



Compounded disturbances in sub-alpine forests in western Colorado favour future dominance by quaking aspen (*Populus tremuloides*)

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Keywords

Disturbance interactions; Fire; Lodgepole pine; *Pinus contorta*; Wind blowdown

Nomenclature

Weber (1976)

Received 8 July 2011

Accepted 1 May 2012

Co-ordinating Editor: Kerry Woods

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Abstract

Question: As the extent, magnitude and/or frequency of various forest disturbances are increasing due to climate change, it is becoming increasingly likely that forests may be affected by more than one type of disturbance in short succession. We studied how compounded disturbances and pre-fire composition influence post-fire tree regeneration. Specifically, do compounded disturbances reduce overall regeneration and favour initial dominance of species that regenerate vegetatively?

Location: Sub-alpine forests in northwestern Colorado.

Methods: The study region was affected by a severe outbreak of *Dendroctonus rufipennis* in the 1940s, a severe wind storm in 1997 and severe fires in 2002. Permanent plots to monitor regeneration were established in 2003 and were re-measured in 2004, 2005 and 2010. Plots were located in stands that varied in long-term disturbance history (stands that originated following fires in 1879 or 1880 vs older stands), recent disturbance history (fire only; outbreak then fire; blowdown then fire) and pre-fire forest dominance (*Populus tremuloides*, *Pinus contorta*, or *Picea engelmannii*–*Abies lasiocarpa*).

Results: Combined density of regeneration of all tree species was highest in stands dominated by *P. tremuloides* prior to the 2002 fires. In *P. contorta* stands that were affected only by the 2002 fires, regeneration density was higher in stands that were younger prior to the fire (those that originated in the 1880s), in which cone serotiny is more prevalent, than in older stands (those that originated >200 yr ago). However, the advantage of relatively young *P. contorta* stands to regenerate following fire was inhibited by compounded disturbances of wind and then fire. Similarly, following compounded disturbances the combined density of conifer seedlings of all species was lower than following only fire. In contrast, the density of *P. tremuloides* was not lower following compounded disturbances than following fire only, and was higher than that of other species.

Conclusions: Pre-fire forest composition and disturbance history influence the abundance and composition of post-fire regeneration. Compounded disturbances generally reduce the regeneration of conifers, which regenerate exclusively from seed, and appear to favour initial stand dominance by *P. tremuloides*, which regenerates both sexually and asexually. Such differential effects may thereby alter trajectories of post-fire regeneration. As *P. tremuloides* are less susceptible than conifers to fires, bark beetle outbreaks and wind disturbances, increased dominance by *P. tremuloides* may contribute to a negative feedback that may diminish the probability and/or severity of future disturbances and thus increase overall forest ecosystem resiliency.

Introduction

An important contemporary challenge in ecology is to understand likely future forest patterns and processes in the face of a changing climate and changing disturbance regimes. Novel climate conditions and/or combinations of disturbances may lead to positive or negative feedbacks that could affect the resilience of some systems and potentially force alternate stable states. Climate change is increasing the frequency, extent and/or magnitude of fires, outbreaks of insects and wind disturbances (Westerling et al. 2006; Raffa et al. 2008; Dutzik & Willcox 2010), which increases the likelihood that ecosystems may be affected by more than one type of disturbance in a short period of time. Such compounded disturbances can affect ecosystem development in ways that are not well understood and may be potentially unpredictable, especially if the time between disturbances is insufficient for the ecosystem to recover from the initial disturbance (Paine et al. 1998) or if earlier disturbances have long-term lingering effects on structure and composition. For example, outbreaks of bark beetles or wind disturbances prior to high-severity fire have the potential to reduce the availability of seed that would otherwise be important to post-disturbance regeneration. Additionally, outbreaks and wind disturbances prior to fires may result in higher burn severity, which in turn may result in unfavourable edaphic conditions or scarcity of microsites sheltered by coarse woody debris. In the present study we examined forest regeneration following individual and compounded disturbances in Colorado sub-alpine forests.

Forest development following disturbance generally varies with disturbance type, disturbance severity and pre-disturbance composition. Disturbances that primarily affect canopy trees, such as wind storms and outbreaks of bark beetles, normally result in the release of previously suppressed shade-tolerant species (Peterson 2000) except in areas where seedling and sapling density is low (e.g. Spurr 1956). In contrast, stand development following stand-replacing fires is dominated by the establishment of new seedlings (Veblen et al. 1991) or by vegetative re-sprouting of clonal species. The most rapid post-fire colonization is likely to be associated with an abundance of species that resprout, that have very good dispersal (e.g. some wind-dispersed species) or that have serotinous cones.

The sub-alpine forests of western Colorado are dominated by *Populus tremuloides* (quaking aspen), *Pinus contorta* (lodgepole pine), *Abies lasiocarpa* (sub-alpine fir) and *Picea engelmannii* (Engelmann spruce). *P. tremuloides* and *P. contorta* both have the ability to dominate early post-fire stand development, but these two species have substantially different life-history traits. *P. tremuloides* clones, which are largely underground, are extremely long-lived (Mitton &

Grant 1996) and reproduce asexually by vegetative re-sprouting. Severe fire or other disturbances can trigger asexual reproduction of *P. tremuloides* (Schier & Campbell 1978), which is often characterized by abundant, rapidly growing root suckers that favour initial stand dominance of this species (Peet 2000). *P. contorta* is also well adapted to dominate post-disturbance environments, but in contrast to *P. tremuloides*, *P. contorta* establishes from large quantities of seed released by serotinous cones and then grows rapidly on favourable sites. The proportion of serotinous cones within a stand can decrease with stand age (Schoennagel et al. 2003), and such variations in serotiny can constrain the availability of *P. contorta* seed across stands of different ages (Tinker et al. 1994).

