

Bark Beetle Demography in Sierra Nevada Mixed Conifer: Variability and Influencing Factors

Walker RF*, Swim SL, Fecko RM, Johnson DW and Miller WW

Department of Natural Resources and Environmental Science, University of Nevada, Reno, Nevada, USA

Abstract

Multiple forest health variables were examined in an eastern Sierra Nevada mixed conifer stand, principal among them bark beetle demography. As indicated by pitch tube counts, California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.), the predominant species, was colonized prodigiously compared to Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.) and sugar pine (*Pinus lambertiana* Dougl.). Across host species, pitch tube abundance was positively related to white fir prevalence and negatively related to tree species diversity. Bark beetles preferentially attacked trees of small to medium DBH in white fir and sugar pine. Attack intensity in small Jeffrey pine was positively correlated with stand basal area and biomass and that in sugar pine of medium size was positively correlated with basal area also. Minor mistletoe infestations were detected in white fir along with incense-cedar (*Libocedrus decurrens* Torr.) and California red fir (*Abies magnifica* A. Murr.), with bark beetle colonization in the smallest and largest white fir positively related to the percentage of this fir thus infested. Mortality in white fir and Jeffrey pine irrespective of size was positively correlated with the pitch tube count in the largest white fir regarding the former and with total tree count regarding the latter.

Keywords: Forest health; Bark beetles; Dwarf mistletoe; White fir; Jeffrey pine; Sugar pine; Fir engraver; Jeffrey pine beetle; Mountain pine beetle

Introduction

Prevalent among vegetative communities at the mid elevations of the Sierra Nevada is a mixed conifer forest cover type that includes among its variants one on the eastern slopes featuring California white fir, Jeffrey pine, incense-cedar, and sugar pine along with occasional California red fir where cold air drainages prevail [1]. The silvics of these species differ markedly, perhaps most prominently in their tolerance of shade with white fir the most tolerant overall although it is presumed to be only marginally more so than red fir, Jeffrey pine the least tolerant, and incense-cedar and sugar pine considered to be intermediate regarding this characteristic [2]. The tolerance classification for white fir is reflected in its ability to regenerate profusely and persist in the shade of an overstory canopy to greater extent than the other constituents in this cover type, resulting in a propensity for it to increasingly dominate the composition of many mixed conifer stands [3,4], although this compositional shift also reflects a legacy that includes selective harvesting of yellow and white pines during the Comstock mining era [5] and fire exclusion during much of the 20th century [6,7]. Among the concerns over this trend is a perception that forest health deteriorates with overabundance of white fir in mixed conifer stands, particularly on sites where moisture availability is a frequent inducer of stress [8]. To a substantial degree, this reflects a propensity for this species to succumb to attack by the Scolytine fir engraver (*Scolytus ventralis* Le Conte), a bark beetle against which the effectiveness of its resin-based defense mechanisms is questionable [9-11]. Additionally, infestation of white fir by the parasitic fir dwarf mistletoe (*Arceuthobium abietinum* [Engelm.] Hawksw. and Wiens), a common occurrence, can imperil the vigor of the host such that its susceptibility to fir engraver attack is exacerbated [8].

Presented here is a study of bark beetle demography encompassing comparisons of the various insect and tree host species associations residing in an eastern Sierran mixed conifer stand. Also examined

were interactions between an array of mensurational and forest health factors and bark beetle colonization.

Materials and Methods

Study site

The stand chosen for study is naturally regenerated, second growth, uneven-aged Sierra Nevada mixed conifer located on the USDA Forest Service Lake Tahoe Basin Management Unit (39.22° N, 120.10° W). Consisting of approximately 8.1 ha, the elevation of this eastern Sierran site is 2050 m, the aspect is generally east, the slope averages 7%, and the average annual precipitation is 81 cm, predominantly snowfall [12]. The soils are derived from volcanic parent material, exceedingly rocky, and of the Jorge-Tahoma Association [13]. Based on dominant and codominant crown class site trees averaging 162 years in age [14], the site quality is class IV according to the Dunning [15] site classification system for Sierra Nevada mixed conifer.

Data collection

Stand attributes were ascertained by measuring trees of pole size and larger (stems ≥ 10.2 cm DBH) within 20 permanent 0.04-ha circular plots established in a square pattern extending over the site in its entirety. All trees in these plots were measured for total height, DBH, and live crown length and tallied by species. Included were free standing dead trees, defined as those exhibiting no live crown, tallied accordingly. Subsequently, tree counts were summed by species and

*Corresponding author: Walker RF, University of Nevada, Department of Natural Resources and Environmental Science, 1664 North Virginia Street, Reno, NV 89557, USA, Tel: 7757844039; E-mail: walker@cabnr.unr.edu

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overall within each plot and then again with dead stems segregated, the percentages by species and of dead stems by species as well as overall were determined, and the number of species within each plot was ascertained as a diversity indicator. Also, tree heights and crown lengths were used to calculate live crown percentage, DBH values were used to derive quadratic mean diameter by plot according to the Curtis and Marshal [16] formula, total tree counts and quadratic mean diameters were used to calculate plot basal area according to the formula of Davis et al. [17], and the above-ground tree biomass by species and overall within each plot was determined using the formulas of Gholz et al. [18] and Ter-Mikaelian and Korzukhin [19]. Ultimately, all tree counts along with basal area and biomass values were expanded to reflect an area of 1.0 ha.

