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ARTICLE

Traumatic resin ducts as indicators of bark beetle outbreaks

R. Justin DeRose, Matthew F. Bekker, and James N. Long

Abstract: The formation of traumatic resin ducts (TRDs) represents an important induced defense in woody plants that enhances oleoresin production and flow in response to environmental perturbations. In some genera (*Pinus*), resin ducts are copious and conspicuous; however, in others (*Picea*), resin ducts are relatively rare. The occurrence and strength of resin ducts, in particular TRDs, in annually resolved rings could be used to reconstruct mechanical damage associated with natural disturbances. We analyzed tree-ring data from paired live and dead Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) that recently experienced a spruce beetle outbreak. The presence of TRDs, defined as resin ducts aligned tangentially and arranged compactly, indicated mechanical damage associated with epidemic spruce beetle (*Dendroctonus rufipennis* (Kirby)) populations. TRD prevalence during the outbreak was significantly higher than over tree lifespans. All other metrics characterizing tree vigor (diameter, age, ring width, and basal area increment) were not significantly different between live and dead trees, suggesting that the inherent capability to produce TRDs that can "pitch out" attacking spruce beetles could be the primary mechanism by which Engelmann spruce survived the outbreak. Because TRD production in our Engelmann spruce was exceedingly rare, this discovery represents a new line of tree-ring-based evidence that can be used to reconstruct other spruce beetle outbreaks.

Key words: bark beetles, dendrochronology, *Dendroctonus rufipennis*, disturbance, resin canals, resin ducts, traumatic resin ducts.

Résumé : La formation de canaux résinifères traumatiques (CRT) constitue un important moyen de défense induit qui augmente la production et l'écoulement d'oléorésine en réaction aux perturbations environnementales chez les plantes ligneuses. Chez certains genres (*Pinus*), les canaux résinifères sont abondants et évidents. Cependant, chez d'autres genres (*Picea*) ils sont relativement rares. L'occurrence et l'intensité des canaux résinifères, plus particulièrement les CRT présents dans les cernes annuels, pourraient être utilisées pour reconstituer les dommages mécaniques associés aux perturbations naturelles. Nous avons analysé des données dendrochronologiques provenant d'épinettes d'Engelmann (*Picea engelmannii* Parry ex Engelm.) mortes et vivantes appariées, frappées récemment par une épidémie de dendroctone de l'épinette (*Dendroctonus rufipennis* (Kirby)). La présence de CRT, canaux résinifères tangentiellement alignés et disposés de façon compacte, indiquait la présence de dommages mécaniques associés aux populations épidémiques de dendroctone de l'épinette. La présence de CRT durant l'épidémie était significativement plus élevée qu'au cours de la durée de vie des arbres. Toutes les autres mesures qui caractérisent la vigueur des arbres (le diamètre, l'âge, la largeur des cernes annuels et l'accroissement en surface terrière) n'étaient pas significativement différentes que les arbres soient morts ou vivants, ce qui indique que la capacité inhérente de produire des CRT capable de stopper les dendroctones qui attaquent les arbres pourrait constituer le principal mécanisme qui permet aux épinettes d'Engelmann de survivre aux épidémies. Parce que la production de CRT chez nos épinettes d'Engelmann était très rare, cette découverte offre un nouvel élément de preuve fondé sur les cernes annuels qui peut être utilisé pour reconstituer d'autres épidémies de dendroctone de l'épinette. [Traduit par la Rédaction]

Mots-clés : scolytes, dendrochronologie, *Dendroctonus rufipennis*, perturbation, canaux résinifères, canaux résinifères traumatiques.

Introduction

Plants exhibit a wide array of constitutive and induced defenses that have evolved to improve survival to environmental perturbations (Krokene 2015). One constitutive line of defense common to the Pinaceae is the production of resin ducts in the xylem by the secondary meristem. A related, commonly induced response to mechanical damage is the production of traumatic resin ducts (TRDs) in the xylem (Lombardero et al. 2000) (Fig. 1). Not to be confused with the "baseline" production of constitutive resin ducts (CRDs), TRDs are conspicuous as a tangentially aligned, compact arrangement of ducts, and TRD formation has been noted in Pinaceae in response to specific disturbances such as fire (Arbellay et al. 2014; Hood et al. 2015), defoliation (McKay et al. 2003), and geomorphological events, i.e., rock fall impact, or snow avalanches (Stoffel 2008; Schneuwly et al. 2009). While CRDs have been used to indicate bark beetle attack in the genus *Pinus* (Ferrenberg et al. 2014), and may indicate lower mortality in response to beetle attacks (Kane and Kolb 2010), rare occurrence in the other Pinaceae species makes them difficult to assess. The increased size (diameter or volume) and density of TRDs compared to CRDs bolsters increased oleoresin transport to damaged areas (Lombardero et al. 2000), which may play a role in helping trees respond to bark beetle attacks. The occurrence of TRDs within an annual ring, therefore, might be useful for determination and (or) reconstruction of other disturbances (e.g., bark beetle outbreaks) in different species. We document the occurrence, strength, timing, and synchrony of TRD formation in *Picea engelmannii* Parry ex Engelm. (Engelmann spruce (ES)) that experienced a recent, landscape-wide *Dendroctonus rufipennis* (Kirby) (spruce beetle (SB))

