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FOLLOWING COMPOUNDED  
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COLORADO

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# Initial Forest Regeneration Following Compounded Disturbances in Western Colorado

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**Abstract:** The forests of the Rocky Mountains are being affected by several major forms of disturbance including outbreaks of bark beetles, wind storms, and fires. We studied how compounded disturbances influence tree regeneration. In the 1940s extensive and severe outbreaks of spruce beetle killed trees over thousands of ha of forest in northwestern Colorado. In 1997, over 10,000 ha of subalpine forest were blow down in nearby forest. In 2002 severe fires burned forest in both of these areas. Following these multiple disturbances, in 2003, we established permanent plots to monitor regeneration in these subalpine forests of Routt and White River National Forests. Plots were located in stands that varied in stand age, recent disturbance history (spruce beetle outbreak then 2002 fire; blowdown then 2002 fire; only 2002 fire), and in pre-fire forest type (aspen, lodgepole pine, and spruce-fir). Following the 2002 fires in western Colorado, regeneration varied with pre-fire conditions including forest type, stand age, and disturbance history.

Densities of lodgepole pine seedlings were most affected by compounded disturbances and were significantly lower following a combination of blowdown and fire in comparison to just fire. Disturbances by both wind storms and fires are expected to increase under climate change scenarios. Our data suggest that the compounding of such disturbances is likely to inhibit the rate of forest regeneration. While regeneration of lodgepole pine was significantly reduced by compounded disturbances, the regeneration of quaking aspen appears not to have been negatively influenced. Densities of aspen ramets/seedlings were high following fire, regardless of whether the fire was preceded by other disturbance. This suggests the possibility that compounded disturbances in Rocky Mountain subalpine forests may favor the dominance of aspen, where viable aspen exists underground.

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## Introduction

Generally speaking, forest recovery following disturbance varies with disturbance type, disturbance severity, and forest composition. Although development following individual disturbances has been studied in many forests, compounded disturbances can sometimes have unpredictable effects on ecosystem development, especially if the time between disturbances is insufficient for the ecosystem to recover from the initial disturbance (Paine et al. 1998).

The forests of the Rocky Mountains are strongly influenced by stand-replacing fires, outbreaks of insects, and wind disturbances. Regeneration following fire is generally dominated by the establishment of new individuals whereas regeneration following outbreaks and wind disturbances is generally dominated by the release of advanced regeneration. Regeneration following individual disturbances in the Rocky Mountains has been studied, but regeneration following compounded disturbances is not well understood.

The subalpine forests of western Colorado are dominated by quaking aspen, lodgepole pine, subalpine fir, and Engelmann spruce. The distribution of these species in western Colorado is strongly related to elevation. Quaking aspen occurs mainly between 2,400 -3,100 m. It forms relatively pure stands in its lower elevational distribution and forms mixed stands with lodgepole pine, Engelmann spruce, and subalpine fir at higher elevations. Within its upper elevational zone, aspen can be successional related to the shade-tolerant spruce and fir. Lodgepole pine forests become increasingly important at higher elevations and occur mostly between 2,600 -3,600 m. On many sites, lodgepole pine is also successional to spruce and fir. Generally, the highest elevation (2,600 -3,300 m) and most mesic forested sites are co-dominated by Engelmann spruce and subalpine fir.

Aspen and lodgepole pine both have the ability to dominate early post-fire stand development but the two species have substantially different life history traits. The underground portion of aspen clones is extremely long-lived, and it has been proposed to be among the oldest living organisms (Mitton and Grant 1996). Aspen have the capacity to reproduce either sexually or asexually, but the predominant mode of reproduction is asexual. Sexual reproduction in this species is thought to be exceedingly rare, with large-scale sexual establishment possibly occurring only once every 200 to 400 years (Romme et al. 1997). Aspen primarily regenerates through asexual vegetative shoots (suckers) which arise from long lateral roots most commonly in response to damage by fire or other disturbances (Schier et al. 1985). Following fire, aspen re-sprouts from underground rhizomes and produces abundant, rapidly growing root suckers that favor the initial dominance of aspen (Peet 2000). Reproduction of aspen in western Colorado is overwhelmingly from suckering, but observations after the 1988 Yellowstone fires suggest that successful seed reproduction may depend on the coincidence of a wet spring, an absence of intense grazing, and good seed production during the year after a fire (Romme et al. 1997). In contrast, lodgepole pine establishes from large quantities of seed released by serotinous cones and initially grows relatively rapidly on sites of favorable habitat. The proportion of serotinous cones within a stand can decrease with stand age (Schoennagel et al. 2003). Such variations in serotiny can

constrain the availability of lodgepole seed to a variable degree across stands of different ages (Tinker et al. 1994).

Engelmann spruce and subalpine fir can successionally replace the shade-intolerant aspen and lodgepole pine and also regenerate directly following fires and can co-dominate the site from the time of stand initiation, especially at sites that lack seed sources of pines or root suckers of aspen (Rebertus et al. 1992). Following fire, Engelmann spruce is likely to establish in greatest abundance, and there may be a lag in the establishment of fir. For example, age-structure studies have shown that fir establishment typically lags that of spruce by many decades (Whipple and Dix 1979, Veblen 1986); however, where seeds are available, both species regenerate immediately following fire (Doyle et al. 1998).

Since climate change is increasing the frequency, extent, and magnitude of fires, outbreaks, and wind disturbances, it is increasingly likely that stands may be affected by more than one disturbance in short succession. The effects of such compounded disturbances on forest regeneration are poorly understood. The most important influence of beetle or wind-caused tree death on post-fire regeneration potential is likely to be the reduction of seed availability of the host species. However, the importance of this reduction will vary with initial stand composition. Additionally, potentially higher burn severity in beetle-or wind-affected stands may result in unfavorable edaphic conditions or scarcity of microsites sheltered by coarse woody debris (CWD), especially if fire occurs after blowdown or after beetle-killed trees have fallen down.

Northwestern Colorado was affected by several severe disturbances over the past half century. In the 1940s a severe outbreak of spruce beetle killed Engelmann spruce over thousands of hectares of forest; in 1997 a severe wind storm blew down over 10,000 hectares of forest; and in 2002 severe fires affected extensive areas of forests, including some forests that were previously affected by outbreak or blowdown. In the current study we address question of whether beetle-kill or blowdown prior to fire significantly alter the abundance and composition of post-fire tree regeneration.

