

Effect of season and interval of prescribed burn on ponderosa pine butterfly defoliation patterns

B.K. Kerns and Douglas J. Westlind

Abstract: Current knowledge concerning the interactions between forest disturbances such as fire and insect defoliation is limited. Wildfires and prescribed burns may influence the intensity and severity of insect outbreaks by affecting the vigor of residual trees, altering aspects of stand structure and abundance of preferred hosts, and by changing the physical environment within forest stands. Prescribed burn timing and frequency are particularly important aspects of the fire regime to consider because they can alter numerous aspects of tree vigor, stand structure, and environmental conditions, and can be manipulated by managers. We evaluated ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) defoliation patterns in relation to season (fall and spring) and interval (5 or 15 years) of prescribed burn in the southern Blue Mountains of Oregon. Beginning in 2008 a pine butterfly (*Neophasia menapia* C. Felder & R. Felder) (Lepidoptera: Pieridae) outbreak coincided with a long-term experimental study, providing a unique opportunity to address this question. Defoliation patterns were measured in 2012. The 5 year interval plots had burned three times with five growing seasons of recovery and the 15 year interval plots had burned once with 15 growing seasons of recovery. Mean pine butterfly defoliation across the study area was about 71%. We found a significant interaction between season of burn and interval of burn on defoliation. Areas burned in the fall every 5 years had marginally less (about 5%) defoliation compared with areas that were burned in the fall 15 years previous. Regression tree analysis revealed that defoliation patterns varied based on stand location, percent mortality since the start of the experiment, and tree height. Our results show that (i) season of burn and interval of burn did not predispose these stands to increased defoliation during a pine butterfly outbreak and (ii) repeat burning may actually lead to lower defoliation. However, the effect we document is small and only marginally significant.

Résumé : Les connaissances actuelles au sujet des interactions entre les perturbations de la forêt, telles que le feu et la défoliation par les insectes, sont limitées. Les feux de forêt et les brûlages dirigés peuvent influencer l'intensité et la sévérité des épidémies d'insecte. À cause de leur impact sur la vigueur des arbres résiduels, ils peuvent modifier les aspects de la structure du peuplement et l'abondance des hôtes préférés et changer l'environnement physique à l'intérieur des peuplements forestiers. La fréquence des brûlages dirigés et le moment où ils sont effectués sont des aspects particulièrement importants du régime des feux à prendre en compte parce qu'ils peuvent altérer plusieurs aspects de la vigueur des arbres, de la structure des peuplements et des conditions environnementales et peuvent être manipulés par les aménagistes. Nous avons évalué les schémas de défoliation du pin ponderosa (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) en fonction de la saison (automne ou printemps) et de la période de récurrence (5 ou 15 ans) des brûlages dirigés dans le sud des montagnes Bleues en Oregon. À partir de 2008, une épidémie de piéride du pin (*Neophasia menapia* C. Felder & R. Felder) (Lepidoptera : Pieridae) qui coïncidait avec une étude expérimentale à long terme a fourni une occasion unique de s'attaquer à cette question. Les schémas de défoliation ont été mesurés en 2012. Les placettes associées à l'intervalle de 5 ans avaient brûlé trois fois et récupéré pendant cinq saisons de croissance et les placettes associées à l'intervalle de 15 ans avaient brûlé une fois et récupéré pendant 15 saisons de croissance. Le taux moyen de défoliation par la piéride du pin dans l'ensemble de l'aire d'étude était d'environ 71 %. Nous avons trouvé une interaction significative entre la saison où a eu lieu le brûlage et l'intervalle entre les brûlages dans le cas de la défoliation. Les zones brûlées à l'automne à tous les 5 ans avaient subi légèrement moins (environ 5 %) de défoliation que les zones brûlées à l'automne 15 ans auparavant. L'analyse de l'arbre de régression a révélé que les schémas de défoliation variaient selon l'endroit où se trouvait un peuplement, le pourcentage de mortalité depuis le début de l'expérience et la hauteur des arbres. Nos résultats montrent que (i) la saison où a eu lieu le brûlage et l'intervalle de temps entre les brûlages n'ont pas prédisposé ces peuplements à une défoliation plus sévère lors d'une épidémie de piéride du pin et (ii) les brûlages répétés peuvent en fait réduire la défoliation. Cependant, l'effet que nous avons noté est faible et seulement légèrement significatif. [Traduit par la Rédaction]

