

Regeneration and Survival of Whitebark Pine After the 1988 Yellowstone Fires

Diana F. Tomback, Department of Integrative Biology, University of Colorado Denver, Denver, CO;

Anna W. Schoettle, USDA Forest Service, Rocky Mountain Research Station, Ft. Collins, CO;

Mario J. Perez and **Kristen M. Grompone**, Department of Integrative Biology, University of Colorado Denver,

Denver, CO; **Sabine Mellmann-Brown**, Institute of Landscape Ecology, University of Münster, Münster, Germany

Introduction

Successional whitebark pine (*Pinus albicaulis*) communities are dependent on fire and other disturbances for renewal (Arno 2001). Where whitebark pine regenerates results from cache site selection by Clark's nutcrackers (*Nucifraga columbiana*) in relation to the environmental tolerances of seeds and seedlings (Tomback 2001). After the 1988 Yellowstone fires, we studied the development of upper subalpine forest communities with particular focus on the regeneration of whitebark pine in two study areas—Mt. Washburn in Yellowstone National Park, and Henderson Mtn. in Gallatin National Forest. Fire history and patterns of community regeneration of the predominantly seral lodgepole pine forests in the southcentral and southwestern regions of Yellowstone National Park have been well studied (e.g., Romme 1982; Turner and others 1997), whereas whitebark pine communities have been less studied.

We examined the following hypotheses: (1) the density of whitebark pine regeneration surpasses the density of the late successional pre-fire canopy forest by 13 years post-fire; (2) growth rates for whitebark pine regeneration are reduced under closed canopies in mid to late-seral forests; and, (3) seedling survival is better correlated with some micro-site attributes than others.

Study Areas and Methods

Both study areas included xeric and mesic study sites with stand-replacing burns, and ranged in elevation from 2560 to 2745 m (for details, see Tomback and others 2001). On Henderson Mtn., we also included unburned study sites and, on Mt. Washburn, a mesic site with mixed severity burn (Table 1). Data were collected at both sites from 1990 to 1995, in every year but 1993, and in 2001 (i.e., up to 13 years post-fire), and also on Henderson Mtn. in 2004 and 2005. A whitebark pine regeneration micro-site was defined as either supporting a solitary seedling or a seedling cluster.

To evaluate study hypotheses, we reconstructed the pre-fire forest from intact tree skeletons on 30 x 30 m quadrats, tracked individual post-fire whitebark pine seedlings on a total of 275 permanent plots, each 20 m² in area, and gathered data on seedling micro-sites throughout the study. Data comparing seedling growth rates under open vs. closed canopy conditions were based on comparisons of seedling

height growth from regeneration on the Henderson Mtn. burned and unburned study sites. Information on whitebark pine regeneration micro-sites came from a combination of description at the initial time seedlings were surveyed and also from information in subsequent years. The position of seedlings in relation to objects, such as rocks and standing trees, and plot aspect, were used to estimate whether shade was present in the morning or afternoon.

Stepwise Poisson Log-linear Regression Analyses were performed to determine the best models predicting whitebark pine occurrence among the study sites, with the response variable comprising the number of whitebark pine regeneration sites per plot. Altogether, 25 different models were examined. Multivariate Logistic Regression and Proportional Hazards Models were used to identify micro-site variables facilitating seedling survival. All statistical analyses were performed using SAS (SAS Institute Inc., 2004). For the Proportional Hazards Model, the known or estimated year of death for each seedling regeneration site was related to the micro-site variables retained in the Multivariate Logistic Regression Model.

Results

The pre-fire forest on Mt. Washburn was dominated by Engelmann spruce (*Picea engelmannii*) and lodgepole pine (*Pinus contorta*), and the pre-fire forest on Henderson Mtn. by subalpine fir (*Abies lasiocarpa*), with whitebark pine a minor pre-fire overstory component in both areas. The density of whitebark pine in the pre-fire forest ranged from 0 stems/m² on the Henderson Mtn. mesic, burned study site to

Table 1. Study sites, ecological conditions, and numbers of plots. Each plot is circular and 20 m² in area.