Picea engelmannii and *A. lasiocarpa* can successional replace the shade-intolerant *P. tremuloides* and *P. contorta* and can also regenerate directly following fires; thus, they can co-dominate the site from the time of stand initiation, especially at sites that lack seed sources of pines or root suckers of *P. tremuloides* (Rebertus et al. 1992). Following fire, *P. engelmannii* is likely to establish at greater abundances than *A. lasiocarpa* and age-structure studies have shown that *A. lasiocarpa* establishment often lags that of *P. engelmannii* by many decades (Whipple & Dix 1979; Veblen 1986). However, where seeds are available, both species can regenerate immediately following fire (Doyle et al. 1998).

The occurrence and ecological effects of large-scale disturbance by fire, outbreaks of bark beetle (*Dendroctonus* spp.) and major windstorms over the past several centuries have been well documented in northwestern Colorado. In the late 19th century widespread and severe fires burned extensive areas of forests, giving rise to young post-fire stands across northwestern Colorado (Kulakowski & Veblen 2002; Sibold et al. 2006; Schoennagel et al. 2007). In the 1940s a severe outbreak of *D. rufipennis* killed *P. engelmannii* over thousands of hectares of forest in White River National Forest, which was preceded by outbreaks of similar magnitude in the mid-19th century and earlier (Veblen et al. 1991, 1994; Eisenhart & Veblen 2000; Kulakowski & Veblen 2006). In 1997 a severe wind storm blew down over 10 000 ha of sub-alpine forest in Routt National Forest (Baker et al. 2002; Kulakowski & Veblen 2002). Finally, in 2002 severe fires burned extensive areas of both of these national forests, including some forests that were previously affected by *D. rufipennis* outbreak or blowdown (Bigler et al. 2005; Kulakowski & Veblen 2007).

In a community that undergoes a second disturbance before recovery from the first disturbance is completed, it is possible that the combined effects may lead to long-term alteration in community state (Paine et al. 1998). Likewise, long-term lingering effects of earlier disturbances may affect regeneration following subsequent disturbances. In

the current study we examine how compounded disturbances affect the abundance and composition of post-fire tree regeneration. Specifically, we test the hypotheses that compounded disturbances reduce overall regeneration and favour initial dominance of species that regenerate vegetatively.

Study areas

The current study was conducted in two areas of north-western Colorado. The 4400-ha Headwaters of Big Creek (BC) study area (106°45' W, 40°45' N; 2400–3400 m a.s.l.) is in northwestern Colorado in the Mount Zirkel Wilderness and surrounding Routt National Forest. Parts of the BC study area were affected by severe fires in 1879 and by a severe blowdown in 1997 (Kulakowski & Veblen 2002). This study area has a continental climate with a mean annual temperature of 3.9 °C, which ranges from a mean monthly temperature of –9.5 °C in January to 13.1 °C in July (Western Regional Climate Center, <http://www.wrcc.dri.edu/>). Mean annual precipitation is 61.0 cm, and ranges from a mean monthly precipitation of 6.4 cm in January to 3.8 cm in July.

The 4600 ha North Fork of the White River (NFWR) study area (107°15' W, 40°00' N; 2450–3250 m a.s.l.) is in northwestern Colorado in the Flat Tops Wilderness and surrounding White River National Forest. Parts of this area were affected by severe fires in 1880, and by a severe outbreak of spruce beetle (*D. rufipennis*) in the 1940s, which reached its peak in 1947 (Kulakowski et al. 2003). The closest climate station to the study area is Marvine Ranch, which is located at 2380 m a.s.l. and has a climate record from 1972 to 1998 (Western Regional Climate Center, <http://www.wrcc.dri.edu/>). The mean January temperature is –8.5 °C and the mean July temperature is 14.3 °C. Mean annual precipitation is 70.5 cm. Forests in both study areas are dominated by *P. contorta*, *P. tremuloides* Michx., *P. engelmannii* and *A. lasiocarpa*. In 1999–2000, we reconstructed the history of fires, *D. rufipennis* outbreaks and wind disturbance from ca. A.D. 1700 to 2000 in both study areas (Kulakowski & Veblen 2002; Kulakowski et al. 2003). Subsequently, large parts of both the BC and NFWR study areas burned in high-severity fires in 2002.

Methods

In 2003 we established 1170 2 m × 1 m permanent plots in forests that had severely burned in 2002 in both study areas. Plots were located based on a stratified random design across a range of pre-fire forest types (*P. tremuloides*, *P. contorta* and *P. engelmannii*–*A. lasiocarpa*), a range of pre-fire stand ages (stands that originated in the 1880s and >200-yr-old stands), and various combinations of pre-fire

disturbance (only 2002 fire, beetle followed by 2002 fire, and blowdown followed by 2002 fire; Table 1). Pre-fire forest type was categorized based on composition of tree species prior to the 2002 fires (Kulakowski & Veblen 2002; Kulakowski et al. 2003) into the following four categories: (1) as *P. contorta* if that species made up ≥40% of canopy trees; (2) as *P. engelmannii*–*A. lasiocarpa* if those species made up ≥90% of canopy trees; and (3) as *P. tremuloides* if that species made up ≥90% of canopy trees in stands that originated in the 1880s or if *P. tremuloides* made up ≥50% of regeneration <1.4-m tall in stands >200 years old.

