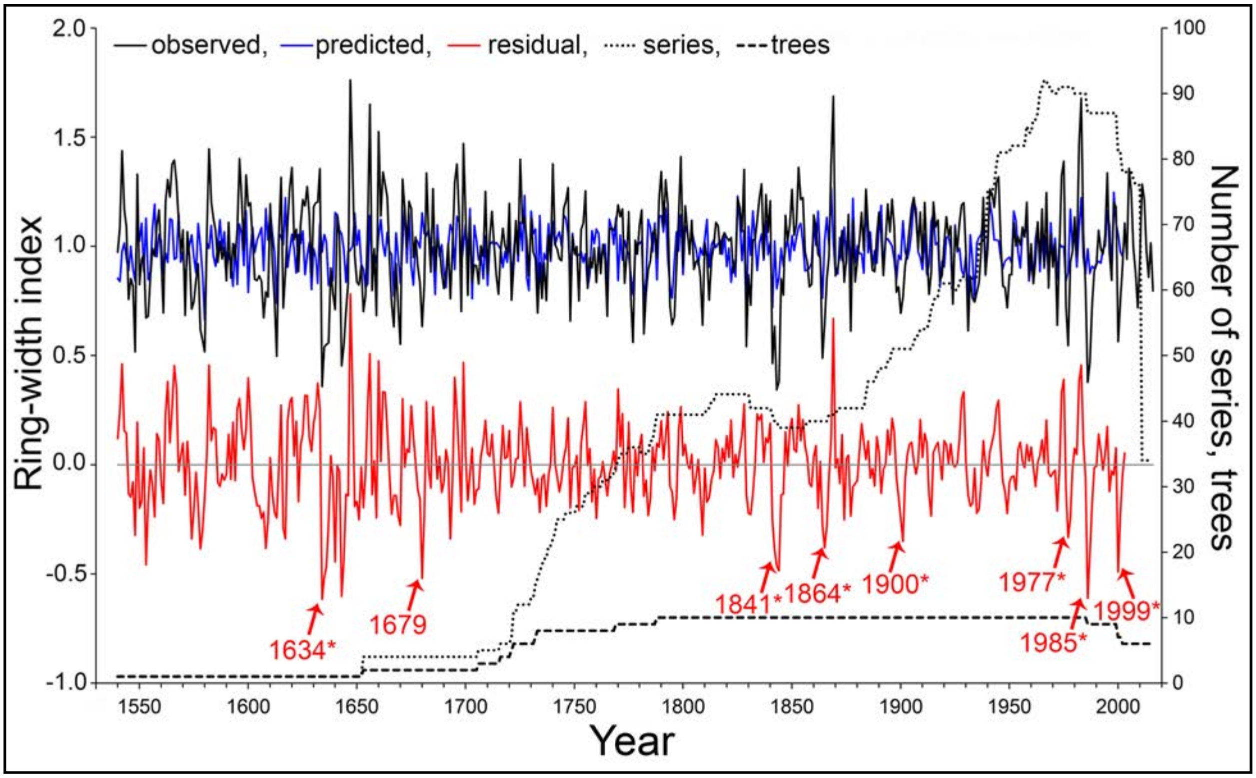

Figure 6. Ring-width index and sample depth for ten redwoods at Landels-Hill Big Creek Reserve (1540 to 2016) and potential fire years identified by post-event low growth relative to drought. Black line shows ring index from seven standing and three downed trees. Blue line shows predicted growth based on drought reconstruction. Red line shows residuals centered on zero. Red years identify potential fires and arrows point to low growth. Asterisks denote anatomical indicators observed on at least one series concurrent with event year.

