Cone production in young post-fire *Pinus contorta* stands in Greater Yellowstone (USA)

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Abstract

Spatial and temporal variability in cone production may influence post-disturbance succession, yet it is not well understood. We sampled 15-year old lodgepole pine (*Pinus contorta* var. *latifolia*) stands ($n = 16$) that regenerated naturally after the 1988 Yellowstone fires and varied in stand density (566–545,200 stems ha^{-1}) and elevation to quantify and explain variation in cone production. Among stands, the percentage of trees bearing cones ranged from 10 to 80% and was greater in stands with larger trees and at lower elevations. Mean cone abundance was 3.7 cones tree^{-1} (range of 0.10–17.85 cones tree^{-1} for the 16 stands) and increased with mean basal diameter and decreasing elevation. The earliest onset of cone production was 1997, and early onset was associated with lower elevations (<2300 m). Cone density ranged from 1082 to 1,015,665 cones ha^{-1} among the stands, with most of this variation explained by a positive relationship with stand density. Although serotinous cones were not expected in such young stands, we observed serotinous cones (albeit infrequently) in five of the 16 stands. Serotinous cones were only recorded at elevations ≤2230 m where fire return intervals are relatively short (<200 years). Among individual trees ($n = 320$), 33% bore cones, and both cone presence and abundance were positively related to tree basal diameter. Cone production in the young post-fire lodgepole pine stands that regenerated after the 1988 Yellowstone fires is both abundant and spatially variable, and lodgepole pine in this system might produce serotinous cones earlier than reported previously. The abundant canopy seed bank in young post-fire stands suggests substantial resilience of this forested landscape to extensive stand-replacing disturbance.

1. Introduction

Understanding tree regeneration following disturbance has long been an important research goal in forest ecology (West et al., 1981; Barnes et al., 1998; Greene et al., 1999). In coniferous forests, the abundance of cones will influence seed availability and hence post-disturbance tree regeneration. Understanding spatial and temporal variability in cone production is increasingly important (Nathan and Ne'eman, 2004) as forest scientists and managers worldwide strive to project the future of coniferous forests in the face of changing disturbance regimes (Greene et al., 1999). Cone abundance may interact with fire regime to influence forest composition, stand structure, and/

or landscape mosaic of stand ages or densities following stand-replacing fire. Climate-induced increases in fire frequency in boreal forests could trigger shifts from one conifer species to another (e.g., *Picea* to *Pinus*, Lavoie and Sirois, 1998), or from conifer- to deciduous-dominated successional pathways (Johnstone and Chapin, 2006). At the northern edge of its range, lodgepole pine (*Pinus contorta* var. *latifolia*) is increasing in dominance following fire and extending its range northward, thus altering forest composition (Johnstone and Chapin, 2003). In subalpine lodgepole pine forests, the stand-age mosaic may shift to younger ages with increased fire frequency without a change in composition (Schoennagel et al., 2006). In this study, we report on the rate and variability of cone production in young, post-fire lodgepole pine forests.

Lodgepole pine is an important species in which to examine cone production because the species is widespread, produces both open and serotinous (closed) cones, is associated with

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infrequent but severe stand-replacing fire, and is invasive in some systems (e.g., New Zealand, Ledgard, 2001; Sweden; Engelmark et al., 2001). Cone production in lodgepole pine begins when trees are between 5 and 10 years of age (Schopmeyer et al., 1974) and increases with tree size (Clements, 1910; Koch, 1987). Cones mature in 2 years (Young and Young, 1992; Koch, 1996), and mature open cones shed their seeds in late summer. Seed availability will typically vary positively with cone abundance; in the Rocky Mountains, the number of seeds in lodgepole pine cones averages 10–24 seeds per cone (Koch, 1996). Seed production in lodgepole pine has been suggested to be an increasing function of basal area (Greene et al., 1999).