In each 2 m × 1 m permanent plot in the years 2003, 2004, 2005 and 2010, numbers of all juveniles (seedlings and ramets) of each tree species were recorded. Plots were grouped for analysis according to pre-fire stand age, composition and disturbance history (Table 1). All plots categorized as burned were located in areas of stand-replacing fires. All reported juveniles established after the 2002 fires. Differences among sites in the same categories were not explicitly considered in the analyses as they were very similar in all factors except for modest differences in precipitation, suggesting that they could justifiably be pooled for analyses. All regeneration data are expressed as number of juveniles per hectare. Significance of differences among groups of plots was tested using Friedman repeated measures (R-M) ANOVA on ranks with a pair-wise Tukey test (Zar 2010). A separate R-M ANOVA tested for the effects of pre-fire composition, stand origin date and combination of disturbances on the abundance and composition of regeneration. The non-parametric Friedman R-M ANOVA on ranks was used because our data did not meet the assumptions of normality and equal variance. Tukey's *P*-values were adjusted to account for multiple comparisons.

Results

The overall density (number per ha) of seedlings and ramets of all tree species combined was contingent on pre-fire composition, but not on pre-fire disturbance history. The density of regeneration in stands dominated by *P. tremuloides* prior to fire was higher than in stands dominated by *P. engelmannii*–*A. lasiocarpa* in all years and higher than in stands dominated by *P. contorta* in 2003, 2004 and 2005 ($P < 0.001$; Tukey test for pair-wise multiple comparison $P < 0.05$; Fig. 1). However, by 2010, there was no difference in the density of regeneration in stands dominated by *P. tremuloides* vs *P. contorta* prior to the 2002 fire. But in 2010 the density of regeneration was higher in stands dominated by *P. contorta* than in those dominated by *P. engelmannii*–*A. lasiocarpa* prior to the fire ($P < 0.001$; Tukey test for pair-wise multiple comparison $P < 0.05$; Fig. 1). In stands that were of the same age and dominated by the same species prior to fire, overall density of

Table 1. Regeneration density (number per ha) of *Populus tremuloides* (PT), *Pinus contorta* (PC), *Picea engelmannii* (PE) and *Abies lasiocarpa* (AL) in various categories of site. Data in each category (i.e. row) are based on 90 2-m² plots. Same subscript letters in columns of "Total" regeneration per year indicate no significant difference based on Tukey pair-wise comparisons ($P < 0.05$).

Origin	Pre-fire Comp.	2003					2004					2005					2010				
		PT	PC	PE	AL	Total	PT	PC	PE	AL	Total	PT	PC	PE	AL	Total	PT	PC	PE	AL	Total
c. 1880	PT	1444	0	0	0	1444 ^b	2389	0	0	56	2445 ^d	1056	0	0	0	1056 ^{a,b,c,d}	278	0	0	0	278 ^a
c. 1880	PT	1056	0	0	0	1056 ^{a,b}	2000	56	0	0	2056 ^{c,d}	2056	0	0	0	2056 ^{c,d}	3111	111	0	0	3222 ^{a,b}
c. 1880	PC	0	0	0	0	0 ^a	0	1722	0	167	1889 ^{b,c,d}	222	1333	222	611	2388 ^d	444	2944	278	500	4166 ^{b,c}
c. 1880	PC	0	0	0	0	0 ^a	0	56	0	0	56 ^a	722	278	0	0	1000 ^{a,b,c,d}	2556	556	0	56	3168 ^{a,b,c}
c. 1880	PE/AL	0	0	0	0	0 ^a	0	0	0	0	0 ^a	0	0	0	0	56 ^a	0	56	0	167	223 ^a
c. 1880	PE/AL	0	0	0	0	0 ^a	0	56	0	0	56 ^a	389	222	0	0	611 ^{a,b}	833	278	0	56	1167 ^{a,b}
c. 1880	PC	0	0	0	0	0 ^a	0	111	56	0	167 ^a	0	167	0	111	278 ^a	0	167	56	111	334 ^a
Old	PC	0	0	0	0	0 ^a	167	56	0	56	279 ^a	722	56	0	0	778 ^{a,b,c,d}	1389	56	0	0	1445 ^{a,b}
Old	PE/AL	0	0	0	0	0 ^a	0	0	56	0	56 ^a	222	0	0	0	222 ^a	500	0	0	0	500 ^a
Old	PE/AL	0	0	0	0	0 ^a	0	56	0	0	56 ^a	56	0	0	56	112 ^a	111	0	0	111	222 ^a
Old	PC	111	0	0	0	111 ^{a,b}	333	0	0	0	333 ^{a,b}	0	0	0	0	0 ^a	1000	56	111	0	1167 ^{a,b}
Old	PE/AL	0	0	0	0	0 ^a	56	0	0	0	56 ^a	0	0	0	0	0 ^a	167	0	0	0	167 ^a
Old	PT	3056	0	0	0	3056 ^c	2333	0	56	0	2389 ^{c,d}	1667	0	0	0	1667 ^{b,c,d}	13 444	0	0	0	13 444 ^c

