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Post-fire epicormic branching in Sierra Nevada *Abies concolor* (white fir)

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Abstract. In California's mixed-conifer forest, which historically had a regime of frequent fires, two conifers, *Sequoiadendron giganteum* and *Pseudotsuga menziesii*, were previously known to produce epicormic sprouts from branches. We found epicormic branching in a third mixed-conifer species, *Abies concolor*, 3 and 4 years after a wildfire in the central Sierra Nevada Mountains of California. Sprouting occurred only from the boles. We investigated (1) whether the degree of crown loss and the extent of epicormic branching were independent; and (2) whether epicormic branching differed by tree size. The vertical extent of epicormic foliage increased with increasing severity of crown loss. There was a significantly greater proportion of large diameter-class (>50 cm diameter at breast height [dbh]) trees with epicormic branching than small/medium diameter-class (25–50 cm dbh) trees. These results suggest large diameter *Abies concolor* may survive high levels of crown loss, aided by crown replacement through epicormic branching, but that reiterative green foliage may not appear for up to 3 years after fire damage. If this response is widespread, it would suggest some 'dying' trees logged under current salvage guidelines could survive, and that higher-intensity fire may substantially reduce the density of small post-fire suppression white fir, while retaining many larger overstory trees.

Additional keywords: California; mixed conifer; salvage logging; traumatic crown reiteration.

Introduction

Epicormic branching can be an important mechanism by which trees maintain or reestablish photosynthetically active foliage as leaves senesce or following crown damage. In general, crown reiteration by epicormic branching has been divided into three types: opportunistic, adaptive, and traumatic (Bégin and Filion 1999). Opportunistic reiteration occurs when epicormic branches are produced by dormant buds on a tree's main stem in response to increased light intensity from thinning, pruning, or windthrow, and is much more common among angiosperms than gymnosperms (Kramer and Kozlowski 1979). Adaptive reiteration occurs continually within the existing crown, allowing rejuvenation of crown foliage and structure. It has been documented in two conifers, *Pseudotsuga menziesii* (Douglas-fir) (Ishii *et al*. 2002) and *Picea mariana* (black spruce) (Bégin and Filion 1999). Traumatic reiteration is a direct response to severe crown loss produced by events such as fire, insect damage, or breakage of the bole or large branches. In these cases, the tree's crown is recreated through the bursting of dormant buds or dedifferentiation of growing axes (Bégin and Filion 1999). Traumatic reiteration has been found in *Picea mariana* due to breakage (Bégin and Filion 1999), *Abies balsamea* (balsam fir) and young *Picea glauca* (white spruce) after defoliation from spruce budworm (Carroll *et al*. 1993; Piene and Eveleigh 1996), *Chamaecyparis nootkatensis* (Alaska cedar) after severe crown loss believed to be caused by environmental stress (Shaw 1985), and after fire in *Pinus rigida* (pitch pine) (Stone and Stone 1943).

Historically, the disturbance regime in the Sierra's largest forest type, mixed conifer, was predominantly low-severity frequent fires, with patchy occurrence of moderate- and high-severity fire. Traumatic reiteration following crown loss due to fire has been previously documented in only one Sierran species, *Sequoiadendron giganteum* (giant sequoia) (Stephens and Finney 2002). Crown fires did occur before fire suppression (Russell *et al.* 1998), but we do not know whether any other Sierran species are adapted to severe crown loss.

In June 2004, we discovered epicormic branching on the boles of white fir (*Abies concolor* [Gord. and Glend.] Lindl.)

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Fig. 1. Epicormic branching on a >50 cm diameter at breast height *Abies concolor*, July 2005.

within a severely burned area in the Tahoe National Forest (Fig. 1). Our goal in the present study was to compare the relative density of white fir with epicormic branching between two size classes, and compare the percentage of the tree bole with sprouts to the extent of crown loss. We used percentage remaining green crown as an indirect measure of fire effects on a tree, which can include bole heating, foliage loss, insect attack, and physiological stress (Ryan and Reinhardt 1988; Stephens and Finney 2002; McHugh and Kolb 2003; van Mantgem *et al*. 2003).

