



Radial growth response and vegetative sprouting of aspen following release from competition due to insect-induced conifer mortality



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ABSTRACT

Eruptive bark beetle outbreaks such as the recent mountain pine beetle epidemic in western North America often result in substantial changes to species composition, abiotic factors, and a highly altered fuel complex. Little is known about the implications of these outbreaks to non-host species, such as aspen (*Populus tremuloides* Michx.), which may be beneficiaries due to release from competition. We investigated radial growth response in aspen following mountain pine beetle-induced conifer mortality in north-central Colorado through dendrochronological analysis using the percent growth change method based on 5-year and 10-year running medians, and we quantified regeneration responses in these areas compared to areas where beetle activity was largely absent. We hypothesized that growth in mature aspen would increase, expressed through wider annual growth rings, while vegetative regeneration (i.e. resprouting from the parent root system) would not increase in forests affected by bark beetles.

Results showed a clear radial growth release in mixed aspen-conifer stands that were subject to extensive conifer mortality but not in forests that remained largely unaffected by beetles. Comparison of extent of suckering showed no significant differences, supporting our hypotheses and suggesting that additional resources due to release from competition were allocated towards radial growth rather than initiation of sucker growth, potentially indicating a trade-off between maintenance of existing stems and regeneration. Results from this study provide the first account of radial release detection in aspen following beetle-induced conifer mortality and help predict aspen persistence and future stand composition in these forests. Additional research, with a higher sample size and more time between sampling and bark beetle disturbance is highly recommended to confirm our findings and optimize release detection methods in aspen.

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1. Introduction

Bark beetles are an important disturbance agent in North American forests. Eruptive bark beetle outbreaks often result in substantial changes to species composition and a highly altered fuels complex (Lynch et al., 2007; Jenkins et al., 2008; Collins et al., 2012; Jenkins et al., 2012). Tree species that are not directly affected by these outbreaks (i.e. non-host species) may be beneficiaries of beetle-induced conifer mortality, including quaking aspen (*Populus tremuloides*), a species of high ecological importance in the Intermountain West due to elevated productivity and taxonomic diversity in aspen-dominated habitats (Chong

et al., 2001; Stam et al., 2008). Although little is known about the immediate implications of beetle-induced conifer mortality on aspen (Pelz and Smith, 2013), two possible responses benefitting the species include (a) elevated growth of individuals that were established prior to disturbance (growth response) and (b) increased rate of suckering (i.e. clonal or vegetative reproduction), the main regeneration strategy of aspen in its southern distribution (regeneration response). This study aims to detect and measure these responses in aspen of the subalpine forests of north-central Colorado.

Mortality of pine trees from bark beetle epidemics increases light to the forest floor and decreases competition; factors that favor both aspen growth and regeneration (Amacher et al., 2001; Shepperd et al., 2006). While the extent of aspen regeneration was included in several studies assessing forest trajectories following bark beetle epidemics (see below), no studies were found that specifically addressed changes in growth of mature aspen in

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beetle-affected areas. Characteristic of a pioneer species, aspen is a weak competitor and very intolerant to shade (Perala, 1990). Therefore, aspen are generally replaced by more shade-tolerant species that regenerate under the aspen overstory as part of typical succession (Peet, 1981; Bartos, 2000; Lieffers et al., 2002; Frey et al., 2004). Mortality of succeeding species temporarily resets this transition, effectively prolonging the lifespan of aspen that would otherwise gradually give way to coniferous species. Such a release from competition should be detectable by wider annual growth rings in the years following the beetle outbreak (i.e. competitor mortality). To assess a possible growth response, we investigated radial growth in aspen by means of dendrochronological analysis.

Dendrochronology and dendroecology are excellent tools to reconstruct past disturbance events (Fritts and Swetnam, 1989). The presence of releases, i.e. abrupt increases in radial growth, are indicative of past disturbance events and can be interpreted at a high spatial and temporal resolution (Frellich, 2002). Although dendrochronological research on aspen is rare due to the difficulty of core preparation and ring identification, and the short life span of aspen compared to other species, tree ring data were successfully used in some Canadian studies to reconstruct western tent caterpillar outbreaks in aspen by comparison of host and non-host chronologies (Cooke and Roland, 2007; Huang et al., 2008) or by identification of pale rings (Hogg et al., 2002).

Besides detecting a possible growth release in pre-disturbance established aspen, initiation of suckering is an area of great interest as aspen are believed to have been declining in the western United States for several decades (Packard, 1942; Krebill, 1972). In addition, the recent loss of overstory trees dubbed “Sudden Aspen Decline” suggests drought as the initial driver of aspen decline (Worrall et al., 2008, 2013; Rehfeldt et al., 2009; Anderegg et al., 2012, 2013). Although not mutually exclusive, growth of existing stems and suckering are controlled by opposing ends of the same regulatory mechanism. New aspen suckers (or ramets) develop from meristems on lateral roots of the parent root system (Schier et al., 1985). In addition to genetics, time of disturbance, pre-disturbance stand conditions, and nutrient and water supply, phytohormones such as auxin play a crucial role in sucker development of aspen (Schier et al., 1985; Frey et al., 2003). Auxin is synthesized in the apical buds and transported to the roots, inhibiting lateral growth on both stem and roots. Loss of overstory stems due to disturbances, such as fire or herbivory, halts the supply of auxin and promotes pulses of regeneration from the surviving parent root system (Romme et al., 1995; Jones et al., 2005). However, after selective disturbances such as bark beetle outbreaks, apical dominance from remaining mature ramets is maintained and may lead to allocation of additional resources towards existing ramets rather than initiation of new sucker growth. Furthermore, increased litter accumulation 5–10 years after bark beetle disturbance (Klutsch et al., 2009, 2011; Collins et al., 2011, 2012; Hicke et al., 2012) may potentially limit sprouting from the parent root system as thicker layers of organic matter have been shown to inhibit suckering (Lavertu et al., 1994; Fraser et al., 2004).

To evaluate a possible regeneration response, we quantified and compared the extent of suckering in areas showing heavy beetle-induced conifer mortality to areas with little beetle activity. Increased aspen suckering has been shown in several studies, although results were not conclusive. A modeling approach based on data spanning 13 western states by Shaw (2004) suggested that mountain pine beetle outbreaks may result in pure aspen stands. Collins et al. (2012) also predict an increase in aspen density in stands affected by mountain pine beetle in north-central Colorado, especially when followed by salvage logging. A moderate increase in relative abundance was found in Rocky Mountain National Park, Colorado, compared to pre-outbreak conditions (Diskin et al., 2011). Contrarily, Klutsch et al. (2009) found no

differences in seedling/sapling densities of aspen between infested and uninfested plots.

To the knowledge of the authors, the present study is the first account to directly assess and contrast growth and regeneration response in aspen following beetle-induced conifer mortality. We hypothesized that (a) pre-disturbance ramets show increased radial growth following disturbance in areas affected by bark beetles, and that (b) suckering from the parent root system does not significantly increase due to allocation of resources towards radial growth.

2. Materials and methods

2.1. Sampling area

Sampling sites were located near the Fraser Experimental Forest, in the Sulphur Ranger district of the Arapaho-Roosevelt National Forest in Grand County, Colorado. All plots were located in the subalpine elevation zone; elevation ranged from 2757 to 3052 m, mean aspect and slope angle were 188.2° and 18.7°, respectively (Table 1).

Dominant overstory species were subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), and aspen (*P. tremuloides*). The most common understory shrubs included *Vaccinium myrtillus*, *Juniperus communis*, and *Shepherdia canadensis*.

