CHARACTERIZING TREE MORTALITY AFTER EXTREME DROUGHT AND INSECT OUTBREAKS IN THE SOUTHERN SIERRA NEVADA

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Abstract—The interplay of past management practices, higher temperatures, extended drought, and insect outbreaks has resulted in unprecedented levels of tree mortality across the southern Sierra Nevada Mountains of California. To characterize patterns in tree mortality, we collected repeated forest measurements on 255 variable-radius plots during 2015 and 2016. From initial measurements in spring 2015, sugar pine (*Pinus lambertiana*) and ponderosa pine (*P. ponderosa*) mortality increased from 30 percent to 80 percent by summer 2016. Incense cedar (*Calocedrus decurrens*) mortality remained relatively stable in 2015 but increased to 40 percent in summer 2016. There were positive relationships for live crown ratios and survivorship for both sugar pine and white fir (*Abies concolor*). In addition, there was a positive effect of diameter on survivorship for ponderosa pine in spring 2015; however, this relationship was reversed in summer 2016. Our results indicate that the effects of this mortality event were variable among species with initial survivorship positively related to tree size.

INTRODUCTION

In recent years, significant drought-induced tree mortality has occurred throughout the United States (Bendixsen and others 2015, Hember and others 2016, Luce and others 2016). Warmer and drier environments, exemplified by “hotter droughts” (Allen and others 2015), can impact trees through greater metabolic demand, reduced carbon fixation, and increased desiccation and cavitation (Luce and others 2016). Between 2012 and 2017, California experienced a record setting, extreme drought event. In 2015, snow pack was only 5 percent of the historical average due to record high temperatures from January to March (Belmecheri and others 2016). Changes in winter weather conditions such as more precipitation falling as rain (Klos and others 2014, Pierce and others 2008), or earlier melting (Cayan and others 2001, Luce and others 2014, Stewart and others 2005), results in a longer dry season in Mediterranean-type climates subsequently increasing the impacts of reduced annual rainfall (Barnett and others 2005) and increased water deficit (Thorne and others 2015). This recent drought event has resulted in an unprecedented level of tree mortality across the Sierra Nevada Mountains with an estimated loss of 102 million trees in California (USDA Office of Communications 2016). Determining the scope and scale of this mortality event is important for informing future silvicultural implementation and understanding the impact of past management practices.

In the southern Sierra Nevada Mountains of California, fire suppression and timber harvests have caused an increase in the density and extent of small diameter, shade-tolerant species from historic averages (McIntyre and others 2015, Stephens and others 2015). The resulting increase in forest biomass and homogeneity couples with warmer temperatures and extended drought to increase the likelihood of insect outbreaks exceeding natural population thresholds from the scale of trees to entire landscapes (Millar and Stephenson 2015, Raffa and others 2008). In addition, high ambient ozone (O_3) concentrations and elevated nitrogen (N) deposition have also been implicated in a fundamental loss in tree vigor and eventual forest decline (Paoletti and others 2009), and the southern Sierra Nevadas have among the highest exposure indices (Cisneros and others 2010). These combined factors have led to severe canopy moisture stress and epidemic levels of insect outbreaks and subsequent tree mortality (Asner and others 2016).

Bark beetles (Curculionidae: Scolytinae) are major disturbance agents in western forests with a larger spatial impact than forest fires (Hicke and others 2016). Trees under drought stress have reduced defenses to beetle attack and drought can increase the occurrence of different beetle species erupting simultaneously, impacting many tree species (Raffa and others 2005). The magnitude of bark beetle outbreaks has increased

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and expanded in recent years (Raffa and others 2008) compared to our knowledge of their historic frequency, severity, location, and extent (Logan and others 2003, Logan and Powell 2001). Bark beetles can act as an integral agent of natural ecological processes, substantially altering forest structure, composition, and function. However, they can also be a major source of economic loss and a challenge to natural resource policy by altering large-scale biogeophysical processes. Outbreaks may also provide valuable insights into environmental threats arising from anthropogenic change (Kurz and others 2008, Raffa and others 2008).

