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Regeneration response and seedling bank dynamics on a *Dendroctonus rufipennis*-killed *Picea engelmannii* landscape

R. Justin DeRose & James N. Long

Abstract

Question: How does regeneration response to a host-specific, high-severity, infrequent *Dendroctonus rufipennis* outbreak differ from our conceptualization of high-severity, infrequent/low-severity, frequent disturbance regimes in *Picea engelmannii-Abies lasiocarpa* communities?

Location: Southern Utah, USA.

Methods: One hundred and seven plots across a high-elevation *P. engelmannii* forest were sampled to reconstruct pre-outbreak overstory and seedling bank densities, and calculate their associated metrics of diversity. Decade of establishment by seedling bank trees indicated "chronic" and "pulse" regenerators.

Results: The post-outbreak overstory and seedling bank were dominated by *A. lasiocarpa*. Although *Pinus flexilis*, *Pinus ponderosa*, *Picea pungens*, and *Psuedotsuga menziesii* were present in the overstory, they were virtually absent in the seedling bank. Seedling bank recruitment of *A. lasiocarpa* and *P. engelmannii* has been occurring chronically for at least the last ~205 and ~152 years, respectively. A pulse response of seedling bank *Populus tremuloides* was apparent; however, results were complicated by intense ungulate browsing.

Conclusions: Despite some similarities to the high-severity, infrequent/low-severity, frequent conceptualization of regeneration response to disturbance, the high-severity *D. rufipennis* outbreak is best described by explicitly considering host specificity and severity. Although, the outbreak simultaneously promoted both a pulse of *P. tremuloides* and a release of chronically regenerated *A. lasiocarpa*, the *P. tremuloides* response was generally masked by ungulate browsing, and the regeneration response came overwhelmingly from the *A. lasiocarpa* seedling bank. In this landscape, once dominated by *P. engelmannii*, the chronically regenerating seedling bank, typically thought to take advantage of canopy gaps associated with low-severity disturbances, is poised to dominate forest reorganization in response to the host-specific outbreak.

Keywords: Advance regeneration; Aspen herbivory; Browsing pressure; Disturbance ecology; Engelmann spruce; Regeneration ecology; Spruce beetle; Subalpine fir.

Nomenclature: Wood(1982); Flora of North America Editorial Committee eds. (1993).

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Introduction

Regeneration response to disturbance is an integral part of forest stand dynamics and is commonly described as a function of the disturbance regime severity. Descriptors of disturbance magnitude such as severity (White & Pickett 1985) are inversely related to disturbance frequency (White & Jentsch 2001). Disturbance regimes are often characterized as high severity and infrequent, low severity and frequent, or mixed in severity and frequency (Turner et al. 2001). Characteristics of mixed-severity disturbances are intricately linked to gap size but are typically intermediate to high- and low-severity disturbances. Regeneration response to mixed-severity disturbance is extremely variable and is often called "gap phase" (Veblen 1992). In this paper, we explicitly focus on the comparison between regeneration response associated with high-severity and low-severity disturbances.

High-severity, infrequent disturbances typically create increased growing space, high light levels, expose mineral soil, and reduce competition (Oliver 1981). Early successional, shade-intolerant species respond to the rapid environmental change caused by the disturbance with a "pulse" of regeneration. As a result, regeneration can be characterized as an event, with establishment occurring over a fairly short time period. In contrast, low-severity, frequent disturbances are commonly associated with limited growing space, low light levels, limited exposed mineral soil, and a high level of competition with existing vegetation (Veblen 1986). In response to low-severity disturbances, seedlings of late succes-

sional, shade-tolerant species, capable of existing in very low light conditions, gradually accumulate as advance regeneration beneath the overstory. This continuous, or "chronic", establishment of regeneration can be characterized as a process whereby a seedling bank (i.e., trees <5 cm diameter at breast height) gradually develops as advance regeneration in the absence of high-severity disturbance.

Disturbance regimes and their characteristic regeneration responses are typically associated with a particular forest type. For example, *Pinus contorta* var. *latifolia* forests are usually comprised of even-aged cohorts resulting from a high-severity, stand-replacing fire (Oliver 1981), whereas subalpine conifer forests in British Columbia are multi-aged as a result of frequent, low-severity mortality of canopy dominants (Lertzman & Krebs 1991).

Southern Rocky Mountain *Picea engelmannii-Abies lasiocarpa* communities are high elevation extensions of the boreal forest (Peet 2000) and are dominated by *P. engelmannii*, *A. lasiocarpa*, and their common associates including *Populus tremuloides*, *P. contorta*, and less commonly *Pinus flexilis* and *Pseudotsuga menziesii* (Long 1994). These forests are typically many centuries old (Aplet et al. 1988); their origin usually attributed to high-severity, infrequent, stand-replacing fires that are indiscriminate with respect to species composition and result in large patches of mineral soil available for establishment (Bloomberg 1950). Shortly after a disturbance, early successional, shade-intolerant species such as *P. tremuloides* or *P. contorta*, which have biological legacies on-site (root stocks or canopy seed banks), are able to quickly establish the site. This establishment, representing a pulse of regeneration, results in domination by these species for 100 years or more. In the long absence of another high-severity disturbance, a suite of disturbances such as root disease, bark beetles, and wind throw, often act in combination to create small, spatially separated gaps by causing species-specific mortality of individuals. The continuous creation of small patches favors chronic regeneration of shade-tolerant *P. engelmannii* and *A. lasiocarpa* in the seedling bank (Veblen 1986). Differences in gap creation can confer an advantage to one species or another e.g., exposed mineral soil associated with a tip-up mound will favor *P. engelmannii*; in contrast, *A. lasiocarpa* is more likely to establish without exposed mineral soil. The process of chronic regeneration will eventually result in a dense seedling bank.