The production of either open or closed cones provides lodgepole pine with a dual strategy for regeneration. Open cones offer a mechanism for ongoing tree recruitment within a stand; the onset of open-cone production promotes the gradual infilling that occurs in stands that are initially sparse (Kashian et al., 2005). In contrast, serotiny offers a mechanism for rapid post-fire seedling establishment. Serotinous cones do not open at maturity but remain closed until subjected to high temperature (Lamont et al., 1991; Johnson and Gutsell, 1993). The closed cones are retained on the tree for many years (15–30 years; Hellum, 1983), but may be reduced in number through foraging by pine squirrels (*Tamiasciurus hudsonicus*; Benkman and Siepielski, 2004). The proportion of trees bearing serotinous cones is a prime determinant of initial tree regeneration following stand-replacing fire (Anderson and Romme, 1991; Turner et al., 1997, 2003).

Variability in lodgepole pine cone serotiny among stands is striking, and many studies have examined its relationship to fire (e.g., Clements, 1910; Critchfield, 1957; Lotan, 1970, 1975; Pfister and Daubenmire, 1975; Muir and Lotan, 1985a,b; Koch, 1987; Tinker et al., 1994; Schoennagel et al., 2003). In the Intermountain and Rocky Mountain regions, the percentage of trees bearing serotinous cones increases with latitude (Koch, 1987). Studies have also reported a greater percentage of serotinous trees at lower elevational zones (Crossley, 1956; Critchfield, 1957; Koch, 1987; Schoennagel et al., 2003), although Lotan (1975) and Muir and Lotan (1985b) found little relationship between cone serotiny and elevation. Serotiny also varies with tree age, with younger trees bearing a greater percentage of open cones, and a potential transition from the open-cone to closed-cone habit suggested to occur between 17 and 60 years (Crossley, 1956; Lotan, 1975; Koch, 1996). However, we are unaware of any studies that have assessed spatial variability in cone abundance and the onset of cone production in young, post-fire even-aged stands.

The 1988 fires in Yellowstone National Park (Wyoming, USA) burned through extensive lodgepole pine forests and were followed by abundant but spatially heterogeneous lodgepole pine regeneration (Turner et al., 1997, 1999). In 1999, post-fire stand density averaged 29,381 stems ha^{-1} (S.E. = 8824) but varied from 0 to 500,000 stems ha^{-1} (Turner et al., 2004). During summer 2000, we observed the onset of cone production in some post-fire stands (personal observation), but cone production rates and the factors that influence

cone production in these young stands are not known. Previous studies of serotiny in mature lodgepole pine forests in Yellowstone have demonstrated landscape-scale variability at scales of one to 10 km (Tinker et al., 1994) and an interaction between stand age and elevation. Trees at elevations >2300 m are characterized by low proportions of serotinous trees across a range of stand ages, whereas trees at lower elevations in stands >70 years of age are characterized by high levels of serotiny (Schoennagel et al., 2003).

Studies of cone production in young stands initiated by the same stand-replacing disturbance may provide new insights into post-fire stand dynamics. In this study, we sampled lodgepole pine stands that regenerated naturally after the 1988 Yellowstone fires to determine how many cones were present on the young lodgepole pines and to identify factors that explained variation in the number and type (open or serotinous) of cones. Among stands, we expected to see a greater proportion of cone-bearing trees and greater cone abundance in low-density stands and at lower elevations. The growing season in Yellowstone is longer at the lower elevations, and our previous studies have demonstrated that aboveground net primary production declines with increasing elevation (Turner et al., 2004). We further hypothesized that serotinous cones would be observed only in areas where pre-fire serotiny was expected to be high (i.e., stands >70 years old at elevations <2300 m, as reported by Schoennagel et al., 2003). Among trees, we expected that larger trees would produce more cones; we also hypothesized an interaction between tree size and elevation, with more cones produced at lower elevations for a given tree size.