By 2014, bark beetle-induced mortality was evident on ponderosa (*Pinus ponderosa*) and sugar pine (*P. lambertiana*) at lower elevations (~ 4,000 feet). The goal of this study was to determine the impact of drought and insect mortality on forest stand structure and composition. The objectives of this study were to determine 1) survivorship by species over time and 2) the effect of mortality on tree size. We hypothesized that 1) pine species would have higher levels of mortality than other species due to the impact of drought coupled with bark beetle outbreaks and 2) larger diameter trees with greater live crown ratios would have higher survivorship due to deeper root systems and larger carbon stores.

MATERIALS AND METHODS

Study Site

The study took place on the High Sierra Ranger District of the Sierra National Forest within the Dinkey Collaborative Forest Landscape Restoration Project (CFLRP) boundary (fig. 1). The Sierra National Forest is located in the southern Sierra Nevada Mountain range of California. The Dinkey CFLRP is located approximately 30 miles east of Fresno, CA. The landscape-level collaborative project was established in 2010, was one of the first projects funded by Title IV of the Omnibus Public Land Management Act of 2009, and lies entirely within the High Sierra Ranger District (Schultz and others 2012). Climate in this area is characterized as montane Mediterranean, with warm, dry summers and cool, wet winters. Most precipitation falls from October to April with 70 percent falling as snow (Bales and others 2011). Soils are in the Gerle-Cagwin families association (NRCS 2009).