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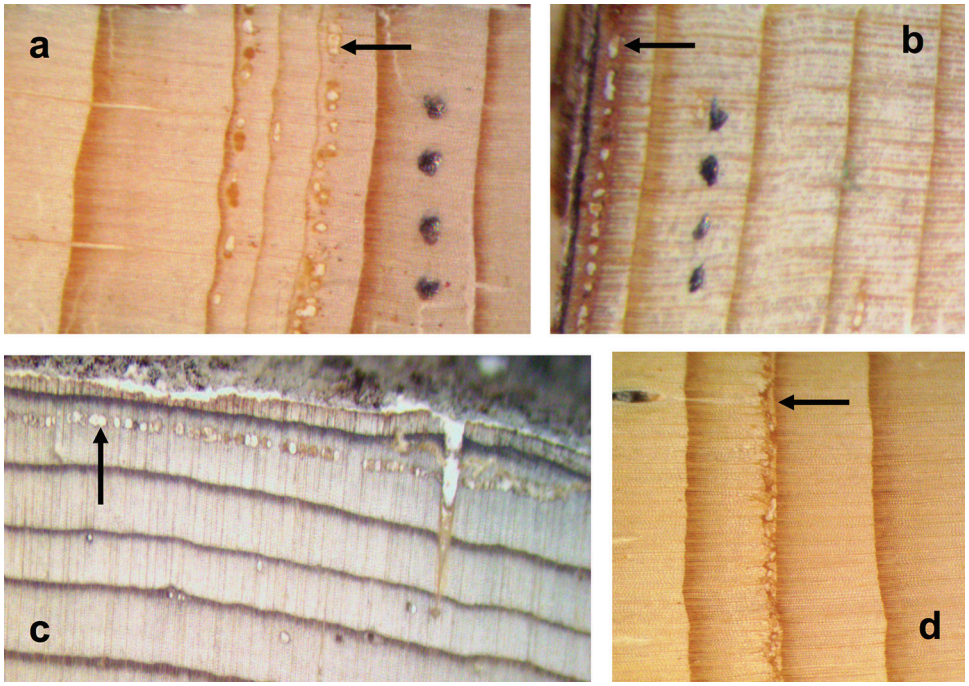
Fig. 1. Examples of traumatic resin ducts in Engelmann spruce (*Picea engelmannii*). (*a*) Live tree; note the traumatic resin ducts in 2001 followed by ring-width release. (*b*) Traumatic resin ducts in a dead tree; date of death was 2001. (*c*) Partial view of an Engelmann spruce cross-section showing tangential rows of traumatic resin ducts from spruce beetle (*Dendroctonus rufipennis*). (*d*) Traumatic resin ducts look distinctly different from frost rings in Engelmann spruce. Direction of xylogenesis in Figs.1*a*, 1*b*, and 1*d* is from right to left and in Fig. 1*c* is from bottom to top. Four pencil dots indicate the year 2000.