## Study Areas

One 4,400 ha study area is located at 106°45' W, 40°45' N in an area of north-western Colorado in the Mount Zirkel Wilderness and surrounding Routt National Forest. Parts of this area were affected by severe fires in 1879 and by a severe blowdown in 1997 (Kulakowski and Veblen 2002). The study area ranges from 2400 to 3400 m above sea level (Figure 1). Forests are dominated by *Pinus contorta* (lodgepole pine), *Populus tremuloides* Michx. (quaking aspen), *Picea engelmannii* (Engelmann spruce) and *Abies lasiocarpa* (subalpine fir). The study area has a continental climate with a mean annual temperature of 3.8° C which ranges from a mean monthly temperature of - 9.6° C in January to 16.5° C in July (Colorado Climate Center <http://climate.atmos.colostate.edu/>). Mean annual precipitation is 60.5 cm and ranges from a mean monthly precipitation of 6.3 cm in January to 3.9 cm in July.

The second 4,600 ha study area is located at 107°15'W, 40°00' N in an area of north-western 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 (*Dendroctonus rufipennis*) in the 1940s, which reached its peak in 1947 (Kulakowski et al. 2003). The study area ranges in elevation from 2450 to 3250 m a.s.l. (Figure 1). Forests are dominated by *P. engelmannii*, *A. lasiocarpa*, *P. contorta*, and *P. tremuloides*. The closest climate station to the study area is Marvine Ranch which is located at 2380 m a.s.l. and which has a climate record from 1972–98 (Colorado Climate Center, <http://climate.atmos.colostate.edu/>). The mean January temperature is -8.5°C and the mean July temperature is 14.2°C. Mean annual precipitation is 66.8 cm.

## Methods

In 1999-2000, we reconstructed the history of fires, outbreaks, and wind damage from c. 1700 A.D. to 2000 in two areas (Headwaters of Big Creek, BC; and the North Fork of the White River, NFWR) that exceed a total of 9,000 ha (Kulakowski & Veblen 2002; Kulakowski et al. 2003). Large parts of both our BC and NFWR study areas burned in 2002. Consequently, in 2003 we established 2160 2-m x 1-m permanent plots in the BC and NFWR areas. These plots were located across a range of forest type (aspen, lodgepole pine, and spruce-fir), a range of stand ages (c. 120 yr old and > 200 yr old), and various combinations of disturbance (no recent disturbance, SB in 1940s, blowdown in 1997, SB followed by 2002 fire, and blowdown followed by 2002 fire) (Table 1). Stands were categorized based on pre-2002 fire species composition. Stands were categorized as *P. contorta* if *P. contorta* made up > 40% of canopy trees; Stands were categorized as *P. Engelmannii/A. lasiocarpa* if *P. Engelmannii* and *A. lasiocarpa* made up > 90% of canopy trees; Stands were categorized as young *P. tremuloides* if *P. tremuloides* made up > 90% of canopy trees; Stands were categorized as old *P. tremuloides* if *P. tremuloides* made up > 50% of juveniles < 1.4 m tall. In 2004 and 2005 mountain pine beetle (MPB) began affecting some plots that we had established as controls. Although we noted the presence of some MPB galleries in control stands, we did not observe mortality of lodgepole pine in our plots. Nevertheless, we anticipate that future remeasurements will include an additional treatment of stands that had been affected by MPB. In each plot we recorded the species and size of all juveniles (seedlings and ramets < 10 years old), saplings, and trees, and % cover of bare ground, litter, herbs, shrubs, trees, and fallen logs. These cover percentages are indicative of fire effects that are likely to affect post-fire regeneration. We re-measured these plots in 2004 and 2005. Analysis of Variance (ANOVA) was used to compare the number of seedlings and ramets of each species among various classes of disturbances.

## Results

In stands that were not affected by any recent disturbances over all three years, the composition of juveniles was dominated by fir (Fig 2). In stands that were affected only by fire, the density of juveniles was dominated by aspen beginning in the year immediately following fire in 2003 (Fig 3). Density of aspen juveniles remained high over the three year period, but decreases each consecutive year. Relatively high numbers of lodgepole pine seedlings were established two and three years following fire. Density of juveniles in stands that were affected only by SB outbreak was strongly dominated by fir (Fig 4). In stands that were affected by outbreak then fire, density of juveniles was dominated by aspen, which was especially dominant in the year immediately following fire (Fig. 5). In stands that were

affected by blowdown in 1997, seedlings of lodgepole were generally not abundant in comparison to other species (Fig. 6). In stands that were affected by blowdown then fire, density of juveniles was dominated by aspen beginning in the year immediately following fire in 2003 and remained high over the three year period (Fig 7). In these stands, relatively high numbers of lodgepole pine seedlings were established two and three years following fire, with greater densities in 2005 than 2004.

Across all stands, densities of aspen stems were higher than any other tree species in stands that had burned, regardless of whether fire was preceded by SB, blowdown, or no recent disturbance (Fig 8). Densities of lodgepole seedlings were high two and three years following fire in stands in which fire was not preceded by blowdown or outbreak (Fig 9). In stands that were affected by compounded disturbances (outbreak then fire and especially blowdown then fire) densities of lodgepole seedlings were much lower than following only fire. Few lodgepole seedlings were established in control stands and none in stands affected by SB outbreak or SB outbreak followed by fire. Density of spruce juveniles varied across years, but was generally highest in control stands and stands affected by blowdown. Density of fir juveniles also varied across years, but was generally highest in control stands and stands affected by blowdown.

## **Discussion**

Single and compounded disturbances had distinct effects on the species and abundance of seedlings and ramets following the stand-replacing fires of 2002. In control stands, the majority of seedlings were subalpine fir. Fir is a shade tolerant species and its life history is characterized by high fecundity and relatively high seedling mortality rates (Veblen 1986). Generally speaking, post-fire density of juveniles was dominated by the shade intolerant quaking aspen and lodgepole pine. Abundance of seedlings and ramets was generally higher following single rather than compounded disturbances.

### Regeneration following single disturbances

In control stands and following blowdown and spruce beetle outbreak, densities of juveniles were generally dominated by fir and spruce, which is consistent with the late-successional role that these two species generally play in Rocky Mountain subalpine forests. The high abundance of fir and spruce in control stands, which is especially high in older (>200 year old) stands, allows a relatively rapid reorganization (*sensu* Marks 1974) following disturbances to the canopy such as those caused by blowdown or spruce beetle outbreak.

Following stand-replacing fires, regeneration in burned stands was dominated by quaking aspen beginning in the year immediately following the fire. Following fire or similar disturbance, aspen reproduces vegetatively from root systems that are often extensive and that survive above-ground disturbances. This vegetative reproduction gives aspen an advantage over species that reproduce from seed and allows it to gain dominance in burned stands immediately following fire. Although the majority of aspen juveniles in our study area was observed in stands that were dominated by aspen prior to the fire, abundant vegetative reproduction of aspen was also observed in some stands in which the canopy was dominated by spruce and fir. Aspen typically gain dominance following stand-replacing disturbance, then in some areas are successional replaced by more shade-tolerant species such as

subalpine fir and Engelmann spruce. Once these shade-tolerant conifers eventually reach the canopy, they can outcompete aspen, which is then no longer able to maintain canopy dominance. Under the light-limited conditions under a spruce-fir canopy, aspen are not able to grow to mature trees, but the underground root system can continue living and ramets can continue to sprout for hundreds of years after losing dominance of the canopy. When a stand-replacing fire occurs in such stands, canopy dominance can change from relatively old spruce-fir stands to quaking aspen.