Recently (1990s), a catastrophic (*sensu* Hardy 2005) *Dendroctonus rufipennis* outbreak occurred on the Markagunt Plateau in southern Utah. In this once *P. engelmannii*-dominated forest, the *D. rufipennis* outbreak resulted in nearly complete overstory mortality (DeRose & Long 2007). High-severity *D. rufipennis* outbreaks (epidemics) selectively kill only overstory *P. engelmannii*, leaving the non-host overstory and the seedling bank to respond. Regeneration response to *D. rufipennis* outbreaks and other disturbances such as catastrophic wind are not adequately described by the conventional disturbance regime conceptualization, which does not take into account disturbance host specificity.

In this study, we describe seedling bank dynamics and regeneration response in the wake of a host-specific, high-severity *D. rufipennis* outbreak. We analyzed species-specific age structures and growth dynamics of the seedling bank to ascertain whether the regeneration response to the outbreak was more characteristically a pulse (high-severity) or chronic (low-severity) disturbance. We also analyzed the influence of pre-outbreak, non-host overstory abundance and composition on the post-outbreak seedling bank to evaluate their roles in regeneration response.

Our objective is to characterize regeneration response to a *D. rufipennis* outbreak, determine how it may or may not differ from the high-severity, infrequent/low-severity, frequent conceptualization of disturbance regimes in *P. engelmannii-A. lasiocarpa* communities, and to determine how an extreme *D. rufipennis* outbreak may influence forest stand dynamics.

Methods

Study area

The study area is located in the subalpine *P. engelmannii-A. lasiocarpa* zone in the Dixie National Forest, Cedar City Ranger District, on the Markagunt Plateau in southwestern Utah (Fig. 1). Prior to the mid-1990s *D. rufipennis* outbreak, the forest was dominated by *P. engelmannii* (Fig. 2; DeRose & Long 2007). Minor components of the forest included *A. lasiocarpa* and *P. tremuloides* at higher elevations, and *P. flexilis*, *P. menziesii*, *P. pungens*, and *Pinus ponderosa* at lower elevations. Shrub species included *Ribes montigenum* and *Mertensia arizonica*, with abundant *Artemisia* spp. in adjacent subalpine meadows. Elevation of the study sites ranged from 2600 to 3300 m a.s.l. (Table 1, Fig. 1). Tertiary deposits of the Claron Lake Formation are responsible for the reddish silty soil over much of the western and northern parts of the plateau (Chronic 1990). Recent (1000-5000 years BP) conspicuous

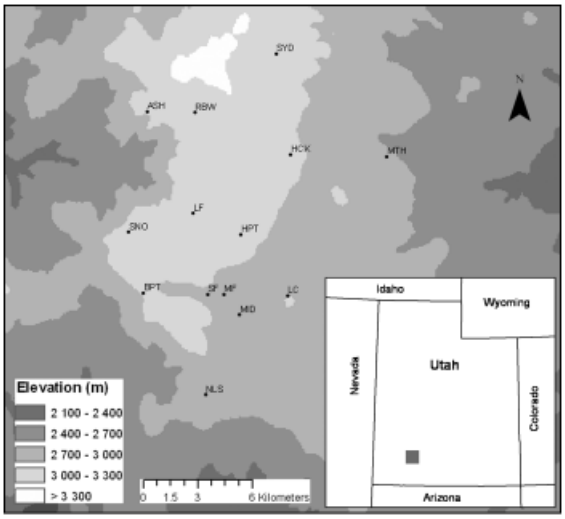

Fig. 1. Map of the Markagunt Plateau showing location of study sites. Study site labels are as follows (see Table 1): ASH – Ashdown, BPT – Bristlecone Pine Trail, HCK – North Hancock, HPT – Hancock Peak Trail, LC – Lava Cone, LF – Lava Flow, MF – Midway Face, MID – Midway Point, MTH – Mammoth Creek, NLS – Navajo Lake, RBW – Rainbow Meadows, SNO – Snotel, SF – South Face, SYD, Sydney Valley.

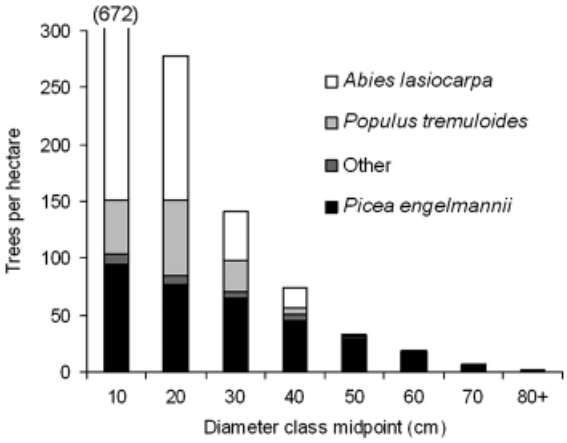

Fig. 2. Composite diameter distribution for all 14 sites constructed from pre-outbreak live overstory (>5-cm DBH) trees per hectare by 10-cm diameter class, showing dominance by *Picea engelmannii*. The 80+ category includes *P. engelmannii* up to 130 cm. Other includes, in order of abundance: *Pseudotsuga menziesii*, *Pinus flexilis*, *Pinus ponderosa*, *Picea pungens*, *Abies concolor*.

basalt flows cover a large portion of the central part of the plateau and are underlain by Tertiary volcanic rock (Chronic 1990). Annual precipitation varied between 369 and 1709 mm over the period 1948-2005. Average annual temperature varied between −0.9 and 3.1°C over the same period (http://www.nrcs.usda.gov/). A general description of regional climate for the plateau can be found in DeRose & Long (2009).