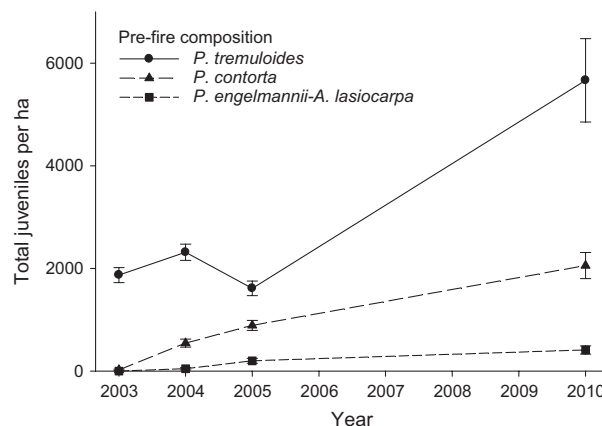


Fig. 1. The overall density of seedlings and ramets (mean + SE) of all species combined in stands that differed in pre-fire composition. The density of juveniles in stands dominated by *P. tremuloides* prior to fire was higher than in stands dominated by *P. engelmannii*–*A. lasiocarpa* in all years and higher than in stands dominated by lodgepole in 2003, 2004, and 2010. In 2010 density of juveniles was higher in stands dominated by lodgepole than in those dominated by spruce fir. Number of 2 m-sq plots = 1170.

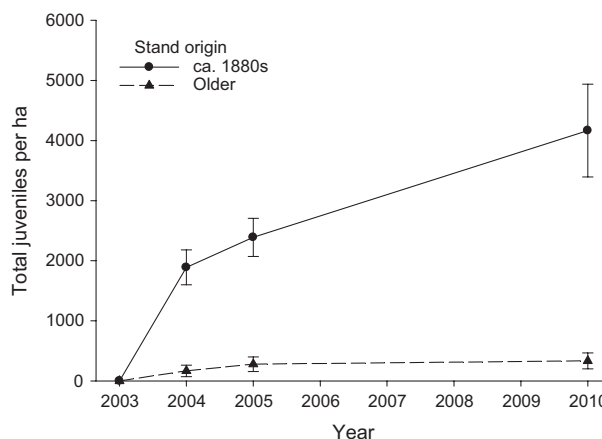


Fig. 2. Total densities of all juveniles (mean + SE) in different categories of stands that were dominated by *P. contorta* prior to fire and that were recently affected only by fire. Overall densities were higher in stands that originated in c. 1880s than in old stands in 2004, 2005, and 2010. Number of 2 m-sq plots = 180.

regeneration did not differ following single vs compounded disturbances (Table 1).

Considering only stands that were dominated by *P. contorta* prior to fire, the total abundance of regeneration in stands affected only by fire was higher in stands that were relatively young prior to the 2002 fire (those that originated in the 1880s) than in older stands in 2004, 2005 and 2010 ($P < 0.05$; Fig. 2). However, there was no difference in total abundance of regeneration between young and old *P. contorta* stands following compounded disturbances by wind then fire in any year ($P > 0.05$; Fig. 3).

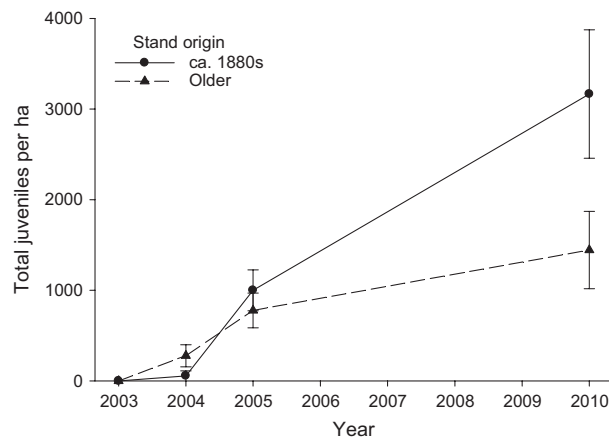


Fig. 3. Total densities of all juveniles (mean + SE) in different categories of stands that were dominated by *P. contorta* prior to fire and that were recently affected by blowdown then fire. Overall densities were not different in stands that originated in c. 1880s than in old stands in any year. Number of 2 m-sq plots = 180.

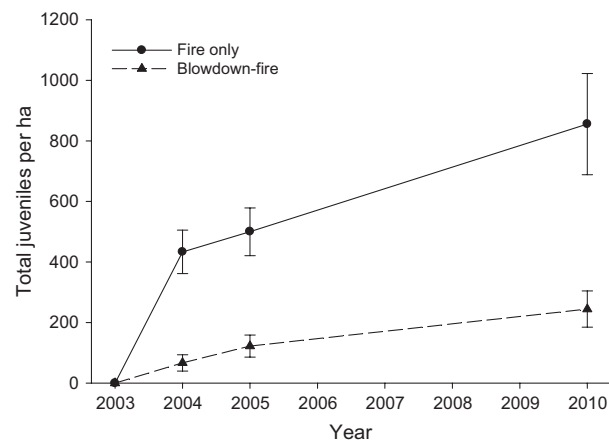


Fig. 4. Combined densities (mean + SE) of all conifer seedlings in stands that were affected only by fire versus those affected by blowdown then fire. In stands that were affected by compounded disturbances (blowdown then fire) densities of all conifer seedlings were lower than in stands affected only by fire in 2004, 2005, and 2010. Number of 2 m-sq plots = 900.

