



Research article

Ecotonal changes and altered tree spatial patterns in lower mixed-conifer forests, Grand Canyon National Park, Arizona, U.S.A.

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Received 27 December 2002; accepted in revised form 27 August 2003

Key words: Dendrochronology, Ecotone, Mixed-Conifer, Patch Structure, Ponderosa Pine, Spatial Analysis, White Fir

Abstract

This research analyzes patch development and determines tree spatial patterns along the lower mixed-conifer ecotone on the North Rim of Grand Canyon National Park in Arizona (U.S.A.). Patterns of patch development were interpreted from spatial analyses, based on tree age and size, and past records of disturbance and climate. Five plots in the ecotone between mixed conifer forests and monospecific stands of ponderosa pine (*Pinus ponderosa*) were studied for patterns of patch development. The methods used include: (1) size-structure analyses, to compare species patch development; (2) dendrochronological dating of tree establishment; (3) tree ring master chronology, to determine periods of suppressed growth, compared to a Palmer Drought Severity Index; and (4) spatial analyses by species composition, size and age, with univariate and bivariate analyses of spatial association and spatial autocorrelation. We found an increased density of shade-tolerant and fire-intolerant species namely clusters of pole-sized white fir, and fewer large ponderosa pine.

Introduction

Disturbances are important factors affecting regeneration dynamics and successional processes in forest communities across landscapes, especially at ecotonal limits. Since plants growing near their physiological tolerances can be sensitive to small change, ecotones may provide detection of alterations of disturbance regimes (Hansen et al. 1988; Sirois and Payette 1991; Mast and Veblen 1999). Moreover, in ecotonal areas the extent of climate induced vegetation change is likely to be indirectly affected by varying degrees of disturbance (Overpeck et al. 1990; Peet 1981; Veblen and Lorenz 1991; Noble 1993; Mast et al. 1998). Movements of conifer forest ecotones have been noted in North America, particularly in the Rocky Mountains (Vale 1978; Veblen and Lorenz 1991; Mast et al. 1997), California (Wright 1966; Parker

1986), the American Southwest (Allen and Breshears; 1998) and the Great Basin regions (Foster 1917; Cottam and Stewart 1940; Johnsen 1962; Burkhardt and Tisdale 1976). Other ecosystems worldwide that contain native or introduced conifer species have also been affected by changes in disturbance regimes, particularly by fire suppression (Richardson and Bond 1991). For example, pine invasions in the Southern Hemisphere are well documented in Argentina, Australia, Chile, Madagascar, Malawi, New Zealand, South Africa, and Uruguay (Richardson et al. 1994; Rejmanek and Richardson 1996).

In the present study, patch development and tree spatial patterns are analyzed along the lower mixed-conifer ecotone on the North Rim of Grand Canyon National Park in Arizona (U.S.A.) (Figure 1). Although ponderosa pine forest dynamics have been studied in Grand Canyon National Park, there has