Introduction

The pine butterfly (*Neophasia menapia* (C. Felder & R. Felder)) (Lepidoptera: Pieridae) occurs in pine and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests throughout western North America. This butterfly is native to western forests of the United States and Canada, and population levels are typically low. However, periodic large outbreaks have occurred, most notably in ponderosa pine (*Pinus ponderosa* P. Lawson & C. Lawson) stands in Montana (Bousfield and Meyer 1972) and eastern Washington and

Idaho (Evenden 1940; Cole 1966). Over the last century, outbreaks of pine butterfly in the Blue Mountains of Oregon have been reported four times, 1908–1911, 1940–1943, 1982, and 2008 to the present (Flowers et al. 2012). Pine butterfly outbreaks generally only last a few years (2–6), but can lead to growth loss and mortality of ponderosa pine across large areas (Evenden 1940; Cole 1966). Adults fly from mid-July to late September (less commonly in October), with a peak in mid- to late August, and lay eggs on current-year foliage (Scott 2012). Eggs overwinter and hatch the

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B.K. Kerns and D.J. Westlind. USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Avenue, Corvallis, OR 97331, USA.

Corresponding author: B.K. Kerns (e-mail: bkerns@fs.fed.us).

following spring (late May or early June) or about the time new ponderosa pine needles appear. Hatching larvae generally feed on older needles, but may consume new foliage during outbreaks, causing extensive defoliation (Scott 2012). Hatching larvae feed in clusters, whereas mature larvae feed individually. Larval development lasts 6–8 weeks and defoliation is generally complete by late July.

While extensive mortality is possible with these outbreaks (Evenden 1940; Weaver 1961), mortality has generally been associated with the interaction of pine butterfly defoliation and bark beetle infestation such as from the western pine beetle (*Dendroctonus brevicornis* LeConte; Hopkins 1908; Evenden 1940; Weaver 1961). Fire-injured trees can be attractive to some forest insects, such as multiple bark beetle species. While there is no evidence that the pine butterfly has a preference for fire-injured trees, prescribed burns may influence the degree of insect infestation and resultant tree mortality by affecting the vigor of residual trees; the size, distribution, and abundance of preferred hosts; and the physical environment within forest stands (Fettig et al. 2010). More trees may be attacked in burned stands, and burned stands may have higher subsequent tree mortality as compared with unburned areas (Schwilk et al. 2006; Fettig et al. 2010; Davis et al. 2012). There might also be direct effects of burning on the pine butterfly population depending on the severity and timing of burning. However, there are no studies quantifying pine butterfly defoliation patterns in relation to fire or prescribed-fire regimes (e.g., season of burn and interval of burn) and subsequent mortality.

In North American coniferous forests, reintroducing fire is a high priority for forest restoration and management, particularly in ponderosa pine ecosystems. Existing policies and legislation emphasize the widespread use of prescribed fire and mechanical thinning, driven by increasing concerns regarding undesirable changes in forest structure and function such as loss of biodiversity; risk of large, uncontrollable, severe, and costly wildfires; insect and disease outbreaks; and low tree vigor and drought-related tree mortality (Covington 2000). Ponderosa pine forests are a major forest type in western North America (Oliver and Ryker 1990) and their ecological history has served as a textbook example for the reintroduction of fire and the use of prescribed fire to restore forest structure and function (Mast et al. 1999; Allen et al. 2002; Hessburg and Agee 2003). The role and importance of fire as a disturbance process in forests (Agee 1993; Fule et al. 1997; Hessburg and Agee 2003) and disruption of fire regimes coinciding with EuroAmerican settlement and associated fire suppression and exclusion (Covington and Moore 1994; Swetnam et al. 1999; Hessburg et al. 2005) have been extensively presented and discussed. Ponderosa pine forests are targeted for restoration using prescribed fire because impacts of fire exclusion and suppression, land use, and climate are thought to be greatest, and treatments most ecologically relevant, in forests that historically experienced very frequent fires and periodic drought (Covington 2000; Brown et al. 2004; Hessburg et al. 2005).