First signs of bark beetle activity were reported in 2003 and by 2006 most of the forests in the sampled area exhibited widespread tree mortality (Hubbard et al., 2013). While data from aerial surveys provided dates for tree mortality at relatively high spatial resolution, ranging between 2003 and 2007 (USDA Forest Service; Table 2), these data “only provide rough estimates of location, intensity and the resulting trend information for agents detectable from the air” (excerpt from the survey data disclaimer).

2.2. Sampling procedure

Plots were chosen based on presence of aspen and ratio of live/dead conifers in the overstory, excluding areas with evidence of other recent disturbances (e.g. wind throw, fire) and avoiding sites in valley bottoms or near bodies of water to minimize confounding factors from different local hydrology. Two types of plots were sampled for comparison: mixed aspen-conifer forests affected by bark beetles (>50% conifers, of those >75% dead) and healthy, mixed aspen-conifer forests (>50% conifers, of those <25% dead). Seven mixed-healthy and eight beetle-killed plots were sampled (Table 2). In addition, two aspen-dominated stands (<10% conifers) were sampled for comparison but not analyzed in depth given the low sample size. Due to the extent of the recent bark beetle outbreak, coniferous components in mixed-healthy were generally comprised of subalpine fir and Engelmann spruce rather than lodgepole pine, since no areas were found with adequate proportions of healthy (alive and without signs of beetle effects) lodgepole pines. In each plot, two 50 m tapes were laid out in cardinal

Table 1
Sampling depth, averages and standard deviations of aspen diameters at breast height, and comparison of averages of abiotic factors per treatment.

Type	Sampling depth			Abiotics			Diameter (cm)	
	Plots	Trees	Cores	Elev. (m)	Aspect (°)	Slope (°)	Average	STDev
Beetle	8	39	76	2891	188.1	23.6	17.4	5.0
Mixed	7	33	62	2811	185.0	11.9	31.9	7.9
Aspen	2	10	19	2817	191.5	20.5	34.4	7.1

Table 2
Years of sampling, initial signs of bark beetle mortality, and releases as detected for each plot using 10-year intervals (first date) and 5-year intervals (second date) on unadjusted and de-trended chronologies.

Type	Plot	Sampled	Mortality	Year of release			
				MRW ^a	Standard	Residual	ARSTAN
Beetle	6	2011	2007	–	–	–	–
	7	2011	2004	–	–	–	–
	8	2011	2004	–	–	–	–
	9	2013	2004	2002/2001 ^b	2003/–	–	2003/2007 ^b
	10	2013	2003	2001/2001	2000/2001	–	2001/2004 ^b
	14	2013	2003	2004/2006	2004/2007 ^b	–	2005/2007 ^b
	16	2013	2005	2003/2005	2002/2005	–	2002/2004
	17	2013	2005	2002/2005	2003/2005	–	2003/2006
Mixed	1	2011	n/a	–	–/2005 ^b	–	–/2005 ^b
	2	2011	n/a	–	–	–	–
	4	2011	n/a	–	–	–	–
	5	2011	n/a	–	–	–	–
	11	2013	n/a	–	–	–	–
	12	2013	n/a	–/2002 ^b	–	–	–
	15	2013	n/a	2003/2001	2003/2001	–	2003/2001
Aspen	3	2011	n/a	–	–	–	–
	13	2013	n/a	–	–	–	–

^a Median ring width (unadjusted).

^b Percent growth change exceeded 100% for less than 3 consecutive years.

directions, intersecting at the 25 m mark. Within each 50 by 50 m plot, ten cores (two per ramet) were extracted from the five largest aspen ramets based on DBH measurements. Sampling two cores per ramet helped account for the asymmetrical growth habit of aspen, as reported by [Cooke and Roland \(2007\)](#) and based on findings by [Copenheaver et al. \(2009\)](#). Cores were extracted at breast height (~1.37 m) parallel to the slope (one core each on the upslope and downslope side of the ramet).

Regeneration was assessed by counting young ramets in 1 m wide transects along the two intersecting 50 m tapes using six size classes (<50 cm height, 50–137 cm height, 0–1 cm diameter at breast height [DBH], 1–2.5 cm DBH, 2.5–5 cm DBH, >5 cm DBH). A visual estimate of canopy cover was made at 1 m intervals along these transects; if canopy cover exceeded 75% at a given interval it was recorded as “shaded”. Using this method yielded a more comprehensive picture of lighting conditions compared to a single canopy cover reading at plot center, especially in forests where dense clusters of live, sub-canopy trees were intermixed in otherwise open, beetle-killed forests. Forest floor covered by downed woody debris was recorded similarly; if the forest floor at any 1 × 1 m interval along the transects was covered more than 75% with downed woody debris it was recorded as “covered”. The resulting proportions of shaded/unshaded and covered/uncovered were summarized as “percent canopy cover” and “percent downed woody debris” for this analysis. In addition, aspect, slope, and GPS coordinates for each plot were recorded at plot center. Elevation measures were derived from GIS data.

2.3. Core preparation and cross-dating

All cores were prepared using standard dendrochronological procedures ([Stokes, 1996](#)). Cores were mounted on prefabricated mounts and sanded using progressively finer sandpaper beginning with 80-grit and ending with 600-grit until the cellular features on all rings could be identified under 10× magnification ([Orvis and Grissino-Mayer, 2002](#)). In some cases, chalk was used to increase visibility of the rings ([DesRochers and Lieffers, 2001](#)). Cores were omitted if they showed significant physical damage or could not be confidently cross-dated. Initial cross-dating was accomplished by constructing skeleton plots ([Swetnam et al., 1985; Stokes, 1996](#)) to demonstrate the replication of ring width variability across cores, and a master chronology was created using ring width

patterns. Tree-ring widths on all cores were measured using a “Velmex” movable stage micrometer to the nearest 0.001 mm and recorded with “Measure J2X” software.

The program “COFECHA” was used to quantitatively verify cross-dating ([Holmes, 1983; Grissino-Mayer, 2001](#)). Any segment with a low correlation with the master (less than 0.328, 99% significance level, one-tailed) was visually re-inspected for anomalous ring patterns or errant cross-dating. Isolated individual rings and pairs of rings that were statistical outliers were re-inspected to ensure measurement error was not the cause. Of the initial 170 samples extracted from 85 ramets, 153 samples from 83 ramets were used for further analyses. A total of 17 samples were discarded due to heavy signs of rot, rendering individual rings indiscernible.

2.4. Release assessment

There are several different methods to detect releases in dendrochronological data; the most common utilizes percent growth changes in yearly increments between intervals in average growth prior and past each year ([Nowacki and Abrams, 1997; Rubino and McCarthy, 2004](#)):

$$\%GC = [(M_2 - M_1)/M_1] \times 100$$

In this formula, %GC is the percentage growth change between preceding (M_1) and subsequent (M_2) means; e.g. the 10-year means $M_1 = 1981–1990$ and $M_2 = 1991–2000$ are used to calculate %GC for the year 1990. The resulting %GC is then compared to a pre-determined threshold. Using adequately long intervals to calculate M_1 and M_2 filters out short-term climate-related responses and eliminates the need to adjust for age-related trends while allowing for a sufficiently high resolution to detect disturbance-related releases ([Leak, 1987; Lorimer and Frelich, 1989; Nowacki and Abrams, 1997](#)). Although different intervals and thresholds are found throughout the literature, 10-year intervals and a 100% threshold are most commonly used ([Fraver and White, 2005](#)) and were adopted for this study except for the intervals 2004–2013 to 2008–2013, where intervals of nine to five years were used, respectively, to allow for percent change calculations several years post disturbance. In addition, an analysis with 5-year intervals was performed for consistency. A response was classified as a release when

percent growth increase was larger than 100% for a period of three or more consecutive years.