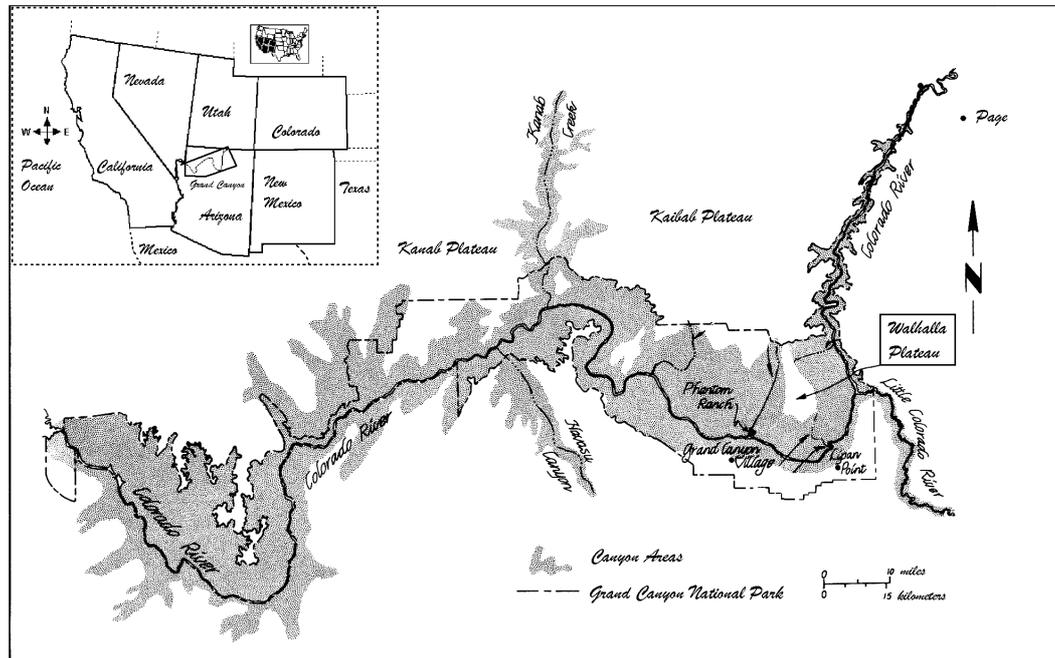


Figure 1. Wahalla Plateau Study Area in the North Rim of Grand Canyon National Park in the southwestern U.S. Map from the School of American Research, used with copyright permission.

been little research on mixed-conifer forests in this area. Situated at higher elevations (c. 2100 m to 2500 m) than ponderosa pine forests, the lower mixed-conifer ecotone consists of ponderosa pine (*Pinus ponderosa*) in the overstory, with white fir (*Abies concolor*) and aspen (*Populus tremuloides*) occurring as subcanopy species. The abundance of aspen is one indication of extensive historical fires on the North Rim (Merkle 1954). A Park policy of fire suppression began in 1919, resulting in lowered fire frequency (Wolf and Mast 1998). Because the National Park Service mandate is to maintain forests in their natural condition, the changes in structure, species composition and spatial patterns at the ponderosa pine/mixed-conifer ecotone should be viewed as “unnatural” if it results from fire suppression management (Bonnicksen and Stone 1985; Parsons et al. 1986; Covington et al. 1994). The objectives of this study are to (1) analyze size structure by tree species to compare species patch development; (2) date tree establishment by species, using dendrochronology; (3) create a tree ring master chronology, to determine periods of suppressed growth and climatic influences on tree establishment; and (4) examine spatial patterns of tree age and size by species at these sites to ascertain if they

are consistent with the expected changes in tree spatial patterns as cohort patches age.

Quantitative analyses of tree age structures and spatial patterns have often been helpful in interpreting patterns of forest development (Veblen et al. 1981; Nakashizuka and Numata 1982; Getis and Franklin 1987; Read and Hill 1988; Mast and Veblen 1999). Although initial spatial patterns may be determined by regeneration mechanisms, subsequent spatial distributions may result from the ability of individual trees to survive competition and dominate the patch (Oliver and Larson 1990; Deutschman et al. 1993). As a forest ages, tree distributions within a patch may shift from a clumped distribution to a random (or regular) distribution due to self thinning and/or succession to shade-tolerant species (Cooper 1961; Laessle 1965; Whipple 1980; Good and Whipple 1982; Peet and Christensen 1987). When age *versus* size class is analyzed, some variance may occur due to the development of a size hierarchy in aging even-aged cohorts (Mast and Veblen 1999). In other words, from a patch of small even-aged trees, only a smaller number of trees can attain dominance and large size within the patch. In a classic study in the White Mountains of Arizona, Cooper (1960, 1961) described a mosaic of even-aged ponderosa

pine groups. He believed that these even-aged patches resulted from simultaneous mortality of nearly all trees in the patch and subsequent higher fire intensities that created favorable seedbed conditions. In a study of regeneration patterns near Flagstaff, Arizona, White (1985) found patches of mixed-sized groups of ponderosa pine, possibly resulting from one or two individual trees in the patch dying and thus creating small areas of seedbed.