Study site conditions	Number of plots
Henderson Mountain, Gallatin National Forest: 2680-2745 m elevation	
Xeric burned	50
Mesic burned	50
Xeric unburned	25
Mesic unburned	25
Mt. Washburn, Yellowstone National Park: 2560-2745 m elevation	
Xeric burned	50
Mesic burned	50
Mesic mixed severity burn	25

Table 2. Density (stems/m²) of whitebark pine in the pre-fire forest and density (regeneration sites/m²) of post-fire regeneration as of 2001, 13 years after the 1988 Yellowstone fires.

Study area	Pre-fire density	Post-fire density
Henderson Mountain		
		Mean (S.D.)
Xeric burned	0.002	0.039 (0.150)
Mesic burned	0	0.020 (0.038)
Xeric unburned	0.009	0.038 (0.044)
Mesic unburned	0.002	0.022 (0.043)
Mt. Washburn		
Xeric burned	0.016	0.026 (0.049)
Mesic burned	0.0005	0.092 (0.110)
Mesic mixed severity burn	0.0055	0.044 (0.055)

0.016 stems/m² on the Mt. Washburn xeric, burned study site (Table 2). Whitebark pine cotyledon seedlings first appeared in all burned study sites in 1991, three years after fire. Combining all seedlings across study sites to generate cumulative numbers over time, there was an exponential increase in seedlings from 1989 to 10 years post-fire, followed by some fluctuation in numbers, possibly drought-related. By 1995, the highest whitebark pine regeneration density was on the Mt. Washburn mesic, burned study site that had experienced stand-replacing fire. By 2001, whitebark pine regeneration density was the lowest on the Henderson Mtn. mesic, burned study site (0.020 regeneration sites/m²) and the highest on the Mt. Washburn mesic, burned study site (0.092 sites/m²). This latter result sharply contrasts with the very low density of whitebark pine in the pre-fire overstory in the mesic, burned study site. The best Stepwise Poisson Regression model predicting whitebark pine distribution was the additive combination of variables: Study area, Burn (unburned, burned, mixed severity burn), and Moisture level (xeric, mesic). Whitebark pine seedling growth rates in the Henderson Mtn. study sites ranged from 0.62 to 2.19 cm/year. The highest whitebark pine seedling growth rates occurred on the two burned Henderson Mtn. study sites.

From the Logistic Regression Model and Proportional Hazards Model, statistically significant positive predictors of seedling survival on Henderson Mtn. included presence of undergrowth vegetation, wood debris, and standing dead trees, whereas survival was reduced by grazing on seedlings. Using these variables to test the performance of the model, 67% of the seedlings were correctly classified as alive or dead. For Mt. Washburn, significant predictors of seedling survival included presence of wood debris, standing dead trees, gopher soil disturbance, and shade; and, survival was reduced by deeper char depth and the presence of duff. In this analysis, 83% of the seedlings were correctly classified as alive or dead. Differences in predictors between the two study areas probably related to different environmental characteristics. For example, Henderson Mtn. is south-facing, and undergrowth vegetation may provide consistent shade and retain moisture. Char depth was much lower on Henderson Mtn., which may explain its lack of significance for that study area.

Discussion

We address each hypothesis, with the following results:

- (1) Whitebark pine regeneration density increased throughout the study, without indication of plateau; by 2001, whitebark pine regeneration densities greatly exceeded those of the pre-fire canopy. These results are in sharp contrast with the pattern of lodgepole pine regeneration after the Yellowstone fires (Turner and others 1997). The numbers of new lodgepole pine seedlings declined from 1990 to 1993, and lodgepole pine regeneration density (seedlings/m²) declined after it peaked in 1992. The seedling recruitment primarily came from 1989 and 1990 cohorts.
- (2) Thirteen years after fire, whitebark pine regeneration densities were similar between the burned and unburned study sites on Henderson Mountain, but seedling growth increments as of 2005 were 2.6 times greater in the burned treatments, indicating seedling suppression in the unburned closed canopy study sites. Thus, fire or other disturbances, which provide canopy openings, appear required for healthy whitebark pine growth in mid to late successional communities.
- (3) The presence of wood debris and standing dead trees predicted seedling survival for both study areas. For Henderson Mtn. other predictors of survival included presence of undergrowth vegetation. For Mt. Washburn, seedling survival was also favored by shade and gopher soil disturbance.

This unique 15 year dataset of repeat observations on post-fire regeneration of whitebark pine provides information on the timeframe and dynamics of seedling establishment and on micro-site correlates of seedling survival, which may be used for restoration planning and the refinement of planting protocols.

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