Similarly, in stands that were affected by compounded disturbances (blowdown then fire) combined densities of all conifer seedlings were lower than in stands affected only by fire in 2004, 2005 and 2010 ($P < 0.05$; Fig. 4). In contrast, abundance of *P. tremuloides* seedlings and ramets following compounded disturbances of blowdown then fire was not different in any year until 2010, when it was higher in stands affected by compounded disturbances ($P < 0.05$; Fig. 5). There was no difference in abundance of seedlings of any species between otherwise similar stands that were affected by only fire vs

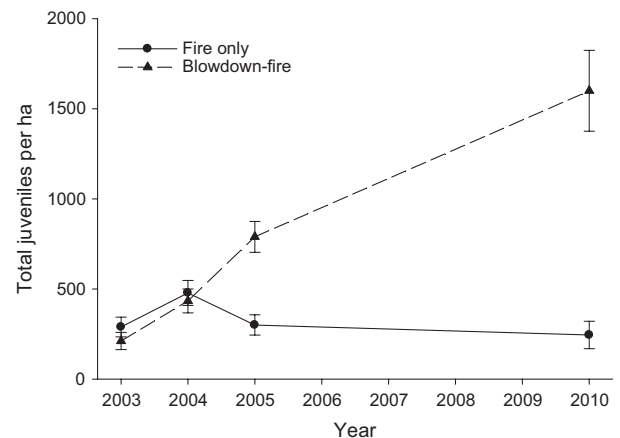


Fig. 5. Combined densities (mean + SE) of all *P. tremuloides* seedlings and ramets in stands that were affected only by fire versus those affected by blowdown then fire. In stands that were affected by compounded disturbances (blowdown then fire) densities of *P. tremuloides* juveniles were higher than in stands affected only by fire in 2010. Number of 2 m-sq plots = 900.

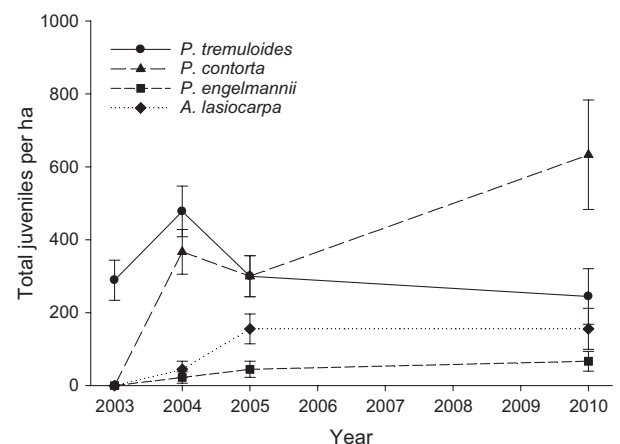


Fig. 6. Density of juveniles (mean + SE) of different species in stands affected only by fire. There was no statistical difference among densities of different species in any year. Number of 2 m-sq plots = 450.

outbreak then fire (Table 1). In both categories of plots (fire and outbreak then fire) the abundance of regeneration was generally low (except in old *P. tremuloides* stands).

In stands affected only by fire, there was no statistical difference among abundance of different species (Tukey test for pair-wise multiple comparison $P > 0.05$; Fig. 6). Although not significant, initial composition of regeneration was dominated by *P. tremuloides*, but later *P. contorta* became more important. In contrast, in stands affected by wind then fire, *P. tremuloides* was more dominant in 2005 and 2010 ($P < 0.001$; Tukey test for pair-wise multiple comparison $P < 0.05$; Fig. 7).

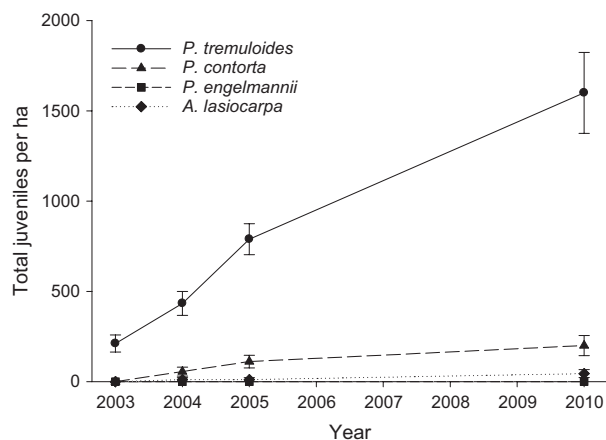


Fig. 7. Density of juveniles (mean + SE) of different species in stands affected by blowdown then fire. Density of *P. tremuloides* was higher than all other species in 2005 and 2010. Number of 2 m-sq plots = 450.

Discussion

In general, it has been recognized that the type and severity of disturbance plays a major role in controlling post-disturbance forest regeneration (Turner & Dale 1998). In the current study we found that the abundance and composition of tree regeneration following stand-replacing fires is also affected by pre-fire forest composition and stand age, as well as pre-fire disturbance history. The density of regeneration was highest in stands dominated by *P. tremuloides* or *P. contorta* prior to the fire. Compounded disturbances generally reduced the abundance of conifer seedlings and favoured initial dominance of *P. tremuloides*. However, the effect of compounded disturbances on regeneration in conifer stands varies with tree species and stand age.

Effect of pre-fire composition on *P. tremuloides* regeneration

Following stand-replacing fires, regeneration was dominated by *P. tremuloides*, beginning in the year immediately following the fire. Following fire or similar disturbance, *P. tremuloides* reproduces vegetatively from root systems that are often extensive and that survive above-ground disturbances (Bartos & Mueggler 1981; Brown & Byle 1987). This vegetative reproduction gives *P. tremuloides* an advantage over species that reproduce from seed and allows it to gain dominance immediately following severe fires (Peet 2000).