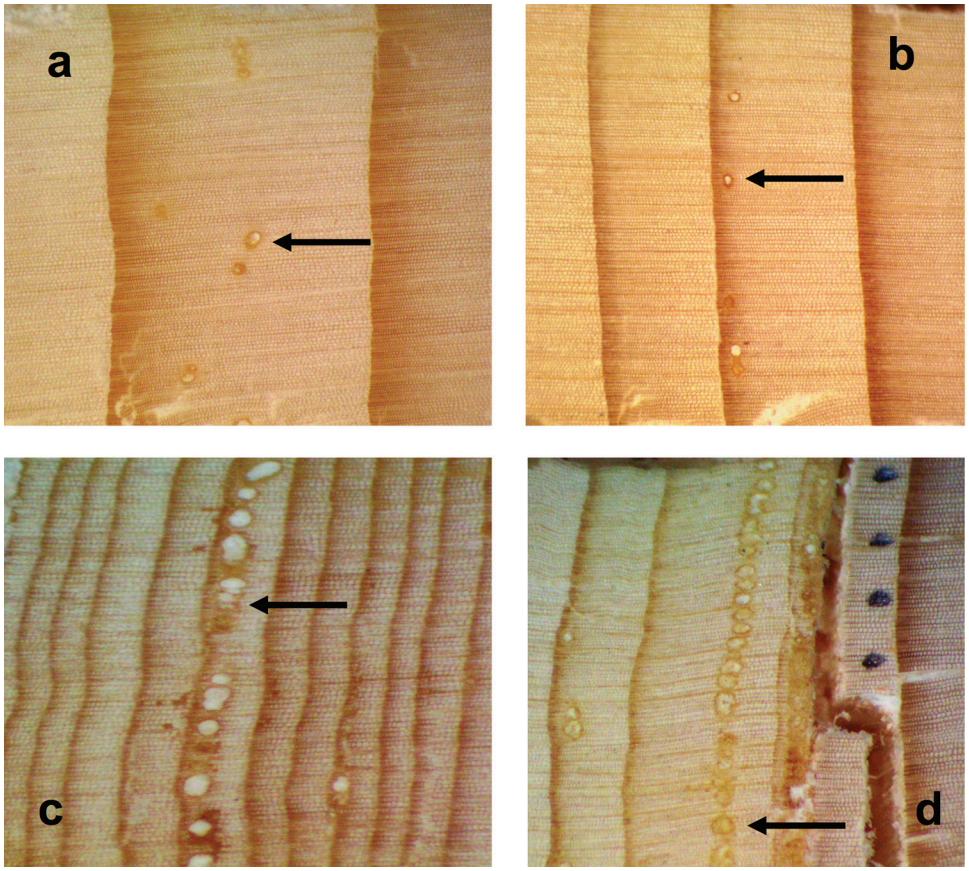
outbreak. Multiple lines of evidence indicate that TRDs formed in response to SB, and therefore, we document the potential for using TRDs to reconstruct past SB outbreaks.

CRDs are formed normally as a part of secondary xylogensis and their occurrence varies by species (Krokene 2015). While resin ducts are a common feature of the *Pinus* spp. of Pinaceae, non-*Pinus* spp., such as *Picea* spp., produce limited CRDs, which appear in the middle-earlywood and latewood and are similar in diameter to tracheids (Markstrom and Alexander 1984). Previous work has shown that similar to CRDs, TRD formation in *Picea* spp. is also rare and typically occurs in response to an environmental perturbation or "event" (Nagy et al. 2000; McKay et al. 2003; Schneuwly et al. 2009). TRDs are much larger and more conspicuous than CRDs (Safranyik et al. 1983; Stoffel 2008), easily identified using the naked eye as a thin, dark band in the annual ring (Krokene 2015). Given the event-specific formation of TRDs and the overall rarity of CRDs, TRD occurrence might indicate past mechanical damage such as attacking SBs. While TRD characteristics per se might not necessarily reveal anything regarding environmental conditions during an outbreak, their occurrence in crossdated annual rings could specifically detail timing (Stoffel 2008; Stoffel and Hitz 2008), although some work has indicated that wound formation during the dormant season (Gärtner and Heinrich 2009) and at different portions of the stem (Angers et al. 2017) may influence precision of dating. Additionally, synchrony in TRD timing across multiple ES might reveal the extent of past SB activity. However, to use TRD formation in ES as a proxy for past SB activity, it must first be demonstrated that ES develops TRDs in response to a SB attack (Berryman 1972).

Sometime between May and August (Schmid and Frye 1977; Safranyik et al. 1983), pioneering female SBs enter ES by excavating through the bark into the phloem, bringing with them a multitude of symbionts (Paine et al. 1997), which act synergistically to overcome host defenses (Krokene 2015). Fungal symbionts have been shown to pre-treat xylem so as to be conducive to SB larvae feeding (Six and Bentz 2003). If the phloem is determined to be suitable, the pioneering beetles emit pheromones that initiate secondary attraction, congregating additional attacking SBs and resulting in a mass-attack (Schmid and Frye 1977). SBs mechanically wound ES by puncturing the secondary meristem (Krokene 2015). Vigorous trees are capable of an almost immediate response via increased oleoresin flow through CRDs, which likely provides baseline protection against an endemic SB population and can rapidly initiate the development of TRDs (1 day to 3 weeks: Safranyik et al. 1983). With extensive resinosis, ES may "pitch out" attacking beetles somewhere between 3 and 6 weeks after wounding, oftentimes evident by resin emerging from excavation holes (Schmid and Frye 1977). Alternatively, nonvigorous ES may not adequately respond to the attack, which could be due to elevated SB numbers or SB attack early in the growing season prior to xylogenesis (Safranyik et al. 1983). The pioneering SB lays eggs, and the larvae will subsequently excavate the phloem, ultimately killing the tree. Therefore, while CRDs may provide baseline protection from pioneering beetles, if ES forms TRDs in response to a SB mass attack and successfully pitches out the beetle, the TRDs ought to be evident within the annual ring that the beetles entered the tree. However, if the tree succumbs to the SBs, we would expect TRDs, if formed at all, to be located in the last ring.

