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Limited seed viability in long-dead serotinous lodgepole pine trees in the Southern Rockies, USA

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ABSTRACT

Serotinous cones, those that remain closed until heated, confer post-disturbance resilience on many lodgepole pine forests throughout the Southern Rockies. The record-breaking extent of wildfires in northern Colorado and southern Wyoming in 2020 raised concerns about tree regeneration in areas where crown fires burned lodgepole pine stands that had experienced high levels of mortality during bark beetle outbreaks occurring more than a decade previously. We measured seed germination and assessed the relationship between cone age and seed viability for serotinous cones on beetle-killed lodgepole pine in eight stands adjacent to four of those wildfires (n = 1160 cones). On average, germination was 34 % with three viable germinants produced per cone. Seed germination declined and the proportion of cones that contained no seed increased across the age range of cones sampled (17–51 yrs at the time of the 2020 wildfires). Germination of seed retained within the canopy seedbank of these long-dead stands was roughly half of that measured on live or recently killed lodgepole pine. Though pre-fire tree mortality from bark beetles can exceed 90 % in this area, serotinous cones on the remaining live trees and cones buried in the soil seedbank will contribute viable lodgepole seeds for tree regeneration on some burned landscapes. The decreased germinant levels from these cones may regenerate into pine stands that are less dense than after harvesting, bark beetles or wildfire alone, but they will likely create forest structure within a range of conditions expected for this region.

1. Introduction

Cone serotiny, a trait where mature cones remain closed until heated, creates resilience for lodgepole pine (*Pinus contorta* var. latifolia) forests after wildfire (Lotan, 1976; Turner et al., 2007). Historic ecological studies documented rapid post-fire tree regeneration and decades-long seed viability in the canopy seed bank of serotinous lodgepole pine stands (Tower, 1909; Clements, 1910). Severe mountain pine beetle (*Dendroctonus ponderosae*, Hopkins) outbreaks that occurred across the range of lodgepole pine during the 2000 s (Raffa et al., 2008) prompted questions about seed viability after tree death. Studies conducted shortly after onset of the beetle outbreak reported that on average, seed germination exceeded 50 % from serotinous cones in both Colorado and British Colombia (Aoki et al., 2011; Teste et al., 2011a). Concurrent field studies documented abundant pine recruitment in beetle-killed lodgepole forests in Colorado, confirming the high regeneration potential of stands with cone serotiny (Collins et al., 2011; Diskin et al., 2011). However, extensive wildfires that burned beetle-killed, lodgepole pine forests in 2020 rekindled questions about the persistence of viability and its effects on tree regeneration, now 15 yrs after tree mortality.

The number of wildfires and extent burned annually has increased across western North America since the early 1980 s (Coop et al., 2020). In 2020, the Cameron Peak (845 km^2), East Troublesome (784 km^2), Mullen (716 km^2), and Williams Fork (60 km^2) fires burned forests at the headwaters of the Colorado, South Platte and North Platte Rivers near the Colorado-Wyoming border (Fig. 1; INCIWEB, 2020); both the Cameron Peak and East Troublesome fires surpassed the previous largest fire in Colorado history (e.g., Hayman Fire 2002; Graham, 2003). More than half of the area burned by these wildfires occurred in lodgepole pine-dominated forests, where beetle outbreaks killed>75 % of overstory trees in many stands and exceeded 90 % in some areas (Collins et al., 2011; Pelz et al., 2018; Rhoades et al., 2020).

Wildfires in high-elevation forests are less frequent than those at lower elevation, though their incidence is increasing (Alizadeh et al., 2021). Owing to the wind-driven, crown-fire behavior typical of those fires (Hart and Preston, 2020), they are often stand-replacing

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disturbances with significant ecosystem effects. High and moderate severity wildfire effects occurred on 37–66 % of the area burned by the aforementioned 2020 fires (INCIWEB, 2020). There is growing awareness that combined or repeated disturbances can create obstacles for tree regeneration (Harvey et al., 2014a; Agne et al., 2016; Stevens-Rumann et al., 2017), and there is evidence of very low conifer recruitment after fires in stands with high lodgepole pine mortality from bark beetles (Rhoades et al., 2018; Turner et al., 2019; Rammer et al., 2021). Given observed and projected increases in wildfire extent and severity (Dennison et al., 2014; Flannigan et al., 2013; Dong et al., 2022), the uncertain recovery of long-dead (i.e., 'gray-phase') beetle-killed stands have broad consequences in the Southern Rockies, both for pine-dominated stands and the mixed-species Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests (Rodman et al., 2022) where lodgepole commonly co-occurs.

The proportion of stands and trees with serotinous cones varies across the range of lodgepole pine (Lotan and Critchfield, 1990) and the factors that control the distribution of the trait are poorly understood (Turner et al., 2007). Serotinous cones predominate in stands in northern parts of lodgepole's range (Koch, 1996) and decline with elevation in the Yellowstone National Park area (Tinker et al., 1994; Schoennegal et al., 2003), but the prevalence of the trait is uncertain in the Southern Rockies. Information about this stand characteristic is incomplete for US Forest Service lands, though the limited, existing data from forests along the Colorado-Wyoming border indicates roughly equal abundance of serotinous and non-serotinous stands (USDA, 2021a). In addition to variability in cone serotiny, the lag between beetle-related tree mortality and the 2020 wildfires has the potential to influence the contribution of serotinous cones in the canopy seedbank to post-fire tree seed availability and tree regeneration in this area (Teste et al., 2011a; Harvey et al., 2014b; Talucci et al., 2019). The 2020 wildfires provide an opportunity to evaluate how bark beetle outbreaks, wildfire, cone serotiny,