Bark beetle prevalence was quantified by counting the pitch tubes on all stand constituents included in the mensurational measurements of each plot. This was accomplished by visually dividing the bole surface into vertically oriented quadrants, counting the pitch tubes in each quadrant, and then totaling the counts for each tree. With ocular aids used as needed, the entire bole length was included in these counts. Principle bark beetle species were identified by the observation of adult and larval forms as well as pitch tube and gallery characteristics as described by Furniss and Carolin [20]. For the purpose of expressing pitch tube counts as the quantity per unit of bole surface area, tree height and DBH were used as approximations of the lateral length and base diameter, respectively, in the geometric formula for the lateral surface area of a right cone, and the counts of individual trees were then divided by their bole surface area thus approximated. Abundance expressed on the basis of the count per unit surface area compensates for the count per tree measure to sometimes overstate attack severity simply because larger trees have more bole surface available to colonize. Nevertheless, for both measures of abundance, values were averaged across and within tree species by plot. Additionally, to better elucidate the influence of tree size on beetle colonization, all stems were segregated by species into six DBH classes, each representing a range inclusive of the low and high values as follows: Class 1, 10.2–20.2 cm; Class 2, 20.3–30.3 cm; Class 3, 30.4–40.4 cm; Class 4, 40.5–50.5 cm; Class 5, 50.6–60.6 cm; and Class 6, ≥ 60.7 cm. Also quantified on all trees included in the mensurational and bark beetle inventories was mistletoe infestation using the Hawksworth [21] rating system with identification of the specific parasitic species based on the descriptions of Scharpf and Hawksworth [22]. Once quantified, the ratings were averaged by species within individual plots and the percentage of stems infested with mistletoe by host species was determined.

Statistical analysis

For purposes of assessing how closely sample means involving compositional and mensurational measures reflected stand attributes, the standard error of the mean (SE) and 95% confidence limits (CL) were calculated from the pertinent plot means and sums, and these statistics were also calculated for the bark beetle demography variables that spanned across the principal tree species represented in the subject stand. Data pertaining to tree mortality, mistletoe infestation, and bark beetle colonization both across and within the DBH classes were subjected to one-way analysis of variance (ANOVA) to test for the effect of host tree species, while within species, one-way ANOVA was also employed to test for the effect of DBH class on beetle colonization. For every ANOVA, effects were considered significant only when $p \leq 0.05$ according to the F test. Subsequently, differences among means

were evaluated using the least significant difference (LSD) test with $\alpha=0.05$, and the SE was calculated to provide an additional indication of the variation among the values from which each mean was derived.

Additional statistical analysis consisted of an extensive array of simple linear regression models used to investigate relationships between variables selected as particularly pertinent to the study. These were divided into five subsets, hereafter denoted the mensuration, species representation, mortality, mistletoe, and biomass subsets. The mensuration subset consisted of models incorporating all possible combinations of tree height, DBH, live crown length and percentage, basal area, and total tree count as independent variables with pitch tube counts per tree and per unit bole surface area across and within species, and within each species by DBH class, along with the mistletoe rating by species, the percentage of trees infested with mistletoe by host species, and the dead tree counts and percentages by species and overall serving as dependent variables. For the species representation subset, the independent variables consisted of the percentages of each species plus species diversity among stand constituents while dependent variables were again those identified above regarding the mensuration subset. The mortality subset featured the dead tree counts and percentages by species as the independent components with the overall dead tree count serving as its dependent counterpart and, matched by species, models with pitch tube counts per tree and per unit bole surface area, both combined and by DBH class, as the former with the dead tree counts and percentages constituting the latter. In the mistletoe subset, where independent and dependent variables were also matched by species, the Hawksworth rating and the percentage of trees infested served as the former and were paired with pitch tube counts per tree and per unit bole surface area, both across and within DBH classes, along with the dead tree count and percentage. As for the biomass subset, independent variables consisted of total biomass by species and overall while the dependent variables were the bark beetle and mistletoe measures included as such in the mensuration subset as noted above. With these models, however, the independent and dependent components were not confined to matches within species. For all regression subsets, models were considered significant only when $p \leq 0.05$ according to the F test, and all statistical analyses were performed using SAS Version 9.3 (SAS Institute, Inc., Cary, NC).

Results

Stand characteristics

Over three-quarters of the trees tallied in the inventory of the subject stand were white fir with neither Jeffrey pine, incense-cedar, sugar pine, nor red fir, the remaining species, constituting as much as one-tenth of the its composition (Table 1). Nevertheless, Jeffrey pine, the second most common species, had more than twice the representation of red fir, the least common stand constituent. Mensurationally, the stand was young sawtimber with approximately one-half of tree height supporting live crown on average and it was moderately stocked for Sierran mixed conifer (Table 2). Regarding above-ground biomass, white fir dry weight (mean=249,538.5, SE=29,071.8, 95% CL= $\pm 60,847.9$ kg ha⁻¹) greatly exceeded that of all other stand constituents, most apparently red fir (mean=6,159.3, SE=3,172.8, 95% CL= $\pm 6,640.7$ kg ha⁻¹) but also Jeffrey pine (mean=29,775.5, SE=9,860.1, 95% CL= $\pm 20,637.4$ kg ha⁻¹), incense-cedar (mean=23,536.8, SE=9,631.9, 95% CL= $\pm 20,159.8$ kg ha⁻¹), and sugar pine (mean=44,802.9, SE=15,126.0, 95% CL= $\pm 31,659.0$ kg ha⁻¹).

ANOVA revealed the species effect on dead tree count to be

Statistic	Composition (%)				
		Jeffrey pine	Incense-cedar	Sugar pine	
Mean	76.73	8.63	5.45	5.42	3.77
SE	0.04	0.03	0.02	0.01	0.02
95% CL (±)	8.05	5.47	3.63	2.41	3.63

¹Data were collected in 20 plots (n=20) from trees ≥ 10.2 cm DBH.

Table 1: Species composition of a mixed conifer stand in the Lake Tahoe Basin selected for assessment of forest health indicators¹.

Statistic	Height (m)	DBH (cm)	Live crown (m)	Live crown (%)	Basal area (m ² ha ⁻¹)	Total trees (stems ha ⁻¹)
Mean	14.13	38.09	7.13	50.10	57.06	530
SE	0.56	1.90	0.28	1.56	3.84	42
95% CL (±)	1.18	3.98	0.58	3.26	8.04	88

¹Data were collected in 20 plots (n=20) from trees ≥ 10.2 cm DBH.

