

Temporal Variability of Soil Seed Banks in Lodgepole Pine Forests

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Abstract

Soil seed banking is a seed dispersal strategy whereby plants increase the chances that their offspring are exposed to suitable habitat. Following disturbance, the soil seed bank is a potential source of new propagules for site colonization. This study used a chronosequence of Rocky Mountain lodgepole pine (*Pinus contorta* var. *latifolia*) stands in the Colorado Northern Front Range to understand how soil seed banks change through time following stand-replacing fire. Seed abundance and richness were estimated using a greenhouse emergence method. A second order polynomial regression of time since fire explained 17% and 23% of the variation in soil seed bank abundance and richness, respectively. Soil seed bank abundance and richness were low in young stands, highest in the 36-year-old stand, and remained low in old stands (> 80 yr). Changes in soil seed bank composition are likely associated with several processes: fire that destroys aboveground vegetation and litter and induces understory development, canopy closure that excludes shade intolerant understory vegetation, and dispersal from surrounding plant communities. Localized disturbance may indirectly contribute to replenishment of the soil seed bank by permitting light to penetrate the forest canopy, encouraging understory growth.

Introduction

The colonization hypothesis of seed dispersal suggests that since habitats change, dispersal in space and time allows parents to produce offspring capable of exploiting uncompetitive environments as they open.¹ Successful plants will be capable of achieving adequate propagule dispersal to ensure colonization of suitable habitat where and when it occurs. Under the colonization hypothesis, seed dispersal is limited by spatial and temporal barriers. Soil seed banking is one strategy plants employ to increase the probability that their offspring are exposed to conditions suitable for establishment and growth.

The composition of a soil seed bank at a given time and location is a function of input through seed rain and outputs through germination or death. These fluxes, and consequently, the composition of the soil seed bank, are modulated by a host of environmental factors, many of which are associated with time since disturbance. Time-related effects are especially apparent in forested ecosystems where the progression of structural processes influence microhabitat conditions at every developmental stage.^{2,3,4}

Canopy closure is a likely driver behind seed bank changes in forests; understory components decline as taller plants outcompete them for light. In a review of 108 articles Hopfensperger found that species in forest soil seed banks tend to be dissimilar from the established aboveground species while dissimilarity increases with time since disturbance (based on Sørensen's index of similarity).⁵ Hopfensperger's findings imply that in older forests, the seeds residing

belowground originate from a different place or time and that seed bank contributions from local aboveground vegetation are negligible.

Revegetation of a disturbed site is contingent upon the regrowth of residuals: organisms or propagules that survive a disturbance event.⁶ Soil seed banks are an important source of propagules in the post-disturbance environment. First colonizers can have priority effects, thus subsequently influencing community structure and composition. In light of the aforementioned temporal variability in forest soil seed banks, it is important to consider the manner in which soil seed banks change through time. This issue is especially pertinent for fire-adapted communities in which regular disturbance is an inherent, formative process.

Rocky Mountain lodgepole pine (*Pinus contorta* var. *latifolia*) is a fast-growing, shade-intolerant conifer common in sub-alpine forests throughout the U.S. and Canadian Rocky Mountains. Lodgepole pine forest is a classic example of a fire-adapted plant community.^{7,8,9,10} Lodgepole pine dominance is perpetuated through the recurrence of fire: adult trees are readily consumed by stand-replacing crown fires causing seeds to release from serotinous cones. These seeds yield the next generation of trees, often resulting in uniformly-aged stands. As stands age, they become structurally and demographically heterogeneous as they are exposed to secondary disturbance from blowdown, low-severity surface fires, and disease. The severity and extent of secondary disturbances determine post-disturbance regeneration and composition of tree species:

high severity disturbances in young stands favors further lodgepole pine establishment while low severity disturbances in old stands favors other species such as subalpine fir (*Abies lasiocarpa*).¹¹ However, the effect of stand age on the composition of the soil seed bank in lodgepole pine forests is poorly documented despite its potential to influence future successional dynamics. In this study, we sought to determine if there is a relationship between stand age and soil seed bank characteristics in lodgepole pine forests by observing differences in soil seed bank species abundance (the count of individual plants from a site) and richness (the number of species represented for each site) across stands of varying ages.