Field sampling

Study sites were carefully chosen where no evidence of past large-scale anthropogenic canopy disturbance was evident (i.e., logging). Each sampled stand appeared homogeneous in terms of overstory structure. Most stands were recently dominated by *P. engelmannii*, with composition varying from ~50% to ~95% *P. engelmannii* basal area ($m^2 ha^{-1}$ at 1.3 m) prior to the outbreak (except for Rainbow Meadows and Sydney Valley, which were dominated by *A. lasiocarpa*). Past elevated beetle populations have been reported as early as 1937 (cited in Hebertson & Jenkins 2008), and a large-scale outbreak occurred during 1916-1918 ~120 km east-northeast of the study site on the Aquarius Plateau (Mielke 1950).

Depending on overall stand size, three to 10 plots were measured at each site during the summers of 2005, 2006, and 2007. A grid sampling network was established in each stand from a randomly located starting point and azimuth. Variable radius plot sampling was used to assess overstory trees [>5 cm diameter at breast height (DBH)] (Bell & Dilworth 2002). DBH and height were measured for each overstory tree, and species and status (live or dead) were noted. Since the outbreak was recent (1990s), nearly every beetle-killed tree was still standing (~99.2%); therefore, both live and dead standing trees were measured to indicate beetle-caused mortality (Veblen et al. 1991b). Rate-of-fall for beetle-killed *P. engelmannii* is thought to be site-specific (E.G. Hebertson, pers. comm., fall 2008, US Forest Service, Forest Health Protection Specialist), and the rate found on nearby Aquarius Plateau (~0.6% per year Mielke 1950) was consistent with our observations. *P. engelmannii* were examined to determine whether mortality was caused by the recent *D. rufipennis* outbreak, which would be indicated by the presence of beetle galleries on the surface of the bole and emergence holes in the bark. Although foresters often differentiate seedlings (<2 m in height) from saplings (>2 m in height but <5 cm in DBH), for ease of interpretation in this study all trees >5 cm in height and <5 cm in DBH were referred to as the seedling bank. The seedling bank was measured on fixed-area subplots (1-3-m radius based on site-specific seedling bank density) in the center of each overstory plot. Height and

Table 1. Site and seedling bank attributes for the sampled stands. *Other: 1 – *Pinus ponderosa*, 3 – *Picea pungens*.

Site	No. plots	Elevation range (m a.s.l.)	Slope (%)	Aspect	Seedling bank density m^{-2}			
					Abies lasiocarpa	*Populus tremuloides*	*Picea engelmannii*	Other*
Ashdown	9	3176-3219	0-5	North	1.48	–	0.03	–
Bristlecone Pine Trail	4	2974-3038	15-40	Northwest	0.16	–	–	–
North Hancock	10	3054-3127	3-30	North	2.55	–	0.37	–
Hancock Peak Trail	10	3062-3101	0-5	Southeast	0.70	1.31	0.06	–
Lava Cone	10	2926-3032	0-20	Variable	1.00	0.29	0.03	–
Lava Flow	3	3125-3147	5-10	Southwest	4.44	0.44	0.11	–
Midway Face	3	2980-3172	5-10	North	1.56	2.33	0.56	–
Midway Point	10	2931-2988	0-3	North	2.33	0.71	0.08	–
Mammoth Creek	10	2618-2723	15-40	North	0.16	0.16	0.02	<0.001
Navajo Lake	10	2845-2914	10-30	Northeast	0.24	0.03	0.02	–
Rainbow Meadow	5	3179-3233	2-10	South	3.07	0.43	0.10	–
Snotel	10	3154-3250	5-45	North	0.21	–	0.02	–
South Face	3	2990-2993	15-30	South	2.00	1.11	–	–
Sydney Valley	10	3073-3117	3-15	Southwest	4.48	0.13	0.08	–
				Averages:	1.74	0.50	0.11	<0.001

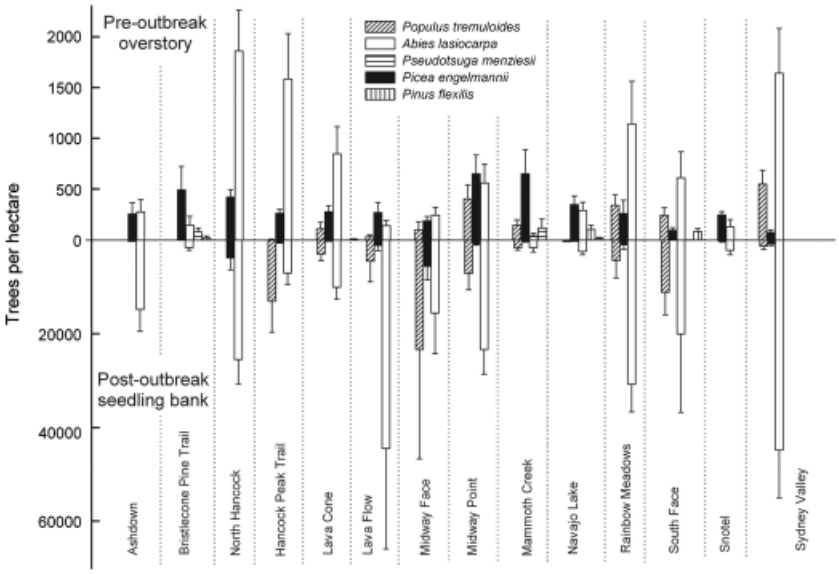

Fig. 3. Pre-outbreak overstory trees per hectare, averaged per site, reconstructed from field data plotted over post-outbreak seedling bank trees per hectare by species shows: (1) the paucity of *Picea engelmannii* in the seedling bank, (2) remaining overstory species after the host-specific beetle outbreak. Individual sites are named and divided by dotted lines (see Table 1).