The regeneration of aspen in stands that were formerly dominated by conifers is significant as there has been much recent concern regarding the decline of quaking aspen in the American West. Much of the aspen that currently dominates Colorado established following stand-replacing fires in the late 19<sup>th</sup> century (Kulakowski et al. 2004; Kulakowski et al. 2006). A portion of these aspen stands have been gradually replaced by conifers during the 20<sup>th</sup> century, leading to substantial concern about the decline of aspen. As recent and projected future climatic conditions are conducive to the occurrence of large, severe fires in subalpine forests, it is likely that some coniferous forests will be converted to aspen following recent and future fires. Data on current understory and sub-canopy composition in coniferous forests would be required to estimate the potential conversion of coniferous forests to aspen forests.

Aspen density in burned stands was higher than any other species in burned stands during the three years following fire, but decreased substantially over this three year period. Thus, although initial trends indicate an initial dominance of aspen in post-fire stands, it is not certain how these initial trends may correspond to long-term stand composition decades after the stand-replacing disturbance and how this dominance may vary with pre-fire cover type.

In the second year following fire, seedlings of lodgepole pine became abundant in burned stands. This finding is consistent with the expectation of lodgepole acting as an early successional species that colonizes well following stand-replacing disturbances. Our data indicate that the abundance of lodgepole seedlings was higher in young (c. 130 year old) stands than in older (>200 year old) post-fire lodgepole pine stands. Previous work in Yellowstone National Park found a higher incidence of serotinous cones on lodgepole pine in young post-fire stands than in old post-fire stands (Schoennagel et al. 2003; Tinker 1994).

#### Regeneration following compounded disturbances

Climate change is increasing the extent, severity, and frequency of various forest disturbances including fires, outbreaks of bark beetles, and wind storms. Therefore it is increasingly likely that forest stands may be affected by compounded disturbances. Initial post-fire development in our study area was contingent upon whether or not fire was preceded by other disturbance. However, regeneration of aspen was not inhibited by compounding disturbances. Stems of aspen were more abundant than any other tree species in all categories of burned stands, regardless of whether or not fire was preceded by another disturbance or not. Generally speaking, compounded disturbances have the potential to alter

post-disturbance regeneration by either reducing seed source or by increasing the intensity of the second disturbance, which in turn may negatively influence micro-environmental conditions and reduce the density of niches that would be suitable for seedling establishment. These two influences may be of minimal consequence for aspen's vegetative reproduction. Although it is conceivable that compounded disturbances may increase overall disturbance intensity so that below-ground aspen roots are killed and therefore post-disturbance re-sprouting is impeded, we found no such effect in our study. Instead, our data suggest that compounded disturbances favor overall aspen dominance in a landscape co-dominated by aspen and conifers. This is especially significant given widespread concern of aspen decline and the increasing likelihood of forest stands being affected by compounded disturbances.

In contrast to aspen, regeneration of lodgepole differed substantially between stands affected by single versus compounded disturbances. In stands that were affected only by fire, lodgepole seedlings became abundant two years after fire and continued to be high in the third year following fire. However, when fire was preceded by blowdown or spruce beetle outbreak, density of lodgepole seedlings was greatly reduced. In the case of blowdown followed by fire, cones of fallen lodgepole would have been close to the ground at the time of the fire. This fuel arrangement would have likely led to a relatively high combustion of lodgepole seeds that were in non-serotinous cones, but the high intensity fire may have also resulted in combustion of some seeds in serotinous cones. The overall higher intensity of fire in blown down stands also likely contributed to greater combustion of organic matter and a reduction of favorable niches in the post-fire environment. Thus, reduced availability of seed combined with a less favorable post-fire environment reduced the density of lodgepole seedlings following compounded disturbances.

In the case of stands in which the 1940s spruce beetle outbreaks was followed by the 2002 fires, the regeneration of lodgepole pine was also inhibited. However, there is a confounding influence in this scenario that probably has an overriding effect. Stands that were categorized as being dominated by lodgepole pine and that were affected by spruce beetle outbreak were several hundred year-old post-fire stands. As older lodgepole stands are likely to have a lower proportion of serotinous cones, they are likely to be characterized by slower post-fire development than younger lodgepole pine stands.

## **Conclusions**

Following the 2002 fires in western Colorado, regeneration varied according to pre-fire conditions including forest type, stand age, and disturbance history. Seedling densities of spruce and fir were generally low following fire, regardless of whether the fire was preceded by other disturbance. This is consistent with the late successional status of both of these species. Densities of lodgepole seedlings were most affected by compounded disturbances and were significantly lower following a combination of blowdown and fire in comparison to just fire. This finding suggests an increased complexity of stand development in stands affected by compounded disturbances. Disturbances by both wind storms and fires are expected to increase under climate change scenarios. Our data suggest that the compounding of such disturbances is likely to inhibit the rate of forest regeneration.

While regeneration of lodgepole pine was significantly reduced by compounded disturbances, the regeneration of quaking aspen appears not to have been negatively influenced. Aspen ramets/seedlings were high following fire, regardless of whether the fire was preceded by other disturbance. This suggests the possibility that compounded disturbances in Rocky Mountain subalpine forests may favor the dominance of aspen, where viable aspen roots exist underground.

### **Acknowledgements**

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## Tables

Table 1. Description of categories of permanent plots. Plots (2 m x 1 m) were stratified by stand age, pre-fire species composition, and by whether the stand was affected by the 1940s spruce beetle outbreak, the 1997 blowdown, and the 2002 fires.