Methods

Study Area and Design

A chronosequence was constructed of lodgepole pine stands (n=9) ranging in age from 2 to 360 years in Rocky Mountain National Park (RMNP), Colorado, USA (one site, BE, was located outside park boundaries) (Figure 1 & Table 1). Elevations of sampling locations ranged from 2500 to 3000 m (8400 to 9800 ft). The study area straddles the continental divide in the Northern Colorado Front Range. The region has a continental climate, and annual precipitation averages just over 500 mm (20 in).¹¹

Sites were selected to represent a broad spectrum of developmental stages: from post-fire conditions (2 years) to the upper limits of the lodgepole pine lifespan and fire regime (360 years). Determination of stand age (time since fire) was based on historic

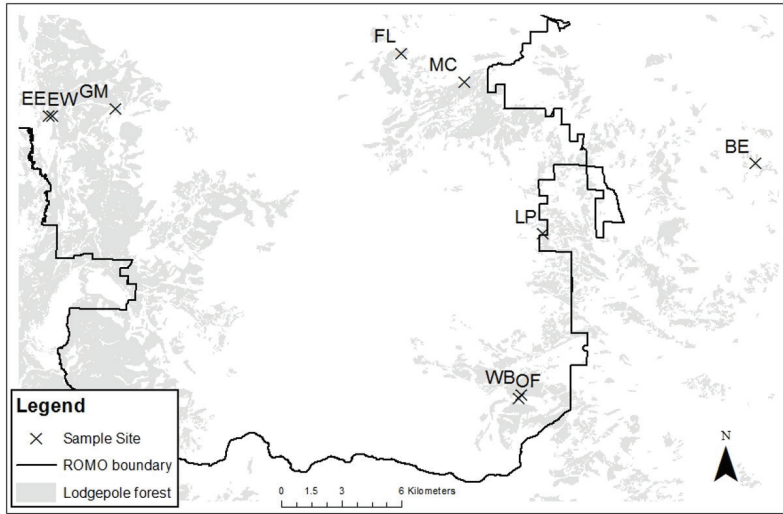


Figure 1: Map depicting the locations of soil seedbank sample sites (marked by "X") within Rocky Mountain National Park (RMNP), Colorado. Gray shading indicates extent of lodgepole pine forests.

Site Name	Age	Elevation (m)	Aspect	Easting	Northing
Fern Lake (FL)	2	2577	349° N	445446.7413	4466790.165
Big Elk (BE)	12	2685	51° NE	452497.2017	4457808.157
Ouzel Fire (OF)	36	2986	302° NW	451271.0952	4449635.541
Longs Peak (LP)	112	2910	75° E	452497.2017	4457808.157
Mill Creek (MC)	114	2566	2° N	448578.5348	4465370.372
Entrance West (EW)	143	2696	189° S	427909.8083	4463659.124
Entrance East (EE)	232	2684	121° SE	428089.8443	4463684.632
Green Mountain (GM)	232	2950	129° SE	431209.1684	4464043.097
Wild Basin (WB)	319	2967	332° NW	451420.8309	4449827.682

Table 1: Summary of sampling sites from lodgepole pine stands of varying ages in the Colorado Northern Front Range. Coordinates are Standard UTM, Zone 13N.

fire occurrences documented by RMNP management and stand reconstructions from Sibold et al.¹² Sibold et al. identified fire rotations (the length of time necessary for an area to burn) ranging from 162 to 216 years in lodgepole pine forests in Rocky Mountain National Park.¹³ Other studies have described similar fire regimes throughout the southern Rocky Mountains.^{14,15,16,17} In recent years, lodgepole forests throughout the region experienced significant die-off from disease spread by the mountain pine beetle (*Dendroctonus ponderosae*). Old lodgepole pine stands (> 80 yr.) were most severely impacted.

Field Sampling

Field sampling took place in June 2014. Each sample site consisted of a 60- x 60-m area containing 16 gridded, uniformly spaced points. At each point, soil samples were extracted to a depth of 5 cm (from the surface of the mineral soil) with a bulb-planter. The point-samples from each stand

were then pooled. If surface litter was present above the mineral soil, it was collected and stored separately. Soil and litter samples were placed on ice throughout transit and were then cold stratified in a refrigerator for approximately three months at 1° C prior to the germination phase.

Germination

Measures of the soil and litter seed banks were based on an emergence method. Following cold stratification, soil and litter samples were introduced to suitable growing conditions in a greenhouse at Colorado State University’s Plant Growth Facility. Soil samples from each site were mixed and divided into two 400 mL portions. Each portion of soil was spread evenly over a sterile plant growth medium in well-drained flats (dimensions: 27.94- x 54.28- x 6.20-cm).

Different types of disturbances produce different post-disturbance conditions.¹⁸ To account for alternative post-disturbance germination conditions and encourage more

complete species representation, subsets of soil from each sample site were subjected to one of two treatments: “heat” and “litter”. To simulate heat from a fire, near-boiling (94° C) water was poured over the heat-treated soil. Heat-treated soil was not covered with litter. The litter-treated soil was covered with 400 mL of litter (collected at sampling sites) and was not heat-treated to represent typical regrowth conditions following non-fire disturbance.