The majority of *P. tremuloides* regeneration in our study area established in stands that were dominated by *P. tremuloides* prior to the fire. However, abundant reproduction of *P. tremuloides* was also observed in some stands in which

the pre-disturbance canopy was dominated by conifers, but that were classified as *P. tremuloides* in our study due to the presence of *P. tremuloides* in the sub-canopy prior to fire. Such stands include the 'old *P. tremuloides*' stands that were affected by *D. rufipennis* outbreak then fire (Table 1). *P. tremuloides* typically gain dominance following stand-replacing disturbance, then in some areas are successional replaced by more shade-tolerant species such as *A. lasiocarpa* and *P. engelmannii* (Peet 2000). Once these shade-tolerant conifers reach the canopy, they can competitively exclude *P. tremuloides*, which is then no longer able to maintain canopy dominance. Under the light-limited conditions beneath a *P. engelmannii*–*A. lasiocarpa* canopy, *P. tremuloides* are not able to grow into mature trees, but the underground root system can continue living and ramets can continue to sprout for hundreds of years after losing dominance in the canopy (Peet 2000). When a stand-replacing fire occurs in such stands, canopy dominance can change from conifers back to *P. tremuloides* (Kulakowski et al. 2004, 2006).

Compounded disturbances in *P. contorta* stands

Shortly following fire, seedlings of *P. contorta* became abundant in burned stands, which is consistent with the expectation of *P. contorta* acting as an early successional species that effectively colonizes following stand-replacing disturbances. Similarly, regeneration in Yellowstone National Park was more abundant after fire in younger, even-aged post-fire stands (Nyland 1998), which was likely due to a higher incidence of serotinous cones on *P. contorta* in young post-fire stands than in old post-fire stands (Tinker et al. 1994; Schoennagel et al. 2003). The higher incidence of serotinous cones in younger stands is expected to contribute to more rapid and abundant post-fire regeneration.

The advantage of relatively young *P. contorta* stands to regenerate following fire was inhibited by compounded disturbances. Higher-intensity fire associated with the abundant surface fuels in blown down stands could have contributed to a relatively high combustion of *P. contorta* seeds in both non-serotinous and serotinous cones. Furthermore, in the years immediately following mortality, *P. contorta* release much of their canopy seed bank through cone opening, cone fall due to breakage and squirrel predation (Teste et al. 2011). Thus the seed bank could have been reduced after the blowdown and viable seeds that were released following the blowdown could have been combusted in the 2002 fire. The overall higher intensity of fire in blown down stands could also potentially reduce the quality of favourable niches in the post-fire environment by exacerbating the effects of unusually warm and dry conditions of the past decade. Thus, reduced availabil-

ity of seed combined with a less favourable post-fire environment is likely to have reduced the density of *P. contorta* seedlings following compounded disturbances. Our data suggest that regeneration in relatively young *P. contorta* stands in the Rocky Mountains following compounded disturbance may follow stand development pathways more typical of non-serotinous stands, in which the seedling recruitment period is more protracted (e.g. Pierce & Taylor 2011).

A study conducted a few kilometers to the north of the BC study area also found that post-fire conifer regeneration was absent or scarce in areas moderately or severely affected by the 1997 blowdown (Buma & Wessman 2011). The same study found that areas affected by salvage logging had significantly higher regeneration than areas of comparable blowdown, suggesting that fuel loading affects post-fire regeneration patterns. Whereas our study found strong influences of pre-fire forest composition on post-fire regeneration patterns, Buma & Wessman (2011) did not consider variability in pre-fire forest composition.

Response of specific species to compounded disturbances

We found only limited conifer regeneration in stands that were affected by the 1940s *D. rufipennis* outbreak and subsequent fire (Table 1). However, the low densities of regeneration in these stands were not different from otherwise comparable stands that were affected only by fire. The *D. rufipennis* outbreak affected only relatively old post-fire stands and not stands that established following fires in the late 19th century (Kulakowski et al. 2003). Our data indicate that conifer regeneration in old stands was generally very slow, regardless of whether the stand was affected by single or compounded disturbances. The scarcity of *P. engelmannii* and *A. lasiocarpa* regeneration is somewhat surprising, given retrospective studies that indicate relatively rapid post-disturbance regeneration of these species (Rebertus et al. 1992), and may be due to unfavourable climate following the 2002 fires. Although we did not detect any difference in regeneration between old stands that were affected only by fire and those that were affected by outbreak then fire, we recognize that further research is necessary to more completely understand the effects of single vs compounded disturbances, especially in relatively old stands.

Generally, compounded disturbances have the potential to alter post-disturbance regeneration by either reducing seed source or by increasing the intensity of the secondary disturbance (Kulakowski & Veblen 2007), which in turn may negatively influence soil and other micro-environmental conditions (Fonturbel et al. 2011). These two influences may be of minimal consequence for the vegetative

reproduction of *P. tremuloides*. Although it is conceivable that compounded disturbances may increase overall disturbance intensity to the point that below-ground *P. tremuloides* roots are killed, and therefore post-disturbance re-sprouting is impeded (e.g. Parker & Parker 1983), we found no such effect in our study. Instead, our data suggest that compounded disturbances favour overall *P. tremuloides* dominance in a landscape co-dominated by *P. tremuloides* and conifers. Similarly, D'Amato et al. (2011) recently reported that stands affected by compounded disturbances (blowdown then fire, as well as blowdown, logging, then fire) in Minnesota were largely dominated by *P. tremuloides* in contrast to those affected by only fire. These findings are especially significant as there has been recent concern about the apparent decline of *P. tremuloides* in some regions (Worrall et al. 2008). However, our data indicate that *P. tremuloides* may be favoured in ecosystems affected by compounded disturbances, which may become more important in the future. As climate change is increasing the extent, severity and frequency of various forest disturbances including fires, outbreaks of bark beetles and wind storms, it is increasingly likely that forest stands may be affected by compounded disturbances. If disturbances in rapid succession become more common in the future, then such conditions may favour *P. tremuloides* and other species that reproduce vegetatively over those that reproduce exclusively from seed. Thus, under more extreme climate conditions and associated disturbance regimes, some coniferous forests may shift to an alternate stable state dominated by *P. tremuloides*. However, the susceptibility of *P. tremuloides* to climate-induced die-off (Anderegg et al. 2012; Hanna & Kulakowski 2012), as well as predicted reductions in its area of suitable habitat under climate warming scenarios (Rehfeldt et al. 2009), create considerable uncertainty about how the interaction of disturbances with climate variability will affect the future extent of *P. tremuloides* communities.