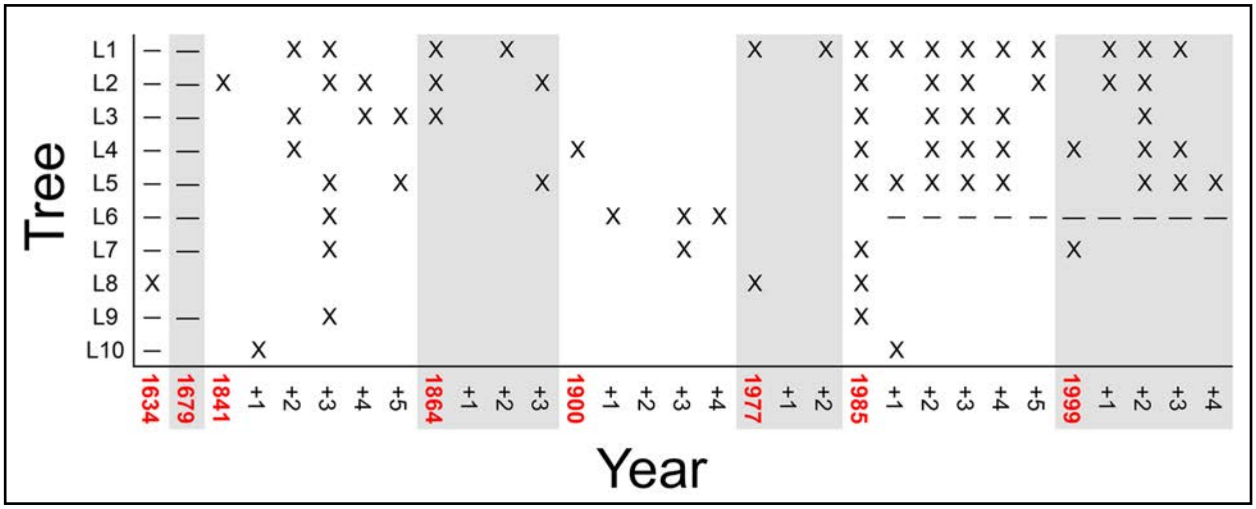

Figure 7. Presence of anatomical indicators associated with potential fire years for ten redwoods at Landels-Hill Big Creek Reserve. Potential fire years listed in red bold and identified by subsequent low radial growth relative to drought. X denotes indicator present on at least one series, blank denotes no indicators present, dash denotes year not sampled or crossdated.

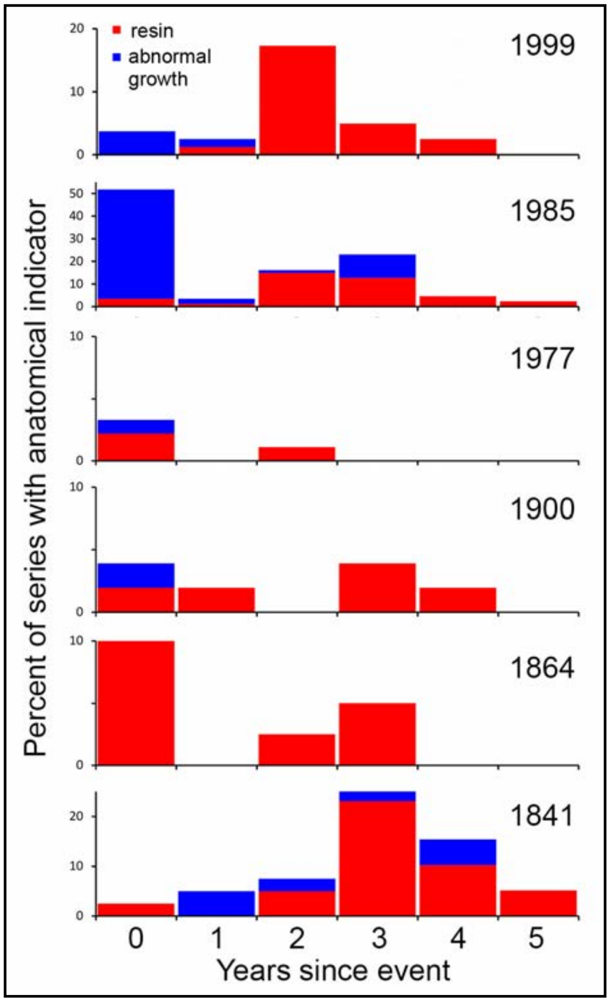

Figure 8. Percent of tree rings at Landels-Hill Big Creek Reserve with anatomical indicators for event year and five subsequent years for ten redwoods. Event year noted in upper right of each panel. Red denotes resin and blue denotes abnormal growth including intra-annual density fluctuations and faint latewood.

wood samples collected at multiple heights, considered climatic drivers of radial growth, and used these anomalies to detect potential fires over several centuries. Rather than relying on stumps and downed trees for samples, we utilized standing redwoods. This strategy provided replication needed for multi-century crossdating at the tree level and allowed living individuals to be used to supplement fire histories.

Fire triggers disruptions to normal cell formation as shown by IADFs, faint latewood, and resin. Fluctuations in earlywood (i.e., false rings) correspond with summer fires in 1985 and 2008, and demonstrate the potential for earlywood to resolve season of burn. Unlike study trees in Redwood National Park, in which double latewood occurs only with late-season fires (Brown and Swetnam 1994), IADFs in latewood follow June, July, and September fires. Faint latewood, a newly noted indicator for redwood, has similarities to light rings but is characterized only by lighter coloration of latewood without the additional component of few cell layers (Filion *et al*. 1986). Faint or thin cell-walled latewood likely corresponds with lower density (Wang *et al*. 2000), reflecting less available resources during the cell wall thickening phase. Trees can experience continued stress as narrow or missing rings often follow faint latewood and resin is produced for several years after fire. TRD in trees at Redwood National Park generally occur within one year of fire (Brown and Swetnam 1994), but also exist up to four years after fire (Swetnam 1987). IADFs and faint latewood can be attributed to several mechanisms, including defoliation, water stress, and constraining climatic conditions (Liang *et al*. 1997, De Micco *et al*. 2006, Liang and Eckstein 2006). Fire commonly occurs during drought, kills foliage, and affects water relations, so it is difficult to determine the exact cause of disrupted xylogenesis.