In the aftermath of a large and severe SB outbreak on the Markagunt Plateau, southwestern Utah, we quantify possible attributes indicating tree vigor (age, ring width) and also the TRD characteristics of rare, surviving ES paired with dead trees of the same diameter to explore possible reasons why some trees survived the outbreak and how we can use this information to document past events. We found that strong TRDs most likely indicate mechanical damage caused by epidemic SB populations, whereas weaker TRDs may indicate nonepidemic SB activity. We compare previously reconstructed SB activity based on ring-width releases (DeRose and Long 2012*b*) to the occurrence of pre-outbreak TRDs. Because our ES (and the *Picea* genus, generally) rarely exhibit

Fig. 2. Guide to the determination of the strength of resin ducts and their position in the annual ring in Engelmann spruce (*Picea engelmannii*). (*a*) Strength = 0, position = middle-earlywood. (*b*) Strength = 1, position = latewood. Both 0 and 1 were considered "baseline" resin duct production. (*c*) Strength = 2, position = latewood. (*d*) Strength = 3, position = earlywood. Both 2 and 3 were considered traumatic resin ducts and are reported to be the result of mechanical damage from spruce beetles (*Dendroctonus rufipennis*). Direction of growth is from right to left in all panels. Four pencil dots indicate the year 2000.



TRDs, we suggest that their formation in annual rings, in multiple trees across stands and landscapes, provides strong proxy evidence for reconstructing past SB outbreaks.

Methods

Previous research detailed the sampling method by which the increment cores used in this study were collected (DeRose and Long 2012*a*). Briefly, a stratified-random sampling design with a randomly located starting point was used to establish plots to characterize ES-dominated forests following a SB outbreak (DeRose and Long 2012*b*). Of 637 ES sampled, 31 (~4.8%) survived the beetle outbreak. The remaining 606 trees died during the outbreak, indicated by SB emergence holes in the bark, the presence of SB galleries inside the bark, and the presence of vertical gallery scars. In other words, any live tree encountered on this landscape represented the very rare situation of having not succumbed to spruce beetle attack. In addition to status (live or dead), diameter at breast height (DBH) was measured for each tree on a plot, and an increment core (using either a 4.3 or 5.15 mm diameter borer) was removed as close as possible to the root collar to determine establishment age.

We retrospectively paired 30 of the 31 live ES to a dead tree from the same stand by matching similar DBHs. One tree was removed from our analysis because annual ring visibility was compromised by decay. DBH was chosen to pair trees because of its relationship to bole surface area, which is where pioneering beetles feed. Although in this retrospective study we could not experimentally control the distance between paired trees, we could minimize variability in attack timing by assigning the pairs within individual stands. Given the magnitude, severity, and extent of the outbreak (DeRose and Long 2007, 2012*a*, 2012*b*), it is likely that this represents the best possible pairing of the data. Of these 30 samples, there were at least two from every site across the ~250 km^2 landscape characterized in DeRose and Long (2012*b*).

Increment cores were sanded and crossdated using the marker year approach (Yamaguchi 1991) and digitized using a microscope and a sliding stage. Ring-width dates were verified using the program COFECHA (Holmes 1983) with an updated ES chronology located on the Markagunt Plateau (Briffa et al. 1992). On each increment core, we noted (*a*) inner-ring year, (*b*) outer-ring year, which was assigned as the date of death (DOD) for dead trees, (*c*) whether the outer ring was partially formed or fully formed, and (*d*) the presence and strength (see below) for every year that exhibited more than one "traumatic" resin duct over the life of the tree (Fig. 1). Strength values were based on the number of ducts, whether they were aligned in a tangential row, and their compactness, which previous research has indicated as strong evidence for mechanical damage (Schneuwly et al. 2009). CRDs were defined as single cells and were not assigned a strength. Strength values of 0 indicated more than one duct without any tangential arrangement or compactness (Fig. 2*a*). As in previous research (Schneuwly et al. 2009), we did not consider level 0 ducts "traumatic". Strength values of 1 indicated more than one resin duct aligned tangentially, but not grouped, and also not likely "traumatic" (Fig. 2*b*). Strength values of 2 indicated groups of TRDs that were tangential but with space between the ducts (Fig. 2*c*).