Conclusions

Following the 2002 fires in western Colorado, tree regeneration varied according to pre-fire conditions, including forest type, stand age (resulting from long-term disturbance history) and recent disturbance history. Densities of conifer seedlings were significantly reduced following a combination of blowdown and fire, in comparison to fire alone. While regeneration of conifers was significantly reduced by compounded disturbances, the regeneration of *P. tremuloides* appears not to have been negatively influenced. This suggests the possibility that compounded disturbances in Rocky Mountain sub-alpine forests may favour the dominance of *P. tremuloides*, where viable *P. tremuloides* roots exist underground. Disturbances by insect outbreaks, wind

storms and fires are expected to increase under climate change scenarios. Our data suggest that the compounding of disturbances is likely to alter post-disturbance ecosystem development and may contribute to an increased complexity of potential stand trajectories that are contingent on combinations of compounded disturbances.

A possible shift in dominance toward *P. tremuloides* resulting from compounded disturbances may in turn reduce future forest susceptibility to fires, bark beetle outbreaks and wind disturbances, as *P. tremuloides* are less susceptible to these disturbance agents than are conifers (van Wagner 1977; Veblen et al. 2001; Kulakowski & Veblen 2002, 2007; Kulakowski et al. 2003). Hence, increased dominance by *P. tremuloides* may contribute to a negative feedback that may diminish the probability and/or severity of future disturbances and thus increase overall forest ecosystem resilience.

Ecological disturbances are increasing in extent, severity and/or frequency in many systems worldwide and are predicted to continue increasing as the climate changes (Dutkik & Willcox 2010). In this context, the current work indicates that combinations of disturbances can affect post-disturbance development in unique ways that are contingent on pre-disturbance composition and on potential disturbance interactions. Future work, especially predictive models of forest development under different climate scenarios, should explicitly consider how potential interactions among disturbances affect trajectories of ecosystem development.

Acknowledgements

This work was supported by the Joint Fire Science Program and the National Science Foundation Awards number 0743351 and 0743498. For research assistance we thank T. Chapman, P. Hanna, N. Malthais, R. Barry and E. Huber. We thank K. Woods and two anonymous reviewers for helpful comments on this work.

References

- Anderegg, W.R.L., Berry, J.A., Smith, D.D., Sperry, J.S., Anderegg, L.D.L. & 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, USA* 109: 233–237.
- Baker, W.L., Flaherty, P.H., Lindemann, J.D., Veblen, T.T., Eisenhart, K.S. & Kulakowski, D. 2002. Effects of vegetation on the impact of a severe blowdown in the Southern Rocky Mountains, USA. *Forest Ecology and Management* 168: 63–75.
- Bartos, D.L. & Mueggler, W.F. 1981. Early succession in aspen communities following fire in western Wyoming. *Journal of Range Management* 34: 315–318.
- Bigler, C., Kulakowski, D. & Veblen, T.T. 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. *Ecology* 86: 3018–3029.
- Brown, J.K. & De Byle, N.V. 1987. Fire damage, mortality, and suckering in aspen. *Canadian Journal of Forest Research* 17: 1100–1109.
- Buma, B. & Wessman, C.A. 2011. Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere* 2: 1–13.
- D'Amato, A.W., Fraver, S., Palik, B.J., Bradford, J.B. & Patty, L. 2011. Singular and interactive effects of blowdown, salvage logging, and wildfire in sub-boreal pine systems. *Forest Ecology and Management* 262: 2070–2078.
- Doyle, K.M., Knight, D.H., Taylor, D.L., Barmore, W.J. & Benedict, J.M. 1998. Seventeen years of forest succession following the Waterfalls Canyon Fire in Grand Teton National Park, Wyoming. *International Journal of Wildland Fire* 8: 45–55.
- Dutkik, A.N. & Willcox, N. 2010. *Global warming and extreme weather: the science, the forecast, and the impacts on America*. Environment Colorado Research & Policy Center Denver, CO, US.
- Eisenhart, K.T.T. & Veblen, T.T. 2000. Dendrochronological detection of spruce bark beetle outbreaks in northwestern Colorado. *Canadian Journal of Forest Research* 30: 1788–1798.
- Fonturbel, M.T., Vega, J.A., Perez-Gorostiaga, P., Fernandez, C., Alonso, M., Cuinas, P. & Jimenez, E. 2011. Effects of soil burn severity on germination and initial establishment of maritime pine seedlings, under greenhouse conditions, in two contrasting experimentally burned soils. *International Journal of Wildland Fire* 20: 209–222.
- Hanna, P. & Kulakowski, D. 2012. The influences of climate on aspen dieback. *Forest Ecology and Management* 274: 91–98.
- Kulakowski, D. & Veblen, T.T. 2002. Influences of fire history and topography on the pattern of a severe wind blowdown in a Colorado subalpine forest. *Journal of Ecology* 90: 806–819.
- Kulakowski, D. & Veblen, T.T. 2006. The effect of fires on susceptibility of subalpine forests to a 19th century spruce beetle outbreak in western Colorado. *Canadian Journal of Forest Research* 36: 2974–2982.
- Kulakowski, D. & Veblen, T.T. 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. *Ecology* 88: 759–769.
- Kulakowski, D., Veblen, T.T. & Bebi, P. 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. *Journal of Biogeography* 30: 1445–1456.
- Kulakowski, D., Veblen, T.T. & Drinkwater, S. 2004. The persistence of quaking aspen (*Populus tremuloides*) in the Grand Mesa Area, Colorado. *Ecological Applications* 14: 1603–1614.
- Kulakowski, D., Veblen, T.T. & Kurz, B.P. 2006. Influences of infrequent fire, elevation and pre-fire vegetation on the persistence of quaking aspen (*Populus tremuloides* Michx.) in the Flat Tops area, Colorado, USA. *Journal of Biogeography* 33: 1397–1413.