Stand age <sup>1</sup>	Species <sup>2</sup>	1940s Outbreak	1997 Blowdown	2002 Fire	n (plots)
YOUNG	PT	N	N	N	45
YOUNG	PC	N	N	N	45
OLD	PC	N	N	N	45
YOUNG	PE/AL	N	N	N	45
OLD	PE/AL	N	N	N	45
YOUNG	PT	N	N	Y	90
YOUNG	PT	N	Y	N	90
YOUNG	PT	N	Y	Y	90
YOUNG	PC	N	N	Y	90
YOUNG	PC	N	Y	N	90
YOUNG	PC	N	Y	Y	90
OLD	PC	N	N	Y	90
OLD	PC	N	Y	N	90
OLD	PC	N	Y	Y	90
YOUNG	PE/AL	N	N	Y	90
YOUNG	PE/AL	N	Y	N	90
OLD	PE/AL	N	N	Y	90
OLD	PE/AL	N	Y	N	90
OLD	PE/AL	N	Y	Y	90
YOUNG	PE/AL	N	N	Y	90
YOUNG	PT	N	N	N	45
OLD	PT	Y	N	N	90
OLD	PT	Y	N	Y	90
YOUNG	PC	N	N	N	45
OLD	PC	Y	N	Y	90
YOUNG	PE/AL	N	N	N	45
OLD	PE/AL	Y	N	N	90
OLD	PE/AL	Y	N	Y	90

<sup>1</sup>Stand age – young stands are those < c. 130 yrs old; old stands are those > 200 yrs old.

<sup>2</sup>Species – Stands were categorized based on pre-2002 fire species composition. Stands were categorized as *P. contorta* if *P. contorta* made up  $\geq 40\%$  of canopy trees; Stands were categorized as *P. Engelmannii/A. lasiocarpa* if *P. Engelmannii* and *A. lasiocarpa* made up  $\geq 90\%$  of canopy trees; Stands were categorized as young *P. tremuloides* if *P. tremuloides* made up  $\geq 90\%$  of canopy trees; Stands were categorized as old *P. tremuloides* if *P. tremuloides* made up  $\geq 50\%$  of juveniles  $\leq 1.4$  m tall.

## Figure captions

Figure 1. Density of juveniles (seedlings and ramets  $\leq 10$  years old) of various species in control stands that were not affected by any major disturbance over the past  $> 70$  years.

Figure 2. Density of juveniles (seedlings and ramets  $\leq 10$  years old) of various species in stands affected by the 2002 fire and no preceding disturbance.

Figure 3. Density of juveniles (seedlings and ramets  $\leq 10$  years old) of various species in stands affected by the 1940s outbreak of spruce beetle.

Figure 4. Density of juveniles (seedlings and ramets  $\leq 10$  years old) of various species in stands affected by the 1940s outbreak then the 2002 fires.

Figure 5. Density of juveniles (seedlings and ramets  $\leq 10$  years old) of various species in stands affected by the 1997 blowdown.

Figure 6. Density of juveniles (seedlings and ramets  $\leq 10$  years old) of various species in stands affected by the 1997 blowdown then the 2002 fires.

Figure 7. Density of aspen juveniles (seedlings and ramets  $\leq 10$  years old) in stands with various histories of recent disturbance.

Figure 8. Density of lodgepole pine juveniles (seedlings and ramets  $\leq 10$  years old) in stands with various histories of recent disturbance.

Figure 9. Density of Engelmann spruce juveniles (seedlings and ramets  $\leq 10$  years old) in stands with various histories of recent disturbance.

Figure 10. Density of subalpine fir juveniles (seedlings and ramets  $\leq 10$  years old) in stands with various histories of recent disturbance.

Figures

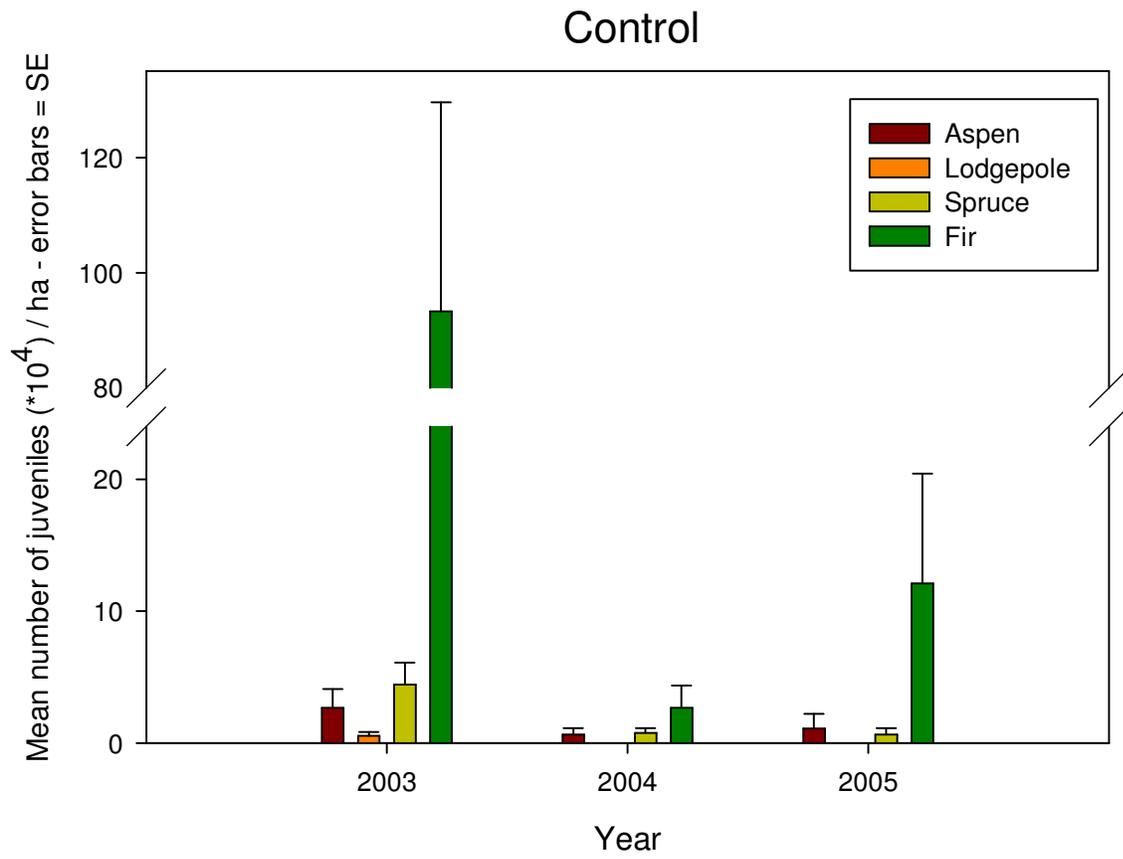


Figure 1.