We examined two hypotheses: (1) vertical extent of epicormic branching is significantly associated with percentage crown loss; and (2) larger diameter-class trees have significantly more epicormic branching than smaller diameter-class trees across different levels of bole scorch. We wanted to examine whether white fir compensate for greater crown damage with increased sprouting up to a threshold of crown loss (hypothesis 1). We were also interested in whether epicormic sprouting varies by tree size (hypothesis 2), which we assessed by comparing the relative density of live, epicormic white fir (the ratio of live, sprouting trees to all trees, live and dead) between two size classes at three different levels of bole scorch.

Methods

Our study was conducted in areas burned by the Star fire, a wildland fire that occurred in August and September 2001. Our study site is 1650–1900 m in elevation, in mature mixed-conifer forest within the Duncan Canyon Inventoried Roadless Area in the Tahoe National Forest (39°7′N 120°72′W). The fire burned in a mosaic pattern of varying severity across ∼7000 ha of mixed-conifer and red fir (*Abies magnifica*) forest.

To address our first hypothesis, that the extent of epicormic response is associated with the degree of crown loss, in August 2004 (3 years post fire) we visually assessed individual white fir in four categories of remaining green crown (50–69%, 30–49%, 15–29%, and 5–14% of total tree height) and epicormic branching (1–14%, 15–29%, 30–49%, or 50–69% of total tree height, with the extent of epicormic branching measured as the vertical length from the lowest epicormic branch to the highest). Only trees with some level of epicormic branching on their boles were recorded. All epicormic trees within 10–15 m of the trail traversing Duncan Canyon were included until sufficient sample size was reached for analysis using a Chi-square R × C independence test, resulting in a total of 158 trees.

Remaining green crown of live trees was recorded for each tree at two distances and from two different directions, recording linear green crown length as a proportion of total tree height within categories (e.g. 5–9%, 10–14%, 15–19%). In an effort to conservatively record the data, if an estimate fell on the boundary between two categories, it was entered into the category with higher remaining green crown.

The accuracy of the visual estimates was assessed by sampling 11 individual trees and comparing visual estimates to those recorded with a laser hypsometer. Visual estimates were within 1–2% of hypsometer data for 10 of the 11 trees, and were within 4% of hypsometer readings for one tree. In all 11 cases, the visual method and the hypsometer placed trees within the same category of remaining green crown. We chose to measure remaining green crown, as opposed to measuring crown scorch directly, owing to the difficulty in estimating crown scorch several years post fire, after most or all dead needles had fallen to the ground.

To address our second hypothesis, that epicormic branching would vary by tree size, twenty-four 0.04 ha plots were established in the study site in 2004 and 2005 to determine the relative density of epicormic trees in two size classes of white fir, 25–50 cm and >50 cm in diameter at breast height (dbh), at three levels of bole scorch, 10–29% (low scorch), 30–49% (moderate scorch), and 50–69% (high scorch) of total tree height. We did not include a fourth bole scorch category (70–89% of total tree height) because observations consistently found no surviving white fir in this category of high fire severity. All plots meeting these criteria were included along a 9 km section of a hiking trail traversing the burned portion of the Duncan Canyon Roadless Area until eight plots were obtained in each of the three scorch categories, for a total of 24 plots.

Plots were spaced at least 35 m apart (greater spacing occurred where landscape features, such as brushfields, separated potential plots). The number of trees 25–50 cm dbh and >50 cm dbh exhibiting epicormic branching, as well as live non-epicormic trees and dead trees, were recorded in each plot. All trees with epicormic branching were counted regardless of the extent of sprouting on a given tree. We were interested in the effects of epicormic branching with respect

Table 1. Extent of epicormic branching in white fir with different levels of crown scorch (expressed in numbers of trees)

Epicormic branching (% of total tree height)	Remaining crown (% of tree height)			
	50–69	30–49	15–29	5–14
1–14	33	9	0	1
15–29	1	21	8	1
30–49	0	7	30	7
50–69	0	0	11	29

Table 2. Ratio of epicormic trees to total tree density (all live and dead trees) for two diameter classes of white fir within eight plots in each of three categories of bole scorch

dbh, diameter at breast height. Values in parentheses are standard deviations.