Median ring widths were calculated using data from all collected samples in respective forest types: beetle kill (76 cores, 39 trees), mixed-healthy (58, 33), pure aspen (19, 10). In addition, responses on the plot scale were assessed using cores obtained only within each plot. As suggested by Rubino and McCarthy (2004), M_1 and M_2 were calculated using medians rather than means to increase statistical robustness in cases of non-normal data. Although radial growth data were not tested for normality, medians approximate means when data are normal and yield similarly accurate release identification (Rubino and McCarthy, 2004).

While not required for release identification using the proposed methodology, chronologies were de-trended using ARSTAN (Version 6.05P) to account for age-related trends and help identify possible climate signals (Cook, 1985). Three de-trended chronologies were created (Cook and Holmes, 1986): Standard (autoregressive modeling), residual (autoregressive modeling using outliers over three standard deviations from the mean), and ARSTAN (combination of previous two). De-trended data were analyzed as described above.

All de-trended chronologies were correlated to monthly precipitation, and minimum and maximum temperatures. To test for possible effects of climate from preceding years on radial growth, data were also lagged up to two years. Climate data were downloaded from PRISM (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, accessed 3 June 2004) for the quadrant located at 39.91000°N, -105.88000°W. Although based on modeling, these data comprised the most complete, continuous data set available to the authors. In addition, de-trended chronologies were correlated to instrumental monthly precipitation data obtained from the Fraser Experimental Forest (39.90500°N, -105.883000°W); however, only data from 1976 to 2003 were available.

An additional analysis was performed using only cores from aspen ranging from 20 to 29 cm DBH to account for a possible size-related signal. The 33 cores from 17 trees in 6 plots in mixed-healthy and 33 cores from 17 trees in 6 plots in beetle-affected forests represented the smallest individuals from mixed-healthy and largest individuals from beetle-affected plots. The resulting average DBH values were 25.0 cm (2.8 cm standard deviation) and 21.9 cm (1.8 cm standard deviation) for mixed-healthy and beetle-affected areas, respectively.

2.5. Regeneration assessment

Regeneration data (i.e. sucker counts) were tested for normality using the Shapiro–Wilk test. Since data were non-normal, differences in sucker counts between areas affected by beetle and mixed-healthy forest were assessed using the Mann–Whitney U test (α : 0.05; H_0 : no difference); pure aspen stands were not included in statistical analysis due to low sample size. To account for multiple testing (multiple size classes), the Holm–Bonferroni adjustment was used. All statistical tests were performed in R (Version 3.0.0).

3. Results

Plots that were affected by bark beetles exhibited a more open canopy, with 31% average canopy cover compared to 45% in mixed-healthy forests. Downed woody debris cover was higher in mixed-healthy plots, with an average of 31% compared to 15% in bark beetle plots; however, none of these differences were significant. The two sampled pure aspen stands exhibited 40% canopy and 0% downed woody debris cover. Percent canopy and debris

cover explained only 1% and 4% of the observed sucker counts, respectively; based on Pearson correlation coefficients (r_{canopy} : 0.08, r_{debris} : 0.20; both not significant).

Mean length of cores was 68.0 and 68.2 years for beetle-affected plots and mixed-healthy plots, respectively; however, many cores showed signs of rot towards the pith, especially in larger individuals, prohibiting precise determination of average tree ages. The oldest, clearly readable series dated back to 1859. Despite the equal series lengths between treatments, average stem diameters of sampled aspen were significantly higher in mixed-healthy (31.9 cm DBH) compared to beetle-affected plots (17.4 cm DBH, p : <0.0001; Table 1).

Quality assessment of cross-dated cores indicated 21 missing rings in all cores measured: 1925 (missing in one series), 1954 (1), 1976 (13), 1998 (3), and 2004 (3). After adjustments, COFECHA showed a series intercorrelation of 0.552 and reported 18 flags in 364 segments (<5%); all flags were of type “A”, indicating that a series was dated correctly but had a correlation below 0.3281 (i.e. critical correlation, 99% confidence interval). Master chronologies and median ring widths per forest type are shown in Figs. 1 and 2, respectively. Clear indicator years used for cross-dating included 1945, 1953, 1976, and 2004. Median annual ring widths indicate generally higher growth rates in mixed-healthy plots compared to beetle-affected plots. While sample size was low, pure aspen plots showed the highest annual growth. This trend reverses after 2009 for the first time since the early 1940s, with bark beetle-affected plots showing higher annual growth than mixed-healthy plots following a rapid increase in median ring widths after 2004 (Fig. 2).

3.1. Radial growth release

A release event was evident for aspen in bark beetle-affected areas, where the 100% threshold of growth increase was passed in 2004 (Fig. 3A, Table 2). No releases were found in mixed-healthy or pure aspen forests (Fig. 3B and C). Similarly, results obtained from using 5-year intervals indicated the only evident release in bark beetle-affected areas (Fig. 3, Table 2); however, the release was delayed by three years to 2007 and it is not clear whether it will sustain at >100% growth change as no calculations using 5-year running medians can be made past 2008 with the available data.

Using de-trended chronologies for release identification yielded similar results. Based on 10-year intervals, releases were evident in beetle-affected sites for both the standard and ARSTAN chronologies after 2005 and 2003, respectively (Fig. 4A and B, Table 2). Using 5-year intervals indicated potential releases after 2008 and 2007 for standard and ARSTAN chronologies, respectively (Table 2). No releases were detected in mixed-healthy and pure aspen stands for either 10- and 5-year intervals, and when analyzed using residual chronologies (Table 2).

There was some notable variability in responses within forest types; in plots affected by bark beetles, releases were only evident in plots sampled in 2013 while 2011 data indicate no releases (Table 2). In addition, plot 15 indicated a release despite its classification as mixed-healthy; a plot with considerably smaller aspen (25 cm average DBH) compared to the average of beetle-affected plots (31.9 cm). Subsequent analysis based on stem diameters ranging from 20 to 29 cm DBH from both mixed-healthy and beetle-affected plots confirmed previous results (Fig. 5). A clear release was detected in 2003 (10-year intervals) and 2005/2007 (5-year intervals); however, a weak release was also detected in mixed-healthy based on 10-year intervals in 2005. No release was detected in mixed-healthy forest based on 5-year intervals.

Correlations to both PRISM (not shown) and Fraser Experimental Forest climate data indicated generally weak climate