Table 2: Mensurational characteristics of a mixed conifer stand in the Lake Tahoe Basin selected for assessment of forest health indicators¹.

significant (p=0.0003), and the LSD test indicated that a relatively high count for white fir significantly exceeded low ones for Jeffrey pine, incense-cedar, and especially sugar pine for which standing dead stems were entirely absent, while the red fir count was the second highest numerically and also surpassed that of the latter species (Table 3). Per hectare, standing dead stems of white fir were 11.0× more abundant than those of Jeffrey pine and 16.5× more prevalent than those of incense-cedar, while the multipliers for red fir in relation to this pine and incense-cedar were 8.3× and 12.5×, respectively. Although unaccompanied by a significant effect as derived from ANOVA, the standing dead percentage was highest overall in red fir and it surpassed that of either Jeffrey or sugar pine according to the LSD test, while white fir and incense-cedar exhibited intermediate, and nearly equivalent, mortality percentages. Proportionally, nevertheless, the mortality rate apparent at inventory was more than twice in red fir that for any of the other species.

Mistletoe infestation

Although mistletoe infestation was exceedingly light overall, ANOVA revealed a significant species (p=0.0067) effect on the Hawksworth ratings (Table 4). In accordance, the LSD test indicated a rating for the white fir that differed significantly from those in either Jeffrey or sugar pine, a reflection of both the relative abundance of fir dwarf mistletoe in the former and the complete absence of the western dwarf mistletoe (*Arceuthobium campylopodum* Engelm.) and sugar pine dwarf mistletoe (*Arceuthobium californicum* Hawksw. and Wiens) in the two pines, respectively, while the ratings for incense-cedar, which reflect infection by its true mistletoe (*Phoradendron libocedri* [Engelm.] Howell), and red fir, another host of the fir dwarf mistletoe (*A. abietinum*), were intermediate in value. Also differing among host species were the percentages of trees in which the various mistletoes were present, led by white and red fir in which infestations occurred most often as compared to Jeffrey and sugar pine where none occurred, while incense-cedar again assumed an intermediate position.

Bark beetle demography

Based on adult and larval forms as well as pitch tube and gallery characteristics, the fir engraver was confirmed as the bark beetle species colonizing white and red fir, the Jeffrey pine beetle (*Dendroctonus jeffreyi* Hopkins) was the principle bark beetle species infesting its namesake host tree, and the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) was the assailant of sugar pine. Because pitch

tubes were entirely absent on incense-cedar and red fir occurred in only a small minority of the inventory plots, bark beetle demography measures specific to these two species were omitted from the analyses undertaken in this study and hereafter in this report. Collectively, and based on the remaining species, namely white fir, Jeffrey pine, and sugar pine, the pitch tube count averaged 54.77 per tree (SE=5.44, 95% CL=± 11.38) and 11.85 per m² of bole surface area (SE=1.33, 95% CL=± 2.78).

Irrespective of DBH class, pitch tube counts per tree and per unit bole surface area were significantly influenced by species (both p ≤ 0.0001) according to ANOVA, and the LSD test divulged that the counts on white fir significantly exceeded those on either Jeffrey or sugar pine according to both abundance measures (Table 5). By way of further comparison between this fir and the two pines, the count per tree on the former was 13.6× that on Jeffrey pine and 25.6× that on sugar pine, while on a surface area basis, the count on the fir was 32.9× and 51.7× those on Jeffrey and sugar pine, respectively. When considered by DBH class, ANOVA revealed the species effect to persist regardless of tree size according to the count per tree measure, specifically within Class 1 (p=0.0014), Class 2 (p ≤ 0.0001), Class 3 (p=0.0002), Class 4 (p=0.0011), Class 5 (p=0.0363), and Class 6 (p ≤ 0.0001), while with the exception of Class 5, this influence was again apparent based on the counts per unit surface area, specifically within Class 1 (p=0.0017), Class 2 (p=0.0002), Class 3 (p=0.0005), Class 4 (p=0.0008), and Class 6 (p=0.0036). To a large extent, the LSD test again confirmed here the propensity of white fir to accumulate pitch tubes in comparative abundance, disclosing as significant the disparities between its counts by both measures and those in either pine species in all except Class 5 wherein its count per tree surpassed that of sugar pine nonetheless. Within the individual diameter classes, the greatest numerical discrepancy between white fir and Jeffrey pine, regardless of abundance measure, was found in Class 1 where the count per tree for the fir was 71.0× that for the pine and the count per unit surface area was 64.3× for the former compared to the latter. However, the diameter class within which the largest numerical difference between white fir and sugar pine existed varied according to the measure considered, as it was found in

Species	Dead Trees (stems ha ⁻¹)	Dead Trees (%)
White fir	33 ^a (8)	8.6 ^{ab} (2.3)
Jeffrey pine	3 ^{bc} (3)	1.1 ^b (1.1)
Incense-cedar	2 ^{bc} (2)	9.1 ^{ab} (9.1)
Sugar pine	0 ^c (0)	0.0 ^b (0.0)
Red fir	25 ^{ab} (13)	21.1 ^a (12.1)

¹Within each measure, means sharing a common letter do not differ significantly at α=0.05 according to the LSD test; each mean is based on values from 20 or fewer plots (n ≤ 20) depending on the presence of trees of the pertinent species within individual plots. ²The SE of each mean is indicated parenthetically.

Table 3: Tree mortality by species in a mixed conifer stand of the Lake Tahoe Basin selected for assessment of forest health indicators^{1,2}.

Species	Mistletoe (Hawksworth rating)	Infested Trees (%)
White fir	0.24 ^a (0.07)	14.2 ^a (3.2)
Jeffrey pine	0.00 ^b (0.00)	0.0 ^b (0.0)
Incense-cedar	0.11 ^{ab} (0.07)	10.6 ^{ab} (7.2)
Sugar pine	0.00 ^b (0.00)	0.0 ^b (0.0)
Red fir	0.06 ^{ab} (0.04)	18.5 ^a (16.4)

¹Within each measure, means sharing a common letter do not differ significantly at α=0.05 according to the LSD test; each mean is based on values from 20 or fewer plots (n ≤ 20) depending on the presence of trees of the pertinent species within individual plots. ²The SE of each mean is indicated parenthetically.