Bole scorch (% of total tree height)	Tree size class (dbh in cm)	
	25–50	>50
10–29	0.27 (0.15)	0.29 (0.45)
30–49	0.36 (0.13)	0.71 (0.21)
50–69	0.12 (0.11)	0.54 (0.29)

to canopy structure, and so did not include understory trees <25 cm dbh.

We analyzed the effect of size class within the three scorch categories using ANOVA (SAS 8.0; SAS, Cary, NC, USA), analyzing diameter class as a split-plot factor and bole scorch as the main plot factor. All data used were current as of the summer of 2005. Of the epicormic trees initially observed in the plots in 2004, only one had died by the summer of 2005.

Results

Percent classes of remaining crown and epicormic branching on the 158 individual trees sampled were not independent ($\chi^2 = 208.05$, d.f. = 9, $P < 0.0001$). Most trees with high levels of remaining crown had less extensive epicormic branching, whereas highly scorched trees with little remaining crown had epicormic branching along a greater percentage of their bole (Table 1).

For the second hypothesis, across the 24 plots the mean ratio of live, epicormic trees to total stem density (all live and dead trees) was higher for trees >50 cm dbh than for those 25–50 cm dbh, except in the 10–30% bole scorch category (low scorch) (Table 2). In the low scorch category, only 40% of all trees without epicormic branching were snags, whereas 89% of all trees without epicormic branches were snags in the 30–50% bole scorch category (moderate scorch), and 97% of all trees without epicormic branches were snags in the 50–70% bole scorch category (high scorch). In low scorch plots, median remaining green crown was 35–40% of total tree height, whereas the median green crown was 15–20% of total tree height in the moderate and high scorch categories. In the moderate scorch plots, 83% of epicormic trees

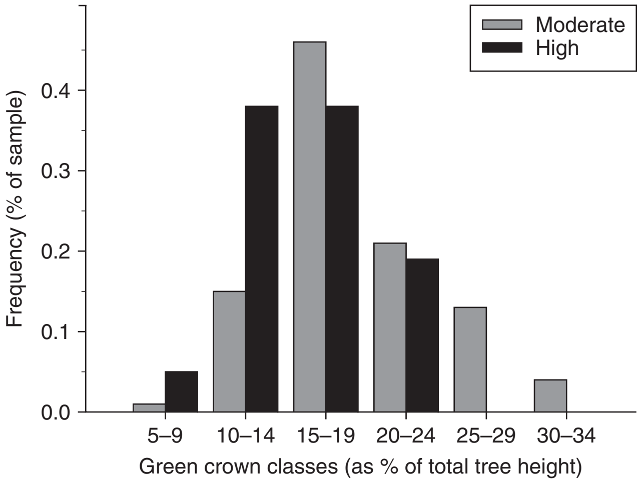

Fig. 2. Relative frequency of epicormic white fir by remaining green crown classes in moderate and high scorch plots.

had remaining green crown on less than 25% of total tree height, and in high scorch plots, 81% of epicormic trees had remaining green crown on less than 20% of total tree height (Fig. 2).

The fact that most live trees in the low scorch plots had no epicormic branches, and many of the plots had no epicormic trees at all, resulted in very high variance in this category, particularly for large trees. As a consequence, the ANOVA assumption of homogeneity of variance for the diameter class factor could not be met with the low scorch category included. In addition, given that 89–97% of live trees in the moderate and high scorch plots had epicormic sprouts, there was a distinct qualitative difference between low scorch and moderate/high scorch plots. At low scorch, the proportion of live, epicormic trees decreased despite an overall increase in tree survival (e.g. 98% survival for trees >50 cm dbh), whereas the overall proportion of epicormic trees declined in the high scorch category, relative to moderate scorch, owing to increased mortality from fire.