## 2002 fire

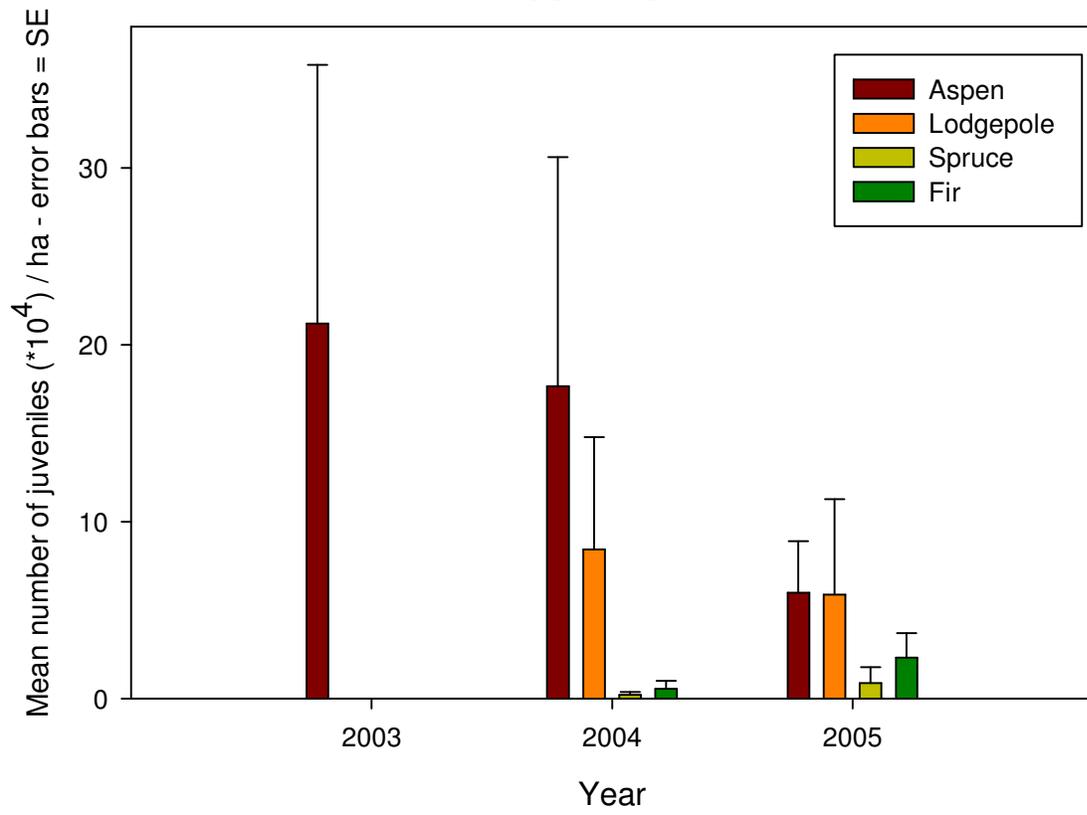


Figure 2

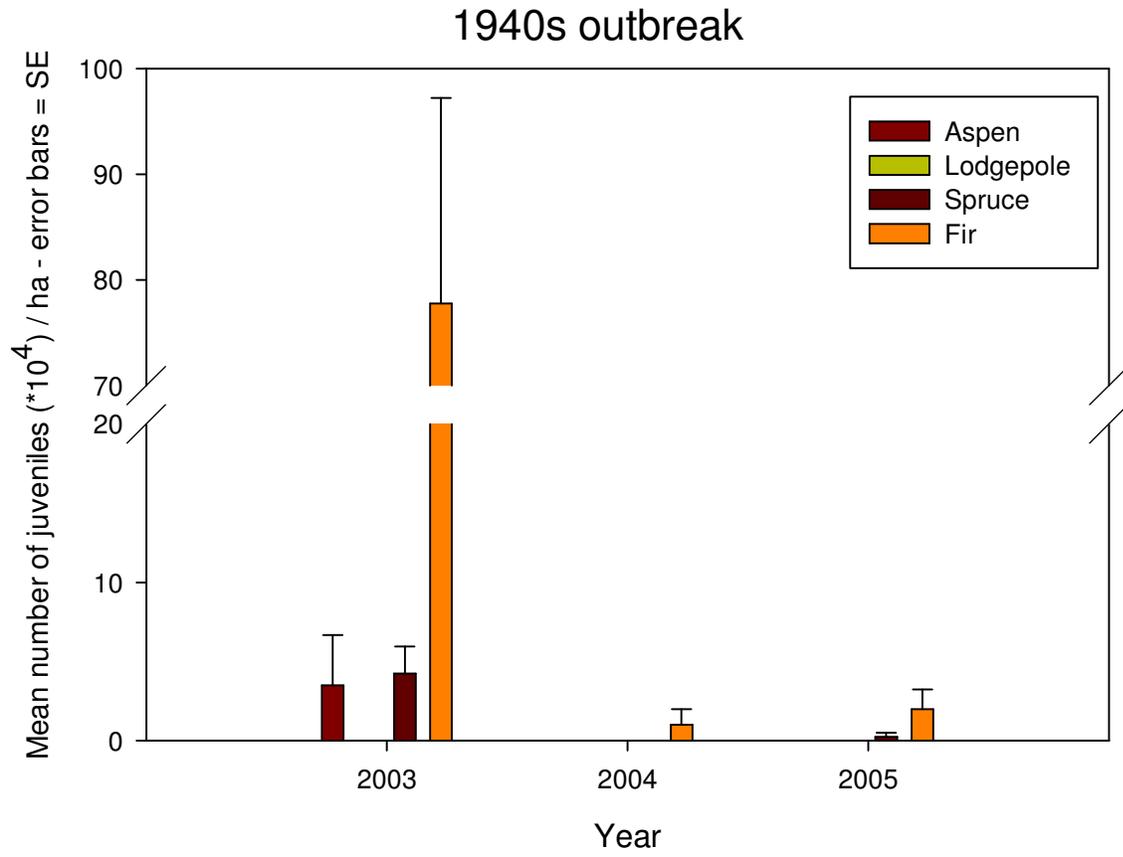


Figure 3