2. Study area and methods

The Greater Yellowstone Ecosystem is comprised of Yellowstone and Grand Teton National Parks and other public and private lands in northwestern Wyoming, southwestern Montana, and adjacent Idaho. Almost 300,000 ha of the Greater Yellowstone Ecosystem were affected by extensive wildfires during the summer of 1988. Approximately 80% of Yellowstone National Park is dominated by lodgepole pine forest, although subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry), and whitebark pine (*Pinus albicaulis* Engelm.) may be locally abundant in older stands and at higher elevations (Despain, 1990). The climate is generally cool and dry with mean January temperature of −11.4 °C, mean July temperature of 10.8 °C, and mean annual precipitation of 56.25 cm (Dirks and Martner, 1982). The summer of 1988 was the driest on record since 1886 (Renkin and Despain, 1992). As with large, infrequent crown fires in other systems, the 1988 fires resulted from synoptic climate patterns and responded little to topography or variation in stand age or structure (Johnson and Wowchuck, 1993; Turner et al., 1994; Bessie and Johnson, 1995; Flannigan and Wotton, 2001). Large fires occur with a return interval of about 170–300 years (Romme and Despain, 1989; Schoennagel et al., 2003).

During summer of 2003, we sampled sixteen 0.25-ha stands that had burned during the 1988 fires. Most (12) stands were a

subset of 90 stands sampled during summer 1999 for post-fire stand density, aboveground net primary production and leaf area index (Turner et al., 2004), two were new stands in Yellowstone National Park, and two were new stands just south of Yellowstone in an area administered by Grand Teton National Park. Sites were chosen to span a range of post-fire stand densities and elevations. At the four new stands, post-fire tree density was estimated following the same procedures employed by Turner et al. (2004). We have seen little evidence of tree mortality in the post-fire stands, and changes in tree density from 1999 to 2003 were not significant in a set of 12 stands that partially overlap with those used in this study (unpublished data). All stands were located on infertile ryholite substrate and between 2050 and 2437 m elevation.

From the center of each stand, 25-m transects were established to the north, south, east and west (4 transects/ stand). A random sample of five lodgepole pine saplings along each transect was obtained by measuring the sapling nearest to the meter tape at 5-m intervals ($n = 20$ saplings/stand). Trees ranged from ca. 0.5 to 3.5 m in height, and we were able to bend the taller trees to count and classify cones. The basal diameter (cm) was recorded for each sapling, and the number of cones present on the tree were counted and recorded by the year in which they were produced. Cone age was assumed to be the age of the branch segment on which the cone was growing, and branch segment age was determined from bud scale scars and whorls of lateral branches. Current-year conelets (produced in 2003) were distinguished not only from their terminal locations but also by their small size and pinkish color. Cones produced in 2002 were full sized but green, closed and immature. Cones produced in 2001 and earlier were brown in color and were scored as either open or serotinous using morphological traits quantified previously for lodgepole pine in Yellowstone National Park (Tinker et al., 1994).

The random sample of 20 trees was used to estimate cones/ tree within each stand, and cone density was then obtained by multiplying mean cones/tree by stand density. If fewer than five of the 20 randomly sampled trees had cones present, we randomly sampled an additional five trees on which cones were present so that cone production could be related to tree morphology in each stand. Thus, we sampled 320 trees using the random sample (16 stands × 20 trees/site) and an additional 60 trees in stands where cones were less frequent for a total of 380 trees.

Among stands ($n = 16$), we used stepwise multiple regression to explore the effects of elevation, stand density and mean basal diameter on the proportion of trees with cones and the mean cone production per tree. Because stand density was correlated with both mean basal diameter and elevation (see Section 3), we used only these latter two variables in the regressions. However, a separate model was tested to determine whether stand density also had a significant influence. Cone data were log transformed prior to analysis to reduce heteroscedasticity in the data. For each stand, we also determined whether the onset of cone production (year in which the oldest cones were produced) was related to elevation and mean basal diameter using stepwise multiple regression. In

addition, we tested for differences in onset of cone production among stands by elevation class (<2300 and >2300 m) using one-way ANOVA. The onset of cone production was coded as the actual year (e.g., 1998). Our prior studies in areas burned by the 1988 fires showed that nearly all lodgepole pine recruitment occurred in 1989 or 1990 (Turner et al., 1997, 1999), and we saw little or no recent recruitment in the stands studied here. The potential relationship between occurrence of serotinous cones (at the stand level) and the same predictors was evaluated using chi-square analysis and logistic regression, and variation in cone density (cones ha^{-1}) among stands was evaluated using stepwise multiple regression.