Table 4: Mistletoe infestation by species in a mixed conifer stand of the Lake Tahoe Basin selected for assessment of forest health indicators^{1,2}.

Species	DBH class						
	Combined	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Pitch tube counts per tree							
White fir	67.69 ^a (5.90)	35.51 ^a (5.15)	76.71 ^a (6.95)	97.85 ^a (10.86)	90.57 ^a (14.45)	57.73 ^a (9.31)	43.28 ^a (5.66)
Jeffrey pine	4.99 ^b (1.59)	0.50 ^b (0.32)	3.90 ^b (1.42)	6.17 ^b (0.50)	9.65 ^b (4.85)	10.00 ^{ab} (—)	3.13 ^b (2.24)
Sugar pine	2.64 ^b (0.73)	0.67 ^b (0.33)	4.50 ^b (2.50)	4.80 ^b (1.93)	0.75 ^b (0.48)	1.50 ^b (1.50)	2.60 ^b (0.51)
Pitch tube counts per m² of bole surface area							
White fir	14.48 ^a (1.34)	21.85 ^a (3.22)	17.38 ^a (1.74)	10.72 ^a (1.30)	6.74 ^a (1.06)	9.80 ^a (5.48)	2.35 ^a (0.48)
Jeffrey pine	0.44 ^b (0.14)	0.34 ^b (0.24)	0.74 ^b (0.27)	0.75 ^b (0.06)	0.56 ^b (0.27)	0.51 ^a (—)	0.10 ^b (0.07)
Sugar pine	0.28 ^b (0.08)	0.42 ^b (0.21)	0.70 ^b (0.09)	0.48 ^b (0.20)	0.06 ^b (0.04)	0.08 ^a (0.08)	0.07 ^b (0.01)

¹Within each Table component, means sharing a common letter do not differ significantly at $\alpha=0.05$ according to the LSD test; each mean is based on values from 20 or fewer plots ($n \leq 20$) depending on the presence of trees of the pertinent species and/or class within individual plots. ²The SE of each mean is indicated parenthetically. ³Denoted parenthetically, “—” indicates that the SE was incalculable due to insufficient sample size.

Table 5: Pitch tube prevalence by prominent tree species across and within DBH classes denoted as counts per tree and per unit of bole surface area in a mixed conifer stand of the Lake Tahoe Basin selected for assessment of forest health indicators^{1,2,3}.

Class 4 regarding the counts per tree, where that in the fir was 120.8× that in this pine, while on a count per unit area basis, it occurred in Class 5, where a multiplier of 122.5× prevailed.

Providing greater illumination of possible size preferences among potential host trees, ANOVA revealed a significant diameter class effect extending to both the count per tree and per unit surface area (each $p \leq 0.0001$) regarding white fir (Table 6). As distinguished by the LSD test, the former measure was higher in Class 3 and 4 than in Class 1, 5, or 6 and was higher in Class 2 than Class 1 or 6 as well. At the most extreme, the count per tree was 2.8× greater in Class 3 than in Class 1, representing the highest and lowest values numerically for this abundance measure, respectively, and was 2.1× higher in Class 4 than in Class 6, which exhibited the second highest and lowest values, respectively. Lower in magnitude, the disparity between Class 2 and either Class 1 or 6 was nonetheless substantial, with the count in the former $\geq 1.8\times$ that in either of the latter. As for pitch tube counts based on bole surface area in white fir, the LSD test denoted as significant the disparities between higher values in Class 1 and 2 than those in all of the other diameter classes plus that between Class 3 and Class 6, and it is perhaps noteworthy that with only a minor deviation involving Class 4 and 5, counts by this measure declined with increasing class designation. Furthermore, the magnitude of the largest difference between classes here was considerably greater than that derived from the count per tree measure, as the value for Class 1 was 9.3× that for Class 6, while other comparisons largely paralleling those detailed above produced substantial discrepancies nonetheless with a count in Class 2 that was 2.6× that in Class 4 and one in Class 3 that was 4.6× the value in Class 6. Unlike the pronounced tree size influence on beetle colonization in white fir, no diameter class effect on pitch tube abundance in Jeffrey pine was disclosed by ANOVA regardless of the measure assessed and the LSD test did not detect any significant differences among the classes for either measure regarding this species. However, specific to the count per unit bole surface area, diameter class imposed an effect on colonization in sugar pine ($p=0.0465$), and the LSD test divulged that this count was significantly higher in Class 2 than in Class 4, 5, or 6 and was such in Class 3 than in Class 4 or 6. Numerically, the magnitude of these disparities was substantial, with a value in Class 2 that was $\geq 8.8\times$ to as much as 11.7× those in Class 4 through 6 and one in Class 3 that was $\geq 6.9\times$ those in Class 4 and 6. Although lacking in a significant influence specified by ANOVA, the LSD test nevertheless detected two significant differences between diameter classes pertaining to the count per tree measure, namely a higher value in Class 3 than in either Class 1 or 4.

Relationships of stand health variables

The first subset of the regressions computed in this study, which was concerned with the relationships of forest health variables to mensurational measures pertaining to tree dimensions and stand density, produced 12 significant models (Table 7). Of those concerned with tree dimensions, all involved live crown with its length the independent variable to which the bole surface area-based pitch tube count across species and DBH classes was negatively related, and its percentage that to which the overall dead tree count and percentage plus the white fir dead tree count and percentage were each negatively related as well. Overall, these models were of modest strength, with a range of 23% to 44% of the variation in the dependent variables explained by that in the independent variables. For models involving stand density measures, the DBH Class 1 surface area-based pitch tube count in Jeffrey pine, the Class 3 sugar pine count per tree, the Hawksworth rating and percentage of infested trees in incense-cedar, and the red fir standing dead percentage were all positively related to basal area, while the Jeffrey pine standing dead and dead percentage were related to the total tree count, and again positively so. These models featured some of the strongest correlations computed in the study, with 49% to 80% of the variation in the dependent variables accounted for by them.