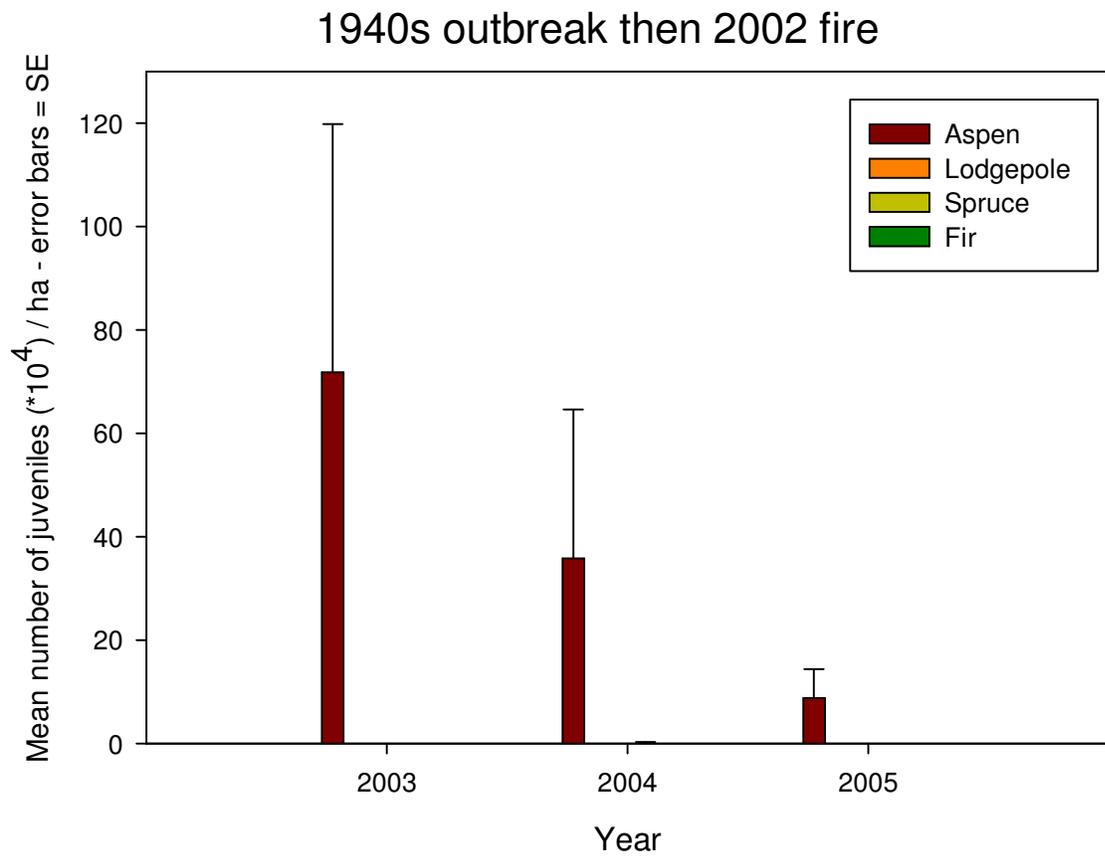


Figure 4

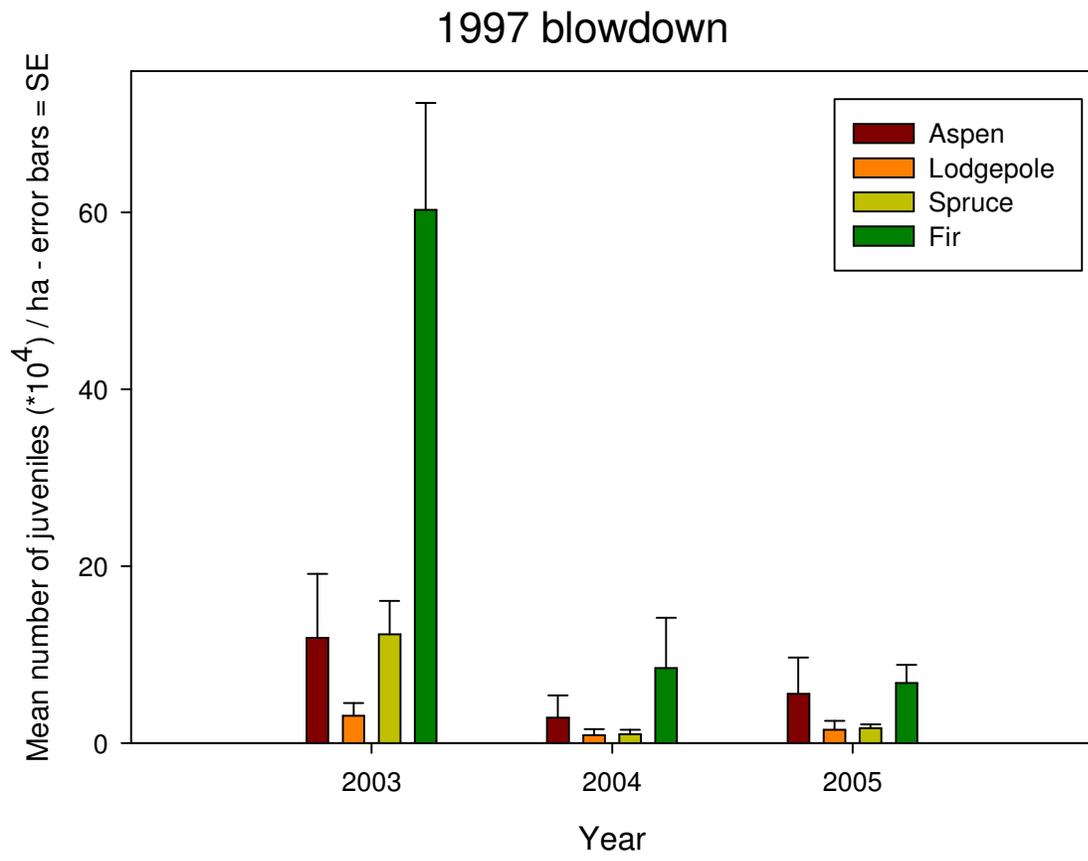


Figure 5