Among individual trees, we used a two-step process to explore variability in cone production. First, cone presence or absence on the randomly sampled trees ($n = 320$) was analyzed using logistic regression with basal diameter, stand density and elevation as independent variables. Second, variation in cone abundance was analyzed for the trees on which cones were present (those observed within the 20 randomly sampled trees plus the additional trees sampled in stands with low cone production). Multiple linear regression was used to predict the number of cones present as a function of tree basal diameter and elevation. Finally, we computed the mean number of cones produced annually on trees that had cones and compared these among years using one-way ANOVA and Tukey's Studentized Range test.

All statistical analyses were conducted using SAS 9.1.3 (SAS Institute, 2003). For all regression models, variables were retained in the models using $\alpha = 0.10$, and models were fitted with a y intercept.

3. Results

3.1. Variation among stands

The mean post-fire lodgepole pine density of the 16 stands we sampled was 53,437 stems ha^{-1} and ranged from 566 to 545,200 stems ha^{-1}. Lodgepole pine was the only tree species present in most of the stands, but we observed occasional seedlings of subalpine fir and Engelmann spruce. The mean basal diameter of the randomly sampled lodgepole pine saplings ($n = 20$) in each stand was 4.20 cm and ranged from 1.64 to 7.45 cm. Stand density was negatively correlated with elevation ($r = -0.51$, $P = 0.04$) and mean basal diameter ($r = -0.60$, $P = 0.0139$), indicating that trees were smaller in denser stands and at higher elevations. Mean basal diameter did not correlate with elevation ($P = 0.36$).

Among stands, the frequency of trees on which cones were present ranged from 0.10 to 0.80, and mean basal diameter and elevation explained 74% of this variation (Table 1). The frequency of trees bearing cones was greater in stands with bigger trees and at lower elevations (Fig. 1). At lower elevations, the frequency of trees with cones spanned the observed range from 0.10 to 0.80, whereas at higher elevations (>2300 m), this frequency was always ≤0.40 (Fig. 1b). Mean cone abundance was 3.7 cones tree^{-1} but ranged from 0.1 to 17.8 cones tree^{-1} among the 16 stands. Multiple regression

Table 1
Results of multiple stepwise regression for: (a) the frequency of trees with cones, (b) the mean number of cones per tree, and (c) the density of cones ha^{-1} in 16 post-fire lodgepole pine stands sampled during 2003

Predictor	Coefficient	Partial r^2	Model r^2	P
(a) Frequency of trees with cones				
Mean basal diameter (cm)	0.1141	0.44	0.44	0.0053
Elevation (m)	−0.0009	0.30	0.74	0.0019
(b) Mean number of cones per tree				
Mean basal diameter (cm)	0.211	0.63	0.63	0.0002
Elevation (m)	−0.001	0.14	0.77	0.0164
(c) Cone density				
Log (stand density, trees ha^{-1})	0.472	0.48	0.48	0.0029
Elevation (m)	−0.002	0.10	0.58	0.0991

P values are for each successive variable added to the model.

revealed that 77% of the variation in cones per tree among stands was explained by mean basal diameter and elevation (Table 1). More cones per tree were observed in stands with larger trees and at lower elevations (Fig. 2).

The earliest year of cone production recorded among the trees sampled in this study was 1997, when trees that germinated in 1989 would have been 8 years old, and all stands were producing cones by 2002, when trees were up to 13 years old. However, the variation in onset of cone production was not related to either tree size or stand density. Results from

Fig. 2. Mean number of cones per lodgepole pine tree (transformed using log $x + 1$) as a function of: (a) mean tree basal diameter and (b) elevation in 16 post-fire stands (15 years since fire) in the Greater Yellowstone Area.

one-way ANOVA revealed a marginally significant influence of elevation class, with the onset of cone production occurring sooner in stands <2300 m in elevation ($r^2 = 0.23$, M.S.E. = 7.56, $F = 4.26$, $P = 0.06$).