basal diameter were measured and species noted before cross-sections were removed at ground level from every tree in the subplot, including root suckers of *P. tremuloides*. In the lab, cross-sections were sanded with progressively finer sandpaper before annual rings were counted under a microscope.

A total of 2093 seedling bank trees were measured in 107 plots on 14 sites across the plateau and used for abundance estimation and comparisons of the overstory composition to seedling bank composition (Table 1). Of these trees, 1850 were successfully aged. In order of abundance they were: *A. lasiocarpa* 1535 (83%); *P. tremuloides* 249 (13%); *P. engelmannii* 62 (4%); *P. pungens* three (<0.01%); and *P. ponderosa* one (<0.001%). Seedling bank age structure and height-age relationships were analyzed using 1846 of these trees (three *P. pungens* and one *P. ponderosa* were removed). Although found in the overstory, neither *P. menziesii* nor *P. flexilis* were present in the seedling bank (Fig. 3).

Abundance by species in the seedling bank was calculated on a per hectare basis and averaged across plots within sites. Although the seedling bank was measured after the outbreak, it reflected

pre-outbreak composition because age data revealed only a small percentage of sampled trees recruited after the outbreak; and of these, most were sprouting *P. tremuloides*. To facilitate analysis, reconstructed pre-outbreak overstory trees per hectare (TPHA) were plotted over seedling bank TPHA (Fig. 3). Overstory abundance of non-host species reflects the presence of biological legacies and potential seed sources post-disturbance.

To quantify timing of establishment by individual species, we generated a frequency distribution of seedling bank recruitment by pooling age data into decadal classes of origin. Evaluating the distribution for consistent or episodic seedling bank recruitment revealed whether a species more typically exhibited chronic or pulse regeneration. Long drawn-out establishment indicated availability for response to overstory disturbance at any time since the earliest decade of seedling establishment, whereas spikes in origin dates indicated rapid establishment of a large number of individuals i.e., a pulse, likely a response triggered by rapid environmental change. Seedling bank tree-ring counts in our analysis were not cross-dated and are therefore conservative.

Composite species-specific height growth rates were estimated by pooling all measured seedling bank individuals and fitting linear models of height and age. Using the fitted equation, average potential growth rates were used to suggest the potential of each species to accede to the canopy. After preliminary inspection, *P. tremuloides* data were split into two groups: one associated with lava flow substrates and another representing an absence of lava flow substrate. The lava flow substrate population is almost entirely from the Lava Cone site, which is surrounded in every direction by ~1.6 km of recent (1000-5000 years) lava flows. Lava flows are composed of large blocky boulders of basalt, making ungulate access both currently and historically impossible. Therefore, lava flow populations represented natural exclosures that have never experienced ungulate browsing, in contrast to the other sites. To evaluate the possibility for *P. tremuloides* canopy accession, approximate browsing height thresholds were juxtaposed over height growth patterns. Height thresholds were: 200 cm for *Cervus elaphus* (elk) (Romme et al. 1995), 130 cm for *Odocoileus hemionus* (deer), and 115 cm for domestic *Ovis aries* (sheep) (Sampson 1923).

Biological legacies of the pre-outbreak forest were represented by remnant, live overstory trees which are a residual seed source, and by a seedling bank of advance regeneration. Relationships between these components were assessed to indicate potential scenarios of future forests and successional dynamics. To determine if pre-outbreak overstory composition influenced the seedling bank composition post-outbreak, three metrics were calculated for both the overstory and seedling bank.

(1) Berger–Parker dominance (D)

$$D = N_{(\mathrm{MAX})}/N,$$

where $N_{(\mathrm{MAX})}$ is the number of individuals in the largest group, and N is the total number of individuals on a given plot.

(2) Shannon diversity (H')

$$H' = \sum_{i=1}^{n} p_i, \ln p_i,$$

where p_i is the proportion of species i and ln is the natural log.

(3) Shannon evenness (E_{H}),

$$E_{\mathrm{H}} = H'/H_{(\mathrm{MAX})},$$

where H' is defined above, $H_{(\mathrm{MAX})}$ is maximum H'.

In order for metrics to be comparable between the overstory and the seedling bank, each was calculated using estimated TPHA. Relationships were assessed by calculating Pearson correlation coefficients. Any predictable relationship could potentially yield important information regarding the hastening or delay of succession as a result of the *D. rufipennis* outbreak.