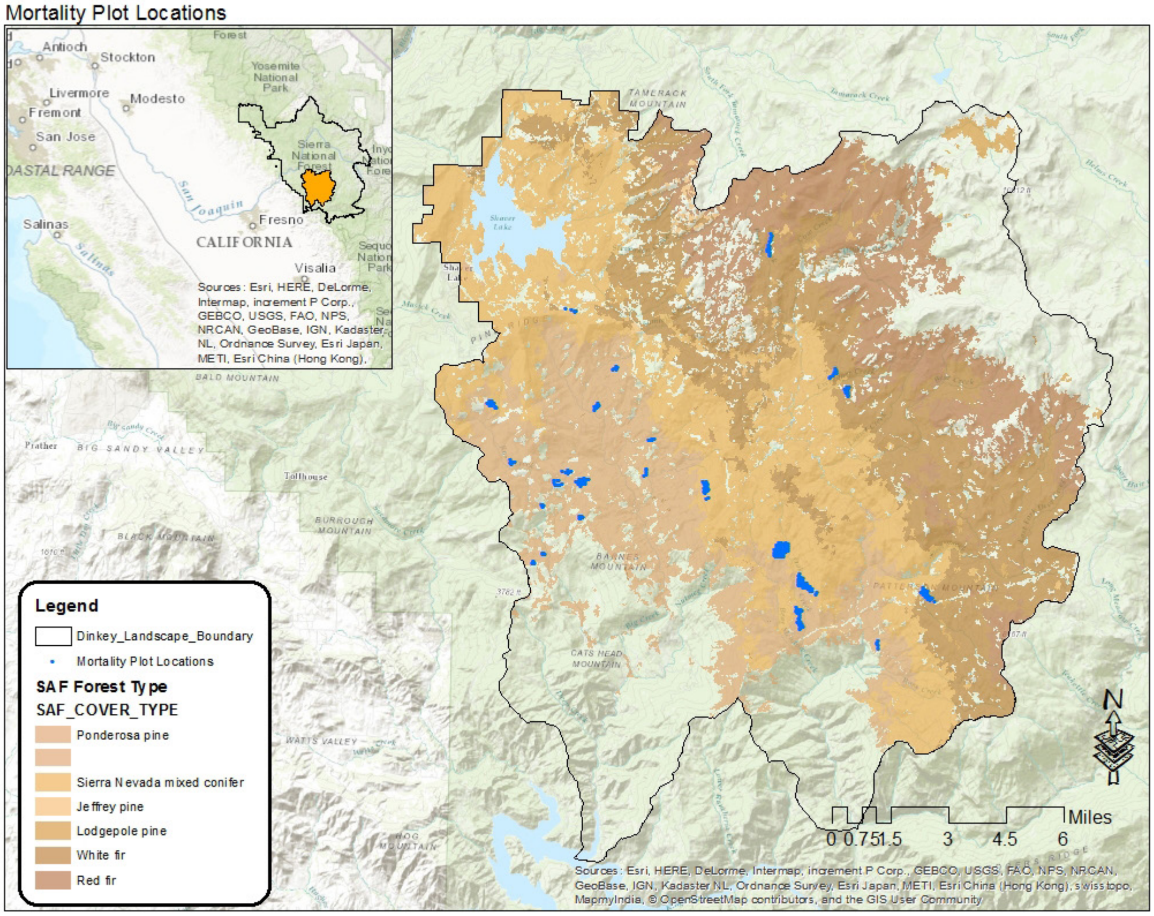

Figure 1—Plot locations on the Sierra National Forest High Sierra Ranger District within the Dinkey Collaborative Forest Landscape Restoration Project (CFLRP) boundary by Society of American Foresters (SAF) cover type.

Plot locations were selected within the Dinkey CFLRP to inform the collaborative planning process for project development and restoration activities as the impact of drought and beetle-related mortality increased across the landscape. To assess our objectives, we established plots outside any recent or active management areas, stratified by forest type, and observed mortality classes based on 2015 aerial detection surveys (ADS). We stratified the ADS into 5 mortality classes (low to very high) based upon dead trees per acre. We limited plot selection to the elevational range of ponderosa pine and mixed conifer zones and stratified by vegetation type, elevational zone, and mortality class. This process identified 25 polygons for measurement with polygons ranging in size from 1 to 10 acres. A randomly placed grid identified plot locations within each of the polygons. This process yielded 255 plots.

Measurements

In the spring of 2015 (SP15), 255 variable-radius plots were established using a 40-factor prism. We permanently tagged trees >5 inches in diameter at breast height (DBH) that were considered "in" the variable-radius plots and recorded each for DBH (inches), height (feet), species, status (dead or alive), and live crown ratio (LCR; percent). Additionally, we established an 11.8-foot offset radius sapling plot to permanently tag and record saplings between 1 and 4.9 inches in DBH. We repeated the measurements in the summer of 2015 (SM15) and the summer of 2016 (SM16).

Data Analyses

Due to relatively small sample sizes, we excluded lodgepole pine (*P. contorta*), Jeffrey pine (*P. jeffreyi*), and canyon live oak (*Quercus chrysolepis*) from the statistical analyses. To assess our first objective, we compared percent survival by species, time (SP15, SM15, and SM16), and their interaction across the three time periods using a repeated measures analysis of variance (ANOVA). Change in overall density (trees per acre) and density by species across the three time periods was analyzed using a one-way ANOVA. To assess our second objective, the probability of survival in relation to DBH and LCR were analyzed by species using logistic regression with a binary response variable for survivorship (0 dead, 1 alive) for each measurement time using GLIMMIX (SAS® 9.1.3 SAS Institute Inc., Cary, NC). Individual tree was nested within plot as a random factor in the model. Data are reported as means and standard errors of the mean. Where necessary, data where transformed prior to analysis or distributions were transformed within the GLIMMIX model, but values are reported in original scale to aid interpretability. Each *p*-value less than 0.05 was considered evidence of a significant difference.

RESULTS AND DISCUSSION

Extended drought and increasing temperatures have been implicated for large-scale mortality events in the Sierra Nevada previously (Guarín and Taylor 2005). Drought, pollution, and high tree density have been implicated in similar drought- and insect-related mortality events in southern California (Paoletti and others 2009). Increases in the frequency of drought-related mortality are often associated with below average moisture levels that occur over multiple, consecutive years (Guarín and Taylor 2005). In our study, a total of 1,683 trees representing nine species were measured (table 1), and live tree density decreased across the three time periods ($F = 5.17$; $p < 0.01$). Average tree density per acre was 209 ± 15 trees per acre in SP15. In SM15, density remained relatively stable to SP15 at 190 ± 15 trees per acre, however in SM16 the density decreased significantly to 145 ± 15 trees per acre. Ponderosa pine

Table 1—Descriptive statistics of the measurements taken across 255 repeatedly measured plots on the Sierra National Forest by species