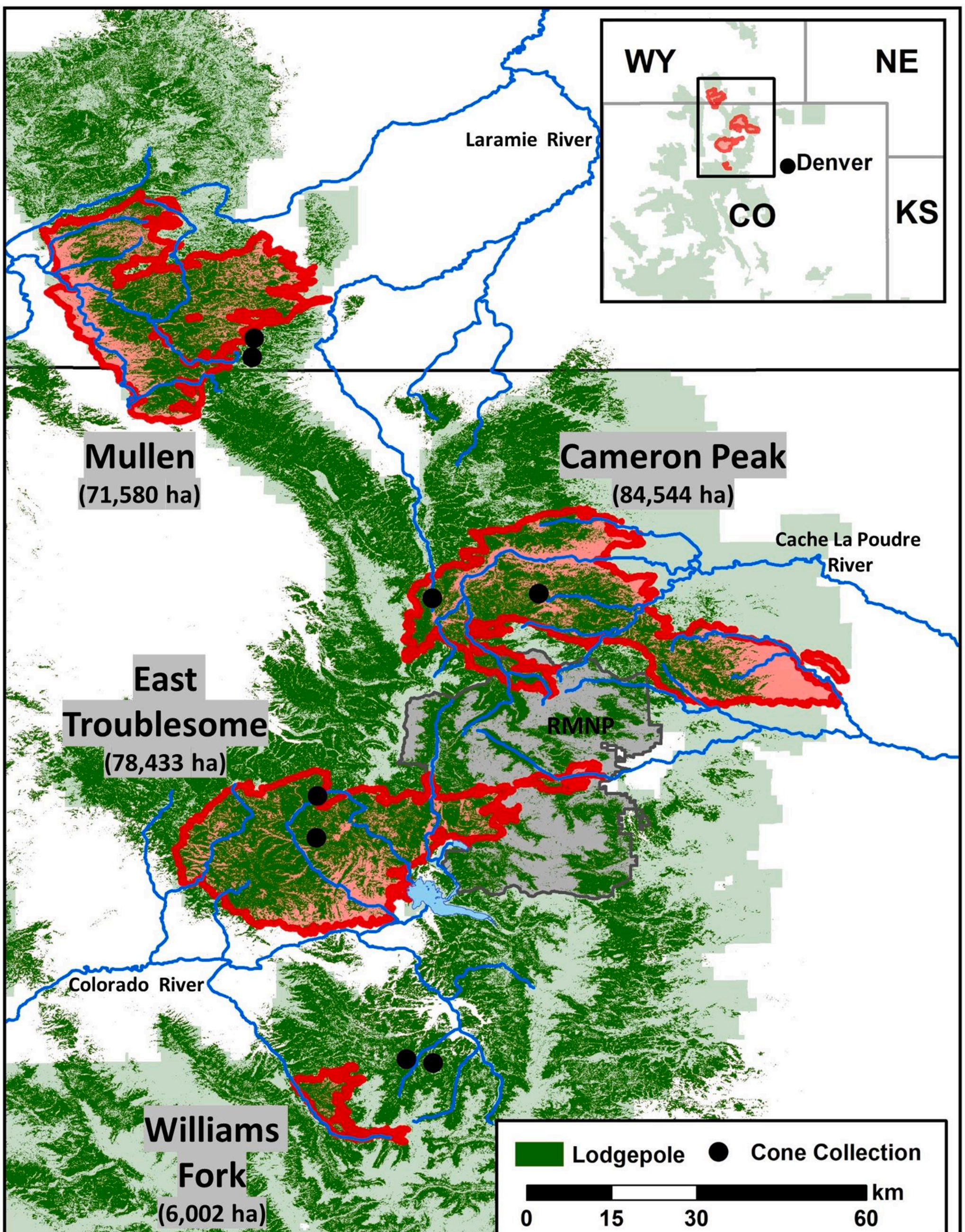

Fig. 1. The perimeter of four wildfires (red area) that burned in lodgepole pine-dominated forests (dark green areas) during 2020 near the Colorado-Wyoming border. Black dots denote eight unburned stands inside or adjacent to the wildfires where serotinous cones were collected. Light green areas denote US Forest Service land (Medicine-Bow Routt and Arapaho-Roosevelt), and the gray area delineates Rocky Mountain National Park (RMNP). Lodgepole pine stands throughout this area underwent a severe mountain pine bark beetle outbreak starting in the early 2000 s and peaking in 2005. Site abbreviations as follows: CP = Cameron Peak, ET = East Troublesome, Mull = Mullen, Wms = Williams Fork. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and seed viability influence regeneration capacity near the southern edge of the tree species' geographic distribution.

Managers working in burned forests require timely information to guide expectations about post-fire tree regeneration potential. As such, this study aimed to rapidly quantify seed viability and availability from serotinous cones in unburned stands adjacent to the aforementioned 2020 fires. Coupled with on-going post-fire regeneration surveys, this assessment will help inform expectations about seed viability in these Southern Rockies stands where lodgepole pine have been dead for more than a decade after bark beetle outbreaks (Hart et al., 2015).

2. Methods

We evaluated seed viability in serotinous cones collected from trees in eight unburned, lodgepole pine-dominated stands, two each within or nearby the four large wildfires (Fig. 1) described above: Cameron Peak (CP1, CP2), East Troublesome (ET1, ET2), Mullen (Mull1, Mull2), Williams Fork (Wms1, Wms2). Within each of the eight stands, we collected ten branches each from ten dead, standing, overstory lodgepole pine trees (n = 800 branches). Intact branches were removed from the mid and upper canopy of felled trees. Trees were felled onto snow or plastic sheeting to reduce loss of branches and cones.

The lodgepole pine forests at each site had undergone significant beetle-related mortality (>75 % in many stands; Kayes and Tinker, 2012; Rhoades et al., 2020). We reviewed photographic images from US Forest Service Annual Aerial Forest Health surveys (USDA, 2021b) and the National Aerial Imagery Program (USDA, 2021c) and determined that beetle-infested trees first appeared between 2005 and 2009 in all the stands sampled. This was consistent with broader temporal patterns of peak overstory mortality between 2005 and 2008 in nearby parts of northern Colorado (Chapman et al., 2012; Meddens and Hicke, 2014). In this area, lodgepole pine were attacked by bark beetles and died over the course of about 3 yrs (Meddens and Hicke, 2014; USDA, 2021b and 2021c), so at the time of this study it was not feasible to assign a precise infestation date. Thus, we assumed each site was infested in 2005 and that trees had been dead for 15 yrs at the time of the 2020 wildfires. All sampled trees had mountain pine beetle galleries, blue-stained wood, or residual pitch tubes.

We examined seed viability across the age range of cones attached to the dead tree branches (n = 1160 cones). To do this we sampled intact, closed cones with serotinous morphology (Tinker et al., 1994) along the length of tree branches. Cone age at the year of tree death was based on annual ring counts on branch cross-sections at the point of cone attachment (Aoki et al., 2011). Cross sections were sanded, and annual rings counted beneath a dissecting microscope. Seed number and viability are known to vary with cone size (Lotan and Jensen, 1970), so we evaluated patterns among sites. Cone dimensions (length and mass) and branch diameter were recorded for 4046 cone-branch cross section pairs.

Cone age, based on branch cross sections, spanned 2 to 36 yrs at the time of tree death across the eight study sites (Fig. 2). Regionally, the beetle infestation peaked in 2005 (Chapman et al., 2012) so these trees would have been dead for fifteen yrs at the time of the 2020 fires, and the cones would have ranged from 17 to 51 yrs. For simplicity, we partitioned cones into three roughly decade-long age classes (Fig. 2): 17–25 yrs (40 % of cones), 26–35 yrs (53 %), and 36–51 yrs at death (7 %).