When only moderate and high scorch plots were included in the ANOVA analysis, there was a highly significant difference between the two diameter classes in terms of the relative density of epicormic trees (i.e. the ratio of surviving trees with epicormic branches to total stem density [$F = 27.91$, $P < 0.0001$]). In both the moderate and high scorch categories there was a significantly higher relative density of large epicormic trees than small/medium-sized (<50 cm dbh) epicormic trees (Tukey pairwise t-test [$P = 0.05$]). In addition, there was a significant effect of bole scorch ($F = 9.46$, $P = 0.0082$) on the proportion of live, epicormic trees, with a smaller proportion of such trees in the high scorch category, as might be expected from increased mortality. This effect was significant only for the 25–50 cm dbh size class (Tukey test, $P = 0.05$). There was no significant interaction between scorch level and diameter class ($F = 0.27$, $P = 0.6119$).

Discussion

Epicormic branching is most common in species exposed to increased light and temperature created by moderate disturbances such as gap-phase replacement (Stone and Stone 1943; Kramer and Kozlowski 1979). Ponderosa pine and mixed-conifer forests in the Sierra Nevada, however, are believed to have had a frequent low-severity fire regime, though patches of higher-severity fire may have been important for shaping forest gap patterns and facilitating regeneration of some species such as giant sequoia. Historically, high-severity fire would have occurred in Sierra Nevada mixed-conifer forests particularly during extreme weather events; however, how often and extensive these fires were is still being debated (Minnich *et al.* 2000; Stephens *et al.* 2003). Traumatic reiteration in conifers following fire is rare and we are only aware of two conifer species in which it has been previously documented, *Pinus rigida* (Stone and Stone 1943) and *Sequoiadendron giganteum* (Stephens and Finney 2002).

Though white fir has been found to be less fire-resistant than some other Sierra Nevada conifers (Stephens and Finney 2002), our observations suggest that individuals that survive their fire-related injuries can compensate for crown loss through epicormic branching. Our findings are limited to one fire event and more extensive surveys are needed to determine how pervasive this phenomenon may be among white fir. Epicormic branching in white fir increased with increasing crown loss. This result is consistent with the theory that such sprouting is an example of traumatic reiteration, which enables trees to survive after severe crown loss due to fire (Stone and Stone 1943). Cosens (1952) documented opportunistic epicormic branching in white fir in which the lower 20–40% of the crown had been pruned. He concluded that epicormic branching is associated with increased sunlight (from pruning) and the small diameter of the tree at the time of pruning (trees averaged 9–15 inches [22–37 cm] dbh, depending on plot). The study did not, however, discuss whether trees with 40% crown removal showed more sprouting than trees with 20% removal. Our results suggest that following fire, traumatic reiteration is associated with the level of crown loss, and occurs in both small and large white fir. We visually inspected trees with epicormic branches on the edge of several openings (either brushfields or edges of stand-replacement patches) but observed no discernable difference in the density of epicormic branches between the sunny and the shaded side of the tree boles. In addition, we observed no epicormic branching on trees with no crown scorch.

There are at least two main limitations to our study. First, our data comes from only one fire, and we cannot say whether similar results can be expected in other fire areas in the Sierra Nevada. As such, these results should be interpreted with caution. Second, we do not know what the long-term survivorship of epicormic trees will be. We considered the possibility that epicormic sprouting may be a last flush of foliage before the tree dies from stress or pest and pathogen damage. However, in 2005 when we resurveyed trees in the 2004 plots, there was only one newly dead tree. Epicormic sprouts we had observed the previous year appeared healthy, and had elongated and added a new branching node. To date (4 years after the fire) all but one of the epicormic trees seem to be thriving.