Species	Scientific name	n	DBH inches	Height feet
White fir	*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.	526	22.5 ± 12.5	89 ± 42
California red fir	*Abies magnifica* A. Murray bis	50	26.1 ± 18.7	93 ± 61
Incense cedar	*Calocedrus decurrens* (Torr.) Florin	419	14.6 ± 12.9	49 ± 36
Lodgepole pine	*Pinus contorta* Douglas ex Loudon	19	18.2 ± 11.0	77 ± 44
Jeffery pine	*Pinus jeffreyi* Balf.	6	35.2 ± 19.7	107 ± 51
Sugar pine	*Pinus lambertiana* Douglas	117	31.5 ± 16.0	112 ± 47
Ponderosa pine	*Pinus ponderosa* Lawson & C. Lawson	416	20.7 ± 12.8	87 ± 49
Canyon live oak	*Quercus chrysolepis* Liebm.	39	5.3 ± 5.8	21 ± 13
California black oak	*Quercus kelloggii* Newberry	91	19.5 ± 10.7	50 ± 23

n = number sampled.

Diameter at breast height (DBH) and height are averages.

decreased in density only a few months after the initial measurement in SP15, with continued reductions in 2016. White fir density remained relatively stable in SP15 and SM15, however by SM16 the density decreased significantly (table 2). Although there were decreases in the densities of incense cedar (*Calocedrus decurrens*) and sugar pine across the three time periods, these decreases were not significant.

Survivorship

Survivorship was significant by time ($F = 144.6$; $p < 0.01$), species ($F = 48.8$; $p < 0.01$), and their interaction ($F = 30.3$; $p < 0.01$). The interaction was due to the variable individual response of different species across the three time periods (fig. 2). In particular, survivorship decreased for white fir ($F = 194.8$; $p < 0.01$), incense cedar ($F = 40.5$; $p < 0.01$), sugar pine ($F = 60.3$; $p < 0.01$), and ponderosa pine ($F = 347.9$; $p < 0.01$) over time, but remained stable for California red fir (*A. magnifica*; $F = 0.29$; $p = 0.75$) and California black oak (*Q. kelloggii*; $F = 0.16$; $p = 0.85$). Species-specific responses likely reflect individual tolerances to both abiotic (e.g., drought) and biotic (e.g., insects) factors. The impact of drought predisposes many conifers to insect attack, resulting in higher levels of episodic tree mortality owing to declines in host defenses, increases in host suitability, and increased incidence of insect mass attacks (Mattson and Haack 1987). In comparison, the higher survivorship rates observed in California black oak may reflect its lower susceptibility to insect attack and relatively minor impact of damaging insects, such as the wood-boring carpenterworm (*Prionoxystus robiniae*) or defoliating California oakworm (*Phryganidia californica*) (McDonald 1990), and relatively lower sensitivity to increases in

Table 2—Change in stand density (trees per acre) by species over the three measurement periods

Species	SP15	SM15	SM16	
White fir	103 ± 10^{a}	99 ± 10^{a}	65 ± 10^{b}	$F = 7.3$; $p < 0.01$
California red fir	187 ± 64	187 ± 64	186 ± 64	$F = 0.01$; $p = 0.99$
Incense cedar	138 ± 16	135 ± 16	110 ± 16	$F = 0.92$; $p = 0.40$
Sugar pine	26 ± 6	20 ± 6	18 ± 6	$F = 0.47$; $p = 0.62$
Ponderosa pine	84 ± 10^{a}	61 ± 10^{ab}	39 ± 10^{b}	$F = 5.48$; $p < 0.01$
California black oak	58 ± 12	54 ± 12	54 ± 12	$F = 0.04$; $p = 0.96$

SP15 = spring 2015; SM15 = summer 2015; SM16 - summer 2016.

Differences in superscript letters indicate a significant difference between measurement periods within species.