Heat from fires variably affects tree components, shifting the availability and allocation of resources. Post-fire reduction in radial growth points to depleted or diverted resources as trees react to damaged roots (Brown 1991, Swezy and Agee 1991), trunks (Seifert *et al*. 2017), or foliage (Douglas and Bendure 2012, Brown 2013). Trees may also be investing in basal sprouts at the expense of trunk wood production as they respond to disturbance (Brown and Swetnam 1994, Sawyer *et al*. 2000, Lazzeri-Aerts and Russell 2014,

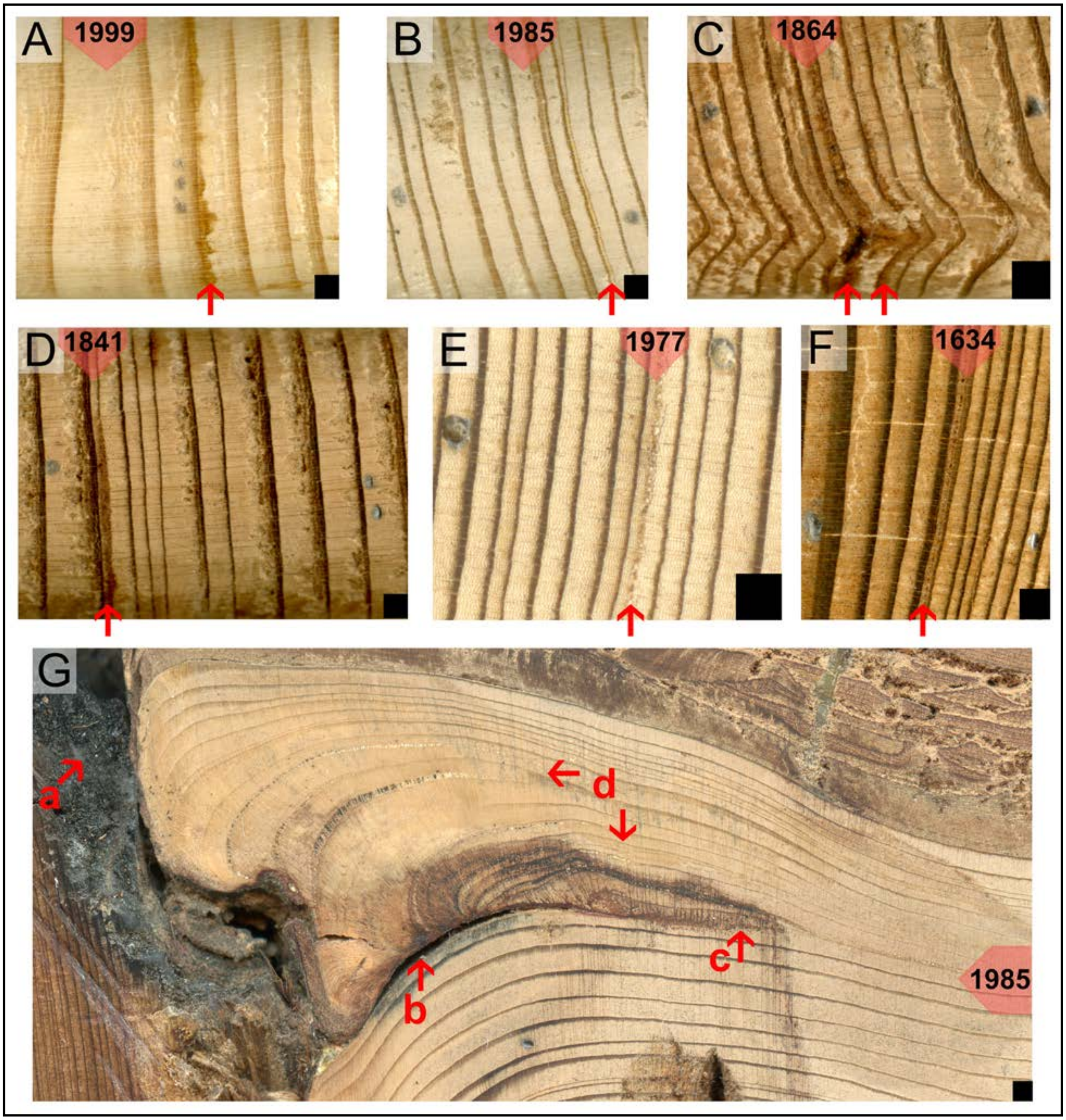

Figure 9. Anatomical indicators of known and suspected fires for redwoods at Landels-Hill Big Creek Reserve. Red boxes show year of event and red arrows point to indicators. Black boxes in lower right corners cover 1 mm^2. Growth proceeds from left to right for A to F, and bottom to top for G. A) Traumatic resin ducts (TRD) and infused resin in the earlywood of 2001 at 70 m; B) TRD in 1988 at 40 m; C) TRD and infused resin in the latewood of 1864 and earlywood of 1866 at 10 m; D) TRD in the latewood of 1841 at 40 m; E) TRD in the latewood of 1977 at 3 m; F) TRD in the earlywood of 1634 at 3 m for remnant; and G) scar from 1985 fire showing a) char, b) ring separation, c) mid-ring scar, d) TRD and discolored wood for subsequent growth rings.

O'Hara *et al*. 2017). Basal sprouting in redwood can be triggered by fire, and ages of the resulting reiterated trunks approximate fire dates (Abbott 1987, Stuart 1987). Investment in sprouting may partially explain why redwood shows initial post-fire growth decreases, even in low-severity to moderate-severity fires, while its closest relative, the non-sprouting giant sequoia, expresses growth releases (Brown *et al*. 1992, Mutch and Swetnam 1995). Increased radial growth following suppressions for the 1985 and 1999 fires suggests a return on investment after trees rebuild their capacity and potentially benefit from neighboring tree injury or mortality. Such patterns may reflect recovery and crown optimization by redwoods after disturbance (Van Pelt *et al.* 2016).

As forests burn, the physiological responses of trees to stress or injury result from a combination of simultaneous processes, and fire behavior can vary from tree to tree. More frequent and robust indicators of the 1985 event suggest that fire severity and intensity affect tree responses. Post-fire measurements of char height, crown scorch, tree mortality, basal sprouting, and fire severity (e.g., Ramage *et al*. 2010, Lazzeri-Aerts and Russell 2014) coupled with increment cores collected several years later from standing redwoods could link growth and anatomical indicators to specific drivers. Although tree size may influence responsiveness to fire due to bark thickness (Sillett *et al*. 