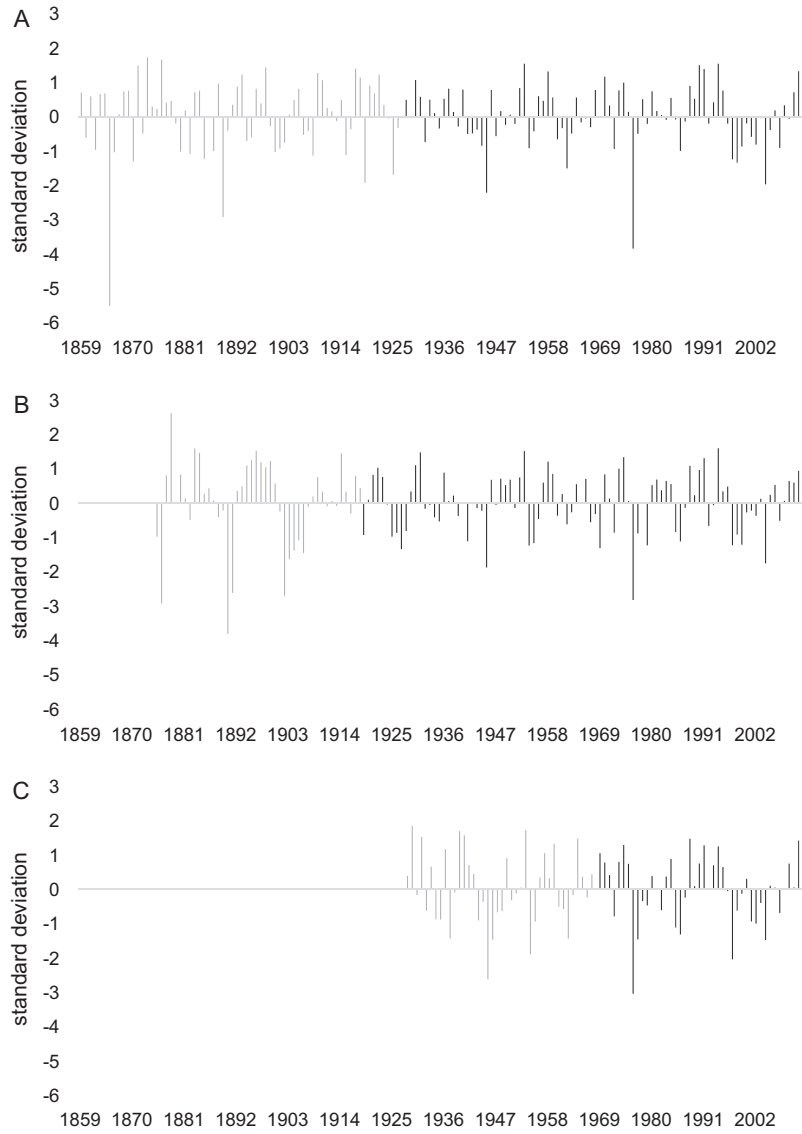


Fig. 1. Master chronologies for aspen (based on standard deviation from mean ring width) per forest type: affected by bark beetles (A), mixed-healthy (B), and pure aspen plots (C). Grey bars indicate values from less than 10 samples.

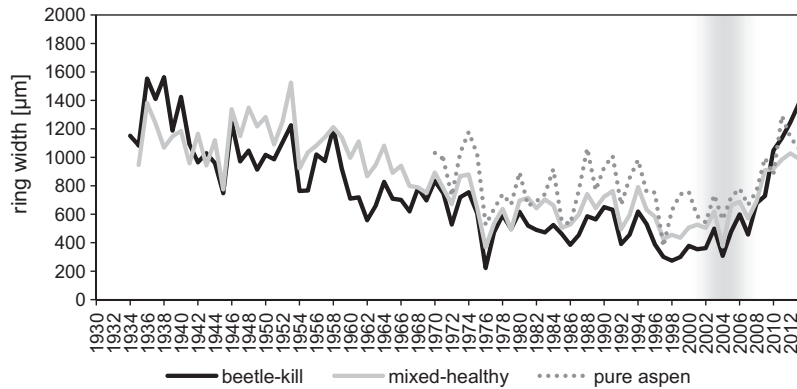


Fig. 2. Median ring widths of aspen growing in plots affected by bark beetles (black), mixed-healthy plots (grey), and pure aspen plots (dotted) show similar growth behavior. The shaded line indicates approximate time of peak bark beetle activity in Fraser Valley. Data were based on least 20 cores per year (beetle-kill and mixed-healthy). Data for pure aspen plots were based on at least 10 cores per year due to low sample size and are only shown for comparison.

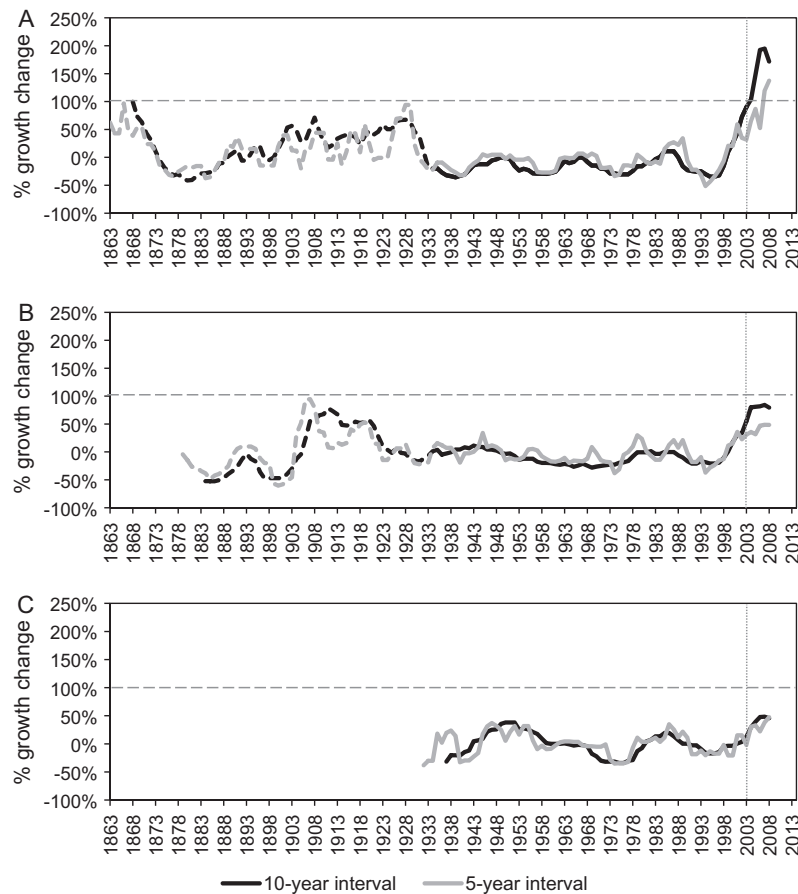


Fig. 3. Percent growth change in plots affected by bark beetles (A), mixed-healthy plots (B), and pure aspen plots (C), based on 10-year (black) and 5-year intervals (grey) of median ring width. For the 10-year analysis, years 2004–2008 were calculated with an M_2 of less than 10, down to 5 years for 2008. A dashed line indicates data based on sample sizes of less than 20 cores. The horizontal line indicates the threshold for a release (100%), the vertical line marks the year of initial bark beetle mortality (2003). Note that all data for pure aspen plots were based on less than 20 cores and are only shown for comparison.

signals (Table 3). While same-year precipitation in March indicated a slightly positive correlation with growth ($r: 0.3$), the strongest signal was found in two-year lagged October precipitation, showing a significant, negative correlation with growth ($r: -0.5$, $p: 0.01$). No significant correlations were found with monthly minimum or maximum temperatures.

3.2. Extent of suckering

Although median number of suckers in the two smallest strata (<50 cm height and 50 cm to breast height) were higher in plots affected by bark beetles, no significant differences in sucker establishment were detected between bark beetle-affected and unaffected plots (Fig. 6). Combining all tallied strata, mixed-healthy plots had an average of 46 suckers, compared to 41 in beetle-affected forests. Median sucker counts were 26 and 31 for mixed-healthy and beetle-affected plots, respectively. Although only represented by two plots, suckering was considerably lower in pure aspen stands, with an average of 6 suckers.

4. Discussion

To assess two possible physiological responses (growth release and regeneration response) in quaking aspen following conifer mortality due to the recent mountain pine beetle outbreak, we evaluated radial growth by means of dendrochronological analysis, and regeneration through quantification of suckering in areas

heavily affected by beetles and in areas of little beetle activity in Fraser Valley of Colorado. Our results indicate a clear radial growth release in aspen based on percent growth changes in 5- and 10-year intervals only in areas heavily affected by bark beetles (Table 2, Fig. 3A) but did not show significantly increased suckering in these areas, suggesting that aspen's primary response is an increase in radial growth of established ramets rather than promoting new sucker growth. While we acknowledge that the number of sampled plots in our study, especially for pure aspen forests, limits conclusive interpretation of the results, we believe our findings are encouraging and warrant further research.