Strength values of 3 indicated nearly complete tangential rows and tightly compact arrangement (Fig. 2*d*). For rings with TRDs present, we also noted their position within the annual ring (i.e., earlywood, middle-earlywood, or latewood), and we noted how many subsequent years TRDs were formed. A Mann–Whitney *U* test indicated differences in TRD position between live and dead trees under the null hypothesis that they come from the same population. To account for unequal variances, we performed this test on *z* scores calculated for each group.

To further verify that TRD formation occurred *in response to* the SB outbreak, and not to other environmental perturbations, the difference between the first year of TRD formation in the live ES minus the DOD (last year of ring increment) from the paired dead tree was calculated, where 0 indicated tree death in the same calendar year as TRD formation, a negative number indicated that DOD was 1 year later than TRD formation in live trees, and positive numbers indicated that DOD was 1 year earlier than TRD formation in live trees. In trees that exhibited multiple sequential years of TRDs, we assumed that the first year with TRDs indicated the earliest response to SB attack. We binned the strength of TRDs across all 60 trees by decade to ascertain whether their prevalence overall was higher during the SB outbreak. The χ^2 test statistic was used to test for significant differences in observed counts of TRDs in live and dead trees during the 1990s and 2000s from their expected occurrence based on the lifetime average. We also compared TRD occurrence to previously reconstructed SB activity (DeRose and Long 2012*b*). To assess potential differences in vigor, we calculated and compared differences in ring width (RW, mm) and basal area increment (BAI, cm^2) between live and dead trees. For each tree pair, cumulative RW and BAI were calculated beginning in the calendar year previous to the dead tree DOD and extending back for 5, 10, 15, 20, and 25 year periods. Average DBH, tree age, RWs, and BAIs between live and dead trees were tested using the nonparametric Mann–Whitney *U* test under the null hypothesis that live and dead trees come from the same population. Unequal variances required that we standardize distributions of the groups, which was done by calculating their *z* score, before tests were performed.

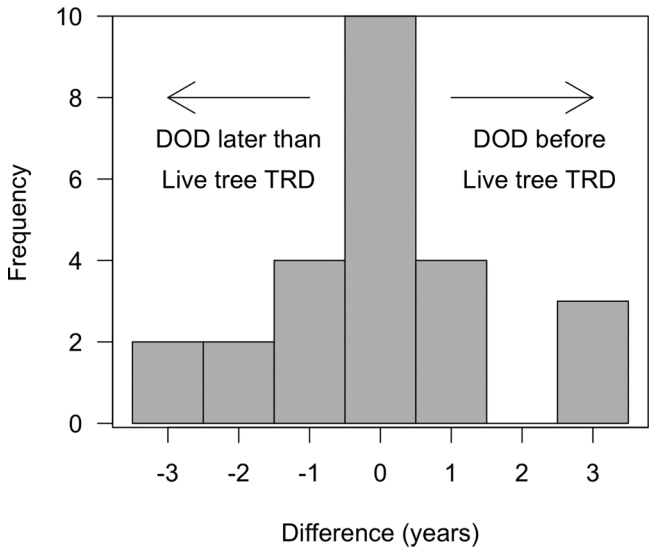
Results

Ninety percent (27 of 30) of the live ES exhibited TRDs (i.e., strength 2 and 3) during a calendar year in close proximity to (1–3 years prior to or after) the DOD indicated by its paired dead tree that succumbed to mass attack during the SB outbreak (Fig. 3). In contrast, 40% (12 trees) of the dead trees exhibited TRDs 1–3 years prior to their DOD.

The prevalence of TRDs over the lifetime of ES was exceedingly rare; of the 9395 rings from 60 trees, TRDs were present in 144 rings or 1.5%. Living ES exhibited 95 rings with TRDs out of 4785 total rings (2.0%), nearly twice as many as the dead trees, which exhibited 49 rings with TRDs out of 4610 total rings (1.1%). Regardless of tree status, approximately half (49%) of all TRDs occurred during the two decades of the SB outbreak (1990s and 2000s) and overwhelmed the rarity of TRDs in the prior three centuries (Fig. 4). In live trees, 42 of the 95 rings (44%) with TRDs occurred during the 1990s and 2000s outbreak, while in dead trees, 23 of 49 rings (47%) with TRDs occurred immediately prior to their death in the late 1990s to early 2000s. The observed number of TRDs in both the 1990s and 2000s for all live trees and in the 1990s for the dead trees was significantly larger than expected ($P < 0.0001$). In addition, the number of weak TRDs (strength 1) in the live trees during the 2000s was significantly greater than expected ($P < 0.0001$) (Fig. 4B).