- Mitton, J.B. & Grant, M.C. 1996. Genetic variation and the natural history of quaking aspen. *BioScience* 46: 25–31.
- Nyland, R.D. 1998. Patterns of lodgepole pine regeneration following the 1988 Yellowstone fires. *Forest Ecology and Management* 111: 23–33.
- Paine, R.T., Tegner, M.J. & Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1: 535–545.
- Parker, J.A. & Parker, K.C. 1983. Comparative successional roles of Trembling Aspen and Lodgepole pine in the southern Rocky Mountains. *Great Basin Naturalist* 43: 447–455.
- Peet, R.K. 2000. Forests of the Rocky Mountains. In Barbour, M.G. and Billings, W.D., eds. *North American terrestrial vegetation*. Cambridge University Press, New York, NY, US.
- Peterson, C.J. 2000. Catastrophic wind damage to North American forests and the potential impact of climate change. *Science of the Total Environment* 262: 287–311.
- Pierce, A.D. & Taylor, A.H. 2011. Fire severity and seed source influence lodgepole pine (*Pinus contorta* var. *murrayana*) regeneration in the southern cascades, Lassen volcanic National Park, California. *Landscape Ecology* 26: 225–237.
- 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.
- Rebertus, A.J., Veblen, T.T., Roovers, L.M. & Mast, J.N. 1992. *Structure and dynamics of old-growth Engelmann spruce–subalpine fir in Colorado*. General Technical Report RM-GTR-213, U.S. Department of Agriculture Forest Service, Fort Collins, CO, US.
- Rehfeldt, G.E., Ferguson, D.E. & Crookston, N.L. 2009. Aspen, climate, and sudden decline in western USA. *Forest Ecology and Management* 258: 2353–2364.
- Schier, G.A. & Campbell, R.B. 1978. Aspen sucker regeneration following burning and clearcutting on two sites in the Rocky Mountains. *Forest Science* 24: 303–308.
- 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.
- Schoennagel, T., Veblen, T.T., Kulakowski, D. & Holz, A. 2007. Multidecadal climate variability and interactions among Pacific and Atlantic sea surface temperature anomalies affect subalpine fire occurrence, western Colorado (USA). *Ecology* 88: 2891–2902.
- Sibold, J.S., Veblen, T.T. & Gonzalez, M.E. 2006. Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park. *Journal of Biogeography* 32: 631–647.
- Spurr, S.H. 1956. Natural restocking of forests following the 1938 hurricane in central New England. *Ecology* 37: 443–451.
- Teste, F.P., Loeffers, V.J. & Landhausser, S.M. 2011. Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. *Ecological Applications* 21: 150–162.
- Tinker, D.B., Romme, W.H., Hargrove, W.W., Gardner, R.H. & Turner, M.G. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. *Canadian Journal of Forest Research* 24: 897–903.
- Turner, M.G. & Dale, V.H. 1998. Comparing large, infrequent disturbances: what have we learned? *Ecosystems* 1: 493–496.
- van Wagner, C.E. 1977. Conditions for the start and spread of crown fires. *Canadian Journal of Forest Research* 7: 23–34.
- Veblen, T.T. 1986. Treefalls and the coexistence of conifers in subalpine forests of the central Rockies. *Ecology* 67: 644–649.
- 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.
- Veblen, T.T., Hadley, K.S., Nel, E.M., Kitzberger, T., Reid, M. & Villalba, R. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *Journal of Ecology* 82: 125–135.
- Veblen, T.T., Kulakowski, D., Eisenhart, K.S. & Baker, W.L. 2001. Subalpine forest damage from a severe windstorm in Northern Colorado. *Canadian Journal of Forest Research* 31: 2089–2097.
- Weber, W.A. 1976. *Rocky Mountain Flora*. Colorado Associated University Press, Boulder, CO, US.
- Westerling, A.L., Hidalgo, H., Cayan, D.R. & Swetnam, T. 2006. Warming and earlier spring increases western US forest wild-fire activity. *Science*, 313: 940–943.
- Whipple, S.A. & Dix, R.L. 1979. Age structure and successional dynamics of a Colorado subalpine forest. *The American Midland Naturalist* 101: 142–158.
- 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 Ecology and Management* 255: 686–696.
- Zar, J.H. 2010. *Biostatistical analysis*. 5th edn. Pearson Prentice-Hall, Upper Saddle River, NJ, US.