4.1. Radial growth release

Based on aerial surveys, actual beetle mortality in plots categorized as beetle-affected was observed between 2002 and 2007, with an average year of 2004 (USDA Forest Service; Table 2). Our results suggest that releases in aspen radial growth occurred between 2003 and 2005 based on 10-year intervals, and between 2007 and 2008 using 5-year intervals, depending on whether median ring widths or de-trended chronologies were used for the analysis (Table 2). Variability in detected release dates is not uncommon. Copenheaver et al. (2009) found varying release signals based on multiple cores even within the same trees and recommended adequate sample sizes and multiple cores per tree to account for this variability. Few other studies focusing on aspen radial growth following release from competition were found. Gendreau-Berthiaume et al. (2012) showed a doubling of aspen

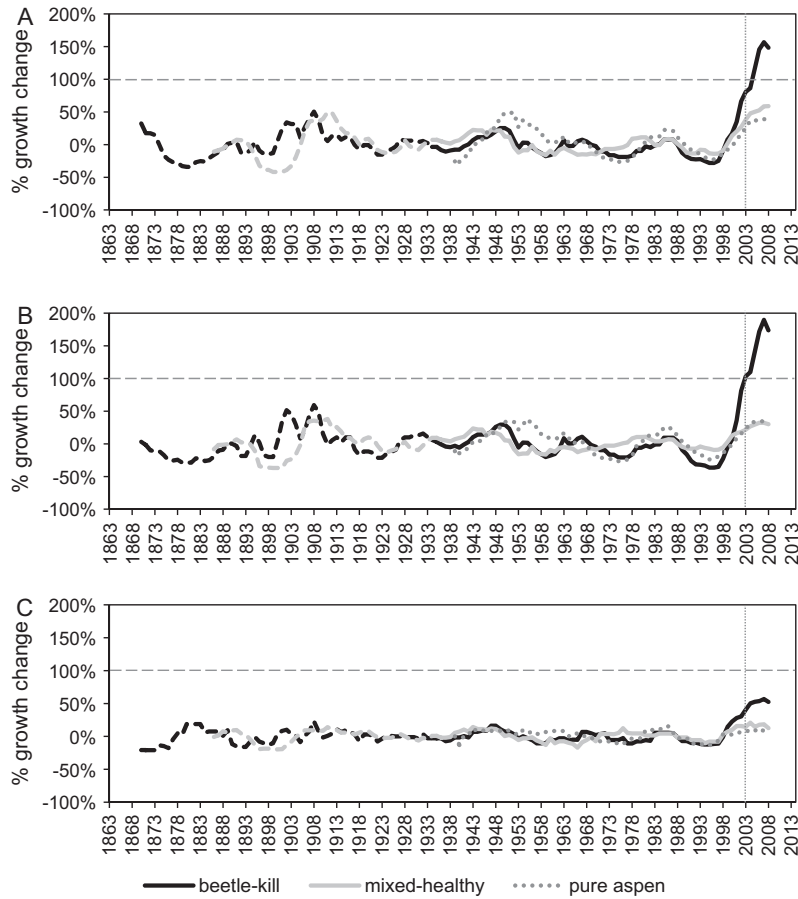


Fig. 4. Percent growth change in plots affected by bark beetles (black), mixed-healthy plots (grey), and pure aspen plots (dotted), based on 10-year intervals of de-trended chronologies (A: standard, B: ARSTAN, C: residual). Years 2004–2008 were calculated with an M_2 of less than 10, down to 5 years for 2008. A dashed line indicates data based on sample sizes of less than 20 cores. The horizontal line indicates the threshold for a release (100%), the vertical line marks the year of initial bark beetle mortality (2003). Note that all data for pure aspen plots were based on less than 20 cores and are only shown for comparison.

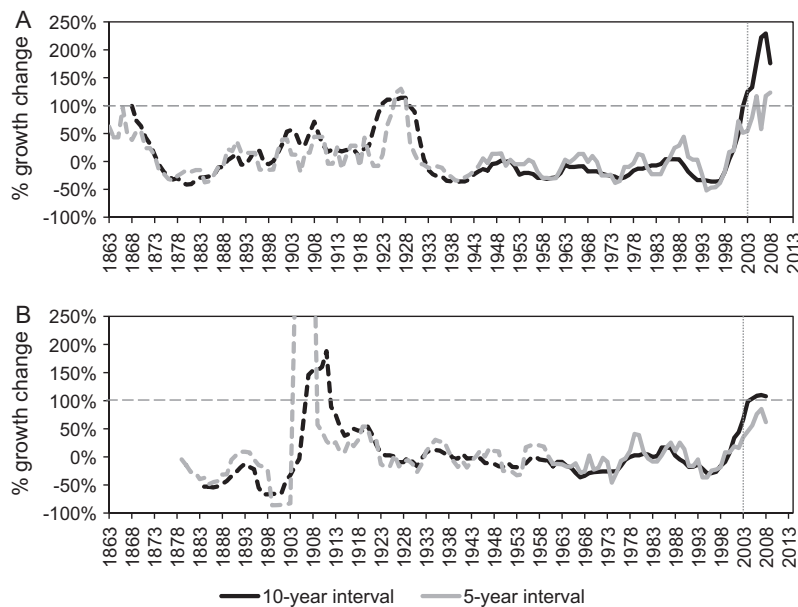


Fig. 5. Percent growth change in plots affected by bark beetles (A) and mixed-healthy plots (B) based on 10-year (black) and 5-year intervals (grey) of median ring width from trees ranging from 20 to 29 cm DBH. For the 10-year analysis, years 2004–2008 were calculated with an M_2 of less than 10, down to 5 years for 2008. A dashed line indicates data based on sample sizes of less than 20 cores. The horizontal line indicates the threshold for a release (100%), the vertical line marks the year of initial bark beetle mortality (2003).

Table 3

Correlation coefficients of standard, residual, and ARSTAN chronologies with monthly precipitation based on instrumental data from Fraser Experimental Forest (1976–2003). Values in bold denote correlations >0.3 .

Chronology	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>no lag</i>												
Standard	-0.16	0.10	0.33	-0.04	0.36	0.00	-0.13	-0.18	-0.12	-0.06	0.19	0.14
Residual	-0.08	0.05	0.30	-0.06	0.26	-0.12	-0.09	-0.01	-0.12	-0.05	0.08	0.13
ARSTAN	-0.18	0.13	0.33	0.02	0.35	0.06	-0.12	-0.24	-0.05	-0.02	0.22	0.12
<i>1 year lag</i>												
Standard	-0.29	0.01	0.20	-0.29	0.21	0.01	-0.17	0.08	-0.19	-0.18	0.15	0.05
Residual	-0.22	-0.05	-0.05	-0.31	0.01	0.01	-0.12	0.24	-0.15	-0.18	0.06	-0.02
ARSTAN	-0.31	0.04	0.28	-0.25	0.25	0.05	-0.18	0.02	-0.16	-0.16	0.20	0.06
<i>2 years lag</i>												
Standard	-0.19	-0.08	-0.05	-0.20	-0.35	-0.13	-0.30	-0.08	-0.28	-0.52*	0.12	-0.25
Residual	-0.06	-0.09	-0.19	-0.05	-0.52*	-0.15	-0.25	-0.11	-0.22	-0.50*	0.05	-0.32
ARSTAN	-0.24	-0.04	0.03	-0.20	-0.28	-0.09	-0.32	-0.08	-0.28	-0.52*	0.16	-0.22

* Significant (α : 0.05).