As expected, the prevalence of all resin ducts (i.e., strength 0 through 3) over the lifetime of ES was rare; all resin ducts were present in 927 rings (9.8%). Living ES exhibited 477 rings with resin ducts out of 4785 total rings (9.7%), and dead ES exhibited resin ducts in 450 rings out of 4610 total rings (9.9%). Resin ducts that occurred prior to the outbreak were primarily weak (strength 0 and 1) and variable in timing compared to those formed during the SB outbreak. The low prevalence of TRDs in previous decades corroborated previous ring-width-based reconstructions that suggested that only endemic-level SB activity occurred prior to the 1990s outbreak (Fig. 4). The peak in TRDs in the 1950s matched previous reconstructions of SB activity in some stands on the Markagunt Plateau.

Fig. 3. Distribution of the difference between the first year of traumatic resin duct formation in live Engelmann spruce (*Picea engelmannii*) trees minus the date of death (DOD) (last year of ring increment) from the paired dead tree. Zero indicates tree death in the same calendar year as TRD formation. Negative values indicate that dead tree DOD was later than TRD formation in live trees.



Additionally, in live trees, 8 of 30 rings (27%) exhibited two or more consecutive years with TRD formation, which suggested possible sustained response to mechanical damage (e.g., lagged physiological response to SB pioneering). Placement of TRDs in the rings occurred primarily in the latewood (53%) and secondarily in the middle-latewood (40%), with the remaining 7% in the earlywood. This pattern of placement did not differ between the dead and live trees ($P > 0.62$). The distribution of occurrence among these three positions remained relatively constant during the 1990s and 2000s outbreak. Except for the prevalence of TRDs during the 1990s outbreak, all comparisons of vigor between live and dead ES (i.e., DBH, tree age, RW, and BAI) were not statistically significant (Table 1). The results for DBH confirmed that pairing by tree size was appropriate.

Discussion

That tree age, RW, BAI, and position of TRDs were not significantly different between paired live and dead ES suggests that the inherent capability to produce enough TRDs to "pitch out" attacking SB could be the mechanism by which a small proportion of ES survived the outbreak. The elevated prevalence of TRDs in the annual rings during the 1990s and 2000s of nearly all surviving ES (and almost half of the dead trees) sampled across the Markagunt Plateau strongly suggested that they were formed in response to mechanical damage caused by SBs. By extension, past SB activity would be recorded as TRDs in any surviving ES. We observed synchrony of TRDs in a relatively short timeframe (e.g., approximately a decade) from multiple ES across a 250 km^2 landscape, providing another line of tree-ring-based evidence for reconstructing past SB outbreaks and their extent. Because resin ducts are normally exceedingly rare in ES, and TRDs are event-specific,

Fig. 4. Distribution of resin ducts for live and dead Engelmann spruce (*Picea engelmannii*) trees binned by decade and sample depth of tree-ring data from 1700–2000. (A) Traumatic resin ducts (strength = 2 and 3) were historically rare until the spruce beetle outbreak (*Dendroctonus rufipennis*) ~1990 (indicated by the broken vertical line). The arrow indicates elevated nonoutbreak spruce beetle activity is in the 1950s (DeRose and Long 2012*b*). (B) "Baseline" resin duct (strength = 0 and 1) production followed (C) sample size of tree-ring data.

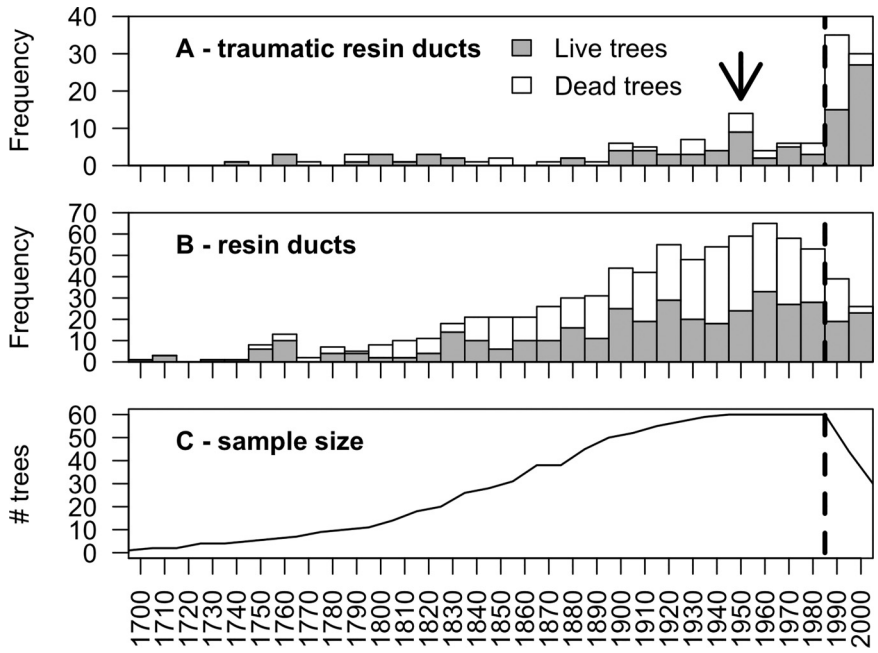


Table 1. Characteristics of paired live and dead Engelmann spruce (*Picea engelmannii*) and statistical tests for their differences.