Focusing on host tree prevalence and the diversity therein, the second subset of regressions yielded six significant models (Table 7). Three of these featured the percentage of white fir among stand constituents as the independent component, to which the overall pitch tube count per tree and per unit surface area irrespective of DBH class along with the white fir standing dead count were all positively related. With negative correlations exclusively, however, the surface area-based pitch tube count across host species and DBH classes plus this same count within Class 2 and 6 white fir were related to host species diversity. Collectively, the models in the second subset explained from 20% to 52% of the variation in the dependent variables.

The third regression subset was concerned with tree mortality exclusively regarding dependent variables although with representation of its measures occurring in different form among its independent variables also, and it produced five significant models (Table 7). Four of these coupled, in all possible combinations and with positive correlations prevailing throughout, overall dead tree count and percentage as the dependent components with the white fir standing dead count and percentage as the independent ones, while the fifth

Species			
DBH class		Jeffrey pine	Sugar pine
Pitch tube counts per tree			
1	35.51 ^c (5.15)	0.50 ^a (0.32)	0.67 ^b (0.33)
2	76.71 ^{ab} (6.95)	3.90 ^a (1.42)	4.50 ^{ab} (2.50)
3	97.85 ^a (10.86)	6.17 ^a (0.50)	4.80 ^a (1.93)
4	90.57 ^a (14.45)	9.65 ^a (4.85)	0.75 ^b (0.48)
5	57.73 ^{bc} (9.31)	10.00 ^a (-)	1.50 ^{ab} (1.50)
6	43.28 ^c (5.66)	3.13 ^a (2.24)	2.60 ^{ab} (0.51)
Pitch tube counts per m² of bole surface area			
1	21.85 ^a (3.22)	0.34 ^a (0.24)	0.42 ^{abc} (0.21)
2	17.38 ^a (1.74)	0.74 ^a (0.27)	0.70 ^a (0.09)
3	10.72 ^b (1.30)	0.75 ^a (0.06)	0.48 ^{ab} (0.20)
4	6.74 ^{bc} (1.06)	0.56 ^a (0.27)	0.06 ^c (0.04)
5	9.80 ^{bc} (5.48)	0.51 ^a (-)	0.08 ^{bc} (0.08)
6	2.35 ^c (0.48)	0.10 ^a (0.07)	0.07 ^c (0.01)

¹Within each Table component, means sharing a common letter do not differ significantly at $\alpha=0.05$ according to the LSD test; each mean is based on values from 20 or fewer plots ($n \leq 20$) depending on the presence of trees of the pertinent species and/or class within individual plots.

²The SE of each mean is indicated parenthetically.

³Denoted parenthetically, “-” indicates that the SE was incalculable due to insufficient sample size.

Table 6: Pitch Tube Prevalence in Prominent Tree Species by DBH Class Denoted as Counts per Tree and Per Unit of Bole Surface Area in a Mixed Conifer Stand of the Lake Tahoe Basin Selected for Assessment of Forest Health Indicators^{1,2,3}.

positively related the white fir dead percentage to the DBH Class 6 pitch tube count per tree for this species. Generally among the strongest models produced by the study, as much as 81% of the variation in the dependent variables was explained by that in their independent counterparts, and none of these models explained less than 42% of such variation.

The penultimate regression subset featured measures of mistletoe infestation as the independent component with either bark beetle colonization or tree mortality measures serving as their dependent counterpart, and six such models were significant with positive correlations prevailing exclusively (Table 7). Of these, the surface area-based pitch tube counts for DBH Class 1 and 6 white fir were paired with the percentage of this species infested with mistletoe in two relatively weak models in which only 23% and 35%, respectively, of the variation in the dependent variables was explained. Additionally, however, the red fir standing dead count and percentage were each related to both the Hawksworth rating and infested percentage for this fir in models accounting for 69% to 85% of such variation.

The stand biomass subset, the final one among the five computed in the study, yielded four significant regressions (Table 7). In two of these, the Hawksworth rating and infestation percentage for white fir were both positively related to the above-ground biomass of this species, while of the remaining two, the surface area-based pitch tube count across all species and DBH classes was negatively related to Jeffrey pine biomass in one while the DBH Class 1 Jeffrey pine pitch tube count by this measure was positively related to stand biomass across all species in the other. For the latter of these models, 84% of the variation in the dependent variable was accounted for, but in the previous three, from 32% to 47% was the extent of such explanation they provided.

Discussion

Within the context of the forest conditions prevailing in the eastern Sierra Nevada at present, the mixed conifer stand in which this study was conducted was largely unremarkable. It exhibited characteristics of a common managerial legacy in the region, namely that of the exclusion of fire for a prolonged period, the reflection of a broad policy