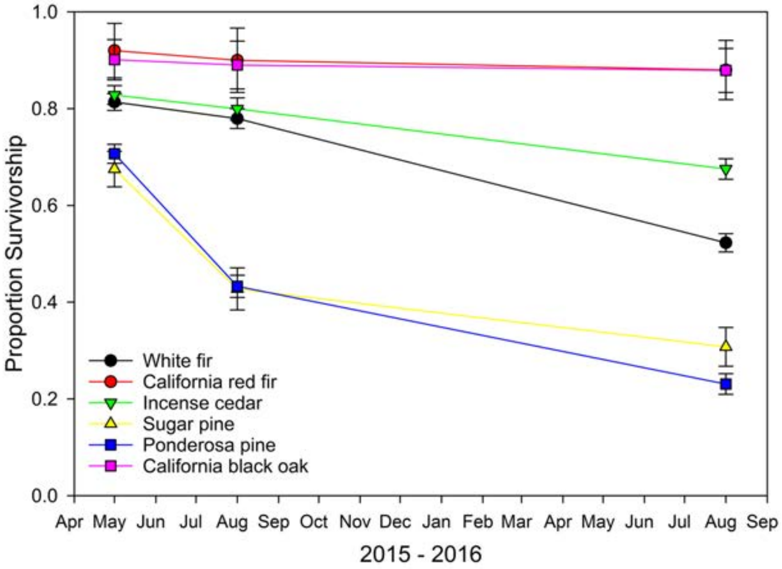

Figure 2—Proportion of survivorship by species during the three measurement periods from spring 2015 to summer 2016 on the Sierra National Forest.

climatic water deficit compared to conifers (McIntyre and others 2015). Previous studies have related drought-induced mortality to insect and pathogen activity coupled with climate change (Logan and others 2003, Millar and Stephenson 2015). Guarín and Taylor (2005) noted that during a drought-related mortality event in California, 62 percent of dead ponderosa pine and 67 percent of incense cedar had beetle galleries or pitch tubes, and 15 percent of dead incense cedar was visibly infected by cedar rust (*Gymnosporanngium libocedri*).

The disproportional impact on pine species from the interaction of drought and bark beetles may have severe ecological consequences as it accelerates a transition from fire-tolerant pine species to fire-intolerant and shade-tolerant white fir and incense cedar following historical logging and fire exclusion beginning in the late 1800s. However, white fir and incense cedar were impacted by the mortality event. White fir survivorship decreased from 88 percent in SP15 to 52 percent by SM16. Incense cedar remained relatively stable with 80 percent surviving throughout 2015 and 68 percent surviving in SM16. The impact to pine species was more dramatic. Sugar pine survivorship was reduced from 68 percent in SP15 to 31 percent in SM16. Ponderosa pine survivorship was reduced from 71 percent in SP15 to 23 percent in SM16. Although the impacts of this mortality event may help to reduce stem densities to levels within the natural range of variation (NRV) prior to fire exclusion, the impact was greatest in large diameter individuals, especially pines (data not reported here), resulting in a significant shift in historic forest stand structure and composition compared to current conditions. This shift will widen the existing deficit of large pines and other conifers in forest landscapes of the southern Sierra Nevada (e.g., Stephens and others 2015).

For several species, the probability of survival could be predicted by either DBH or LCR over the three measurement periods (table 3). Diameter at breast height was significant for determining the probability of survival for incense cedar and California black oak in all three measurement periods (fig. 3; right panel). It was also significant for determining the survival of ponderosa pine in SP15 and SM16, however the relationship of DBH and survivorship was reversed. This reversal indicates the greater survivorship of smaller diameter understory ponderosa pine in some areas compared with larger diameter trees. Live crown ratio was significant for determining the probability of survival for white fir and

Table 3—Species-specific parameter estimates using diameter at breast height (DBH) and live crown ratio (LCR) for logistic binary regression models for each measurement time