When tree density was multiplied by the mean cones per tree in each stand, we found an expected cone density ranging from 1082 to 1,015,665 cones ha^{-1}. Stand density was the strongest predictor of cone density (Fig. 3), but an additional (albeit marginally significant) negative influence of elevation was also identified (Table 1).
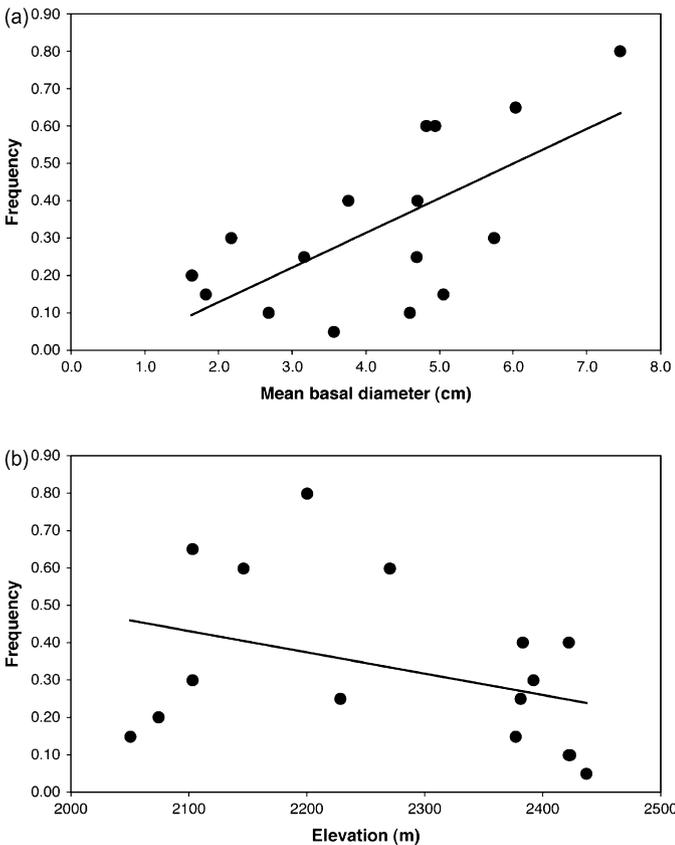

Fig. 1. Frequency of lodgepole pine trees producing cones as a function of: (a) mean basal diameter and (b) elevation in 16 post-fire stands (15 years since fire) in the Greater Yellowstone Area.
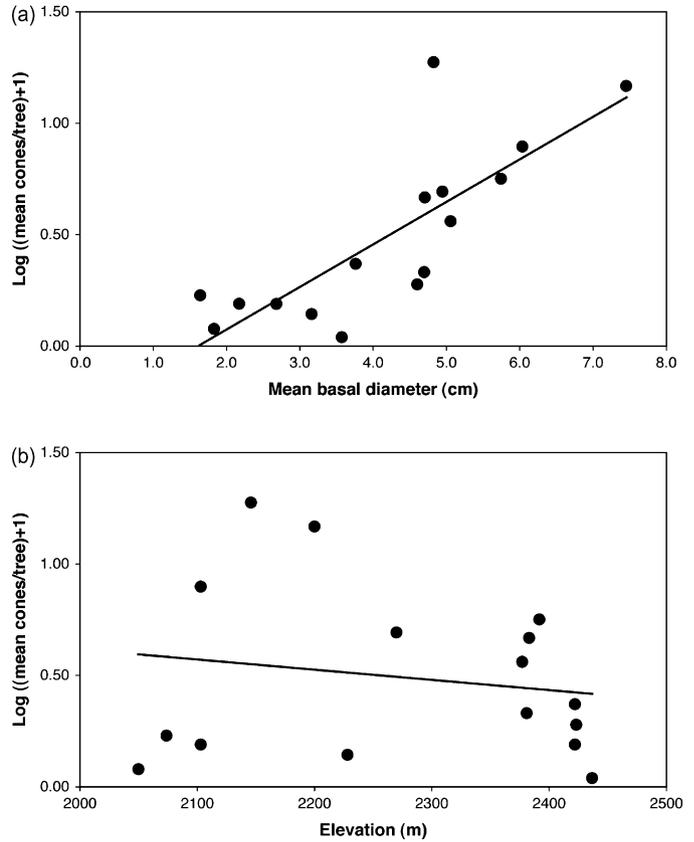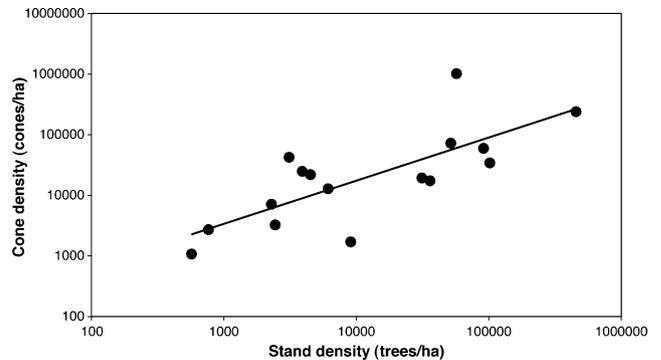