that encompassed much of the 20th century. Additionally, it has been subjected to occasional partial harvests targeting its yellow and white pine components, which probably intensified in the years leading up to the transfer of ownership from the private to the public sector approximately three decades past, and with minimal extraction of white and red fir, species with little commercial value until the last half of the 20th century. In combination, these factors have culminated in a stand that exhibits a moderate level of stocking for the cover type [23], rendering it somewhat of an aberration regarding density but one that conforms to the long-term trend of rising white fir representation and diminishing Jeffrey and sugar pine prevalence in Sierran mixed conifer forests generally [24]. Despite the moderate stand density, however, a vestige of self-thinning induced by between-tree competition was apparent in mortality that was concentrated in its fir component, although the sheer preponderance of white fir on the site somewhat masked the magnitude of its demise when expressed as a percentage of its overall representation. Any question about the magnitude of the impact of white fir mortality on that of the stand in total, however, was negated by four simple regressions that positively related, in all possible combinations and with moderate to strong correlations prevailing throughout, overall standing dead count and percentage to each of these measures in white fir alone. Another regression model, although weaker, positively related the standing dead count in this fir to its prevalence specifically. It is probable that a factor in the mortality of this species is an annual precipitation for the site that is below the range considered common for white fir [8]. Undoubtedly, such was the case for red fir as well inasmuch as precipitation at this site is near the bottom of the range for those typically occupied by this fir, and its limited residence there is largely a reflection of cold air drainage that settles locally [25]. What is also likely is that the mistletoe infestation here in fir generally, and in the incense-cedar as well, was too anemic to be considered a direct causal agent in their mortality other than in isolated cases. Several strong regression models involving red fir, specifically those positively correlating its standing dead stem count and percentage to both its Hawksworth rating and infestation percentage,

Independent variable	Dependent variable	Correlation	Model F test p-value	Model r ²
Mensuration subset				
Live crown length	Overall combined pitch tube count per m ²	Negative	0.0312	0.2329
Live crown percentage	Overall dead tree count	Negative	0.0014	0.4399
Live crown percentage	Overall dead tree percentage	Negative	0.0046	0.3682
Live crown percentage	White fir dead tree count	Negative	0.0189	0.2698
Live crown percentage	White fir dead tree percentage	Negative	0.0331	0.2283
Basal area	Jeffrey pine DBH Class 1 pitch tube count per m ²	Positive	0.0390	0.8049
Basal area	Sugar pine DBH Class 3 pitch tube count per tree	Positive	0.0474	0.7790
Basal area	Incense-cedar mistletoe rating	Positive	0.0171	0.4862
Basal area	Incense-cedar percentage infested with mistletoe	Positive	0.0171	0.4862
Basal area	Red fir dead tree percentage	Positive	0.0344	0.7132
Total tree count	Jeffrey pine dead tree count	Positive	0.0083	0.6024
Total tree count	Jeffrey pine dead tree percentage	Positive	0.0083	0.6024
Species representation subset				
White fir prevalence	Overall combined pitch tube count per tree	Positive	0.0073	0.3366
White fir prevalence	Overall combined pitch tube count per m ²	Positive	0.0014	0.4430
White fir prevalence	White fir dead tree count	Positive	0.0353	0.2234
Species diversity	Overall combined pitch tube count per m ²	Negative	0.0113	0.3064
Species diversity	White fir DBH Class 2 pitch tube count per m ²	Negative	0.0480	0.2000
Species diversity	White fir DBH Class 6 pitch tube count per m ²	Negative	0.0084	0.5169
Mortality subset				
White fir dead tree count	Overall dead tree count	Positive	<0.0001	0.6102
White fir dead tree count	Overall dead tree percentage	Positive	<0.0001	0.6910
White fir dead tree percentage	Overall dead tree count	Positive	0.0005	0.4997
White fir dead tree percentage	Overall dead tree percentage	Positive	<0.0001	0.8079
White fir DBH Class 6 pitch tube count per tree	White fir dead tree percentage	Positive	0.0223	0.4216
Mistletoe subset				
White fir percentage infested with mistletoe	White fir DBH Class 1 pitch tube count per m ²	Positive	0.0335	0.2275
White fir percentage infested with mistletoe	White fir DBH Class 6 pitch tube count per m ²	Positive	0.0442	0.3462
Red fir mistletoe rating	Red fir dead tree count	Positive	0.0091	0.8485
Red fir mistletoe rating	Red fir dead tree percentage	Positive	0.0210	0.7728
Red fir percentage infested with mistletoe	Red fir dead tree count	Positive	0.0400	0.6920
Red fir percentage infested with mistletoe	Red fir dead tree percentage	Positive	0.0145	0.8098
Biomass subset				
White fir total biomass	White fir mistletoe rating	Positive	0.0059	0.3506
White fir total biomass	White fir percentage infested with mistletoe	Positive	0.0008	0.4704
Jeffrey pine total biomass	Overall combined pitch tube count per m ²	Negative	0.0087	0.3251
Overall total biomass	Jeffrey pine DBH Class 1 pitch tube count per m ²	Positive	0.0287	0.8398

¹Each model is based on values from 20 or fewer plots ($n \leq 20$) depending on the presence of trees of the pertinent species and/or class within individual plots.

Table 7: Significant Simple Linear Regression Models Relating Pitch Tube and Mistletoe Abundance Along with Tree Mortality to an Array of Pertinent Influencing Factors in a Mixed Conifer Stand of the Lake Tahoe Basin Selected for Assessment of Forest Health Indicators¹.

would appear to dispute this assertion, but these probably reflect impacts of secondary contributors to a demise mostly caused by the marginality of the host species for this site. Lending further credence to this interpretation is that such regressions did not materialize for white fir, which had the highest rating overall and an infestation percentage near that of the red fir. In fact, the only contribution of the regression analysis to an understanding of the interactions between either white fir or incense-cedar and their respective mistletoes is that higher stand density favored infestation, as the Hawthorn rating and infestation percentage for the latter was related to one stand density measure, specifically basal area, and those for the former were related to a surrogate density measure specific to this fir, that of above-ground tree biomass, all positive correlations of mostly moderate strength. In light of the paucity of Jeffrey pine on this site, a compositional feature of the stand rendered even more distinctive because its silvics are relatively well matched to the site [26], it is perhaps noteworthy that mortality in this species, denoted as either the standing dead count or its percentage, was positively related to another density measure

employed in the study, that of the total tree count, in regressions of some strength. And, lending further evidence to the assertion that the mortality in red fir was, to a large extent, caused by between-tree competition for resources exacerbated by its marginal adaptation to the site, which would leave it at a competitive disadvantage, another regression model revealed that the standing dead percentage for this fir was positively, and strongly, correlated with stand basal area.