Throughout the 150-day growth phase from October 2014 to February 2015, the flats were maintained at 30.6° C on warming pads to stimulate germination. Flats were watered regularly (3-4 times weekly) and subjected to a 16-hour day/8-hour night photoperiod. Germinants were differentiated and identified with unique codes per species. Germinants were removed and counted after the growth phase. Germinant counts from “heat” and “litter” samples were pooled by site for analysis.

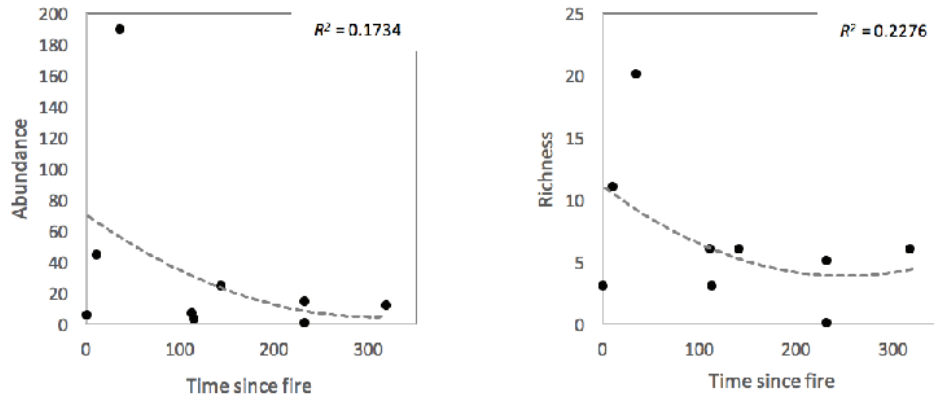


Figure 2: Scatterplots of time since fire versus species abundance and richness of lodgepole pine soil seed banks. Dotted lines are polynomial regressions fitted to the data.