Seed release from serotinous cones is sensitive to cone moisture content. Live, serotinous cones typically open and release viable seed when heated at 60 °C for 24 hrs (Hellum and Barker, 1981). Seed release can be limited at moisture content below 12 %, even after many hours of heating (Hellum and Barker, 1980). Serotinous cones on our long-dead, beetle-killed trees had 5.4 % moisture content on average (n = 578). During a pilot study, no cones (n = 50) opened after the standard heating treatment (i.e., 60 °C for 24 hrs; Knapp and Anderson, 1980; Hellum and Barker, 1981; Teste et al., 2011b), or at higher temperatures (65, 80,

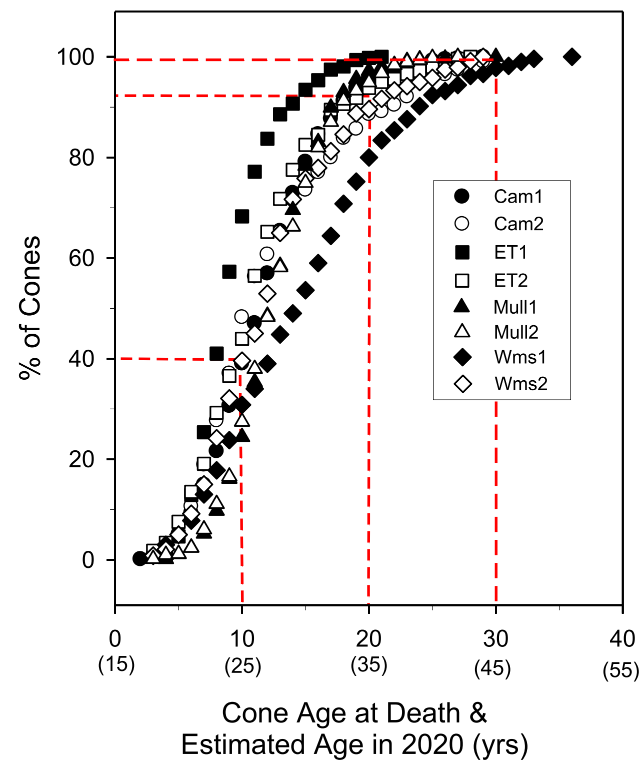

Fig. 2. Age distribution of serotinous cones sampled at eight stands adjacent to wildfires that burned in Colorado and Wyoming during 2020 (n = 4046 branch cross section – cone pairs). Cone age at the time of tree death was based on the number of annual rings at the point of branch attachment (Top line of X-axis). Lodgepole pine trees were killed by bark beetles during the mid-2000 s at all study areas, so we estimate that the age of cones and seeds at the time of the 2020 fires ranged from 17 to 51 yrs (Bottom line of X-axis). The red dashed lines differentiate three age classes that we summarized and compared. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

105 °C) or longer durations (48–168 hrs). However, cones opened and released seed after soaking in tap water and then heating them at 60 °C for 24 hrs (Perry and Lotan, 1977). Moisture of soaked cones averaged 54 %.

Open cones were tapped 20 times on a hard surface to release seeds. Seed wings were removed, the firmness of each seed embryo was examined with forceps, and sound seeds were counted and collected. On a subset of cones, we destructively opened every scale and determined that our soaking, tapping and heating procedure recovered > 95 % of stored seeds. All seeds were dusted with a powdered fungicide (Captan, Drexel Chemical Co., Memphis, TN), placed between sheets of sterile, wetted filter paper and incubated within petri dishes at 27 °C. Seeds were placed in a germinator with alternating light and temperature (27 °C for 8 hrs in the light, 20 °C for 16 hrs in the dark (Knapp and Anderson, 1980; Aoki et al., 2011). Seeds were checked and rewetted multiple times weekly. Seeds were considered germinated if a 2 mm root tip emerged over the course of 21 days.

We also evaluated seed germination and water content of cones that had been stored under field conditions in the soil seed bank. In November 2021, five cones each per sampling site were embedded 2 cm deep within the soil O-horizon of a lodgepole pine forest in northern Colorado. Cones remained buried beneath the winter snowpack (~1.5 m deep at peak snowpack) and then retrieved after snowmelt (mid-April 2021). Cones were not subsequently soaked, but seed germination trials were conducted as previously described.

Table 1
Branch diameter at the point of cone attachment, cone dimensions and moisture content for serotinous, beetle-killed lodgepole pine trees (n = 4046 branch cross section - cone pairs). Letters denote which means differed at α = 0.05 according to Tukey's-adjusted pairwise comparisons.

Cone Age (yr)	Branch Diameter (mm)			Cone Mass (g)			Diameter (mm)			Length (mm)			Moisture (%)		
	Mean		Max	Mean		Max	Mean		Max	Mean		Max	Mean		Max
17–25	8.6	a	37.4	6.0	a	14.0	16.2	a	27.4	32.2	a	43.9	5.2	a	9.7
26–35	10.5	b	40.8	5.9	a	14.0	16.8	a	28.5	32.1	a	47.4	5.0	b	9.9
36–51	12.4	c	54.5	5.3	b	11.9	14.8	b	19.4	30.1	b	41.6	4.9	b	9.5

2.1. Statistical analyses

We compared germination and germinant production (germinants per cone) across eight independent stands. Differences in germination and cone dimensions were tested among cone age classes using oneway analysis of variance (SPSS, Inc., V 26 IBM, Chicago, IL). We also evaluated whether germination or cone dimensions differed among the study sites within age classes. Levene's statistic was used to test assumptions of homogeneity of variance. Where means differed significantly, pairwise Tukey-adjusted comparisons were used to identify differences between age classes or sites. Relations between germination and cone age and size were evaluated using multiple least-squares linear and non-linear regression (SPSS, Inc., V 26 IBM, Chicago, IL). Throughout the manuscript, statistical significance is reported when α ≤ 0.05, unless otherwise stated.

3. Results

3.1. Cone dimensions and moisture

Branch cross section diameter increased, and cone mass, diameter, length, and moisture content decreased with cone age (Table 1). The mean mass and diameter of cones in the oldest age class were 11 % lower than those in the younger classes. Cone dimensions and moisture content differed significantly among sites (Table 2). Cones from Mull1 had the lowest moisture content across all cone age classes; Mull2 cones had the second lowest moisture content for two of the three age classes. Conversely, the two ET sites had the highest cone moisture content overall, with ET2 as the top-ranked site for cone moisture across age classes. Cone size patterns were less consistent, though the two CP sites and ET1 generally had the highest mass, diameter and lengths for all age classes and cones from the Wms sites were generally among the smallest.

