CAUSES AND CONSEQUENCES OF ALTERNATIVE SUCCESSIONAL TRAJECTORIES FOLLOWING THE 1988 YELLOWSTONE FIRES

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✦ INTRODUCTION

The 1988 Yellowstone fires created a strikingly heterogeneous pattern of severely burned, lightly burned, and unburned forests across a large portion of Yellowstone's subalpine plateau (Turner et al. 1994). Equally striking has been the variation in post-fire tree seedling density throughout the burned forests (Table 1). In 1999 we initiated a 3-year study of post-fire succession, with three principal objectives:

(1) to document the variation in post-fire tree sapling density and to map the spatial patterns of sapling density
(2) to explain the causes of the variation in post-fire sapling density
(3) to explore the consequences of variable post-fire sapling density for ecosystem processes, specifically aboveground net primary productivity (ANPP) and leaf area index (LAI).

We addressed the first objective by obtaining new, high-resolution aerial photographs of the entire park, sampling a number ground-truth points, and generating a map of sapling density within all of the areas that burned in 1988. For the second objective, we will test three hypotheses about causes of pattern by generating a predicted map of sapling density in a GIS environment (based on the hypotheses) and comparing the patterns generated by the predicted map with actual patterns documented in our empirical map produced from the aerial photos. The three hypotheses about causes of pattern were derived from our previous work (Turner et al. 1997) which showed that residual vegetation that survived the fire was the principal source of biotic cover in the first decade after fire. The most important biotic residual for tree establishment was lodgepole pine seeds that survived in the burned canopy, especially within

Table 1. Comparison of three areas (large patches described in Turner et al. 1997) exhibiting different initial successional pathways following the 1988 Yellowstone fires. All three areas were forested at the time of the fires. Data are from 1996 in areas of crown fire. "Nonforest" refers to areas that were forested at the time of the fires.

Geographic location	Initial successional pathway	Pine seedling density (mean stems ha^{-1})	Mean cover of trees + shrubs	Mean cover of forbs + graminoids	Mean # vascular plant species in 10-m^2 plots
Cougar Creek	High-density lodgepole pine	43,000	32%	7%	10
Fern Cascades	Low-density lodgepole pine	4,700	6%	19%	10
Yellowstone Lake	Nonforest	14	2%	40%	16

serotinous cones (Tinker et al. 1994). The three hypotheses that we will test in this second objective are:

(a) Where pre-fire serotiny was high, high-density stands have developed after the fires. Fire size and severity make little difference in this situation.
(b) Where pre-fire serotiny was low, fire severity largely determines post-fire sapling density. Moderate-density stands have developed in areas of severe surface fire, while low-density stands have developed in areas of crown fire (because of greater seed mortality in crown fires).
(c) Where pre-fire serotiny was zero, patch size largely determines post-fire sapling density. Low-density stands have developed in small burn patches (because of seed dispersal from adjacent unburned areas), while "non-forest" stands have developed in large burn patches. By "non-forest," we mean stands that were forested before the fire but that now have < 100 saplings / ha.

For the third objective, we focused on ANPP and LAI, because these are indicators of overall ecosystem function. ANPP is highly correlated with total energy flow in the system, and provides the base of the food web. LAI is strongly correlated with primary productivity and transpiration rate.

In addition to the three main objectives described above, in 2000 we planned to re-sample all of the permanent plots that we established in 1990 throughout the areas burned in 1988. We have sampled these plots in 1990, 1991, 1992, 1993, 1996, and now again in 2000. The objective of this sampling is to document long-term plant recovery in relation to fire size, severity, and geographic location (Turner et al. 1997).

✦ METHODS

For the first objective, we obtained new GPS-controlled aerial photos (1:30,000 color infrared) of the entire Park in August, 1998. During the winter, we processed the photos to create a preliminary map of sapling density. During the 1999 field season we tested the predictions of the preliminary map in 88 stands distributed throughout the areas burned in 1988. In each of the 88 stands (each ca. 1 ha in extent), we measured sapling density in a belt transect, and also collected data for the third objective (below). We were not entirely satisfied with the correspondence between predicted sapling densities based on the map and the actual densities measured in the field. Therefore, we developed a new map of sapling density using an objective supervised classification of the imagery, with the 88 stands described above serving as training sites (described in Results below). This new map was tested by means of 50 independent field samples collected in the 2000 field season.