Fig. 3. Double-log plot of overall cone density vs. stand density for 16 post-fire stands (15 years since fire) in the Greater Yellowstone Area. Cone density was estimated as stand density (trees ha^{-1}) × mean cones tree^{-1}.
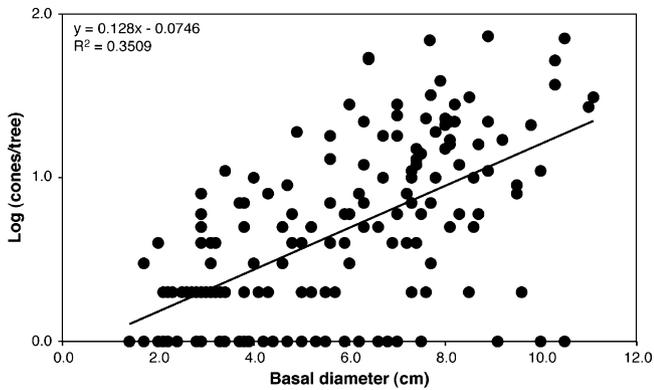
Fig. 4. Number of cones observed on 15-year old post-fire lodgepole pine trees ($n = 165$) that had at least one cone present as a function of basal diameter. (Cones per tree were transformed using log $x + 1$).

negatively to elevation ($\beta = -0.0062$, $P < 0.0001$); the overall model was fairly strong ($P < 0.0001$, 85% concordance).

Considering only trees on which cones were present ($n = 165$), we observed an average of 9.5 cones tree^{-1} (S.E. = 1.0) and a maximum of 73 cones tree^{-1}. Trees with cones had an average basal diameter of 5.7 cm (S.E. = 0.19 cm), but cones were present on trees ranging from 1.4 to 11.1 cm basal diameter. However, more cones were present on larger trees (Fig. 4). Variability in cone abundance among individual trees was explained by basal diameter ($\beta = 3.08$, $r^2 = 0.45$, $P = 0.005$). Cone production also varied among years ($P < 0.0001$, $F = 75.37$, d.f. = 6) with the greatest annual mean cones per tree produced during 2002 (Fig. 5).

4. Discussion

This study has documented abundant cone production in 15-year old stands of lodgepole pine that regenerated naturally following the 1988 fires. As expected, we found a strong positive relationship between mean tree size (as measured by basal diameter) and both the frequency of trees with cones and the mean number of cones per tree. A positive relationship between stem diameter and cone production has also been observed in other conifers, such as ponderosa pine (*Pinus ponderosa*, Krannitz and Duralia, 2004) and black spruce (*Picea glauca*, Greene et al., 2002; Sirois, 2000). In addition, elevation influenced cone production, with more cones produced at lower elevations and an earlier onset of cone production (9–10 years after fire). This may reflect the longer growing season at lower elevations, where the snow-free period is about a month longer than at the higher elevations.