White fir was the predominant conifer species in our study area, but several other species were present, including incense-cedar (*Calocedrus decurrens* [Torr.] Floren.), sugar pine (*Pinus lambertiana* Dougl.), ponderosa pine (*Pinus ponderosa* Laws.), red fir and Douglas-fir. No epicormic branching, however, was observed on the boles of these species, despite high levels of crown loss in some stands. In some conifer species, such as ponderosa pine, terminal buds may survive in portions of the crown where foliage is otherwise killed (Harrington 1987; Swezy and Agee 1991), allowing the tree to recover crown foliage even after high levels of crown scorch. Douglas-fir showed some evidence of epicormic branching on limbs but not on the boles of the trees. In white fir, however, epicormic branching was observed only on tree boles.

In our study area, the density of trees with epicormic branching was relatively high in moderate- and high-severity burn patches, with $\sim$210 stems/ha $>$25 cm dbh. The percentage of a tree's bole with sprouts also increased as remaining green crown decreased. These findings suggest white fir may be capable of developing new branch structure even after high levels of crown damage. All epicormic branches initially observed in 2004 were bright green and generally 3–5 cm in length with only one node, indicative of new growth. By July 2005, epicormic branches on the same trees were generally 10–17 cm in length, with two nodes visible, though some apparent 2005 sprouts were also observed (3–5 cm in length, with only one node) on trees amidst the sprouts presumably from 2004. We observed no epicormic branching in the study area in 2003, but in July 2005 we did locate two trees that had epicormic branches 30–35 cm in length with three visible nodes, indicating that sprouting on these two trees may have begun 2 years post fire in 2003.

If other studies also find that large white fir commonly produce epicormic branches, this would suggest mature white fir can survive and continue to be prevalent in mixed-conifer composition even with higher-intensity fires, except where bole scorch generally exceeds 70% of total tree height. Our results indicate, however, that small- and medium-sized white fir, which have become denser in many areas since fire suppression, are greatly reduced by higher-intensity fire, leaving widely spaced, epicormic overstory trees. These open, high-light conditions may facilitate regeneration of shade-intolerant pine species, while retaining large, old white fir.

Forest Service salvage guidelines allow harvesting of most conifers with $>$65% crown height scorch because some studies have found low survivorship at this level of damage generally in small trees (Cluck and Smith 2001). Our results suggest that post-fire survivorship among white fir could be maintained through traumatic crown reiteration, particularly for larger trees. In our 16 moderate and high scorch plots, 71% and 54% respectively of all white fir >50 cm dbh were alive and producing epicormic branches 4 years post fire with remaining green crown on only 10–20% of total tree height. This is generally consistent with Stephens and Finney (2002), who found that survival rates increased with diameter, given equal crown scorch. In that study, at 75% crown volume scorch, ~40% of white fir with a dbh of 25 cm survived, whereas ~70% of white fir with a 50 cm dbh survived. Even higher rates of survival were found for incense-cedar and ponderosa pine with 50 cm dbh at the same level of crown scorch.

Our study did not examine the physiological response of white fir to crown scorch, so we can only speculate on the mechanisms that might produce epicormic sprouts. One hypothesis that might explain the 3-year delay is that the epicormic sprouts may not have come from dormant buds. Heavily scorched white fir may need to dedifferentiate cambial tissue and differentiate it into new buds along the scorched bole (e.g. Kramer and Kozlowski 1979). These buds, which eventually produce the epicormic sprouts, would take time to develop. Stored photosynthate may need to drop below a threshold level before cambial tissue is differentiated into buds that can produce epicormic sprouts. Other factors, such as edaphic conditions and post-fire precipitation patterns, may also affect the extent of the delay between the fire and sprout development.

Post-fire tree mortality is affected by many factors. Crown loss may be the best general indicator of post-fire conifer survival rates (Ryan *et al*. 1988; Stephens and Finney 2002), but mortality can also occur from other less visible causes such as cambial damage from long duration duff and litter burning (Peterson and Ryan 1986; Ryan and Reinhardt 1988). Long-term studies could reveal whether additional delayed mortality occurs and whether epicormic branches fully reiterate crown structure. Further research is needed to understand both the physiological responses triggering epicormic branching in white fir, and the tree characteristics associated with traumatic reiteration.

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