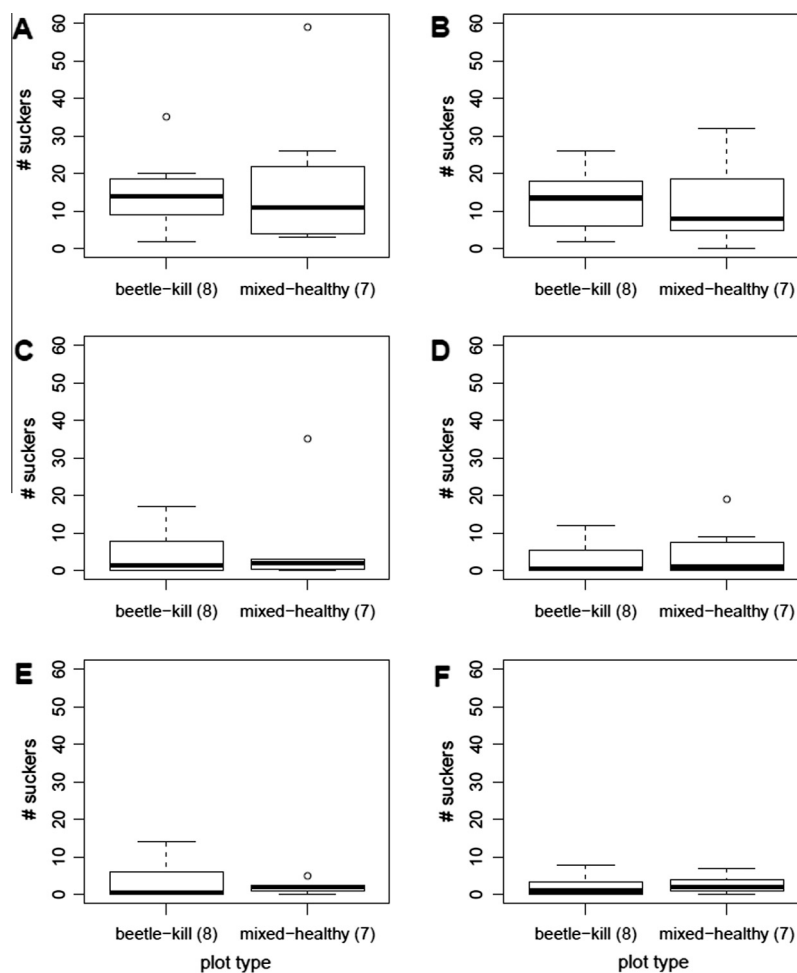


Fig. 6. Regeneration data for all sucker size categories: **A:** <50 cm height, **B:** 50–137 cm height, **C:** 0–1 cm DBH, **D:** 1–2.5 cm DBH, **E:** 2.5–5 cm DBH, **F:** >5 cm DBH. Numbers in parentheses denote sample sizes, i.e. plots per treatment. No significant differences were detected for any comparison.

growth four years after partial cutting of overstory in boreal mixed hardwood-conifer forests in western Quebec, Canada. Outbreaks of western spruce budworm (*Choristoneura occidentalis*) and Douglas-fir beetle (*Dendroctonus pseudotsugae*) in Rocky Mountain National Park, Colorado, resulted in growth releases of non-host species with variable responses depending on outbreak severity, pre-outbreak physiognomy, and non-host species (Hadley and Veblen, 1993); aspen exhibited weaker responses than other non-host species, including ponderosa pine (*Pinus ponderosa*) and lodgepole pine (*Pinus contorta*). Despite records of previous outbreaks of bark

beetles in Colorado, e.g. in the 1940s (Veblen et al., 1991; Eisenhart and Veblen, 2000), no releases were detected in our data, suggesting that growth response in aspen is dependent on the severity of the outbreak and resulting overstory mortality as well as other factors, including perhaps climate, composition, and age.

Our results show a generally weak climate signal. October precipitation two years prior to the year of growth was significantly correlated to growth (Table 3), although only accounting for 25% of the observed trend. The lack of a release in mixed-healthy and pure stands suggests that climate alone, specifically the wetter

conditions following the 2002 drought in Colorado, was not the main factor responsible for the observed growth release, although contributing to overall increased growth across treatments (Fig. 2). Leonelli et al. (2008) showed that aspen in sites with higher productivity responded stronger to climate. In our study, the highest growth response was evident in plots with lower productivity based on the comparison of annual median ring widths of aspen since the 1940s (Fig. 2), further lending support to the assumption that climate was not the main driver for the detected release. While we did not measure soil moisture or nutrient pools, we excluded areas in valley bottoms or near bodies of water during site selection; however, the significant difference in slopes (Table 1) and consequent changes to local hydrology (e.g. runoff and retention behaviors) between treatments may be a contributing factor to the elevated annual growth of aspen in mixed-healthy plots prior to beetle disturbance. Based on our results, we suggest that beetle-induced competitor mortality was the main factor responsible for the observed growth release (Fig. 3). Transpiration of infested lodgepole pines was 60% lower compared to control trees within two months after infestation, and water uptake was near zero at the beginning of the following year of infestation as a result of xylem obstruction caused by blue stain fungus (Hubbard et al., 2013), leading to increased water availability in affected areas shortly after disturbance (Clow et al., 2011).

Although average chronology lengths in our study were similar and the oldest, clearly identifiable individual was found in a beetle-affected plot, cores from large trees could often not be dated to the pith due to rot and aspen stem diameters were significantly larger in mixed-healthy plots (Table 1). While the latter may in part be the result of decade-long differences in annual growth (Fig. 2), it may be indicative of differences in average stand age. Results from our analysis held up when accounting for stem diameters (Fig. 5). Although the 100% release threshold was surpassed in mixed-healthy plots as well, the release was much stronger in beetle-affected areas.

Competitive status strongly influenced growth of aspen in intraspecific competition, with complex interactions between age, genetics, O₃ and CO₂ concentrations, and magnitude of competition (McDonald et al., 2002). In their study, the response to elevated CO₂ was greater for competitively advantaged trees. Likewise, beetle-induced conifer mortality likely aggravated the effects of a wetter climate past 2003, further supporting the notion that aspen were beneficiaries of the synergistic effect associated with simultaneous competitor mortality due to bark beetles and shift towards more favorable climate conditions.

4.2. Extent of suckering

Although coarse woody debris cover was lower and canopy more open in forests affected by beetles, both conditions that should benefit sucker growth (Lavertu et al., 1994; Romme et al., 1995), these differences were non-significant and were reflected in no significant difference in suckering across treatments (excluding pure aspen forests due to low sample size; Fig. 6). The presence of a clear growth release paired with the lack of significantly increased suckering suggests a trade-off between the two responses, although more rigorous testing is needed to support this claim. Regeneration from the parent root system was likely inhibited by the continuous release of auxin from remaining aspen terminal shoots (Frey et al., 2003) and suppressed by high litter accumulations typical during the so-called “grey phase” 3–5 years after initial beetle infestation (Edburg et al., 2012). Fraser et al. (2004) showed that the number of suckers generated per root was significantly affected by duff depth, with up to 65% more suckers growing on roots under shallow layers of organic matter compared to roots under deep duff layers.

Since aspen's main regeneration strategy in its southern distribution is by suckering (Mitton and Grant, 1996), the lack of a regeneration response following bark beetle disturbance in Colorado poses important implications for the species' persistence in the landscape. Sexual reproduction may only occur every 200–400 years in the Intermountain West during a “window of opportunity” with favorable abiotic conditions (Jelinski and Cheliak, 1992) and is considered extremely rare in Colorado (Zeigenfuss et al., 2008), leaving vegetative regeneration as the only major mode of reproduction. Due to aspen's strong apical dominance, pulses of suckering are generally associated with stand-replacing disturbances such as fire (Romme et al., 2005). While pulses of regeneration following bark beetle disturbances have been found in southern Utah, they had the potential to be suppressed by intense ungulate herbivory (DeRose and Long, 2010); however, no signs of heavy ungulate activity were found in this study.