Table 2
Cone moisture content and dimensions for stands within or adjacent to four large wildfires in northern Colorado and southern Wyoming (n = 1160 cones). Within each age class, letters denote which means differed at α = 0.05 according to Tukey's-adjusted pairwise comparisons.

		17–25 yrs				26–35 yrs				36–51 yrs			
	Site ID*	N	Mean	SD		N	Mean	SD		N	Mean	SD	
Cone Moisture (%)	CP1	51	5.3	1.0	abc	65	5.1	1.0	ab	29	4.9	1.5	abc
	CP2	60	5.2	0.8	abc	62	4.7	0.8	ab	46	4.8	0.7	abc
	ET1	60	5.2	1.4	abc	61	5.2	1.1	b	5	5.8	0.5	c
	ET2	65	5.7	1.4	c	61	5.3	1.4	b	32	5.9	1.8	c
	Mull1	37	4.7	0.9	a	68	4.5	0.9	a	22	3.9	0.8	a
	Mull2	37	4.9	0.9	ab	65	5.1	1.1	ab	27	4.4	1.1	ab
	Wms1	56	5.1	1.3	abc	60	4.7	1.5	ab	62	4.9	1.3	abc
	Wms2	41	5.4	1.4	bc	63	5.1	1.3	ab	25	5.1	1.6	bc
Cone Mass (g)	CP1	51	6.6	1.9	c	65	6.9	2.3	c	29	6.9	2.3	c
	CP2	60	7.1	1.6	c	62	7.0	1.7	c	46	6.6	1.3	bc
	ET1	60	6.6	1.9	c	61	5.4	1.5	b	5	4.5	1.1	a
	ET2	65	4.4	1.3	a	61	4.1	1.2	a	32	4.4	1.3	a
	Mull1	37	6.4	1.2	c	68	6.9	1.3	c	22	6.5	1.7	bc
	Mull2	37	5.6	1.3	b	65	6.2	2.4	ab	27	5.4	2.0	ab
	Wms1	56	4.4	1.3	a	60	4.2	1.0	a	62	4.5	1.0	a
	Wms2	41	5.4	1.4	b	63	5.5	1.5	b	25	5.0	1.9	a
Cone Diameter (mm)	CP1	11	17.0	3.5	ab	8	18.6	2.0	ab	2	18.4	1.4	b
	CP2	28	15.0	1.4	b	15	14.5	2.3	a	11	14.4	1.3	a
	ET1	26	16.3	2.2	ab	6	17.1	1.1	ab	2	18.8	0.6	b
	ET2	19	13.6	1.2	a	17	14.3	2.5	a	3	14.6	2.2	a
	Mull1	10	20.2	3.1	c	13	20.6	3.9	b	7	16.7	1.2	ab
	Mull2	14	16.1	3.4	ab	24	17.7	4.5	ab	4	14.1	0.8	a
	Wms1	22	15.1	2.2	ab	15	15.3	1.8	a	13	13.6	1.6	a
	Wms2	5	16.2	1.2	ab	4	14.4	1.3	a	0	—	—	—
Cone Length (mm)	CP1	11	41.3	5.5	d	8	42.1	5.5	e	2	47.5	1.3	b
	CP2	28	38.3	3.8	bcd	15	37.1	3.2	bcd	11	37.3	2.8	a
	ET1	26	42.6	4.0	d	6	41.5	3.3	de	2	34.4	0.4	a
	ET2	19	34.0	4.4	ab	17	32.1	2.9	a	3	32.1	2.1	a
	Mull1	10	39.4	3.6	cd	13	40.5	3.1	cde	7	40.2	6.1	ab
	Mull2	14	34.9	2.7	abc	21	34.2	3.5	ab	4	32.8	3.3	a
	Wms1	22	35.5	4.1	abc	15	36.1	4.2	abc	13	34.3	3.9	a
	Wms2	5	33.5	3.6	a	4	36.9	3.2	bcd	0	—	—	—

* CP = Cameron Peak, ET = East Troublesome, Mull = Mullen, Wms = Williams Fork.

Table 3
Seeds released and seed germination for serotinous lodgepole pine cones collected in unburned stands within and adjacent to four wildfires that burned in 2020 near the Colorado-Wyoming border, USA. For each response variable, letters denote which age-specific means differed at a = 0.05 according to Tukey's-adjusted pairwise comparisons.

Cone		Seeds / Cone				Germination (%)				Germinants / Cone			
Age Class	N	Mean		Min	Max	Mean		Min	Max	Mean		Min	Max
17–25	407	9.8	a	0	38	38.7	a	0	100	3.5	a	0	24
26–35	505	8.5	ab	0	44	32.4	b	0	100	2.4	b	0	24
46–51	248	8.0	b	0	39	26.8	c	0	100	1.8	b	0	14
All	**1160**	**8.9**				**33.6**				**2.7**			

3.2. Seed availability and germination

Of the 1160 cones we examined, 977 (84 %) contained seed. There were 8.9 seeds per cone on average, with as many as 44 seeds in some cones (Table 3). On average, 34 % of the released seeds germinated, yielding 2.7 germinants per cone (Table 3). Seed germination declined from about 40 to 10 % within increasing cone age (Fig. 3). Germination was 39 % with 3.5 germinants were per cone for the youngest age class compared to 27 % and 1.8 germinants per cone for the oldest class. In addition to the 183 cones that contained no seed, 350 of the cones containing seed produced no germinants. The proportion of cones that produced no germinants increased from 24 % in the youngest cone class to 33 and 35 % in the middle and oldest classes, respectively.

Germination and the number of germinants produced per cone varied significantly across the eight sites (Fig. 1; Fig. 4). Overall, germination averaged from 26 to 41 % across all sites. Averaged across age classes, germination and germinant production were highest in CP1 and the two ET sites and were generally lowest in Mull1 and Wms2. For the youngest cone class, germination ranged from 25 to 47 % per cone, yielding from 1.9 to 6.2 seeds per cone. Germination declined by 41 % between the youngest and oldest cone classes in all but the Mull sites where it increased.

Other than cone age and site, cones attributes were only weakly related to seed germination. For example, Mull1 had both the lowest germination (Fig. 4) and cone moisture of all sites (Table 2), and conversely, CP1 and the two ET sites had the highest germination and cone moisture. However, in general across all eight sites, germination was unrelated to cone moisture. Similarly, germination was only weakly related to cone size. Across ages, cone mass explained 8 % of variability in germinants produced per cone. The linear relations between cone mass and germinant number were significant at all sites except Mull1 and explained as much as 25 % of the site-level variation in germinant number.