From 2008 to 2012 the largest outbreak of pine butterfly recorded in Oregon occurred in the southern Blue Mountains encompassing over 250 000 acres of moderate to heavy defoliation (Flowers et al. 2012). This outbreak impacted a long-term experimental study known as the Season and Interval of Burn Study (SIB). Located in six upland ponderosa pine stands on the Malheur National Forest, this study is unique in the western United States. Established at the request of local land managers to investigate the influence of spring and fall prescribed-fire treatments on black stain root disease and its potential insect vectors (Thies et al. 2005), the original study was significantly expanded in 2002 to include 5 and 15 year burn intervals, a grazing component, and the addition of an array of ecosystem response variables — tree growth and mortality, interactions with insect and diseases, fuels, understory vegetation and exotic plant species, and soil properties, and biota. The objectives of the overall study are to evaluate

the long-term effects of repeated (5 or 15 years) prescribed fire in the spring versus fall to achieve desired vegetation and fuel conditions. In 2008, the pine butterfly outbreak was detected in the study area (minor defoliation), where it reached epidemic proportions by 2010 and continued through 2012. This outbreak provided a unique opportunity to evaluate pine butterfly defoliation patterns in relation to season and interval of burn, and continued research will allow the assessment of subsequent mortality in relation to pine butterfly defoliation, prescribed-fire regime, and other disturbance interactions (e.g., bark beetle attacks). Sampling occurred 15 years after the first burns (one 15 year burn) and after completion of three 5 year interval burns. The timing of the latest set of prescribed burns in fall 2007 and spring 2008 coincided immediately before the outbreak beginning in 2008.

Methods

Study area

The study was conducted using six upland ponderosa pine forested stands located on the Emigrant Creek Ranger District, Malheur National Forest, Oregon. Estimated mean annual cumulative precipitation was 466 mm per year (1982–2012), falling mostly as snow between October and April (USDA-NRCS 2012). Annual cumulative precipitation for water year 2012 (October 2011 through September 2012) was 76% of historical. Parent materials consisted of basalt, andesite, rhyolite, tuffaceous interflow, altered tuffs, and breccia (Carlson 1974). Soils are generally dominated by Mollicsols, but Inceptisols and Alfisols are also present (Hatten et al. 2008). The stands are dominated by mixed-aged ponderosa pine, but western juniper (*Juniperus occidentalis* Hook.) and curl-leaf mountain mahogany (*Cercocarpus ledifolius* Nutt.) also occur. Ponderosa pine trees in the study area are approximately 80–100 years old with infrequent individuals of about 200 years old (Emigrant Creek Ranger District, unpublished data). Understory species composition varies among the sites (Kerns et al. 2006, 2011), but *P. ponderosa*/*Pseudoroegneria spicata* (Pursh) Á. Löve and *P. ponderosa*/*Carex geyeri* Boott are the major plant associations. Each stand was thinned in 1994 or 1995. More extensive details on the study area and the experiment can be found in Thies et al. (2005, 2006); and Kerns et al. (2006, 2011).

The pine butterfly outbreak was not widely apparent in the study area until 2010 and 2011. The stands experienced minor defoliation in 2008 and 2009 and more moderate defoliation in 2010 and 2011. In 2011, no major trends in defoliation among the stands were detectable, although our assessment at that point was rapid and qualitative. The worst defoliation occurred in 2012. We explored using the USFS Region 6 Forest Health Protection aerial survey data to examine annual patterns in defoliation for the stands from 2008–2012. However, the data conflicted with our on-the-ground knowledge (e.g., only two stands were shown as highly defoliated in 2012), and we suspect that this was caused by edge errors associated with the scale of data collection. We determined that use of the annual aerial survey data to track temporal patterns in defoliation at the stand scale would not be appropriate.