In the semi-arid American Southwest, we hypothesize that altered disturbance regimes may decrease ponderosa pine regeneration at the mixed-conifer forest ecotone due to increased competition with other conifer species. Ponderosa pine regeneration requires a combination of several factors, such as sunlight (seedlings are shade-intolerant), a good seed year, adequate seedbed conditions, and absence of drought or fire. Historically, frequent surface fires maintained open conditions, favoring shade-intolerant ponderosa pine while reducing invasion from shade-tolerant conifer species (Dieterich 1983; Veblen et al. 1991; Harrington and Sackett 1992; Wolf and Mast 1998). Subsequent cessation of periodic surface fires resulted in increased density and distribution of shade-tolerant conifer species, and the subsequent fuel accumulation could lead to stand-replacing fires (Kilgore and Sando 1975; Burkhardt and Tisdale 1976; Parsons and DeBenedetti 1979; Vale 1982; Savage 1989). In addition, overgrazing by domestic livestock can decrease fire frequency and fire spread, altering the natural evolution of a forest (Leopold 1943; Covington and Moore 1992; Covington et al. 1994).

Our research hypotheses are twofold. First, from the size analyses, tree aging, and chronology development, we hypothesize that ponderosa pine establishment in this lower ecotonal habitat is episodic at stand-scales of c. 0.1 ha, while shade-tolerant white fir establishment has occurred continuously since fire suppression and cessation of livestock grazing. In addition, we hypothesize that these current mixed-conifer lower ecotone forests were actually ponderosa pine forests (white fir absent or uncommon) prior to the 1870s. Second, from the spatial pattern analyses and following the cohort aging theory (Kenkel 1988; Szwagrzyk 1992), we hypothesize that internal patch structure should become less clumped as single cohort patches age due to self-thinning with only a few trees attaining size dominance in a small patch. Specifically, within the altered species composition, internal patch structure should be comprised of white fir poles and small trees with a scattered remnant

large ponderosa pine in the overstory. Based on this hypothesis, the spatial analysis questions addressed are: Are there differences between and within conifer species in the spatial patterns of tree ages and tree sizes that imply development of a size hierarchy in an aging patch? In addition, what are the human impacts on the spatial patterns of species composition and densities at the lower ecotone of the mixed-conifer forest? Specifically, how does the hypothesized shift in species composition from ponderosa pine overstory to white fir understory affect within-patch spatial patterns?

Study area

General study area

The areas sampled are in the lower mixed-conifer ecotone of the North Rim of Grand Canyon National Park, part of the Kaibab Plateau located at 36° 00' to 36° 21' N and 111°46' to 112°30' W in north-central Arizona (Figure 1). The Kaibab Plateau is the highest plateau on the North Rim of the Grand Canyon, rising to 1300 m above the plateaus bordering it on the east and west (Maurer 1990). The study sites are on the lower elevations of the Walhalla Plateau, a sub-unit of the larger Kaibab Plateau, which gradually slopes from 2200 m in the most southern points to 2500 m in the northern region. The uppermost layer of rock is Kaibab limestone (100 m thick), which explains the lack of surface water due to the highly porous and soluble nature of this rock (Maurer 1990). Soldier Series soil, underling the conifer forests in the North Rim, is well drained with high percolation (Bennett 1973). Mean annual precipitation in the study area is 642 mm (White and Vankat 1992). May and June are drought months, while July and August have monsoon precipitation. Temperature averages -6.05°C in January and 16.5°C in July, with substantial winter snowfall (Bennett 1973, White and Vankat 1992).

Although lightning provides ignition sources for July and August fires, fires historically were also started by Native American Indians. For thousands of years prior to European settlement, Paiute and Navajo Indians lived on the North Rim in the summers and contributed to frequent fire occurrence (Hughes 1978, White and Vankat 1992). Some researchers hypothesize that Native American Indians created fires to keep forests open for hunting and agriculture (Stew-

Table 1. Plot Information for five 20×50 m plots on the Walhalla Plateau, Grand Canyon National Park.