Naturally, disturbances can only induce asexual regeneration where the root system is still present (Jones et al., 2005). As a pioneer species, aspen is intolerant to shade (Perala, 1990) and is in most cases eventually replaced by more shade-tolerant species (Peet, 1981; Bartos, 2000; Lieffers et al., 2002; Frey et al., 2004), rendering frequent disturbances essential to the species' persistence. When growing in shaded conditions, aspen predominantly allocates resources to the root system (Landhäusser and Lieffers, 2001). Carbon storage in the parent root system enhances aspen's ability to resprout following stand-replacing disturbances, but it takes a long time (>80 years) to fully restock this reserve to pre-disturbance conditions in Colorado (Shepperd and Smith, 1993). Although no pulse in suckering was found in our study, the increased growth of mature stems ensures that these aspen will sustain for an extended time in the landscape, both enhancing the ability to restock carbon storage and maintaining a higher density of aspen stands until a stand-replacing disturbance resets succession, or until optimal conditions for seed germination are present.

More rigorous studies are required to test our results. The apparent lack of releases in plots sampled in 2011 and the discrepancies in release detection between interval lengths and chronologies require further attention, and our data should be subject to evaluation through resampling in 10+ years when more running medians post disturbance can be calculated. To exclude potential confounding factors, we propose a study in homogeneous mixed aspen-conifer forests that utilizes artificial introduction of conifer death through girdling. While girdling does not precisely mimic beetle-induced mortality (Hubbard et al., 2013), it is a better alternative to mechanical thinning as girdled trees remain standing similar to trees affected by bark beetles. In addition, more knowledge of radial growth patterns in aspen is needed to calibrate percent growth change thresholds and interval lengths, and allow for application of potentially more precise release-detection methods such as the absolute-increase method (Fraver and White, 2005).

5. Conclusion

In summary, our results suggest that aspen are beneficiaries of the recent bark beetle epidemic in north-central Colorado, as indicated by a radial growth release that approximately corresponds to timing of beetle-induced conifer mortality. Furthermore, our results indicate that aspen do not exhibit increased vegetative regeneration but allocate increased growth capacities resulting from reduced competition to ramets that were established pre-disturbance. These findings provide important insights into persistence of aspen, future stand development, and aid in the development of optimum management strategies to preserve this ecologically important species. Our results provide the first

account of this response and beg for further investigation of a possible trade-off in aspen growth following beetle-induced conifer mortality.

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References

- Amacher, M.C., Johnson, A.D., Kutterer, D.E., Bartos, D.L., 2001. First-year postfire and postharvest soil temperatures in aspen and conifer stands. Res. Pap. RMRS-RP-27-WWW. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 24 p.
- Anderegg, W.R., Berry, J.A., Smith, D.D., Sperry, J.S., Anderegg, L.D., Field, C.B., 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences U.S.A.* 109, pp. 233–237.
- Anderegg, W.R.L., Plavcová, L., Anderegg, L.D.L., Hacke, U.G., Berry, J.A., Field, C.B., 2013. Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. *Global Change Biol.* 19, 1188–1196.
- Bartos, D.L., 2000. Landscape dynamics of aspen and conifer forests. *Aspen Bibliography*. Paper 782.
- Chong, G.W., Simonson, S.E., Stohlgren, T.J., Kalkhan, M.A., 2001. Biodiversity: Aspen stands have the lead, but will nonnative species take over? In: Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G., comps. *Sustaining aspen in western landscapes: Symposium proceedings*; 13–15 June 2000. Grand Junction, CO. Proceedings RMRS-P-18. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 261–272.
- Clow, D.W., Rhoades, C., Briggs, J., Caldwell, M., Lewis Jr, W.M., 2011. Responses of soil and water chemistry to mountain pine beetle induced tree mortality in Grand County, Colorado, USA. *Appl. Geochem.* 26 (Supplement), S174–S178.
- Collins, B.J., Rhoades, C.C., Battaglia, M.A., Hubbard, R.M., 2012. The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. *Forest Ecol. Manage.* 284, 260–268.
- Collins, B.J., Rhoades, C.C., Hubbard, R.M., Battaglia, M.A., 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. *Forest Ecol. Manage.* 261, 2168–2175.
- Cook, E.R., 1985. A time series analysis approach to tree ring standardization (Dendrochronology, Forestry, Dendroclimatology, Autoregressive Process). Thesis. University of Arizona, Tucson, Arizona, USA.
- Cook, E.R., Holmes, R.L., 1986. Users manual for program ARSTAN. Laboratory of Tree-Ring Research, University of Arizona, Tucson, USA.
- Cooke, B.J., Roland, J., 2007. Trembling aspen responses to drought and defoliation by forest tent caterpillar and reconstruction of recent outbreaks in Ontario. *Can. J. Forest Res.* 37, 1586–1598.
- Copenheaver, C.A., Black, B.A., Stine, M.B., McManamay, R.H., Bartens, J., 2009. Identifying dendroecological growth releases in American beech, jack pine, and white oak: within-tree sampling strategy. *Forest Ecol. Manage.* 257, 2235–2240.
- DeRose, R.J., Long, J.N., 2010. Regeneration response and seedling bank dynamics on a *Dendroctonus rufipennis*-killed *Picea engelmannii* landscape. *J. Veg. Sci.* 21, 377–387.
- DesRochers, A., Liefers, V.J., 2001. The coarse-root system of mature *Populus tremuloides* in declining stands in Alberta, Canada. *J. Veg. Sci.* 12, 355–360.
- Diskin, M., Rocca, M.E., Nelson, K.N., Aoki, C.F., Romme, W., 2011. Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. *Can. J. Forest Res.* 41, 782–792.
- Edburg, S.L., Hicke, J.A., Brooks, P.D., Pendall, E.G., Ewers, B.E., Norton, U., Gochis, D., Gutmann, E.D., Meddens, A.J., 2012. Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. *Front. Ecol. Environ.* 10, 416–424.
- Eisenhart, K.S., Veblen, T.T., 2000. Dendroecological detection of spruce bark beetle outbreaks in northwestern Colorado. *Can. J. Forest Res.* 30, 1788–1798.
- Fraser, E.C., Liefers, V.J., Landhäusser, S.M., 2004. Wounding of aspen roots promotes suckering. *Can. J. Bot.* 82, 310–315.
- Fraver, S., White, A.S., 2005. Identifying growth releases in dendrochronological studies of forest disturbance. *Can. J. Forest Res.* 35, 1648–1656.
- Freligh, L.E., 2002. *Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-deciduous Forests*. Cambridge University Press, New York.
- Frey, B.R., Liefers, V.J., Hogg, E., Landhäusser, S.M., 2004. Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. *Can. J. Forest Res.* 34, 1379–1390.
- Frey, B.R., Liefers, V.J., Landhäusser, S.M., Comeau, P.G., Greenway, K.J., 2003. An analysis of sucker regeneration of trembling aspen. *Can. J. Forest Res.* 33, 1169–1179.
- Fritts, H., Swetnam, T., 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Adv. Ecol. Res.* 19, 111.
- Gendreau-Berthiaume, B., Kneeshaw, D.D., Harvey, B.D., 2012. Effects of partial cutting and partial disturbance by wind and insects on stand composition, structure and growth in boreal mixedwoods. *Forestry* 85, 551–565.
- Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Res.* 57, 205–211.
- Hadley, K.S., Veblen, T.T., 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. *Can. J. Forest Res.* 23, 479–491.
- Hicke, J.A., Johnson, M.C., Hayes, J.L., Preisler, H.K., 2012. Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecol. Manage.* 271, 81–90.
- Hogg, E.H., Brandt, J.P., Kochtubajda, B., 2002. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Can. J. Forest Res.* 32, 823–832.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43, 69–78.
- Huang, J.-G., Tardif, J., Denneler, B., Bergeron, Y., Berninger, F., 2008. Tree-ring evidence extends the historic northern range limit of severe defoliation by insects in the aspen stands of western Quebec, Canada. *Can. J. Forest Res.* 38, 2535–2544.
- Hubbard, R.M., Rhoades, C.C., Elder, K., Negron, J., 2013. Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling. *Forest Ecol. Manage.* 289, 312–317.
- Jelinski, D.E., Cheliak, W., 1992. Genetic diversity and spatial subdivision of *Populus tremuloides* (Salicaceae) in a heterogeneous landscape. *Am. J. Bot.* 728–736.
- Jenkins, M.J., Hebertson, E., Page, W., Jorgensen, C.A., 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecol. Manage.* 254, 16–34.
- Jenkins, M.J., Page, W.G., Hebertson, E.G., Alexander, M.E., 2012. Fuels and fire behavior dynamics in bark beetle-attacked forests in Western North America and implications for fire management. *Forest Ecol. Manage.* 275, 23–34.
- Jones, B.E., Rickman, T.H., Vazquez, A., Sado, Y., Tate, K.W., 2005. Removal of encroaching conifers to regenerate degraded aspen stands in the Sierra Nevada. *Restor. Ecol.* 13, 373–379.
- Klutsch, J.G., Battaglia, M.A., West, D.R., Costello, S.L., Negrón, J.F., 2011. Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in north-central Colorado. *Western J. Appl. Forest.* 26, 101–109.
- Klutsch, J.G., Negrón, J.F., Costello, S.L., Rhoades, C.C., West, D.R., Popp, J., Caissie, R., 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *Forest Ecol. Manage.* 258, 641–649.
- Krebill, R.G., 1972. Mortality of aspen on the Gros Ventre elk winter range. Landhäusser, S.M., Liefers, V.J., 2001. Photosynthesis and carbon allocation of six boreal tree species grown in understory and open conditions. *Tree Physiol.* 21, 243–250.
- Lavertu, D., Mauffette, Y., Bergeron, Y., 1994. Effects of stand age and litter removal on the regeneration of *Populus tremuloides*. *J. Veg. Sci.* 5, 561–568.
- Leak, W., 1987. Comparison of standard and actual tree-growth trends for deciduous and coniferous species in New Hampshire. *Can. J. Forest Res.* 17, 1297–1300.
- Leonelli, G., Denneler, B., Bergeron, Y., 2008. Climate sensitivity of trembling aspen radial growth along a productivity gradient in northeastern British Columbia, Canada. *Can. J. Forest Res.* 38, 1211–1222.
- Liefers, V.J., Pinno, B.D., Stadt, K.J., 2002. Light dynamics and free-to-grow standards in aspen-dominated mixedwood forests. *Forest. Chron.* 78, 137–145.
- Lorimer, C.G., Freligh, L.E., 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Can. J. Forest Res.* 19, 651–663.
- Lynch, H.J., Renkin, R.A., Crabtree, R.L., Moorcroft, P.R., 2007. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone Fires. *Ecosystems* 9, 1318–1327.
- McDonald, E.P., Kruger, E.L., Riemenschneider, D.E., Isebrands, J.G., 2002. Competitive status influences tree-growth responses to elevated CO₂ and O₃ in aggrading aspen stands. *Funct. Ecol.* 16, 792–801.
- Mitton, J.B., Grant, M.C., 1996. Genetic variation and the natural history of quaking aspen. *BioScience* 46, 25–31.
- Nowacki, G.J., Abrams, M.D., 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecol. Monogr.* 67, 225–249.
- Orvis, K.H., Grissino-Mayer, H.D., 2002. Standardizing the reporting of abrasive papers used to surface tree-ring samples. *Tree-Ring Res.* 58, 47–50.
- Packard, F.M., 1942. Wildlife and aspen in rocky Mountain National Park, Colorado. *Ecology* 23, 478–482.
- Peet, R.K., 1981. Forest vegetation of the Colorado front range. *Plant Ecol.* 45, 3–75.
- Pelz, K.A., Smith, F.W., 2013. How will aspen respond to mountain pine beetle? A review of literature and discussion of knowledge gaps. *Forest Ecol. Manage.* 299, 60–69.
- Perala, D.A., 1990. *Populus tremuloides* Michx. quaking aspen. In: Burns, R.M., Honkala, B.H. (Eds.), *Silvics of North America*. United States Department of Agriculture, Forest Service, Washington, DC.