With bark beetle demography constituting the main thrust of this study, perhaps the most profound finding regarding this subject was the pronounced disparities in the level of colonization sustained by the various tree species represented in the stand, and more specifically that sustained by white fir in comparison to the other two species considered, namely Jeffrey and sugar pine. In part, it is reasonable to attribute the magnitude of the difference to the abundance and close proximity, and therefore ready availability, of this host species, factors that likely facilitated expansion of the fir engraver population. Prior studies by DeMars, Ferrell, and Otrosina [27], Ferrell, Otrosina, and DeMars [28], Walker et al. [4], and Egan et al. [29] have all provided

evidence that an important influence on populations of this bark beetle was the proportional prevalence of its host, with greater availability exacerbating attack severity. Inasmuch as the overwhelming majority of the pitch tubes found on the tree boles, which served as the quantitative basis here for assessment of colonization level, was found on white fir, two regression models that positively related the overall pitch tube count, i.e. across host species, denoted as both the count per tree and that per unit of bole surface area, to white fir prevalence provided some credence to this assumption. Somewhat related were two other models that negatively related the overall surface area-based count to tree species diversity and to Jeffrey pine biomass. However, suggesting that host availability was not the sole explanation for the exceptional size of the engraver population was that these regressions were not of notable strength and that significant models matching pitch tube abundance in white fir specifically to the prevalence of this host species failed to materialize. Inevitably, this leads to the second of the probable causes of the large engraver population, that of deficiencies in white fir defense mechanisms which are pronounced to such extent that they provide relatively little protection against attack [4, 9-11] and therefore do not exert much control on population levels of this beetle because its reproductive success is only nominally imperiled by them. To a large extent, the vulnerability of white fir is attributable to a resin duct system that is typically underdeveloped relative to those of pine species [30-32] reflecting that its development, rather than perpetual, is initiated only when an attack commences [33] and is largely confined to bark rather than arrayed across both bark and wood as in the pines [34]. An already precarious defense capability is further jeopardized by moisture stress, particularly that chronically induced by drier sites, and a minimum annual precipitation threshold of 89 cm has been established for this species to thrive in the Sierra Nevada [8,35], which is more than that deposited over the long term on the site of this study. Moisture stress induces stomatal closure, thus disrupting photosynthate production by limiting gas exchange, which in turn diminishes the availability of carbohydrates that can be dedicated to the production of defense compounds, primarily oleoresin [36], and such stress likely exacerbates the conundrum of assimilate partitioning because any dedicated to defense is unavailable for growth and reproduction [37]. In a study conducted on a drier site but near that of the one presented here which illustrated the debilitating interaction of defensive mechanisms of dubious efficacy and limited moisture availability in this species, pitch tubes on scattered white fir in a pure Jeffrey pine stand were far more numerous than on the latter species according to both of the abundance measures used herein [38]. As an aside, its relatively subdued presence here belies the status of the Jeffrey pine beetle as the single greatest threat to the health of its namesake host species [26, 39]. Although direct examination of the functionality of the defense mechanisms embodied in the species constituting this stand was beyond the scope of the present study, a relatively weak regression model negatively related overall pitch tube count on a surface area basis to live crown length, suggesting that reduced energy production due to restricted crown development may have resulted in marginally elevated levels of beetle attack. Indirect evidence of the vital role of energy production in stand health may have also been manifested in four other models, specifically two each that negatively correlated dead tree count and percentage both across species and for white fir alone with live crown percentage. Undoubtedly, these reflect in part the distinction employed to detect dead trees, which was a complete lack of live crown, and are moderate in strength at most, but they may be somewhat indicative of the ultimate effect of diminishing vigor on viability as well.

The pronounced inequality between the overall pitch tube prevalence in the white fir and those in the pines here essentially extended to include disparities of substantial magnitude within every one of the six DBH classes. In fact, only in Class 5 were statistically significant differences between the fir and both Jeffrey and sugar pine lacking, and even therein, such was extant between the former and sugar pine according to the count per tree measure. Numerically, the largest difference between white fir and Jeffrey pine occurred in Class 1 regardless of the abundance measure considered, which in and of itself suggests an inclination for the fir engraver to colonize small trees of its host species more so than the Jeffrey pine beetle. In a comparison of this fir and sugar pine, however, the greatest numerical discrepancies occurred in Class 4 on a count per tree basis and in Class 5 according to the surface area-based count, suggesting that the engraver beetle had somewhat more of a proclivity toward colonizing larger host trees than the mountain pine beetle. Nevertheless, somewhat greater clarity regarding the respective host tree size preferences of the three bark beetles in question here was provided by comparisons within species among the diameter classes. Thus evaluated, the preference of the fir engraver was for trees in Class 3 and 4, or white fir from 30.4 cm to 50.5 cm DBH, followed by those of the next smallest size in Class 2, when assessed on the basis of pitch tubes per tree, while the smallest and largest classes were the least colonized overall. Alternatively, when assessed according to the surface area-based counts, targeted sizes were the small stems of Class 1 and 2 with the large Class 6 trees the least preferred. Interpretively, it may be reasonable to explain the discord in these findings as that the count per tree result possibly demonstrates an actual size preference by the fir engraver while that derived from the surface area-based measure probably reflects the size most likely to succumb under concentrated, and therefore lethal, attack. Regardless, what is abundantly clear in either result is that on this site, the fir engraver did not gravitate toward the largest host trees available, which is a departure from the findings of earlier studies [4,27,28] in which a marginal preference of this beetle for larger fir was revealed. Given that resin ducts develop almost exclusively in the bark of white fir as noted previously, and that the thicker bark of larger diameter trees could conceivably accommodate greater resin duct formation, it is possible that the comparative avoidance of larger fir was a de facto avoidance of those with the best developed resin production capability. Extrapolating management implementations from this finding, it suggests that in the selection of stems for removal during thinnings of Sierran mixed conifer, and perhaps especially so for stands of this cover type in which white fir is predominant, eliminating those of smaller stature, the directive of the commonly employed low thinning procedure and one that best mimics the mortality inherent in natural self-thinning [40], would ultimately prove to be the approach most conducive to the enhancement of stand health. Unlike the fir engraver, there was little evidence here to indicate that the Jeffrey pine beetle was discriminating as to the size of its namesake host tree. Although substantial numerical differences among the DBH classes were apparent, more so in the pitch tube quantity per tree than in that per unit bole surface area, excessive variability in the data from which these means were derived rendered them statistically non-significant. Nevertheless, the mountain pine beetle demonstrated clear proclivities regarding the size of the sugar pine it colonized as well as some level of consistency between the two pitch tube abundance measures. Specifically, the highest count per tree occurred in Class 3 followed by that in Class 2, while the highest surface area-based count was found in Class 2 followed by that in Class 3, which collectively would seem to indicate a preference for trees of small