Seed germination from cones stored overwinter in the soil seedbank were comparable or better than for cones in the canopy seedbank. Germination was 36 % on average for all sites for cones buried under the snowpack (n = 40; 26 to 35 yrs old cones). Cones produced 5.8 germinants on average with up to 18 per cone. Meltwater from the snowpack increased mean cone moisture from 5 % (Table 1) at the time of burial to 55 % at the time of retrieval and the germination trials.

4. Discussion

Cone serotiny is a reliable source of post-disturbance resilience in many lodgepole pine forests. However, our study documents a significant decline in the number of seeds produced by serotinous cones that could reduce seedling density following the 2020 wildfires that occurred more than a decade after widespread tree mortality. At the onset of the bark beetle outbreak in British Colombia and Colorado, germination of young lodgepole pine cones (<10 yrs old) was high (70–100 %) and similar to that measured in live trees (Aoki et al., 2011; Teste et al., 2011b). For those recently killed trees, germination declined sharply for cones >15 yrs old, was 30–60 % for 25 yr-old cones, and 22 % when they reached age 37. At the time of the 2020 fires, beetle-killed trees had been dead for 15 yrs. At that time, germination was 34 % on average and declined from 40 % to <20 % across the range of cone age from 17 to 51 yrs (Fig. 3).

Most of the cones we sampled on the long-dead, beetle-killed trees were >25 yrs old (Fig. 2), and overall, they were dry, had low seed viability and many contained no seed (35 % in the oldest age class). Preferential loss of young cones from branch extremities and transfer to the soil surface has been observed shortly after tree mortality during beetle infestation of lodgepole pine stands in British Colombia (Teste et al., 2011a; Talucci et al., 2019). Within six years of tree death, nearly half of the canopy seedbank was transferred to the soil, leaving older cones in the canopy, and as we report here, seed availability from older cones on long-dead trees is reduced relative to live trees or recently infested stands.

The soil seedbank may be an increasingly important source of lodgepole pine seedlings with time since tree mortality. For example, germination from cones in the soil seed bank was relatively high (82 %) and comparable to the seeds from canopy cones following beetle infestation of lodgepole pine in British Colombia (Teste et al., 2011b). The dense lodgepole pine recruitment common in clear cut harvest units in bark beetle salvage projects (Collins et al., 2010) is evidence that transfer of cones to the soil seedbank represents a significant pathway for post-fire lodgepole pine regeneration following bark beetles and wildfire. The abundance of pine seedling recruits in the understory of uncut stands the initial decade following beetle infestation further demonstrates the importance of this regeneration pathway (Collins et al., 2011; Diskin et al., 2011). In this study we found that germination from our soil seedbank trial was equal or better than comparable age cones in the canopy seedbank (36 vs 32 %) and that moisture from the melting snowpack was adequate to promote cone opening. Similarly, Sharpe and Ryu (2015) found that serotinous lodgepole cones from beetle-killed trees were able to absorb moisture to levels that promoted cone opening.

However, the number of lodgepole pine seeds in the soil seedbank is a small fraction of those typically found in the canopy seedbank (Teste et al., 2011a) and buried seed is susceptible to losses during surface fires and from predation and decay. Rodents, for example, are known to decimate cones and conifer seeds in the soil seedbank (Zwolak et al., 2010; Lobo, 2014) following both wildfire and beetle outbreaks (Teste et al., 2011a). Seed predation has also been observed in burned areas created by pile burning and may inhibit tree recolonization in those areas (Rhoades et al., 2021). Earlier research found that the vigor of tree seedlings originating from the soil seedbank declined with time since beetle infestation in Canadian lodgepole pine stands (Teste et al., 2011b). A combination of declining seed viability, predation pressure and seedling vigor may progressively restrict the seedling regeneration potential of the soil seedbank with time following beetle infestation, both following wildfire and within unburned forests.

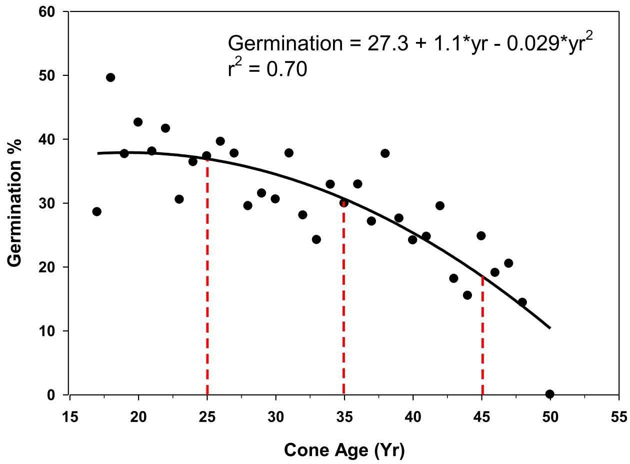

Fig. 3. Germination relative to cone age for 1160 serotinous cones collected from mountain pine beetle-killed lodgepole pine trees. Data points show mean rates for 15–91 cones per year between 18 and 44 yrs. There were fewer cones per year (i.e., 1–8) for the oldest (45–51 yrs) or youngest cone ages. The red dashed lines differentiate three age classes that we summarized and compared. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

5. Implications for post-fire regeneration

Lodgepole pine often produces high seed loads (Lotan and Jensen, 1970) that can generate abundant post-fire seedlings (>500,000 ha^{-1}; Turner et al., 2004), so the reduction in seed availability we observed in gray-phase stands may or may not result in unacceptable tree stocking levels (Hansen et al., 2018). Combining the average number of germinants we tallied (3 cone^{-1}), with average tree (1500 t ha^{-1}) and cone density (450 cones t^{-1}) in mature lodgepole stands in the Southern Rockies (Lotan and Jensen, 1970; Koch, 1987; Pearson et al., 1987; Ryan and Waring, 1992), we estimate around 2 million germinants ha^{-1} (range: 1 to 3 million ha^{-1}) from gray-phase, serotinous stands. Losses of seed and seedlings to predation, drought, competition, and other factors vary widely (Hansen et al., 2018), though regional estimates indicate that 2500 to 15,000 seeds are needed to produce one seedling on moderate and challenging sites (i.e., dry sites with high competition), respectively (Lotan and Perry, 1983). Based on these values for gray-phase stands, we estimate post-fire pine recruitment of 120 and 700 seedlings ha^{-1} on challenging and moderate sites. These estimates of pine recruitment density are below those measured 3 and 10 yrs after clear-cut harvesting (5000 t ha^{-1}: Collins et al., 2011; 1500–2500 t ha^{-1}: Rhoades et al., 2020) at nearby sites, and 10–50 % of the density of mature lodgepole pine in local forests (Ryan and Warring, 1992; Collins et al., 2011).