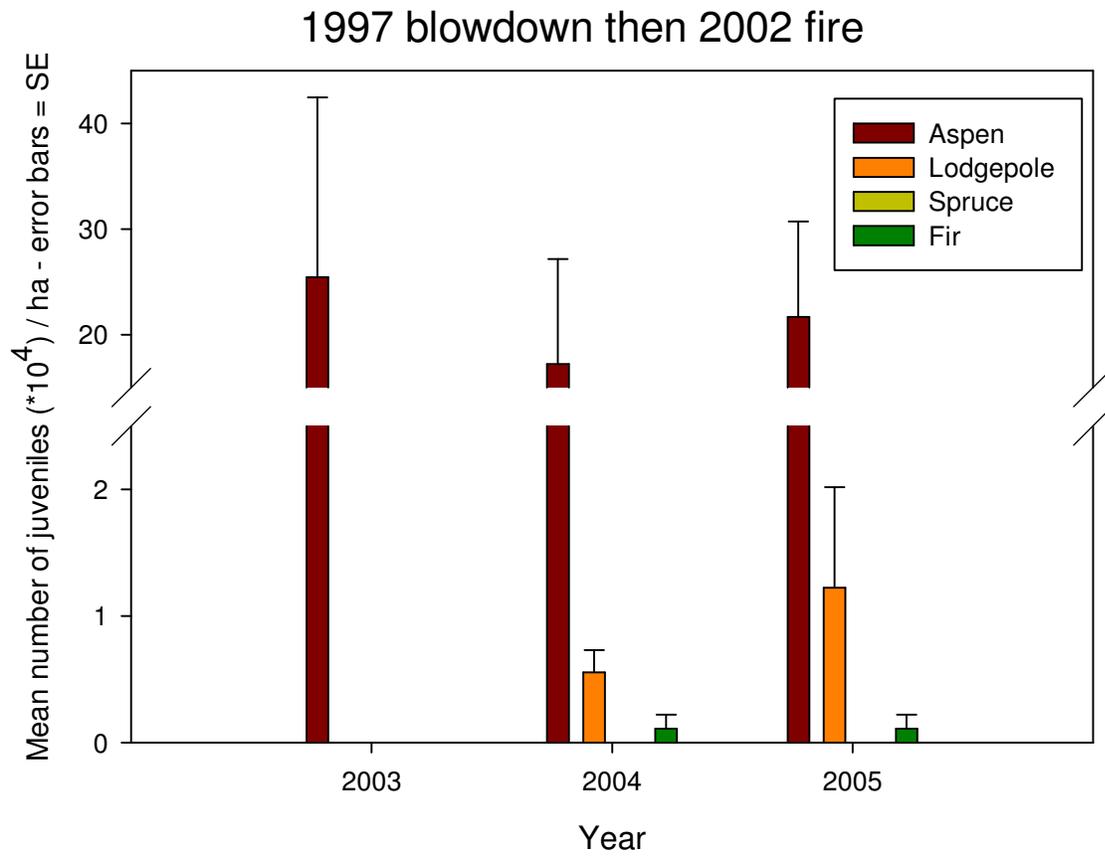


Figure 6

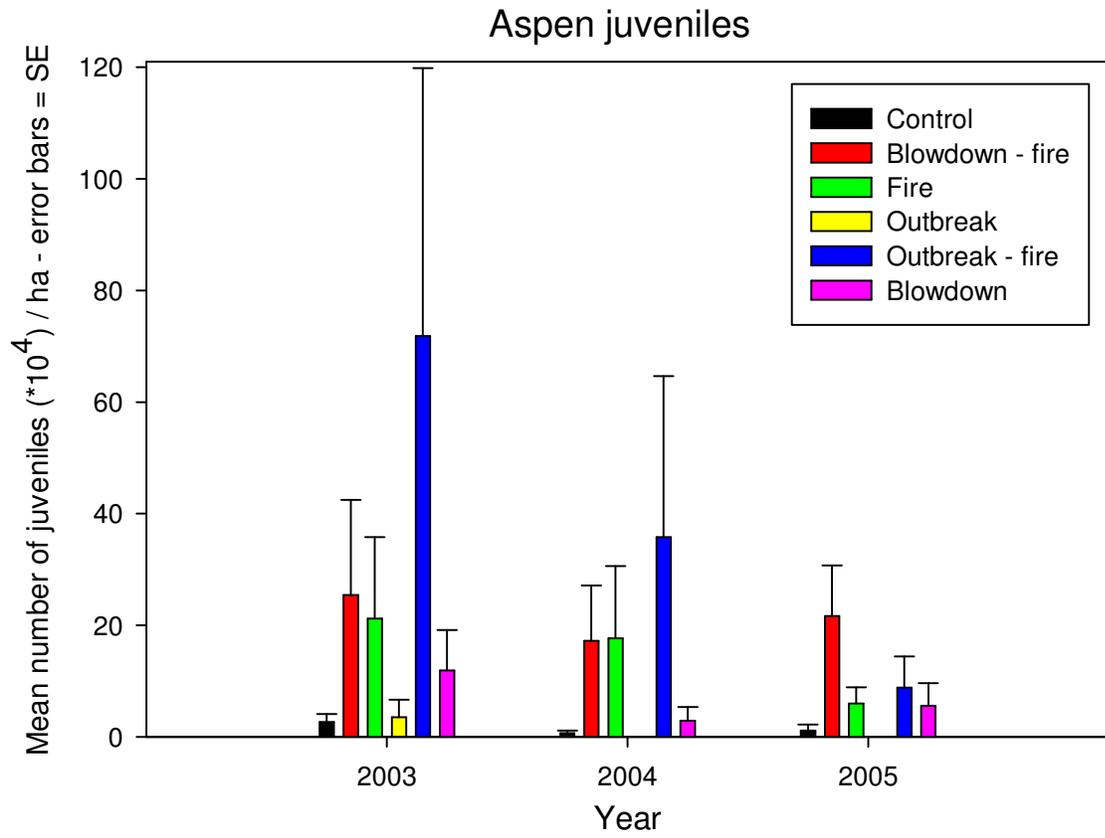


Figure 7

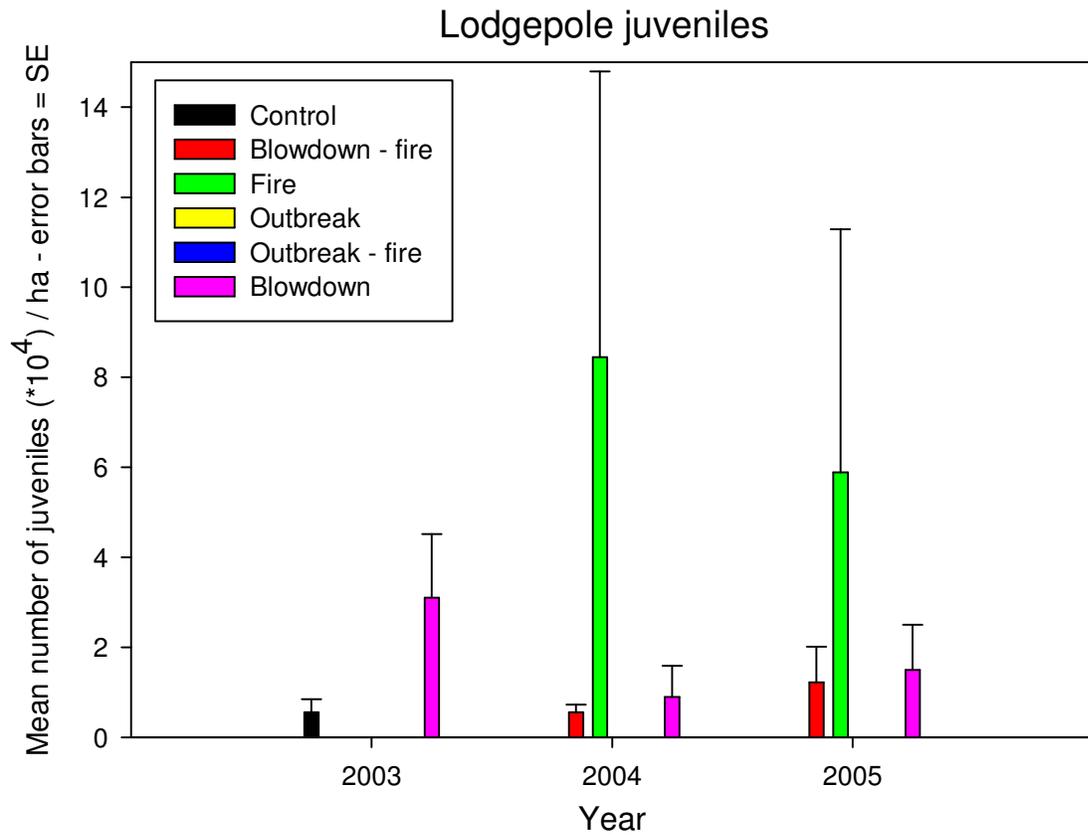