		DBH estimates			***LCR estimates***		
Species	**Time**	**Intercept**	**Estimate**		**Intercept**	**Estimate**	
White fir	SP15	1.6068	-0.0059	F = 0.5; *p* = 0.50	0.0414	0.2621	F = 2.29; *p* = 0.13
	SM15	1.4291	-0.0073	F = 0.8; *p* = 0.37	**0.1841**	**0.0962**	**F = 19.0; *p* <0.01**
	SM16	-0.0398	0.0059	F = 0.7; *p* = 0.40	**-0.7955**	**0.0343**	**F = 31.8; *p* <0.01**
California red fir	SP15	1.7691	0.0310	F = 0.8; *p* = 0.37		-	
	SM15	1.9643	0.0097	F = 0.1; *p* = 0.72	2.3970	0.0288	F = 0.3; *p* = 0.59
	SM16	1.7793	0.0088	F = 0.1; *p* = 0.72	2.9975	0.0019	F = 0.0; *p* = 0.97
Incense cedar	SP15	**0.4574**	**0.1108**	**F = 32.2; *p* <0.01**	3.9686	0.0386	F = 0.7; *p* = 0.40
	SM15	**0.4400**	**0.0855**	**F = 29.5; *p* <0.01**	2.7083	0.0132	F = 0.8; *p* = 0.37
	SM16	**-0.0185**	**0.0589**	**F = 29.3; *p* <0.01**	**0.8242**	**0.0190**	**F = 6.3; *p* = 0.01**
Sugar pine	SP15	0.5337	0.0064	F = 0.3; *p* = 0.61	**-1.7661**	**0.0532**	**F = 10.0; *p* <0.01**
	SM15	-0.6355	0.0108	F = 0.8; *p* = 0.36		Did not converge	
	SM16	-0.8653	0.0017	F = 0.0; *p* = 0.89	**-2.1345**	**0.0426**	**F = 7.9; *p* <0.01**
Ponderosa pine	SP15	**0.5156**	**0.0182**	**F = 4.5; *p* = 0.04**	2.9985	0.0569	F = 1.6; *p* = 0.20
	SM15	-0.2382	-0.0016	F = 0.0; *p* = 0.83	0.2730	0.0048	F = 0.5; *p* = 0.49
	SM16	**-0.7850**	**-0.0213**	**F = 5.1; *p* = 0.02**	-0.5114	-0.0064	F = 0.78; *p* = 0.38
California black oak	SP15	**0.5326**	**0.1088**	**F = 4.8; *p* = 0.03**		Did not converge	
	SM15	**0.3335**	**0.1145**	**F = 5.5; *p* = 0.02**		Did not converge	
	SM16	**0.5288**	**0.0917**	**F = 4.6; *p* = 0.04**		Did not converge	