The scattered live serotinous trees that are typically present even within stands with severe beetle infestation (Rhoades et al., 2020) will augment post-fire seed availability and seedling regeneration (Kemp et al., 2016), and the soil seedbank will contribute additional germinants (Teste et al., 2011b). In beetle-killed lodgepole pine forests in British Colombia, fire severity combined with cone abundance determined seedling recruitment and mean post-fire density exceeded the mean pre-outbreak canopy tree density (Talucci et al., 2019). However, our initial approximation suggests that some forests burned by the 2020 fires may not reach the seedling density threshold (370 t ha^{-1}; USDA, 1997) that often triggers tree planting on US Forest Service land in the Southern Rockies.

Coupled with seed limitations in long-dead, beetle-killed serotinous stands, other conditions may have consequences for post-fire regeneration and potential reforestation activities. Non-serotinous stands are an obvious example, but so are young, regenerating stands that have yet to produce abundant viable seed or to develop cone serotiny (Lotan, 1976; Keeley et al., 1999). This maturation period can persist for multiple decades (Hodson, 1908; Tower, 1909; Lotan and Perry, 1983). Extensive areas of high-severity crown fire with high cone consumption and surface fires that combust soil organic layers and the soil seedbank (Turner et al., 1999; Romme et al., 2011; Talucci et al., 2019) would exacerbate low seed viability. Managers responding to these 2020 wildfires are prioritizing reforestation in areas with extensive high-severity crownfire, young regenerating stands, recent harvest units, non-serotinous stands and stands with high levels of beetle-related mortality. Conversely, small patches of high-severity crownfire adjacent to live tree seed walls (Kemp et al., 2016; Talucci et al., 2019) are ranked lower. Ultimate planting decisions balance logistical considerations and post-fire seedling recruitment, as well as the need to prioritize sensitive headwater ecosystems and riparian corridors where forest recovery is critical for protecting drinking water supply, watershed condition and aquatic habitat.

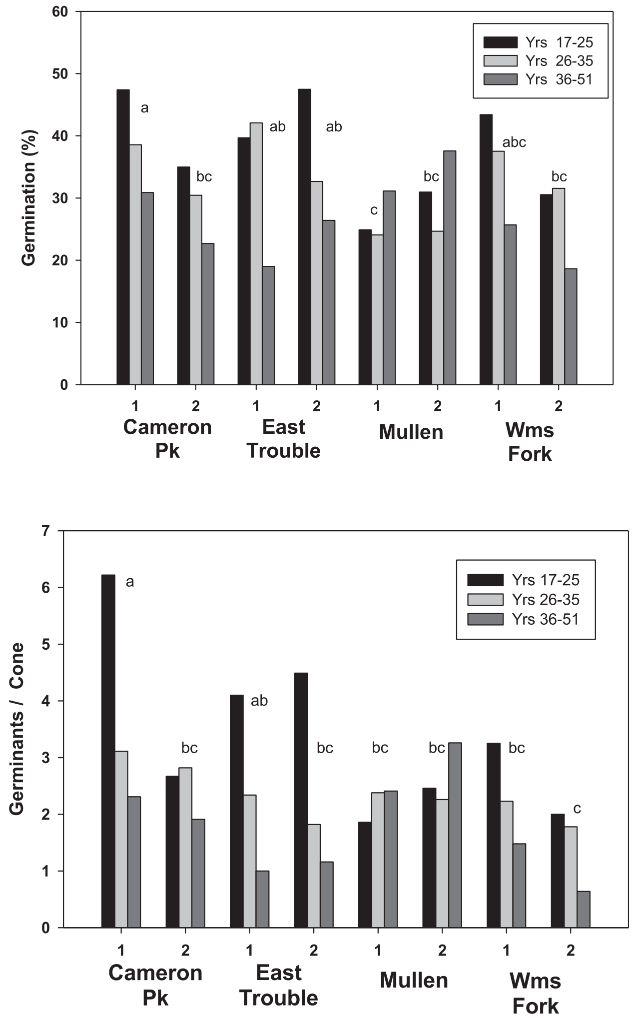

Fig. 4. Germination and the number of germinants produced per cone in long-dead lodgepole pine trees (n = 1160 cones). Data are averages for the eight study areas (i.e., two per fire, labelled 1 and 2) and three age classes. Letters above each cluster of bars denote site-level differences in germination and germinant number averaged across the three age classes. Site differences were assigned with α = 0.05 using Tukey's-adjusted pairwise comparisons.

6. Conclusion

This study was prompted by concerns regarding seed availability and tree regeneration following large wildfires that burned more than a decade after severe bark beetle outbreaks (Aoki et al., 2011, Teste et al., 2011a). Our findings may also apply to post-beetle salvage logging, large windstorms, or other compound disturbances (Stevens-Rumann and Morgan, 2019). Across a range of site conditions, we found that the cones retained within the canopies of long-dead trees were very dry and germination was roughly half that of cones on live or recently dead lodgepole pine. Cone dimension and moisture varied among sites, but cone age was the dominant control on germination and seed availability. Based on our measured germination and seed production, we estimate that the canopy seed bank might produce between 120 and 700 seedlings ha^{-1} across a range of local site conditions. Thus, on some sites, seedling recruitment is likely to fall short of regional stocking thresholds, below densities typical after wildfire, harvesting or under mature stands shortly after beetle infestation, and below the density of lodgepole pine in nearby mature forests (Ryan and Waring, 1992; Smith and Resh, 1999; Collins et al., 2011). The majority of beetle-killed lodgepole pine remained standing through the first decade after the infestation in Colorado forests (Rhoades et al., 2020), but the continued pace of windthrow and the persistance of those snags and the canopy seedbank is unknown. We found that germination of seed transferred with cones buried in the soil seedbank can augment seedlings recruitment, though this is unlikely to offset the general decline in tree regeneration potential. These findings coupled with the high spatial variability in cone serotiny in these forests, highlight the need for extensive monitoring of post-fire seedling establishment. Land managers responding to the 2020 fires are currently determining the extent of post-fire planting needs and prioritizing areas based on pre-fire stand conditions, wildfire severity, post-fire recruitment and landscape sensitivity. In some of these areas, planting may compensate for reduced seed viability in severely burned areas dominated by long-dead, serotinous lodgepole pine (Stephens et al., 2013; Malcom et al., 2021).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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References

Agne, M.C., Woolley, T., Fitzgerald, S., 2016. Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire. For. Ecol. Manage. 366, 73–86.

Alizadeh, M. R., Abatzoglou, J. T., Luce, C. H., Adamowski, J.F., Farid, A., Sadegh, M. 2021. Warming enabled upslope advance in western US forest fires. Proceedings of the National Academy of Sciences 118: e2009717118.