- Rehfeldt, G.E., Ferguson, D.E., Crookston, N.L., 2009. Aspen, climate, and sudden decline in western USA. *Forest Ecol. Manage.* 258, 2353–2364.
- Romme, W.H., Turner, M.G., Tuskan, G.A., Reed, R.A., 2005. Establishment, persistence, and growth of aspen (*Populus tremuloides*) seedlings in Yellowstone National Park. *Ecology* 86, 404–418.
- Romme, W.H., Turner, M.G., Wallace, L.L., Walker, J.S., 1995. Aspen, elk, and fire in Northern Yellowstone Park. *Ecology* 76, 2097–2106.
- Rubino, D.L., McCarthy, B., 2004. Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia* 21, 97–115.
- Schier, G.A., Jones, J.R., Winokur, R.P., 1985. Vegetative regeneration. Aspen: Ecology and management in the western United States. USDA, For. Serv. Gen. Tech. Rep. RM-119. Rocky Mt. For. and Range Exp. Sta., Ft. Collins, CO, pp. 29–33.
- Shaw, J.D., 2004. Analysis of aspen stand structure and composition in the Western US: implications for management. In: Proceedings: Canadian Institute of Forestry and Society of American Foresters Joint 2004 annual general meeting and convention, pp. 2–6.
- Shepperd, W.D., Rogers, P.C., Burton, D., Bartos, D.L., 2006. Ecology, biodiversity, management, and restoration of aspen in the Sierra Nevada. Gen. Tech. Rep. RMRS-GTR-178. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 112 p.
- Shepperd, W.D., Smith, F.W., 1993. The role of near-surface lateral roots in the life cycle of aspen in the central Rocky Mountains. *Forest Ecol. Manage.* 61, 157–170.
- Stam, B.R., Malechek, J.C., Bartos, D.L., Bowns, J.E., Godfrey, E.B., 2008. Effect of conifer encroachment into aspen stands on understory biomass. *Rangeland Ecol. Manage.* 61, 93–97.
- Stokes, M.A., 1996. *An Introduction to Tree-ring Dating*. University of Arizona Press.
- Swetnam, T.W., Thompson, M.A., Sutherland, E.K., 1985. Using dendrochronology to measure radial growth of defoliated trees. United States Department of Agriculture, Forest Service. Agricultural Handbook No. 639. 39 p.
- Veblen, T.T., Hadley, K.S., Reid, M.S., Rebertus, A.J., 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology* 72, 213–231.
- Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., Shepperd, W.D., 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. *Forest Ecol. Manage.* 255, 686–696.
- Worrall, J.J., Rehfeldt, G.E., Hamann, A., Hogg, E.H., Marchetti, S.B., Michaelian, M., Gray, L.K., 2013. Recent declines of *Populus tremuloides* in North America linked to climate. *Forest Ecol. Manage.* 299, 35–51.
- Zeigenfuss, L.C., Binkley, D., Tuskan, G.A., Romme, W.H., Yin, T., DiFazio, S., Singer, F.J., 2008. Aspen ecology in Rocky Mountain National Park: Age distribution, genetics, and the effects of elk herbivory. p. 52.