Significant (alpha of 0.05) GLIMMIX model effects indicated in **bold.**

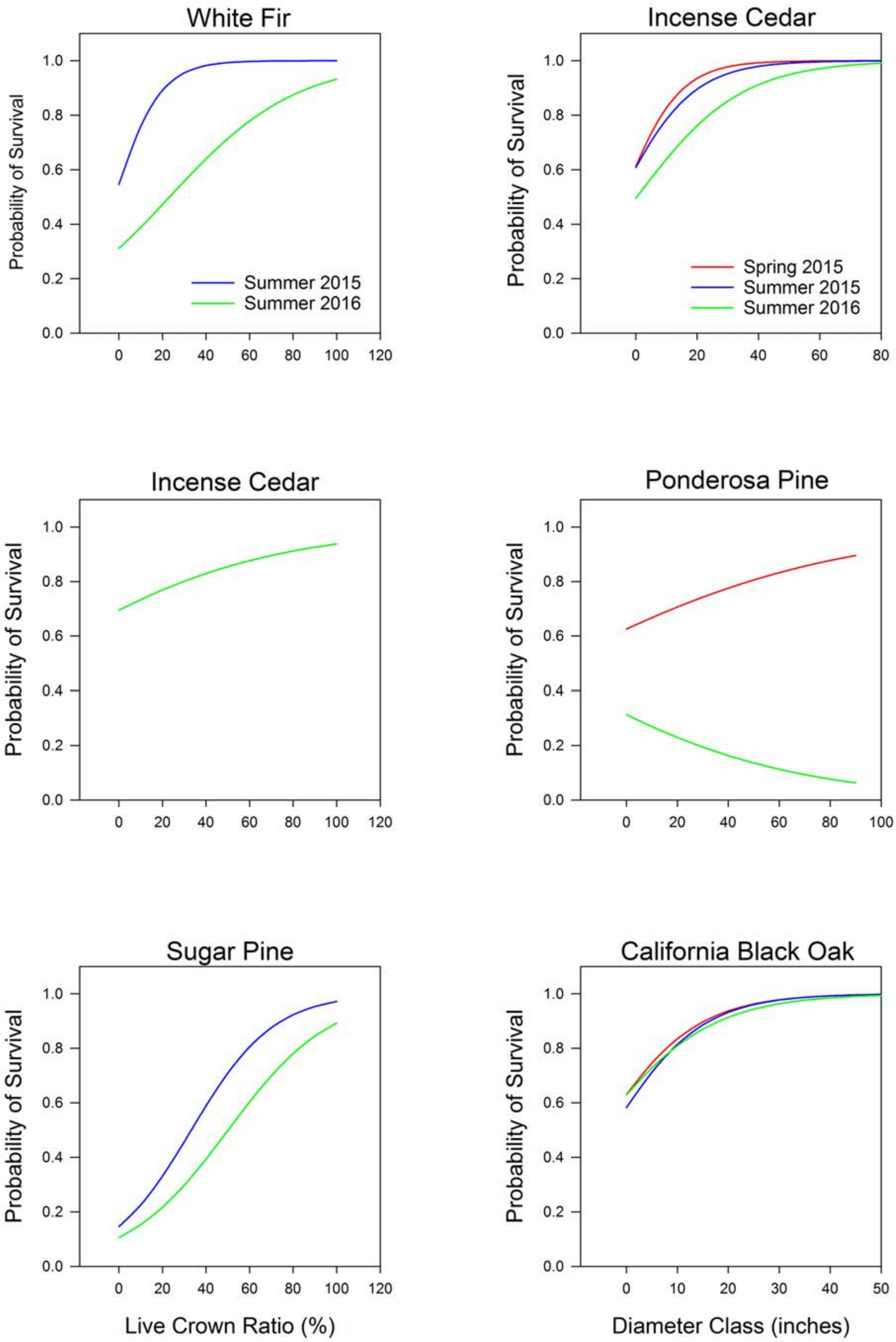

Figure 3—The probability of survival by live crown ratio (LCR in percent; left panel) and diameter at breast height (DBH in inches; right panel) by species and measurement time (red line = spring 2015; blue line = summer 2015; green line = summer 2016).

sugar pine in SM15 and SM16 (fig. 3; left panel). Live crown ratio was also significant for determining the probability of survival for incense cedar in SM16.

Management Implications

Lessons for managers are that treatments that increase tree diameter and LCR may provide for increased survivorship during periods of drought. However, during periods of extended or extreme drought and epidemic insect outbreaks, other landscape-level ecological factors can negate individual tree characteristics. Proactive silvicultural manipulations, such as thinning, may reduce stand-level insect eruptions because they can increase the defensive capacity of a tree by ameliorating the effects of drought, but may be ineffective at reducing landscape-scale eruptions (Fettig and others 2007). Once landscape level thresholds have been breached, no known feasible management action will stop an eruption until hosts are depleted or unseasonably cold temperatures occur over large areas (Raffa and others 2008).

The dramatic loss of mature pine species will require restoration efforts to reforest and promote the ecological conditions necessary for pine to be productive in this landscape. Providing increased growing space for individual trees by increasing stem diameter and maintaining large crowns may help to reduce tree stress. Promoting these characteristics to increase tree vigor has been found to be important for reducing the effects of drought- and insect-related mortality in Mediterranean-type ecosystems (Kolb and others 2016, O'Brien and others 2017). Incorporating a mixed-species approach that includes both pine and other species such as California black oak that have proved more resistant to extreme drought may help increase forest resilience. This will include planting and efforts to control competing vegetation, including shrubs and abundant incense cedar and white fir regeneration, which may include the use of mastication, herbicide, and re-establishing frequent, low intensity fire regime where appropriate. Landscapes that are vertically and structurally heterogeneous including a mixture of species and size classes are likely to result in greater forest resilience. However, as our study shows, individual tree traits such as large DBH and LCR show limited improved survivorship during landscape-level disturbances.

CONCLUSIONS

Our results indicate that trees with larger diameters and LCRs had the greatest initial probability of survival. However, as bark beetle populations reached unprecedented levels, large diameter ponderosa pine were negatively impacted, and mortality was temporally variable among species. In comparison, patterns of high survivorship and low mortality in California black oak suggest that this species and others (e.g., canyon live oak) may be favored over conifers at low to mid elevations of the Sierra Nevada with increasing climatic water deficit associated with warming climate (McIntyre and others 2015). New silvicultural regimes may be needed in this era of megadisturbances to support the health and vitality of future forests (Millar and Stephenson 2015).

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