Mean tree size was a stronger predictor of among-stand variation in cone production than was stand density, although these two predictors are correlated. Trees are smaller in the high-density stands, and thus the effect of stand density may be manifested primarily as tree-size variation. Alteration in stand density through tree thinning is associated with growth release (e.g., Sullivan et al., 2006), which may then promote cone production. For example, Scots pine (*Pinus sylvestris* L.) trees in stands that were thinned produced 65% more conelets than trees in control stands that were not thinned, and needle concentrations of nitrogen, potassium and phosphorus were positively correlated with numbers of conelets (Karlsson and Orlander, 2002).

Stand density was the primary determinant of cone density among stands; stands with the highest density of trees also had the most cones (Fig. 3). Although this may seem circular, either tree density or the average number of cones per tree could determine the cone density. However, the extremely wide range of stand densities appears to overwhelm the more modest variation in average cone production. Thus, the initial patterns of tree density that established within the first 2 years after the fires may exert a strong influence upon landscape patterns of reproduction, although we did not measure seed production or viability. Other studies suggest that stand density might positively influence seed production. In Mediterranean fir (*Abies pinsapo*), low-density stands had reduced fruit set and seed viability (21% compared to

Although infrequent, serotinous cones were observed in our sample of these 15-year old stands. Considering only the 20 trees sampled randomly in each stand, serotinous cones were recorded in three stands, occurring on 10–15% of the trees. When the trees added to increase the sample size of trees with cones are included, the number of stands with serotinous cones increased to five. Serotinous cones were only present in stands at elevations <2230 m, but they were observed across a very wide range of stand densities (3100–101,800 stems/ha for the five sites) and mean basal diameters (1.83–7.45 cm). Chi-square analyses confirmed the increased likelihood of observing serotinous cones at elevations <2300 m ($\chi^2 = 7.27$, d.f. = 1, $P = 0.007$), and logistic regression showed no effects of stand density, the frequency of trees with cones, or mean basal diameter on the occurrence of serotinous cones.

3.2. Variation among individual trees

Thirty-three percent of the 320 randomly sampled trees had at least one cone present. Logistic regression revealed that the presence of at least one cone on an individual tree was related positively to basal diameter ($\beta = 0.6612$, $P < 0.0001$) and
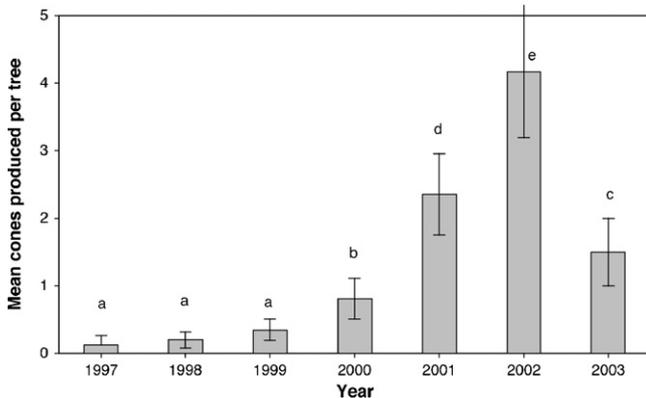

Fig. 5. Mean number of cones produced annually per tree between 1997 and 2003 for 165 post-fire lodgepole pine trees on which cones were observed in 2003. Error bars indicate ±2S.E. The oldest cones observed in this study were produced in 1997. Letters indicate significant differences among means based on Tukey's Studentized Range Test ($P < 0.05$).

82% in the high density stands; Arista and Talavera, 1996), suggesting that pollen availability and origin influenced the frequency and quality of seed. The relatively high cone densities observed in our study also suggest that these young lodgepole pine stands are already developing a substantial canopy seed bank, which, if it persists, should enhance stand regeneration following future disturbance.