Aoki, C.F., Romme, W.H., Rocca, M.E., 2011. Lodgepole Pine seed germination following tree death from mountain pine beetle attack in Colorado, USA. Am. Midland Nat. 165, 446–451.

Chapman, T.B., Veblen, T.T., Schoennagel, T., 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. Ecology 93, 2175–2185.

Clements, F.E., 1910. The life history of lodgepole burn forests. Dept. of Agriculture, Forest Service, Washington, D.C, U.S, p. 74.

Collins, B.J., Rhoades, C.C., Underhill, J., Hubbard, R.M., 2010. Post-harvest seedling recruitment following mountain pine beetle infestation of Colorado lodgepole pine stands: a comparison using historic survey records. Can. J. For. Res. 40, 2452–2456.

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. For. Ecol. Manage. 261, 2168–2175.

Coop, J.D., Parks, S.A., Stevens-Rumann, C.S., Crausbay, S.D., Higuera, P.E., Hurteau, M. D., Tepley, A., Whitman, E., Assal, T., Collins, B.M., Davis, K.T., Dobrowski, S., Falk, D.A., Fornwalt, P.J., Fulé, P.Z., Harvey, B.J., Kane, V.R., Littlefield, C.E., Margolis, E.Q., North, M., Parisien, M.-A., Prichard, S., Rodman, K.C., 2020. Wildfire-driven forest conversion in Western North American landscapes. Bioscience 70, 659–673.

Dennison, P.E., Brewer, S.C., Arnold, J.D., Moritz, M.A., 2014. Large wildfire trends in the western United States, 1984–2011. Geophys. Res. Lett. 41, 2928–2933.

Diskin, M., Rocca, M.E., Nelson, K.N., Aoki, C.F., Romme, W.H., 2011. Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. Can. J. For. Res. 41, 782–792.

Dong, C., Williams, A.P., Abatzoglou, J.T., Lin, K., Okin, G.S., Gillespie, T.W., Long, D., Lin, Y.-H., Hall, A., MacDonald, G.M., 2022. The season for large fires in Southern California is projected to lengthen in a changing climate. Comm. Earth & Env. 3, 22. https://doi.org/10.1038/s43247-022-00344-6.

Flannigan, M., Cantin, A.S., de Groot, W.J., Wotton, M., Newbery, A., Gowman, L.M., 2013. Global wildland fire season severity in the 21st century. For. Ecol. Manage. 294, 54–61.

Graham, R.T. (Ed.) 2003. Hayman Fire Case Study. Gen. Tech. Rep. RMRS-GTR-114 USDA Forest Service, Rocky Mountain Research Station, Ogden, UT, 396 p.

Hansen, W.D., Braziunas, K.H., Rammer, W., Seidl, R., Turner, M.G., 2018. It takes a few to tango: changing climate and fire regimes can cause regeneration failure of two subalpine conifers. Ecology 99, 966–977.

Hart, S.J., Preston, D.L., 2020. Fire weather drives daily area burned and observations of fire behavior in mountain pine beetle affected landscapes. Environ. Res. Lett. 15, 054007.

Hart, S.J., Schoennagel, T., Veblen, T.T., Chapman, T.B., 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proc. Natl. Acad. Sci. 112, 4375–4380.

Harvey, B.J., Donato, D.C., Turner, M.G., 2014a. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proc. Natl. Acad. Sci. 111, 15120–15125.

Harvey, B.J., Donato, D.C., Romme, W.H., Turner, M.G., 2014b. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecol. Appl. 24, 1608–1625.

Hellum, A.K., Barker, N.A., 1980. Cone moisture content influences seed release in lodgepole pine. Can. J. For. Res. 10, 239–244.

Hellum, A.K., Barker, N.A., 1981. The relationship of lodgepole pine cone age and seed extractability. For. Sci. 27, 62–70.

Hodson, E.R., 1908. Silvical notes on the lodgepole pine. Proc. Soc. Am. For. 3, 82–89.

INCIWEB, 2020. Interagency Incident Information https://inciweb.nwcg.gov [accessed May 2021].

Kayes, L.J., Tinker, D.B., 2012. Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. For. Ecol. Manage. 263, 57–66.

Keeley, J.E., Ne'eman, G., Fotheringham, C.J. 1999. Immaturity risk in a fire-dependent pine. Journal of Mediterranean Ecology 1:41-48.

Kemp, K.B., Higuera, P.E., P. Morgan, P. 2016. Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. Landscape Ecology 31: 619-636.

Knapp, A.K., Anderson, J.E., 1980. Effect of heat on germination of seeds from serotinous lodgepole pine cones. Am. Midland Nat. 104, 370–372.

Koch, P., 1996. Lodgepole pine in North America Forest Products Society. Madison, WI.

Koch, P. 1987. Gross characteristics of lodgepole pine trees in North America. Gen Tech Rep INT 227 USDA Forest Service, Intermountain Research Station, Odgen, UT. 311pp.

Lobo, N., 2014. Conifer seed predation by terrestrial small mammals: A review of the patterns, implications, and limitations of top-down and bottom-up interactions. For. Ecol. Manage. 328, 45–54.

Lotan, J.E., Critchfield, W.B. 1990. Pinus contorta Dougl. ex. Loud. lodgepole pine, p. 302-315, *In* Burns R.M., Honkala, B.H. eds. Silvics of North America. Volume 1. Conifers, Vol. Agric. Handb. 654. U.S. Department of Agriculture, Forest Service, Washington, DC.

Lotan, J.E., Jensen, C.C. 1970. Estimating seed stored in serotinous cones of lodgepole pine. Res. Note INT-83. Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 10 p.

Lotan, J.E., Perry, D.A. 1983. Ecology and regeneration of lodgepole pine, Agric. Handb. 606 U.S. Department of Agriculture, Forest Service., Washington, DC.

Lotan, J.E. 1976. Cone serotiny - fire relationships in lodgepole pine. Tall Timbers Fire Ecology Conference Proceedings 14, Tall Timbers Research Center, Tallahassee, FL. 267-278.

Malcolm, A., Hay, A., Januta, A. 2021. Tree planting efforts aren't replacing burned U.S. forests — not even close Reuters September 9, 2021. https://www.reuters.com/world/us/tree-planting-efforts-arent-replacing-burned-us-forests-not-even-close-2021-09-09/.