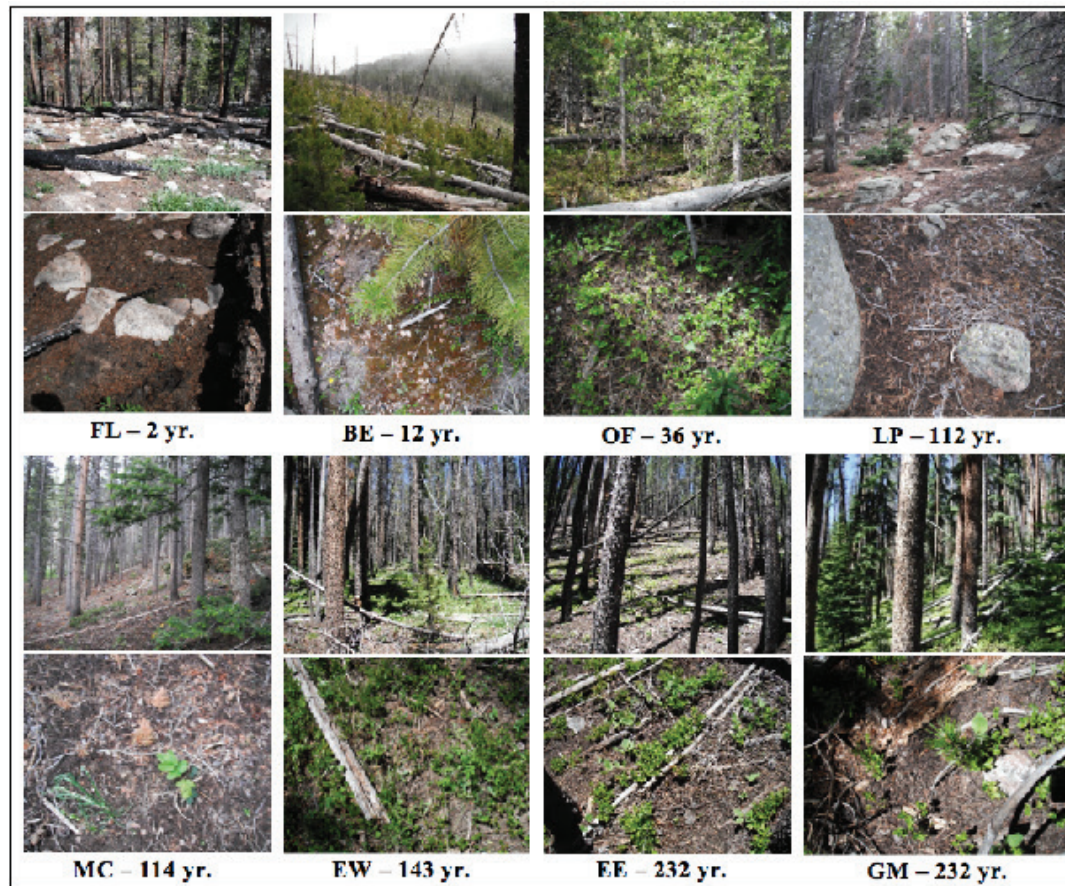


Figure 3: Photos of the understory (top) and forest floor (bottom) of eight lodgepole pine stands varying in age (2-232 yrs) in the Northern Colorado Front Range. Evidence of mortality from mountain pine beetle was observed in all old stands (> 80 yrs).

Statistical Analyses

Seedling emergence data were used to characterize each site's soil seed bank in terms of abundance and richness. Abundance is the count of individual plants from a site and richness is the number of species represented for each site. All statistical tests were conducted with Microsoft Excel (2013). A second order polynomial regression was performed to determine whether time since fire was associated with a curvilinear trend in abundance ($y = 0.0007x^2 - 0.4303x + 70.357$) or richness ($y = 0.0001x^2 - 0.0578x + 11.081$).

Results

Time since fire (age) did not significantly predict abundance ($R^2 = 0.1734$, $F(1,7) = 0.6235$) or richness ($R^2 = 0.2276$, $F(1,7) = 0.8348$) of germinants. Richness and abundance of seedbanks were both low in the youngest stands, highest in the 36-year-old stand, and remained at low levels throughout all older age classes (Figure 2). The polynomial regressions of abundance and richness begin high and gradually decline as time since fire increases. Evidence of recent disturbance was apparent at all sites. Young stands (< 80 yr.) were the products of stand-replacing fires.

Older stands (> 80 yr.), where the legacy of fire was less obvious, experienced varying degrees of mortality due to beetle-kill. No lodgepole pine seedlings were observed.

Discussion

Although a small sample size limited statistical inference, the data portrays a pattern of changing soil seedbanks over time. Species abundance and richness in the soil seed bank of lodgepole pine forests appear to be influenced by at least three ecological processes: fire, canopy closure, and dispersal.

The rapid abundance and richness gains

in the four decades following fire is likely a consequence of the accumulation of seeds from a burgeoning understory. As canopies in aging stands close over time, species richness and abundance in the soil seed bank appear to decline and then stabilize. These results concur with previous studies. Vose and White found that seed rain from grasses and forbs in ponderosa pine forests was 10-times greater beneath canopy gaps than below dense forest canopies.¹⁹ Additionally, Abella and Springer observed larger soil seed banks associated with species-rich understories, sparse litter, and tree canopy openings.²⁰

Following canopy closure, localized, secondary disturbances may contribute to the soil seed bank by freeing light resources to favor understory development. High seed abundance in the soil seed bank does not appear to be maintained throughout stand development, suggesting that seed longevity is generally short. Although the aboveground plant community was not quantitatively sampled, photographs of the sites suggest an association between understory development and the abundance and richness of the soil seed bank (Figure 3), with very little understory present in older closed-canopy stands.

Despite a century of fire suppression policy during the twentieth century, lodgepole pine forests in RMNP have not been excluded from the historic range of variability by altered fire regimes.¹³ The oldest stand in this study (WB: 319 yr.) yielded abundance and richness values comparable to those of a stand over two centuries younger (LP: 112 yr.). Given the lack of complete soil seed bank demise with age it is reasonable to assume that substantial seed bank expiration occurs within the first hundred years of stand development for lodgepole pine forests. Thus, in the event of further stand-replacing disturbance, sites occupied by young stands may experience less understory seed limitation than sites occupied by older stands.

Conclusion

This study suggests that soil seed bank composition varies over time and is linked to stand development processes including disturbance, canopy closure, and seed rain from surrounding plant communities. The soil seed bank appears to increase initially after a disturbance and then to decline but not expire as stands age. Low-severity secondary disturbance may indirectly contribute to soil seed bank renewal by permitting light and encouraging understory development. Understanding the apparent linkages between the soil seed bank and aboveground conditions can help restoration practitioners and resource managers anticipate post-disturbance dynamics. Perhaps restoration treatment efficiency could be improved by

targeted re-seeding of areas that are known to have fewer propagules residing in the soil seed bank. Future research should seek to identify and quantify the specific biotic and abiotic processes driving changes in soil seed bank composition and investigate the soil seed bank's role in shaping future communities.

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