	Live			Dead		
	Mean SD	Min.	Max.	Mean SD	Min.	Max.
DBH (cm)[a]	21.0±9.1	7.3	43.4	23.8±8.88	6.5	43.1
Age[a]	155±68.4	65	342	157±52.4	66	275
Ring width (mm) tests[a]						
5 years	0.661±0.579	0.096	0.579	0.655±0.463	0.08	2.257
10 years	0.688±0.613	0.092	2.635	0.679±0.488	0.072	2.273
15 years	0.727±0.607	0.131	2.483	0.744±0.524	0.079	2.409
20 years	0.722±0.561	0.155	2.235	0.768±0.522	0.094	2.360
25 years	0.726±0.539	0.167	2.011	0.780±0.520	0.106	2.337
Basal area increment (mm^2)[a]						
5 years	453±484.5	27.3	1873	481±403.5	65.3	2125
10 years	466±526.3	33.2	2036	480±389.9	57.1	2058
15 years	478±528.6	40.2	2174	506±389.0	59.5	2080
20 years	463±489.2	41.8	1973	508±373.2	53.5	1957
25 years	456±476.0	42.0	1940	505±361.5	56.2	1855

[a]The Mann–Whitney *U* test indicated no significant difference in diameter at breast height (DBH), age, ring width, or basal area increment (5 to 25 year periods) between live and dead paired trees.

we suggest that differences in the strength (tangential alignment and compact or not) of TRDs might be used to help differentiate between past endemic versus epidemic SB populations. For example, the lack of any peaks in strong TRDs on the Markagunt Plateau suggests that from ~1700 to the 1990s there were no SB outbreaks.

The ability to rapidly respond to pioneering beetles through the production of oleoresin could have long-term implications for the natural selection of ES, and *Picea* spp. in general, when faced with attacking SB populations. Furthermore, this response is potentially influenced by environmental factors such as tree age, vigor, and possible level of hybridization among congeners. Safranyik et al. (1983) found that wound healing and resin flow generally occurred faster in younger *Picea* than in older, which suggested that vigor plays a role in tree response. We were unable to demonstrate any effect of vigor, as indicated by tree age, RW, or BAI, between our paired ES. Of the variables measured in this study, only the prevalence of TRDs differed, both between the live and dead trees and over the lifetime of the trees. We found that the preponderance of TRDs were formed during the 1990s outbreak compared to the previous three centuries. The only other noticeable peak in TRD production occurred in the 1950s and was relegated to Sydney Valley, which was previously reconstructed as SB activity by analyzing tree-ring releases (DeRose and Long 2012*b*).

We found that 40% (12 of 30) of the dead ES had a partial outer ring, which clearly indicated the putative DOD during the growing season and likely represents initial beetle mass attack during the previous year due to the SB 2 year life cycle. The remaining 60% of dead trees likely succumbed to SB brood mining after initial mass attack in the previous growing season (or during the dormant season). That is, ES were unable to respond by forming TRDs because initial attack or brood excavation occurred outside of the growing season, and therefore, differentiation of TRDs during cell division was not yet underway in the cambium. Safranyik et al. (1983) noted that resin-forming tissue was absent in some attacked trees, which indicated that phloem and cambium were rapidly killed by the beetle–fungi symbiont complex, thereby preventing the tree from forming TRDs during xylogenesis. In this regard, early beetle flight and (or) early brood mining represents an advantage to attacking SBs because ES may be unable to respond via induced defenses (Safranyik et al. 1983).

Weaker TRD formation may be background noise associated with endemic SB pioneering or other potentially confounding TRD-forming perturbations. Based on our results, the occurrence of TRDs in ES likely spans a continuum, where level 0 represents baseline CRD production, up to level 3, which likely indicates a SB mass attack. Levels 1 and 2 represent a middle ground in that level 1 ducts are not necessarily "traumatic" although they appear tangential, perhaps indicating endemic beetle pioneering (i.e., low SB population) via the production of a few TRDs, whereas at level 2, TRDs are tangentially aligned and compact, perhaps indicating the shift from endemic to epidemic SB populations. Therefore, as the strength in production of induced resin ducts in ES

increases, so does our confidence that they are due to SB mass attack.