Experimental design

The experiment is a randomized complete block split-plot design with stand serving as the blocking unit ($n = 6$). Season of burn is the whole plot treatment (fall, spring, and control), and burn interval is the split plot at two levels (one burn 15 years prior or three burns at 5 year intervals prior). Before burning, each stand was divided into three experimental units with boundaries (average size 13 ha) established along roads and topographic features to aid in the control of burn treatments. Treatments (control, spring burn, and fall burn) were then randomly assigned to whole plots. Burns were originally completed in October of 1997 and June of 1998. Six half-acre subplots were then systematically established within each treatment and used for sampling. In 2002,

the experimental units were divided and each half was randomly assigned a 5 or 15 year treatment. Five year interval reburns were conducted in the fall of 2002 and 2007 and spring of 2003 and 2008. Fifteen year interval reburns were planned for the fall of 2012 and spring of 2013, but did not occur prior to sampling for this study.

All fires were ignited by hand-carried drip torches using a multiple-strip head-fire pattern spaced with a goal to maintain an average 60 cm flame length. Temperature, humidity, and wind speed and direction were similar during the application of all burns (Thies et al. 2013), although fuel moisture conditions between spring and fall burns were different. Higher surface fuel moisture occurs during late spring after snow melt, while lower surface fuel moisture conditions occur in the fall. Conditions for the prescribed fires are summarized in Thies et al. (2013).

Sampling

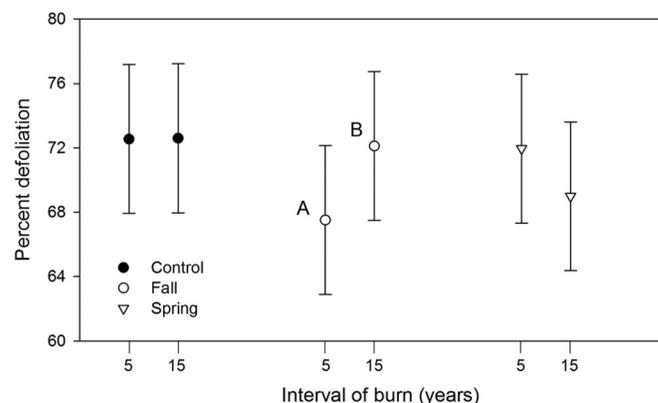
Defoliation sampling was done in 2012 using established plots. Four trees in each plot were systematically chosen for assessment using the plot tree nearest to each cardinal direction as measured from the plot center. The percentage of defoliation was visually assessed to the nearest 10% by ground-based observers. Defoliation was measured in September of 2012, about 2 months after defoliation was complete (Scott 2012). Because this is a long-term permanent plot study, destructive branch samples were not taken for comparison. We made no distinction between old and current-year needles. All observers participated in daily standardization with a technician experienced in ocular estimation of crown symptoms. This method of estimating defoliation has proven to be consistent and accurate to within 10% of defoliation estimates taken from branch samples. Ocular estimates are especially accurate at the defoliation rates of 50% or more experienced in this study (MacLean and Lidstone 1982). Other tree and fire severity data were used for multivariate regression tree analysis. Tree density data were collected in 1998 and 2012 by tallying all plot trees >7.5 cm. Tree diameter breast height (DBH), total height, height of lowest live crown, crown scorch height, and bole scorch height were measured following the initial fires in 1998. Tree diameter was measured with a diameter tape and recorded to the nearest 0.25 cm. Tree heights were measured to the nearest 3.0 cm with a laser hypsometer. Crown scorch was calculated as a percentage of the crown length. Bole scorch was calculated as a percentage of the total tree height. After the initial fires, crown and bole scorch cannot be reliably repeatedly measured. The initial fires were the most severe, resulting in the greatest amount of tree damage and subsequent mortality (unpublished data). In 2008, all trees on the plots were remeasured for DBH and total tree height. Total plot mortality from 1998 to 2012 was summed and the percentage of tree mortality for each plot calculated.