Results

It is likely that *A. lasiocarpa* has been continuously establishing in the seedling bank for many centuries. We measured individuals with establishment dates to 1800 (age range 6-205 years). A decreasing percentage of those individuals persisted through time because of the balance between establishment and mortality that occurs in the seedling bank when canopy accession is restricted (Fig. 4). *P. engelmannii* also likely had continuous establishment for centuries. We measured individuals as old as 152 years, although *P. engelmannii* never represented >1% of the seedling bank in any given decade (Fig. 4). Clearly both *A. lasiocarpa* and *P. engelmannii* were chronic regenerators prior to the *D. rufipennis* outbreak, although at drastically different levels (Fig. 4). *P. tremuloides* exhibited a pulse response immediately following the death of canopy *P. engelmannii* associated with the recent outbreak, which varied by year across the plateau but was manifest in the spikes of establishment seen

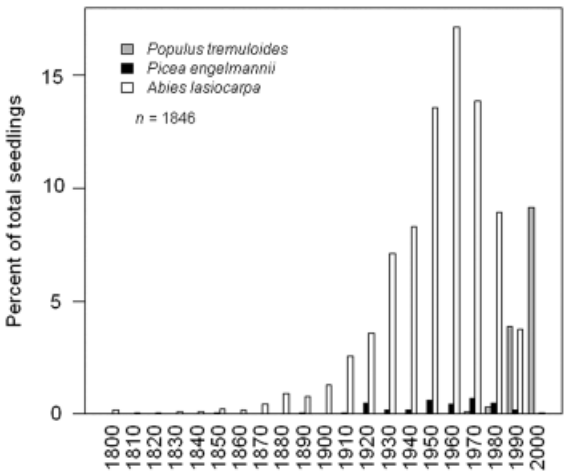

Fig. 4. Frequency distribution (percentage of total seedlings) of decade of establishment by species for the seedling bank. Chronic regeneration of *Abies lasiocarpa* dated to 1800. *Picea engelmannii* establishment dated to 1850, but was chronically occurring from 1910 to 2000. A pulse of *Populus tremuloides* establishment occurred in 1990 and 2000. *Picea pungens* was recruited once in 1900 and twice in 1940 (not shown in legend).

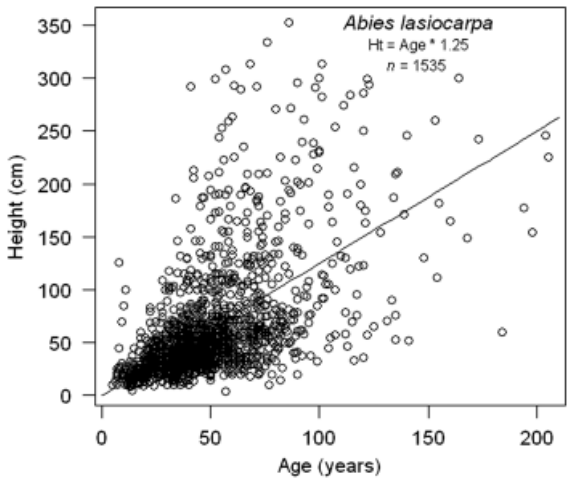

Fig. 5. Height (cm)-age (years) relationship for *Abies lasiocarpa*. Data pooled across all sites.

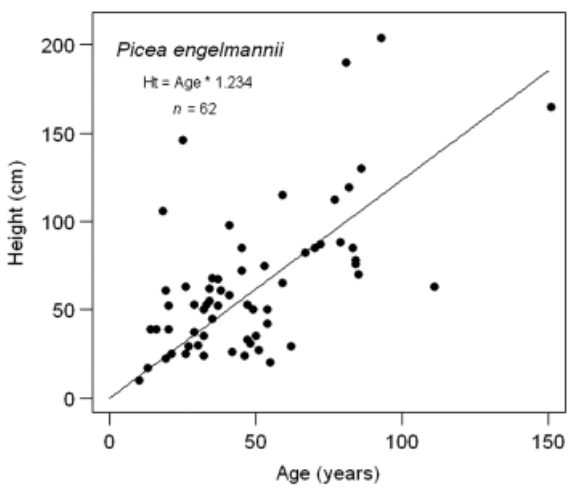

Fig. 6. Height (cm)-age (years) relationship for *Picea engelmannii*. Data pooled across all sites.

in the 1990s and 2000s (Fig. 4). Although *P. tremuloides* ranged in age from 1 to 36 years, the few individuals present during the 1970s and 1980s established under ungulate-free circumstances on lava substrates. The only other seedling bank species sampled were one *P. ponderosa* and three *P. pungens*, all at Mammoth Creek. The three *P. pungens* were recruited into the seedling bank in 1900 (1) and 1940 (2).

The chronically regenerating species *A. lasiocarpa* and *P. engelmannii* had similar height growth patterns of 1.2 cm yr^{-1} (Figs 5 and 6); although for *A. lasiocarpa* they were extremely variable and ranged from ~8 to < 0.25 cm yr^{-1}. Average growth rate suggested that by the time ~2.0-3.5 m in height was reached, the species were capable of accession to the overstory (threshold of 5-cm DBH used in this study); however seedling bank ages (Fig. 4) suggested canopy accession is a very rare event. The post-outbreak *P. tremuloides* (< 20 years) from two different populations, lava (non-browsed) and non-lava (browsed), have drastically different net height growth rates (Fig. 7). It is clear *P. tremuloides* from all sites without a lava substrate were unable to attain heights above the minimum browsing threshold, masking the expected pulse response to the high-severity *D. rufipennis* disturbance.