Site	Elevation (m)	Slope (%)	Aspect	Ground Cover % Litter	Ground Cover % Wood	Dominant Understory Species
WL-1	1568	13	SW	72	1	<i>Achillea millefolium</i> , <i>Verbena ciliata</i>
WL-2	1576	2	NW	34	11	<i>Amelanchier utahensis</i> , <i>Lupinus argenteus</i>
WL-3	1583	8	SW	70	6	<i>Berberis repens</i> , <i>Fragaria ovalis</i>
WL-4	1570	0	SW	44	33	<i>Eriogonum</i> spp., <i>Bromus ciliatus</i>
WL-5	1578	4	SE	75	3	<i>Achillea millefolium</i> , <i>Geranium richardsonii</i> , <i>Robinia neomexicana</i>

art 1956; Laven et al. 1992; Covington et al. 1994; Parsons and van Wagtenonk 1996; for a review of the debate, see Allen, C. D. 2002). Spanish explorers generally did not establish settlements in the North Rim, and Euro-Americans did not settle in northern Arizona until the late 1800s (Altschul and Fairley 1989; Moore et al. 1999). Between 1870 and 1880, the Euro-American population grew to 40,000 on the Kaibab Plateau and the surrounding region (Hughes 1978). These homesteaders, primarily Mormon settlers and ranchers, impacted the North Rim forests through logging and livestock grazing. In addition to removing harvested wood, loggers also burned the resulting debris during timber removal, and this activity may have increased fire frequency (Cooper 1961; Swetnam and Baisan 1994).

The North Rim became part of Kaibab National Forest in 1883, and then was included in Grand Canyon National Preserve in 1906. As early as 1890, the estimated head of cattle on the North Rim was > 100,000 with an additional 250,000+ head of sheep grazing the land (Hughes 1978). When the North Rim became part of Grand Canyon National Monument in 1908, sheep and cattle grazing were still permitted. Cessation of livestock grazing began in 1919 when the North Rim became part of Grand Canyon National Park, established to preserve the scenery and natural or historic landscapes (Hughes 1978). In addition, heavy grazing at the turn of the century had decreased the capacity of the grasslands to support cattle and sheep. The formal policy of fire suppression also began in 1919 when the North Rim became part of Grand Canyon National Park (Hughes 1978), although de facto fire exclusion began with the introduction of livestock decades earlier. Silvicultural activities also stopped in 1919 because it was seen as destructive and contrary to the image of pristine wilderness (Parsons and van Wagtenonk 1996).

Study sites

Five plots were randomly located in the lower mixed-conifer forest ecotone in the North Rim (Table 1). Overstory species present were ponderosa pine, white fir and aspen. Understory species included Sweet William (*Verbena ciliata*), yarrow (*Achillea millefolium*), lupine (*Lupinus argenteus*), serviceberry (*Amelanchier utahensis*), strawberry (*Fragaria ovalis*), locust (*Robinia neomexicana*), geranium (*Geranium richardsonii*), creeping barberry (*Berberis repens*), buckwheat (*Eriogonum* spp.) and brome grass (*Bromus ciliatus*). All of the stands contained ponderosa pine established prior to 1860 (i.e., the stands are > 140 years old).

Fire histories, determined from crossdated fire-scars (Wolf and Mast 1998), show these five plots experienced fires in the period 1732-1938. Based on a total of 30 fire-scar trees sampled within a 300 m search radius of each plot, our study areas show pre Euro-American settlement (prior to 1870) fire intervals were less frequent (mean 8.5 years, standard deviation 9.38 years) than the Euro-American settlement era (1870-1919) (mean 4.88 years, standard deviation 3.87 years), but more frequent than the suppression era (1920-1995) (mean 18.75 years, standard deviation 8.08 years). Subsequent increases in white fir densities and distributions are hypothesized to be a direct result of the dramatic decline in fire frequencies on the North Rim.