For the second objective, we plan to predict sapling density in a large number of locations, based on our GIS coverages of % serotiny, elevation, and 1988 burn patterns. We will then compare these predictions with actual sapling density as revealed by our final map derived from the aerial photos.

For the third objective, we harvested lodgepole pine saplings in five stands and determined ANPP and LAI using techniques of dimension analysis (Reed et al. 1999). From these samples we developed regression equations to predict ANPP and LAI from sapling basal diameter and height. We also developed regressions between % cover (based on visual estimates) and ANPP and LAI for herbaceous species. Using these regressions we estimated total ANPP and LAI in all 88 stands sampled for developing the aerial photo interpretation (described above). Finally, we scaled up to the entire landscape by predicting ANPP and LAI in all burned patches on the basis of our measured relationship between sapling density and total stand ANPP and LAI.

We re-sampled the permanent plots using methods described in Turner et al. (1997).

✦ RESULTS

The preliminary map, based on visual interpretation of the aerial photos, was useful in identifying areas for field sampling. However, it failed to capture the degree of complexity that actually existed on the ground. Our field measurements revealed that post-fire sapling density ranged from < 10 to > 500,000 stems/ha – some six orders of magnitude! Sapling density may vary 10 to 100-fold over distances of only hundreds of meters.

We have just completed the development of a new sapling density map using supervised classification of the imagery. A test of predicted density against actual density measured in the field in 50 stands resulted in 76% accuracy; which is generally regarded as quite adequate for a remotely sensed map of this kind.

The testing of hypothesized causes of the observed variation in sapling density (objective #2) has not yet been completed, because of delay in completing the final density map (objective #1). Now that we have a satisfactory sapling density map, we will test the hypotheses in objective #2 within the near future.

For the third objective, we found that total ANPP was closely related to sapling density (positive correlation), but that herbaceous productivity declined with sapling density: 78% of the total ANPP was herbaceous in the stands with 1000 stems/ha or less, but only 5-16% was herbaceous in stands with >25,000 stems/ha. The ratio of herbaceous to tree ANPP varied over four orders of magnitude. Additional analyses are in progress.

We re-sampled nearly all of our permanent plots, and analysis of the data is in progress. We were unable to access one of our remote study areas on the Two Ocean Plateau (Lake Large patch) because of logistical difficulties, but we hope to return to this area in 2001 to complete the sampling.

✦ DISCUSSION

The 1988 Yellowstone fires created a remarkably heterogeneous landscape. Post-fire sapling density varies over six orders of magnitude, and exhibits a very fine-grained pattern. Highest density is found in areas where pre-fire serotiny was high, and lowest density is found in large burned patches where none of the trees that burned had serotinous cones. To date, little thinning of the pine saplings that germinated after 1988 has taken place, even in very dense stands.

Parameters of ecosystem function, viz. ANPP and LAI, are strongly correlated with post-fire sapling density. Overall, recovery of ecosystem function (as measured by ANPP and LAI) has been very rapid (Romme and Turner, in review). Indeed, ANPP and LAI in high-density stands are within or nearly within the range reported for mature pine forests Reed et al. (1999).

This research on spatial variation in pine sapling density and resulting variation in ANPP and LAI after the 1988 fires, has laid the groundwork for more general studies of spatial heterogeneity in ecosystem processes. The Yellowstone landscape provides a unique opportunity to combine the perspectives and questions of ecosystem ecology and landscape ecology within a largely untrammeled setting. In December, 2000, we were awarded a 5-year grant from the Mellon Foundation to continue our research on spatial and temporal variation in post-fire succession, primary productivity, nitrogen dynamics, and the role of coarse woody debris in ecosystem processes. We plan to conduct this new round of research through the UW-NPS Research Center, which provides ideal support for long-term studies of this kind.

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