The outbreak resulted in ~96% mortality of overstory *P. engelmannii* (R.J. DeRose, unpubl. data). Furthermore, almost none of the seedling bank established after the outbreak. As a result, the site-by-site comparison of pre-outbreak overstory TPHA and post-outbreak seedling bank TPHA highlights the drastic reduction in *P. engelmannii* site dominance as a result of the outbreak (Figs 2 and 3). In some stands there were virtually no *P. engelmannii* in the seedling bank (e.g., Bristlecone Pine Trail, South Face) whereas in a few stands there was some *P. engelmannii* regeneration (e.g., Midway Face, North Hancock); however, there is a paucity of *P. engelmannii* across the 14 sites. In most cases, *A. lasiocarpa* was well represented in the overstory and abundant in the seedling bank. Indeed, the species composition of the seedling bank is almost certainly indicative of potential future dominance

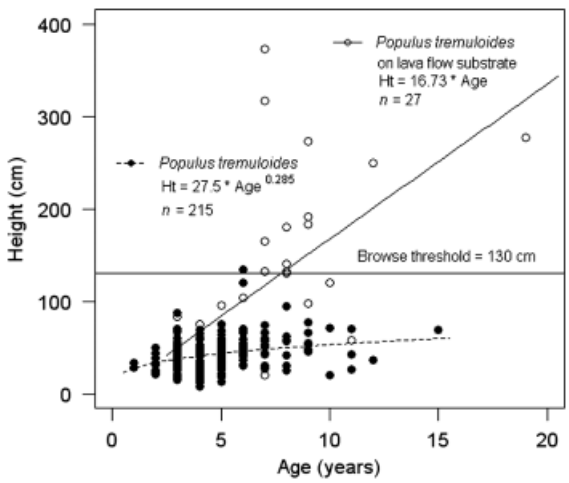

Fig. 7. Height (cm)-age (years) relationships for post-outbreak (<20 years) *Populus tremuloides* across the Markagunt Plateau. Aspen height growth rate calculated separately for sites with (absence of lava flow) and without (lava flow substrate) browsing pressure, to show the potential difference due to grazing history. See text for explanation. Regression lines plotted to suggest average height growth rates.

Table 2. Correlation coefficients for overstory and seedling bank diversity metrics.

	Overstory			Seedling bank		
	D	H'	E_H	D	H'	E_H
Overstory						
D	1.0					
H'	−0.95	1.0				
E_H	−0.84	0.81	1.0			
Seedling bank						
D	0.13	−0.16	−0.07	1.0		
H'	−0.10	0.12	−0.04	−0.94	1.0	
E_H	0.12	−0.13	0.05	−0.90	0.96	1.0

by *A. lasiocarpa* and, to a lesser degree, *P. tremuloides* (Fig. 3).

Comparisons of three metrics relating to composition revealed little relationship between pre-outbreak overstory and post-outbreak seedling bank composition. In all cases, regressions of the metrics between overstory and seedling bank components showed no significant relationship ($\alpha = 0.05$ level), and there was little correlation among the metrics (Table 2). Only for *A. lasiocarpa* was there a relationship overall between overstory and seedling bank abundance ($R^2 = 0.41$, $P < 0.001$). Many plots contained only *A. lasiocarpa*, i.e., $D = 1$ and for these plots $H' = 0$, which indicated complete dominance and no diversity, respectively. Similarly, there was no relationship in E_H between the overstory and the seedling bank.

Discussion

Our purpose in this study was to characterize regeneration response to a *D. rufipennis* outbreak and to describe its effects on stand dynamics. We also evaluated how it compared with the high-severity, infrequent/low-severity, frequent conceptualization of *P. engelmannii-A. lasiocarpa* disturbance regimes. We found the regeneration response to the outbreak did not fit the conceptual disturbance regime model. Instead, the host-specific, high-severity, infrequent *D. rufipennis* outbreak promoted a regeneration response dominated by the pre-existing seedling bank.

Had the recent high-severity disturbance been a stand-replacing fire instead of a host-specific beetle outbreak, most individuals in both the overstory and the seedling bank would have been killed, regardless of species, not just *P. engelmannii*. The resulting forest reorganization would have included a pulse of *P. tremuloides*, vigorously resprouting from root suckers on sites where rootstocks were present prior to the fire. In many *P. engelmannii-A. lasiocarpa* forests *P. contorta* also responds favorably to stand-replacing fire; however, the Markagunt Plateau is outside the geographic range of this species. It is possible that mature, thick bark *P. menziesii*, and, to a lesser extent, *P. flexilis* would survive the fire in rare refugia, and be available as seed sources. Somewhat counter-intuitively, it is possible that a stand-replacing fire would have been more advantageous for *P. engelmannii* recolonization, since post-fire there is a window of establishment possibility i.e., the "colonization phase" prior to the *P. engelmannii* "exclusion phase" (*sensu* Aplet et al. 1988), and it is likely fire is what initially regenerated at least some of the recently killed stands on the Markagunt Plateau (DeRose & Long 2007). In addition, a large-scale fire would have exposed mineral soil, necessary for *P. engelmannii* establishment (e.g., see Kulakowski & Veblen 2006), and the seed source would have come from biological legacies on rocky outcrops and in moist refugia. Finally, a stand-replacing fire would have killed most canopy and seedling bank *A. lasiocarpa*, a drastically different outcome than the recent *D. rufipennis* outbreak (Fig. 3). The result would be few *A. lasiocarpa* legacies and a possible lengthening of the time (decades) before *A. lasiocarpa* regenerated on the burned site (Little et al. 1994).