Figure 8

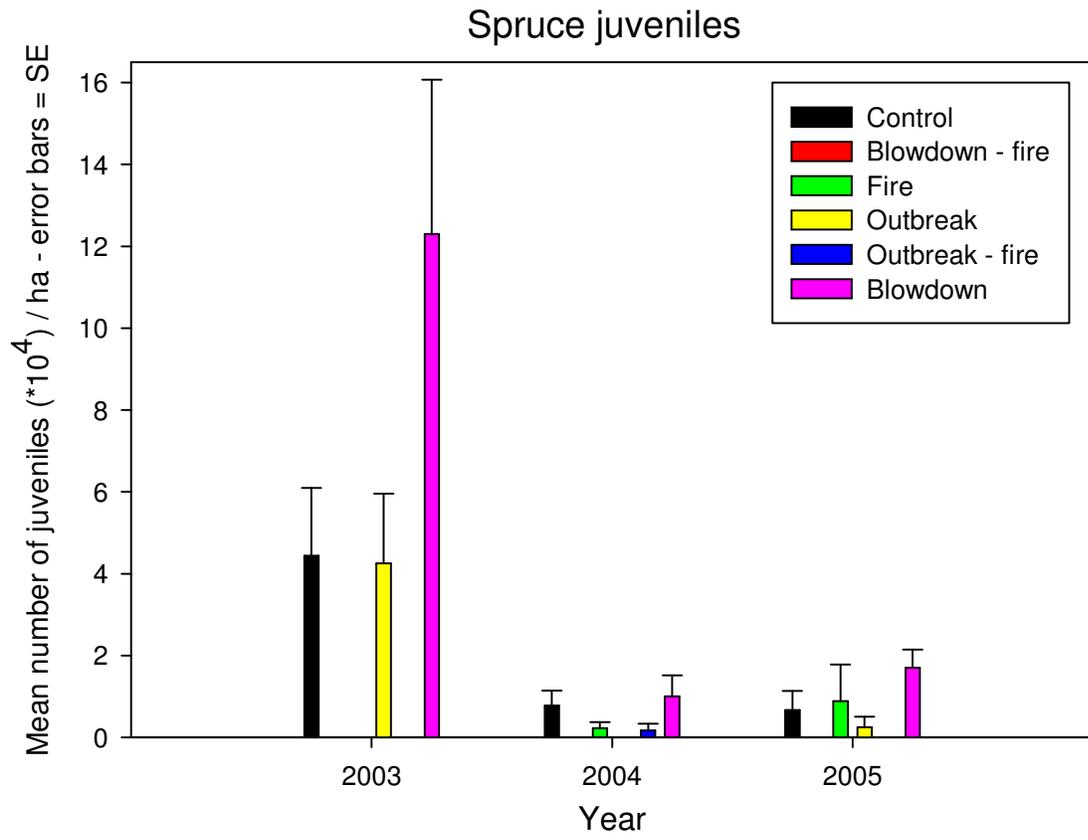


Figure 9

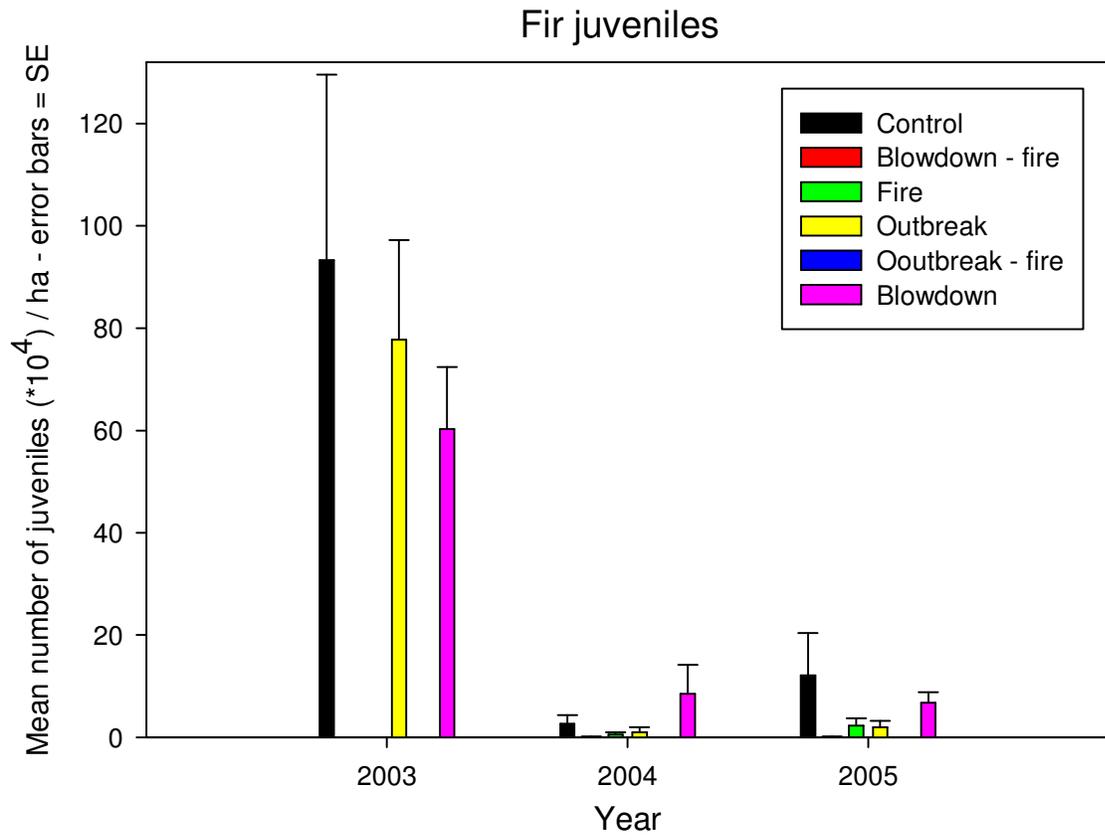


Figure 10