A variety of other factors not measured in this study may also influence cone presence and abundance. In the western US, pine squirrels and Red Crossbills (*Loxia curvirostra* complex) are seed predators on lodgepole pine, although we have not measured their abundance in our study area. Seed predation on lodgepole pine is receiving increased attention (Sjoberg and Danell, 2001; Strong et al., 2001; Bates et al., 2002; Siepielski and Benkman, 2004). Studies have also shown that cone production and cone serotiny may be influenced by branch age (Gauthier et al., 1993) and the amount of intercepted radiation on the tree crown (Despland and Houle, 1997; Greene et al., 2002). Nutrient status of trees also influences cone and seed production (Karlsson and Orlander, 2002).

Although the production of serotinous cones was not expected in such young stands of lodgepole pine, we observed serotinous cones (albeit infrequently) in five of 16 stands sampled. This suggests that lodgepole pine might produce serotinous cones earlier than reported previously. All five stands were at relatively low elevation in areas of high pre-fire serotiny (Tinker et al., 1994) and where fire return intervals are <200 years (Schoennagel et al., 2003). This observed pattern across the Yellowstone landscape is consistent with the dual strategy of lodgepole pine (post-fire seeder with serotinous cones were fire is more frequent, and a colonizer with open cones in areas with a longer fire-free period). Interestingly, another serotinous pine (*Pinus halepensis*) that occurs in the Mediterranean region reproduces at an early age, but young reproductive trees produce a high percentage of serotinous cones that declines with increasing time since fire (Goubitz et al., 2004; Ne'eman et al., 2004).

The genetic controls on cone production and serotiny are not understood, although the role of fire as a selective force on production of serotinous cones has been suggested (Perry and Lotan, 1979; Lamont et al., 1991; Schwilk and Ackerly, 2001; Schoennagel et al., 2003), and Yeaman and Jarvis (2006) report an influence of regional heterogeneity on genetic variance in lodgepole pine. Radeloff et al. (2004) suggest the potential for spatial control of genetic variability within jack pine (*Pinus banksiana*), also a serotinous species, in relation to landscape variation in fire regime. In jack pine, the appearance of the first serotinous cone was more strongly related to dbh than to age or height; most trees that bore no serotinous cones were <7 cm dbh (Gauthier et al., 1993). Cone production in black pine (*Pinus nigra* Arnold) appears to be under strong genetic control (Matziris, 1993). In our study, elevation was the only variable that we measured that was associated with the occurrence of serotinous cones, and this is consistent with a selective influence of fire frequency. However, other environmental factors also differ with elevation, and fire frequency similarly may vary with other unmeasured variables.

The production of serotinous and non-serotinous cones may be associated with variation in other seed traits that influence stand regeneration, but this appears to have received relatively little study. In experimental studies in which seeds from serotinous and non-serotinous cones of *Pinus halepensis* were germinated, Goubitz et al. (2003) found that seed from serotinous cones were more tolerant to fire-related factors (higher pH and high heat). Because open cones are expected to be more prevalent in stands where the fire return interval is longer than the expected lifespan of the tree (Schoennagel et al., 2003), such adaptations of the seeds may also promote successful germination following fire (for seeds from serotinous cones) or in suitable microsites produced by other disturbances (for seeds from open cones). Future studies of the onset, frequency, and potential genetic controls on cone serotiny in lodgepole pine are warranted.

In conclusion, this study revealed that cone production in the young post-fire lodgepole pine stands that regenerated after the 1988 Yellowstone fires is both abundant and spatially variable. Among stands, the frequency of trees with cones and the number of cones per tree was explained by tree size and elevation, but the presence of serotinous cones was influenced only by elevation. However, variation in the density of cones across the burned landscape was controlled largely by stand density. Demographic studies that elucidate the spatio-temporal dynamics of lodgepole pine growth, reproduction and mortality will enhance understanding of the successional trajectory that follows large infrequent disturbances.

Acknowledgements

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