Unfortunately, the retrospective pairing did not allow us to choose live–dead tree pairs ideally proximate to each other, which likely explains some of the variability between dead tree DOD and live tree TRD formation (Fig. 3). However, over one third of TRDs formed in live trees occurred in the same year as the DOD for the paired dead tree, and another approximately one third of trees died in the growing season immediately prior to, or after, their live pair. Because TRDs begin forming within days of wounding (Safranyik et al. 1983), both positive and negative differences between TRD formation and DOD might be due to spatial variability in pioneering SBs at the stand scale. Previous research has indicated that mechanical damage outside of the growing season (Gärtner and Heinrich 2009) could play a role in the observed variability in DODs. In our study, dead tree DODs ranged from 1997 to 2002, whereas the range in the first year of TRD formation in live trees was 1995–2003. Within-stand variability of DOD among all measured stands affected by the Markagunt Plateau outbreak was approximately 1 decade (DeRose and Long 2012*a*).

Additional variability in timing of TRD formation between paired live and dead ES may be due to spatial variability of TRD formation within individual trees and the fact that some trees exhibited multiple successive years of TRDs. Although TRDs form primarily in the secondary xylem to increase oleoresin flow immediately after wounding, it is unknown how variable the within-bole production of TRDs is in response to SB. Nonconformity of wood formation along the stem during the time of tree death for four boreal conifers (Angers et al. 2017) has been demonstrated and is likely possible in ES. These researchers suggested taking full sampling cross-sectional disks from breast height to minimize variability in determining DODs. Our cores were obtained near the root collar, which may have also contributed to some of the observed variability (Fig. 3). In general, *Picea* has been reported to produce nearly continuous tangential TRDs around the circumference of the bole (Krokene 2015) and we noticed this for ES as well (Fig. 2*c*). However, it appeared that even the strongest TRD production still included some tangential gaps. As a result, TRD detection will be more limited when sampling with increment borers versus cross-sections.

Previous research has noted that location of trees (site) and their risk to perturbations (situation) are critical when ascertaining TRD formation in wood (Stoffel 2008). Other possible mechanical damage leading to TRD production (i.e., false positives) includes tree falls (wind throw or logging), landslide events, rock fall events, avalanches, and fire. However, in most of these situations, it is unlikely that TRDs would be formed synchronously in time (similar rings) *and* space (multiple trees) on a landscape, especially when ES does not occur on steep slopes where mass movement would be likely. In the case of fire, TRD formation has not been documented for *Picea* spp. and it is likely to be rare given the sensitivity of ES meristems to heat. While previous research in *Pinus* spp. (Kane and Kolb 2010; Ferrenberg et al. 2014; Hood et al. 2015) has indicated that resin duct characteristics (increased quantity, volume, and diameter) were associated with decreased mortality risk from bark beetles, the rarity of resin ducts in ES, and specifically TRDs in our study, makes similar comparisons difficult. Instead, if thought of as a definitive induced response, TRDs represent an alternative line of evidence for SB population levels that can be used in addition to synchrony in ring-width release, historic documentation, aerial detection surveys, and remote sensing data to reconstruct past endemic or epidemic SB-caused mortality. Specifically, TRDs formed in response to mechanical wounding (i.e., rock fall: Stoffel 2008) have been documented as more reliable indicators of timing than ring-width releases because they are formed relatively quickly in response to the damage, whereas release may be delayed by many years (DeRose and Long 2012*b*). Therefore, careful attention to both site and situation will be important for future studies attempting to document TRDs in ES.

Conclusions

We report compelling evidence that TRDs in ES were produced primarily in response to a historical SB outbreak. As a result, quantifying the prevalence, strength, and timing among multiple, surviving ES on a landscape could likely be used to differentiate endemic from epidemic populations in the distant past. Because the production of resin ducts is under strong genetic control, these results are relevant across the range of ES. Preliminary results from two other study locations also indicate TRD production occurred in response to SB activity at both endemic and epidemic SB population levels (unpublished data). One limitation that also holds for other tree-ring-based approaches is that during particularly severe outbreaks, there are only few living trees to record the event. Future research to reconstruct past SB outbreaks could use TRD presence in ES tree rings. This approach would focus on quantifying the presence and strength of TRDs in crossdated annual rings of ES. First, the presence of TRDs indicates the likelihood that mechanical damage has occurred. Second, the strength of TRDs (tangential alignment and compact arrangement) likely indicates that the damage was the result of mass attacking SB. Third, the synchrony in timing (less than approximately a decade) of TRD formation on multiple ES located in many different stands across a larger landscape would be very strong evidence for large-scale SB outbreaks.

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