Data analysis

Data were analyzed as a randomized complete block split-plot ANOVA design using the mixed models procedure in SAS 9.2 (SAS Institute Inc. 2008). The response variable was percent defoliation, the main treatment effects (interval of burn and season of burn) were fixed, and block (stand) and block*season were random. During the analysis, model assumptions of normality and equal variance were tested using normal probability plots and plots of residuals (observed versus predicted), respectively. Percent defoliation was not transformed based on these assessments. Overall treatment differences were considered significant at $\alpha = 0.05$ and marginally significant at $\alpha = 0.10$. Where differences exist, P values and confidence limits (CL) were adjusted for multiple comparisons using Tukey's honestly significant difference method. Means and 95% CL are present from the ANOVA results.

We also used nonparametric classification and regression tree analysis to analyze pine butterfly defoliation patterns in relationship to prescribed-fire treatments, burn severity, forest structure,

Fig. 1. Mean pine butterfly defoliation (%) ($\pm 95\%$ confidence limits) of current- and previous-year foliage in relation to season (spring versus fall) and interval (5 versus 15 years) of prescribed burn from six eastern Oregon ponderosa pine stands. Different letters denote marginally statistically significant differences among treatments (Tukey's adjusted).



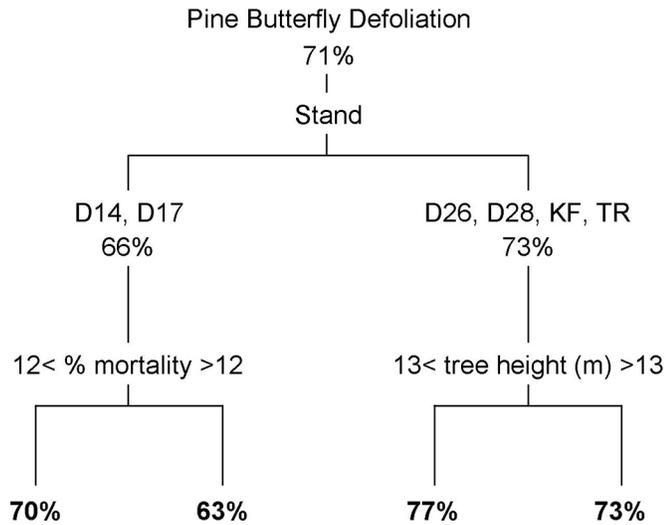
and stand location (Breiman et al. 1984). Regression tree models are decision trees and both descriptive and predictive. They are nonparametric and ideal for capturing relationships that make sense ecologically but are difficult to reconcile with conventional linear models (McCune and Grace 2002; Kerns and Ohmann 2004). Regression tree modeling uses binary recursive partitioning based on reduction in deviance (sum of squares) to split the data into increasingly homogeneous groups. This method first fits an overly large tree that is then "pruned" back using established procedures to remove branches that do not contribute significantly to reduced deviance (Breiman et al. 1984; Clark and Pregibon 1993). For model development, we used 14 independent variables at the plot scale: season of burn (control, spring, and fall), interval of burn (5 and 15 years), stand, 2012 tree density, 2008 average tree height, 2008 basal area, 1998 average crown scorch, 1998 average bole scorch, total tree mortality (since 1998), percentage of tree mortality (since 1998), and heat load ($(1 - \cos(\text{aspect} - 45))/2$). A full model was developed using default settings in S+ 8.2 (TIBCO Software Inc. 2010) (stopping criteria = 0.01, minimum group size = 10, and minimum split = 5). Final optimum model size was selected using the average of 10 sets of 10-fold cross-validation (Clark and Pregibon 1993). The optimum model size is equal to the number of final homogeneous groups referred to as tree nodes. Explanatory power for the model was assessed using proportional reduction in deviance (PRD), which is analogous to the multiple r^2 of regression.