2015), epicormic sprouting (Abbott 1987), and ability to survive fire (Ramage *et al*. 2010, Douglas and Bendure 2012), no size-related trend in fire indicators is evident in this study of trees 93 cm *f*-DBH to 481 cm *f*-DBH. While individuals show varying degrees of radial growth and wood anatomy effects following the MW and LH events, sampling trees regardless of external signs of fire reliably capture tree-ring indicators when viewed in aggregate.

To further resolve redwood fire histories, we applied a detection method applicable to standing trees, broadening the scope of individuals and forests available for study. Non-climatic growth suppression and anatomical indicators left a fingerprint in the tree-ring history revealing five additional events at LH. Since disturbances other than fire also cause reduced radial growth and atypical wood anatomy (Stoffel and Bollschweiler 2008), these dates isolate potential fire years and would ideally be used in combination with fire scars to document spatial extent. The inclusion of two samples outside of the plot provided evidence of the July 1977 Marble Cone Fire, which burned the nearby Ventana Wilderness. In 1841, fires burned forests in northern and central California (Skinner *et al*. 2009), and we infer that this regional event extends to the Big Sur coast. Declining sample depth limits the interpretation of results prior to the 1700s. The relationship between radial increment and fire should be considered if climate reconstructions are generated from redwoods. Reconstructions are likely for southern locations near LH, where ring widths show strong sensitivities to drought (Carroll *et al*. 2014) and crossdated chronologies now extend to 1540.

Using anatomical and growth indicators captured by increment cores from standing trees provides a valuable tool for better resolving fire histories in the redwood region. A complementary methodology sampling both fire-scarred stumps and non-scar indicators from living trees would help to crossdate basal scars, further ascertain the applicability of the non-scar indicators (e.g., prior to fire-exclusion fuel buildups, under varying fire severities and seasons), and better quantify fire extent in redwood forests. A more robust understanding of redwood's fire regime remains a goal for improved conservation (Varner and Jules 2017) of the 7.1 % of redwood forests that are large and complex (Cowan *et al*. 2017), as well as for promoting old-growth characteristics in young redwood forests (Engber *et al*. 2017). As we continue to expand the network of crossdated redwood tree-ring records (Carroll *et al*. 2017), we will utilize these methods to understand the role of fire in redwood forests.

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