Methods

Field methods

Plot size (0.1 ha plots, 20 m×50 m) and sampling design followed the U.S. National Park Service criteria for fire-monitoring permanent plots (Western Re-

gion Fire Monitoring Handbook 1992), to serve as assessment on pre-prescribed fire conditions, and later to monitor both immediate postfire effects and long-term change. The plots were located randomly on the lower elevations of the Walhalla Plateau by using an overlay grid system of topographic maps. Plots were rejected if they were located within 0.5 km of a road or did not fit the criteria of the dominant vegetation characteristics (ponderosa pine and at least one other conifer tree species present in the overstory). Understory species were also surveyed along two 50 m line transects in each plot using the point-line-intercept method (Veirs and Goforth 1988) to measure the frequency of species occurrence, relative cover and density by species. Size data for all trees and poles was determined from diameter measurements taken at breast height (dbh) for trees (defined as > 15 cm dbh) and poles (defined at > 2.5 cm but < 15 cm dbh). Tree cores were taken near the base (c. 10 cm) of every live and dead tree and pole in each plot for age analyses and master chronology development. For the spatial analysis, locations of trees and poles were measured and mapped to the nearest 0.5 m using 50 m tapes in order to record X and Y coordinates in a grid system.

Lab analyses

Size structure was analyzed in 5-cm size classes by species and status (live *versus* dead). Tree age data consisted of ring counts from increment cores that were mounted and fine-sanded with successively finer grades of sand paper to reveal annual rings (following technique in Stokes and Smiley 1968). Rings were counted using a binocular microscope to determine marker years which are annual rings with very narrow ring widths or signatures (Visser 1995). Samples were cored near the ground to reasonably determine establishment period (no estimate of stem age at coring height was added). Given the establishment dates could be 1 to 3 years earlier than the tree ring record, age structure was then analyzed in 10-year age classes. Ring counts were corrected for false and missing rings by use of marker years. Although there are shortcomings of using static age distributions to interpret population dynamics (which include both recruitment and mortality), given the dry climate, longevity of the three tree species, and lack of local disturbance by fire, logging, or firewood collection within our sampled stands, we believe that the

record of tree mortality during the last century is adequately preserved in dead snags and logs.

In addition to visually cross-dating the cores for the age structure analysis, the tree-ring program MEASURE (Krusic 1992) was used to determine ring widths to the nearest 0.01 mm for a subset of ponderosa pine to create a master chronology using a binocular microscope with an incremental measuring machine. The tree-ring program COFECHA (Holmes 1983; Grissino-Mayer and Holmes 1993) helped to detect dating problems, such as false or missing rings, by shifting series in time (Dieterich and Swetnam 1984; Fritts and Swetnam 1989). Once dating problems were eliminated, a master chronology was created using the tree-ring computer program ARSTAN (Cook and Holmes 1984) and skeleton plot strips. ARSTAN creates master chronologies by standardizing and reducing variances by assigning a dimensionless index to each ring width. To better detect disturbances, a horizontal line detrending option was chosen to avoid masking the growth trend of each tree, i.e., the narrowing of rings due to the tree's geometry (Fritts and Swetnam 1989; Visser 1995). In order to obtain the longest possible record, seventy-six percent of the samples for the ponderosa pine master chronology came from dead trees, with the ages of trees sampled ranging from 126 years to 340 years (1757-1995). In addition, we obtained Palmer Drought Severity Index (PDSI) data to determine any relationships between climate and our master chronology. PDSI data was obtained from the Paleoclimatology Program of the NOAA Climate and Global Change Program (<http://www.drought.noaa.gov/index.html>).

Spatial statistics

Tree and pole spatial patterns from mapped locations by size and age classes were analyzed by computing Ripley's $K(t)$, Ripley's $K_{12}(t)$ and Moran's I (Moran 1950; Ripley 1977; Legendre 1993; Haase 1995). Duncan's (1990) spatial statistics program was used for these computations. All analyses were based on a distance step size of 0.5 m and calculated up to 10 m (one half the distance of the shortest plot) since edge effects become a concern at greater distances. The edge effects were accounted for by using Ripley's (1977) toroidal correction. Statistical significance was determined by computing 95% confidence intervals using 99 simulations (Besag and Diggle 1977; Marriott 1979). After testing the sites for directional ori-

entation of trees (anisotropy), all were found to meet the assumption of isotropy (no directional orientation in the point pattern) necessary for K-analysis.