Meddens, A.J.H., Hicke, J.A., 2014. Spatial and temporal patterns of Landsat-based detection of tree mortality caused by a mountain pine beetle outbreak in Colorado, USA. For. Ecol. Manage. 322, 78–88.
Pearson, J.A., Knight, D.H., Fahey, T.J., 1987. Biomass and nutrient accumulation during stand development in Wyoming lodgepole pine forests. Ecology 68, 1966–1973.
Pelz, K.A., Rhoades, C.C., Hubbard, R.M., Smith, F.W., 2018. Severity of overstory mortality influences conifer recruitment and growth in mountain pine beetle-affected forests. Forests 9.
Perry, D.A., Lotan, J.E. 1977. Opening temperatures in serotinous cones of lodgepole pine. USDA Forest Service, Research Note INT-228. Intermountain Forest and Range Experiment Station, Ogden, UT. 6 p.
Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. Bioscience 58, 501–517.
Rammer, W., Braziunas, K.H., Hansen, W.D., Ratajczak, Z., Westerling, A.L., Turner, M. G., Seidl, R. 2021. Widespread regeneration failure in forests of Greater Yellowstone under scenarios of future climate and fire. Global Change Biology doi: 10.1111. gcb.15726.
Rhoades, C.C., Pelz, K.A., Fornwalt, P.J., Wolk, B.H., Cheng, A.S., 2018. Overlapping bark beetle outbreaks, salvage logging and wildfire restructure a lodgepole pine ecosystem. Forests 9, 15.
Rhoades, C.C., Hubbard, R.M., Hood, P.R., Starr, B.J., Tinker, D.B., Elder, K., 2020. Snagfall the first decade after severe bark beetle infestation of high-elevation forests in Colorado, USA. Ecol. Appl. 30, e02059.
Rhoades, C.C., Fegel, T., Zaman, T., Fornwalt, P.J., Miller, S.P., 2021. Are soil changes responsible for persistent, slash pile burn scars in lodgepole pine forests? For. Ecol. Manage. 490, 1119090.
Rodman, K.C., Andrus, R.A., Carlson, A.R., Carter, T.A., Chapman, T.B., Coop, J.D., Fornwalt, P.J., Gill, N.S., Harvey, B.J., Hoffman, A.E., Kelsey, K.C., Kulakowski, D., Laughlin, D.C., Morris, J.E., Negrón, J.F., Nigro, K.M., Pappas, G.S., Redmond, M.D., Rhoades, C.C., Rocca, M.E., Schapira, Z.H., Sibold, J.S., Stevens- Rumman, C., Veblen, T.T., Wang, J., Zhang, X., S.J. Hart, S.J. 2022. Rocky Mountain forests are poised to recover following bark beetle outbreaks, but with altered composition. Journal of Ecology *under review*.
Romme, W.H., Boyce, M.S., Gresswell, R., Merrill, R., Minshall, E.H., Whitlock, C., Turner, M.G., 2011. Twenty Years After the 1988 Yellowstone Fires: Lessons About Disturbance and Ecosystems. Ecosystems 14, 1196–1215.
Ryan, M.G., Waring, R.H., 1992. Maintenance respiration and stand development in a subalpine lodgepole pine forest. Ecology 73, 2100–2108.
Schoennagel, T., Turner, M.G., Romme, W.H., 2003. The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. Ecology 84, 2967–2978.
Sharpe, M., Ryu, S.R., 2015. The moisture content and opening of serotinous cones from lodgepole pine killed by the mountain pine beetle. For. Chron. 91, 260–265.
Smith, F.W., Resh, S.C., 1999. Age-related changes in production and below-ground carbon allocation in Pinus contorta forests. For. Sci. 45, 333–341. https://doi.org/10.1093/forestscience/45.3.333.
Stephens, S.L., Agee, J.K., Fulé, P.Z., North, M.P., Romme, W.H., Swetnam, T.W., Turner, M.G., 2013. Managing forests and fire in changing climates. Science 342, 41–42.
Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D. C., Morgan, P., Veblen, T.T., 2017. Evidence for declining forest resilience to wildfires under climate change. Ecol. Lett. 21, 243–252.
Stevens-Rumann, C.S., Morgan, P.T., 2019. Tree regeneration following wildfires in the western US: a review. Fire Ecology 15. https://doi.org/10.1186/s42408-019-0032-1.
Talucci, A.C., Lertzman, K.P., Krawchuk, M.A., 2019. Drivers of lodgepole pine recruitment across a gradient of bark beetle outbreak and wildfire in British Columbia. For. Ecol. Manage. 451, 117500.
Teste, F.P., Lieffers, V.J., Landhäusser, S.M., 2011a. Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. Ecol. Appl. 21, 150–162.
Teste, F.P., Lieffers, V.J., Landhäusser, S.M., 2011b. Viability of forest floor and canopy seed banks in Pinus contorta var. latifolia (Pinaceae) forests after a mountain pine beetle outbreak. Am. J. Bot. 98, 630–637.
Tinker, D.B., Romme, W.H., Hargrove, W.W., Gardner, R.H., Turner, M.G., 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. Can. J. For. Res. 24, 897–1303.
Tower, G.E., 1909. A study of the reproductive characteristics of lodgepole pine. Proc. Soc. Am. For. 4, 84–106.
Turner, M.G., Romme, W.H., Gardner, R.H., 1999. Prefire heterogeneity, fire severity and plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. Int. J. Wildland Fire 9, 21–23.
Turner, M.G., Tinker, D.B., Romme, W.H., Kashian, D.M., Litton, C.M., 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems 7, 751–775.
Turner, M.G., Turner, D.M., Romme, W.H., Tinker, D.B., 2007. Cone production in young post-fire Pinus contorta stands in Greater Yellowstone (USA). For. Ecol. Manage. 242, 119–206.
Turner, M.G., Braziunas, K.H., Hansen, W.D., Harvey, B.J., 2019. Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. Proc. Natl. Acad. Sci. 116, 11319–11328.
USDA Forest Service. 1997. United States Department of Agriculture. Revision of the land resource management plan. Arapaho and Roosevelt National Forests and Pawnee National Grassland, Fort Collins, CO. https://www.fs.usda.gov/Internet/FSE_Documents/fseprd641737.pdf [accessed April 2022].
USDA Forest Service. 2021a. United States Department of Agriculture. Forest Inventory and Analysis National Program. https://www.fia.fs.fed.us/tools-data/ [accessed April 2022].
USDA Forest Service. 2021b. United States Department of Agriculture. USFS Forest Health Projection Program Aerial Detection Survey Team. https://www.fs.usda.gov/detail/r2/forest-grasslandhealth/?cid=STELPRDB5165873 [accessed April 2022].
USDA Forest Service. 2021c. United States Department of Agriculture. National Agriculture Imagery Program. https://naip-usdaonline.hub.arcgis.com/ [accessed April 2022].
Zwolak, R., Pearson, D.E., Ortega, Y.K., Crone, E.E., 2010. Fire and mice: Seed predation moderates fire's influence on conifer recruitment. Ecology 91, 1124–1131.