In the absence of a high-severity disturbance, the Markagunt Plateau would eventually begin to have gap-forming disturbances, in which primarily mature trees, individually or in small groups, would be killed. The continuous creation of small patches

would favor the chronic regeneration of shade-tolerant *P. engelmannii* and *A. lasiocarpa* in the seedling bank (Veblen 1986). Gaps with tip-up mounds, dead and down wood (Zielonka 2006), or mineral soil would favor *P. engelmannii* establishment, whereas gaps due to broken stems or crowns and thick litter layers would favor *A. lasiocarpa*. In the continued absence of a high-severity disturbance, the process of chronically regenerating species would have maintained a multi-aged *P. engelmannii-A. lasiocarpa* forest, where species coexistence would be mediated by a balance between long-lived *P. engelmannii* and prolifically regenerating *A. lasiocarpa* (Veblen 1986; Aplet et al. 1988).

Regeneration response to some disturbance regimes does not necessarily fit the high-severity, infrequent/low-severity, frequent model. For example, mixed-severity disturbance regimes operate at different spatial and temporal scales. Fire regimes in Rocky Mountain *P. menziesii* forests create spatial heterogeneity of burned patches on the landscape (Klenner et al. 2008). Catastrophic wind and bark beetle outbreaks are disturbances that are more difficult to characterize with the conventional disturbance regime conceptual model. Although high severity and infrequent, they are both fundamentally different from stand-replacing fire. Like fire, severe wind storms are not fundamentally species-specific, and create large patches of growing space (Foster & Boose 1992). However, wind storms mostly affect overstory individuals, leaving biological legacies such as shade-tolerant, late seral species, which have chronically established in the seedling bank and can persist in low light conditions until released by canopy disturbance. Regeneration response to high-severity wind throw is likely a combination of new establishment of pulse species and a release of chronic species from the seedling bank (Cooper-Ellis et al. 1999; Kulakowski & Veblen 2003).

Unlike both catastrophic wind and stand-replacing fire, the high-severity *D. rufipennis* outbreak on the Markagunt Plateau resulted in beetle populations that selectively killed only overstory *P. engelmannii*, leaving the non-host overstory trees and the seedling bank to respond. Moreover, prior to the outbreak the canopy was heavily dominated by dense, mature (many centuries old) *P. engelmannii* with a sub-canopy of *A. lasiocarpa* (Fig. 2), so that when the outbreak killed the dominant *P. engelmannii* it left almost entirely *A. lasiocarpa* in both the overstory and seedling bank (Figs 3 and 4). The dominance of *A. lasiocarpa* in both the overstory and seedling bank (in terms of TPHA) is likely the reason metrics of pre-outbreak overstory and post-outbreak seedling bank composition were unrelated (Table 2), not unlike that found by Lecomte et al. (2005). Overstory *P. engelmannii* were rare or completely absent from our sites post-outbreak, and since seed-bearing *P. engelmannii* exhibit irregular years of good seed production (Long 1994) and do not form a soil seed bank that persists longer than 9 months (Greene et al. 1999), seed from *P. engelmannii* will not effectively contribute to the future forest. Overstory biological legacies of species other than *A. lasiocarpa*, such as *P. tremuloides* and, less commonly, *P. menziesii* and *P. flexilis*, occurred on the plateau (Fig. 3); however, they were rare and unlikely to effectively contribute to the regeneration response. In Canada, Astrup et al. (2008) found little evidence for a post-*Dendroctonus ponderosae* outbreak pulse of regeneration, as would be expected after fire, and instead, concluded that the response was likely dominated by previously established individuals (advance regeneration) composed almost entirely of *A. lasiocarpa*. In contrast to our data and Astrup et al. (2008), Axelson et al. (2009) found *D. ponderosae*-affected *P. contorta* forests had adequate representation of live *P. contorta* in the canopy (29%) and sub-canopy (25%) post-outbreak that would contribute to forest reorganization.

A regeneration response to the recent outbreak characteristic of low-severity, frequent disturbance was evident in our data. The process of chronic seedling bank regeneration has likely been occurring for centuries (Fig. 4); however, it was much more pronounced for *A. lasiocarpa* than for *P. engelmannii*, which is consistent with their relative shade tolerances (Kobe & Coates 1997). Moreover, the large difference in numbers between these two species suggested *A. lasiocarpa* was better able to establish in the thick litter associated with this *P. engelmannii-A. lasiocarpa* forest floor (Noble & Alexander 1977), and likely relied on a long-lived seedling bank to maintain its position as a sub-canopy associate of *P. engelmannii* (Veblen 1986; Antos & Parish 2002). In contrast, *P. engelmannii* has more exacting seedbed requirements and, as reflected in our data, only rarely establishes, probably when an appropriate microsite becomes available. Indeed, *P. engelmannii* regeneration has been found to be limited to sites with thin to no litter layer (Noble & Alexander 1977; Knapp & Smith 1982). The bell-shaped age frequency distribution of the chronic regenerators was likely a result of the gradual mortality of most of the seedling bank over time, suggesting they cannot survive indefinitely (Fig. 4). However, our data were not inconsistent with the observation by Veblen et al. (1991a) of an overall

increase in seedling bank *A. lasiocarpa* in general in *P. engelmannii-A. lasiocarpa* communities of Rocky Mountain National Park during the last 100 years, possibly as a result of increased regional moisture.