Results

Mean pine butterfly defoliation across the study area was about 71% and ranged from 53% to 87%. Defoliation was lowest in the 5 year interval fall burn and 15 year interval spring burn treatments (Fig. 1). We found a significant interaction between season of burn and interval of burn ($F_{2,15} = 5.54$, $P = 0.016$; Fig. 1) with defoliation marginally lower (Tukey's adjusted $P = 0.10$, difference ranged from 1.2% to 8.0% less defoliation, and average 4.6% based on 95% CL) in the 5 year interval fall burn compared with the 15 year interval fall burn treatments (Fig. 1). All other treatments were statistically similar.

Regression tree analysis results revealed several interesting patterns for pine butterfly defoliation that differed based on stand, percent mortality, and tree height. The regression tree model is displayed graphically and can be read as a decision tree or flow chart (Fig. 2). The undivided data and the overall mean value are at the top of the tree and splits and final nodes are beneath. The model explained 46% of the variability in pine butterfly defoliation using

Fig. 2. Pruned regression tree model results for pine butterfly defoliation from six eastern Oregon ponderosa pine stands ($n = 107$). The model can be read as a hierarchical decision tree or flow chart with the undivided data and the overall mean value at the top of the tree and splits and final nodes beneath. The first split is based on stand location, with two stands forming the left portion of the tree and four stands forming the right portion of the tree. Proportional reduction in deviance (roughly equivalent to r^2) is 0.46. Terminal nodes (mean defoliation for the group) are in boldface type.



three explanatory variables, with a final tree size of four nodes. The first split in the model is based on stand. Two stands (D17 and D14, mean = 66%) had lower defoliation compared with the four other stands (D28, D26, KF, and TR, mean = 73%). At D14 and D17 (left side of the tree), the next split in the tree is based on percent mortality. Plots with more mortality had about 7% less pine butterfly defoliation compared with plots that had less mortality. At the other four stands (right side of the tree), pine butterfly defoliation patterns depended on tree height. Plots with taller trees had about 4% less defoliation.

Discussion

Pine butterfly defoliation was relatively high and surprisingly consistent across our stands and treatments, although we did detect some patterns that explain variability in our results. All plots displayed mean defoliation values $>50\%$, with some values exceeding 85%. Our results show that prescribed burning in the fall or spring 15 years previous or at 5 year intervals does not predispose ponderosa pine stands to increased defoliation during a pine butterfly outbreak. The timing of the latest set of prescribed burns in fall 2007 and spring 2008 coincided immediately before the outbreak beginning in 2008, yet no increase in defoliation was detected in the burned stands. The effect we document is marginally significant, but we found lower defoliation in our 5 year interval fall burns, but only as compared with the 15 year interval fall burns. However, the difference that we found (about 5%) could also be within the margin of sampling error.

The limited impact of season and interval of burn on defoliation patterns may stem from the small size of the treatment areas compared with the massive landscape that was affected by the pine butterfly outbreak. While our treatment areas are operational in size, they are small areas within the larger landscape impacted by the outbreak. Pine butterflies are present in high numbers, are highly mobile, and there is likely strong competition for food. Consequently, they are dispersed over a large area and are feeding on any available host. Had our treatment areas been proportionally much larger, there may have been a more pronounced treatment effect.