to moderate size. However, these findings must be contemplated with caution, as although reasonably well distributed throughout the stand, sugar pines were so widely dispersed that few subject specimens were available from which to collect data. This may partially explain their low overall colonization level, especially when contrasted against the engraver beetle in white fir, which is perhaps most noteworthy because the mountain pine beetle is a formidable damaging agent in sugar pine capable of highly intensive attacks [20,41, 42].

Given the extreme variability typically existing within forest stands in the degree to which their individual constituents are colonized by bark beetles, discerning causation as to localized conditions and beetle responses has often proven to be elusive, but several significant regression models computed in this study provide insight regarding relationships specific to some of the individual diameter classes. Among them, the count per unit bole surface area in Class 1 Jeffrey pine and that per tree in Class 3 sugar pine were each strongly correlated with basal area, so at least for the narrow diameter ranges embodied therein, these species displayed the propensity for higher stand density to elevate beetle populations that has been documented in several western North American forest types [4,43-46]. Closely collaborative here was another strong model featuring a positive correlation between the surface area-based count in Class 1 Jeffrey pine and stand biomass. Conversely, surface area-based counts in Class 2 and 6 white fir were negatively related to tree species diversity, with the former a weak model but the latter much stronger, which indirectly reiterates the aforementioned contribution of host tree availability to expansion of the engraver population. More directly, however, these models infer that a mixed composition presents a complexity for bark beetles in terms of detecting suitable host trees for colonization [47]. The low occurrence of mistletoes in this stand notwithstanding, two models specific to white fir regarding both the dependent and independent components revealed positive, albeit weak, correlations between the pitch tube counts per unit surface area of Class 1 and 6 and the mistletoe infestation percentage. Because of their capacity to weaken trees and therefore compromise their defense mechanisms against a multitude of damaging agents, including bark beetles, dwarf mistletoe infestations are assumed to have considerable diagnostic value in detecting the threat of rapid escalation in beetle populations within western North American forest stands [8,25,48,49]. Nevertheless, in the only significant regression model providing any evidence that fir engraver attacks on white fir caused any of the mortality therein, a positive correlation of moderate strength was detected between its standing dead percentage across the full spectrum of tree sizes and the pitch tube count per tree in Class 6. Regardless, the lack of additional models revealing similar relationships but based on other diameter classes indirectly suggests that the fir engraver population here had not risen to the level known to induce the heavy mortality for which this species is known [4,11], and perhaps further suggests that although a likely contributor, attacks by this beetle were not the sole cause of mortality in its host species.

In summary, this study involved an examination of forest health variables in an eastern Sierra Nevada mixed conifer stand focused on bark beetle demography and its interrelationships with mensurational features as well as other stand maladies. The fir engraver in white fir, the Jeffrey pine beetle in its namesake host species, and the mountain pine beetle in sugar pine constituted the three insect and host associations of interest. Quantified through pitch tube abundance on the tree boles denoted as both the count per tree and that per unit of bole surface area, beetle colonization in white fir greatly exceeded that in either Jeffrey pine or sugar pine regardless of measure considered, likely a reflection

of the degree to which the former dominated stand composition, its limited capacity to defend itself against attack, and the stress-induced loss of vigor it incurred due to its marginal adaptation to the site upon which the study was conducted. Pitch tube abundance across host species was positively related to white fir prevalence according to both measures and was negatively related to tree species diversity according to the surface area-based count. Both the fir engraver and mountain pine beetle displayed discriminating behavior concerning the size of their host trees as discerned through the segregation of the diameter dimension into multiple classes encompassing the full range of tree sizes in residence, with both species revealing a propensity to attack small to medium stems rather than the largest ones available to them. Any size preference of the Jeffrey pine beetle was not sufficiently pronounced to induce statistical distinctions. Nevertheless, Jeffrey pine beetle attack intensity in the smallest diameter class was positively correlated with stand basal area and biomass according to surface area-based pitch tube quantities, and the count per tree measure in sugar pine of medium size was positively related to the former as well. Fir engraver attack intensity in the second smallest and the largest host diameter classes was negatively related to tree species diversity and that in the smallest and largest classes was positively related to the percentage of white fir infested with dwarf mistletoe, all cases in which pitch tube prevalence was enumerated on a surface area basis. Extant in white and red fir, the latter an exceedingly minor stand constituent, along with incense-cedar, mistletoe infestations were very light overall, and although red fir mortality was positively correlated with its Hawksworth rating and infestation percentage, it is unlikely that mistletoe infestations were the principal cause of mortality in any of the resident species. Somewhat similarly, within the white fir mortality was linked to the pitch tube count per tree of the largest diameter class, and although considerable mortality occurred in this species, it is probable that deaths resulted from multiple causes of which bark beetle attack was not preeminent. Exemplifying that the latter assumption was likely even more applicable to the other stand constituents was that mortality in Jeffrey pine was found to be induced by higher total stem counts only among factors examined in this study. These findings advance the understanding of forest health indicators, stand attributes, and pertinent interactions thereof as often encountered in Sierra Nevada mixed conifer and similar cover types.

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