In contrast to a *D. rufipennis* outbreak, disturbances that expose mineral soil increase the likelihood of *P. engelmannii* establishment. Canopy gaps in old-growth forests as a result of low-severity, gap-phase dynamics create and maintain the necessary seedbed conditions (i.e., fallen logs, tip-up mounds, and mineral soil) for *P. engelmannii* establishment and also allow it to increase its representation in the seedling bank (Kulakowski & Veblen 2003). There was limited evidence of pit and mound topography on our sites (R.J. DeRose, in prep.), which may partially explain the very low numbers of *P. engelmannii* in the seedling bank. Relatively low abundances of *P. engelmannii* have been found in other systems; e.g., Schulze et al. (2005) suggested seedling bank density of *Picea obovata* in the Dark Taiga forest ranged from 100 to 400 TPHA but did not state over what time period these trees established. Similarly, Antos & Parish (2002) found 7.6% of the *P. engelmannii-A. lasiocarpa* forest seedling bank was *P. engelmannii* in British Columbia. If we assume the ~1% establishment of *P. engelmannii* per decade on our sites in the mid- to late-1900s (from Fig. 4) represented average decadal recruitment into the seedling bank, then ~50 seedlings $ha^{-1} yr^{-1}$ became established, whereas the ~10% establishment, on average, of *A. lasiocarpa* over the same time period translated into ~550 seedlings $ha^{-1} yr^{-1}$. Therefore, although *A. lasiocarpa* exhibits a more rapid extinction in numbers over time than *P. engelmannii* (from right to left on Fig. 4), it maintained much larger quantities in the seedling bank overall. Furthermore, although overall seedling bank abundances appeared high enough to be adequate for forest regeneration (Fig. 3, *sensu* Nigh et al. (2008), in beetle-killed *P. contorta*), *A. lasiocarpa* makes up a vast majority of that total. Antos et al. (2000) suggested the paucity of *P. engelmannii* observed on two sites in British Columbia is partially offset by its' increased height growth; however, we found no height growth advantage for *P. engelmannii* in our data (Figs 5 and 6).

In contrast to *A. lasiocarpa* and *P. engelmannii*, the regeneration response of *P. tremuloides* was a characteristic pulse, as expected given the high-severity 1990s beetle outbreak (Fig. 4). Nevertheless, with the exception of sites with a lava flow substrate (i.e., Lava Cone and Mammoth Creek), virtually none of the *P. tremuloides* pulse achieved heights above the minimum browsing threshold (Fig. 7). *P. tremuloides* on lava flow substrates reflect height growth in the absence of browsing, whereas the balance of *P. tremuloides* on the plateau are simply unlikely to attain appropriate height for canopy accession due to browsing pressure from both domestic and native ungulates. *Odocoileus hemionus* (deer), *Cervus elaphus* (elk), *Ovis aries* (domestic sheep), and *Bos* spp. (domestic cattle) are primarily responsible for browsing pressure on the Markagunt Plateau. In general, *O. aries* browse choice is similar to *O. hemionus*, with a preference for leaves and tender stems, whereas *C. elaphus* eat a more varied diet. As a result, *O. aries* browsing should directly increase the grass component by removing the herbaceous component that the *C. elaphus* prefer; however, if there are too many *O. aries, C. elaphus* might have to find something else to eat (i.e., *P. tremuloides*; Sampson 1923). In addition to *O. aries*, if *Bos* spp. are present they will compete with *C. elaphus* for grass, further pushing *C. elaphus* to rely on *P. tremuloides*. Indeed, recent work has found evidence of top-down regulation of *P. tremuloides* by *C. elaphus* in Yellowstone National Park (Halofsky & Ripple 2008), where increased *P. tremuloides* growth has resulted from the coupling of recent fire and reduced *C. elaphus* herbivory, presumably from increased *Canis lupus* (wolf) presence (Halofsky et al. 2008).

In sharp contrast to other large-scale, high-severity disturbance types such as fire, the recent *D. rufipennis* outbreak did not destroy the non-host overstory or seedling bank, nor did it create environmental conditions generally associated with pulse regeneration of early seral species as we would expect, given the conventional disturbance regime conceptualization. Instead, the loss of the dominant overstory *P. engelmannii* has opened growing space for the few non-host overstory species, where they occur, and released the seedling bank of primarily *A. lasiocarpa*, which has been chronically regenerating for centuries. Although *P. tremuloides* exhibited a pulse regeneration response to the outbreak, it will not dominate post-outbreak stands (except on lava substrates) because of intense browsing pressure. In this once *P. engelmannii*-dominated landscape, the relatively few residual, non-host overstory trees will not be able to fully reoccupy the growing space; instead, the seedling bank will play the primary role in regeneration response. The chronically regenerating seedling bank, typically associated with canopy gaps, created by low-severity disturbances, is posed to dominate forest reorganization in response to the high-severity, host-specific *D. rufipennis* outbreak.

The regeneration response to this high-severity, host-specific outbreak may not be typical of what has happened previously on our site. However, such atypical regeneration response in western North America might become more common in the future due to changing bark beetle dynamics. Beetle outbreaks, both *D. rufipennis* on the Kenai Peninsula of Alaska (Berg et al. 2006) and *D. ponderosae* in western Canada (Wulder et al. 2006) and northern Colorado (D. Kulakowski & T.T. Veblen, unpubl. report), are affecting larger areas than previously documented. Increasing area of susceptible hosts, predicted shifts in *D. rufipennis* populations from one generation every 2 years to one generation in a single year (Bentz et al. submitted), and a predicted shift in *P. engelmannii* habitat to higher elevations (Rehfeldt et al. 2006) may all contribute to altered disturbance dynamics of *P. engelmannii* and a reduction in area of *P. engelmannii* forest in the western US.

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