Regression tree analysis indicated that the lowest defoliation was found at two stands that had experienced $>12\%$ total mortality over the past 15 years. Past studies have indicated that fall burning is generally more severe and results in more mortality compared with spring burning (Thies et al. 2005). Initially we suspected that this lower defoliation and relationship to mortality was related to lower tree densities. That is, plots that had experienced more mortality were more open, and perhaps either canopy gaps influenced pine butterfly behavior or trees in more open areas may be more vigorous (Kolb et al. 1998). However, we found no relationship between pine butterfly defoliation and tree structure variables such as density, basal area, or stand density index. Indeed, the plots at D14 and D17 that had low defoliation exhibited a range of values for these forest structure variables. It is possible that repeat burning in the fall may alter other aspects of forest structure (tree distribution or tree canopy architecture), or the physical environment within the stand that we have not measured, and that this unmeasured aspect may better explain our results. The patterns we detected might also be less related to forest structure and more related to changes in remnant tree vigor in plots that experienced more mortality. While repeat fall burning and subsequent tree mortality may not have greatly altered forest structure, areas burned in the fall did experience significantly more immediate and delayed tree mortality (Thies et al. 2005). It is possible that remnant trees might have experienced a change in resource availability and increased tree vigor or growth owing to this mortality. Evenden (1940) found that, in central Idaho, trees with high growth rates prior to a defoliation event were better able to recover from defoliation and experienced less mortality. We have evidence that areas burned in the fall have higher growth rates during the second 5 year postfire period relative to the first 5 year postfire period (data from 1998 to 2007) (Thies et al. 2013). However, this result was found for both burn intervals. It is also possible that repeat burning reduces competition from the understory, which might also lead to an increase in tree vigor. However, understory results from prior studies do not support this (Kerns et al. 2006, 2011).

Regression tree analysis indicated that four stands had higher than average pine defoliation. Thus, we might expect higher future tree mortality within these stands. For these stands, plots with taller trees (>13 m) had slightly lower defoliation. Trees taller than 13 m in the study area tended to be scattered older canopy-dominant or co-dominant trees. Evenden (1940) noted that, in central Idaho, the tall mature trees were defoliated in the beginning of the outbreak, but in subsequent years the defoliation was largely confined to smaller trees. The mature trees in our study area were possibly defoliated in 2008 and have partially recovered and that the defoliation event is now focused on smaller less mature trees, or the pattern may simply reflect pine butterfly behavior (e.g., feeding across the denser canopy at lower heights).

Studies that compare pine butterfly defoliation with subsequent mortality are limited for pine butterfly in western ponderosa pine stands. However, Evenden (1940) noted that, in central Idaho, mortality only occurred in severely defoliated trees (75–100% defoliation). Twenty-nine percent of our plots (31 out of 107) had defoliation values 75% or greater. Earlier reports of ponderosa pine mortality associated with the pine butterfly occurred in unmanaged mature stands in conjunction with western pine beetles (Hopkins 1908; Evenden 1940). It is unknown what mortality, if any, to expect in our mixed-age managed stands, and whether the small treatment difference we detected will significantly impact future mortality or subsequent bark beetle attack and mortality. While there are larger diameter trees in our stands, the majority are smaller and less desirable to western pine beetles, which usually attack mature, slow-growing, or diseased trees (DeMars and Roettgering 1982). Currently, western pine beetle populations in the area are low (Flowers et al. 2012). If these stands do experience mortality or significant top kill it is more likely to

result from infestation by the pine engraver *Ips pini* (Say) or *Ips emarginatus* (LeConte), which have shown both a preference for trees of smaller diameter and insect-defoliated pines (Dewey et al. 1974).

Conclusion

Our data provide information about a relatively rare event that is rarely studied — a widespread and severe pine butterfly outbreak in ponderosa pine. We examined pine butterfly defoliation patterns in relation to season of burn and interval of burn. Our results suggest that (i) prescribed burning in the fall or spring 15 years previous, or repeat burning at 5 year intervals, does not predispose ponderosa pine stands to increased defoliation during a pine butterfly outbreak and (ii) areas repeatedly burned at 5 year intervals in the fall may experience slightly less defoliation (about 5%) as compared with areas that only burned once 15 years prior in the fall. However, the effect we detected was small, marginally significant, and should be interpreted with caution, particularly (ii). For some stands, season and interval of burn may alter pine defoliation patterns by altering mortality patterns. Areas that experience more mortality from repeated fall burning may experience less defoliation. In other stands, tree height appeared to be important as trees greater than about 13 m experienced less (about 4%) defoliation compared with shorter trees. Future data collection in these stands will allow us to examine subsequent mortality patterns and potential interactions with bark beetle attacks.

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