Ripley's $K(t)$ is a univariate analysis of single-species (or single group) spatial distributions based on point locations in a rectangular plot:

$$K(t) = \lambda^{-1} E[\text{number of events within distance } (t) \text{ of an arbitrary event}] \quad (1)$$

where (t) is the distance, λ is the mean number of events per unit area, and E is the expectation (Ripley 1977; Ripley 1981; Diggle 1983). The observed $K(t)$ value is compared with that expected from a randomly distributed set of point locations and confidence intervals are derived from Monte Carlo simulations. Regular (or uniform) distributions are indicated by low values and clumped distributions by high values of $K(t)$ for the various distances (t) . For the $K(t)$ analyses, spatial analyses were performed for two size classes, trees and poles. Classes were then further divided into species groups (ponderosa pine and white fir).

Spatial associations of ponderosa pine *versus* white fir were determined using Ripley's $K_{12}(t)$ (Lotwick and Silverman 1982, Diggle 1983, Upton and Fingleton 1985):

$$K_{12}(t) = \lambda_2^{-1} E[\text{number of type 2 events within distance } t \text{ of an arbitrary type 1 event}] \quad (2)$$

where (t) is the distance, λ is the mean number of type 2 events per unit area, and E is the expectation. The null hypothesis is spatial independence. Values of $K_{12}(t)$ that exceed the 95% confidence interval indicate significant positive associations (attraction) while values below the 95% confidence interval indicate significant negative associations (repulsion).

Moran's I , a measure of spatial autocorrelation, was computed for tree ages ($Z = \text{years}$) and tree sizes ($Z = \text{dbh}$) for trees and poles for all trees species combined and also by species. The calculated $Z(d)$ value of Moran's index for each distance class was based on:

$$Z(d) = \{I(d) - E[I(d)]\} / \sqrt{\text{Var}[I(d)]} \quad (3)$$

where (d) is the distance class, $I(d)$ is the value of Moran's coefficient for distance class (d) , E is the expectation, and Var is the variance species (Moran 1950; Cliff and Ord 1973; Cliff and Ord 1981; Upton and Fingleton 1985; Odland 1988; Legendre and Fortin 1989). Trees are spatially defined as neighbors if within stated distance class (then given a weight = 1, *versus* a weight = 0 if not within stated distance class). The null hypothesis is no spatial autocorrelation ($I(d)=0$) for the variable (age or size). Significant positive or negative spatial autocorrelations indicate the values of the variable (age or size) are spatially dependent.

Results

Size analyses

A total of 113 ponderosa pine, 312 white fir and 50 aspen were sampled for size and age analyses in the five plots. With regards to the live trees and poles, ponderosa pine at these lower ecotone sites exhibited a full range of sizes, from the smallest size to 95 cm dbh class, yet few ponderosa pine (average of 16 per ha) occurred in the 0-10 cm size classes (Figure 2). The mean number of ponderosa pine trees and poles for the five plots was 246 per ha, with 190 ponderosa pine trees/ha *versus* 56 ponderosa pine poles per ha. In comparison, there was an average of 968 white fir trees and poles per ha (216 white fir trees/ha *versus* 752 white fir poles per ha). Moreover, 91% of the white fir were in the 0-29 cm dbh size classes, while only 3 white fir trees were > 50 cm dbh. Aspen were similarly sized, with 60% in the < 10 cm dbh category. The mean number of aspen per ha was 104 (36 trees per ha *versus* 68 poles per ha). There were on average 6 dead ponderosa pine trees per ha (ranging up to 50-54 cm size class) but no dead ponderosa pine poles. The mean number of dead white fir per ha was 54 (34 dead trees per ha *versus* 20 dead poles per ha), also ranging up to 50-54 cm size class. On average there were 28 dead aspen per ha, with 12 dead aspen trees per ha (up to 20 cm size class) and 16 dead aspen poles per ha.

Age analyses

Ponderosa pine establishment peak (42%) occurred in 1880 to 1919. The oldest ponderosa pine established in 1721, and almost no ponderosa pine establishment

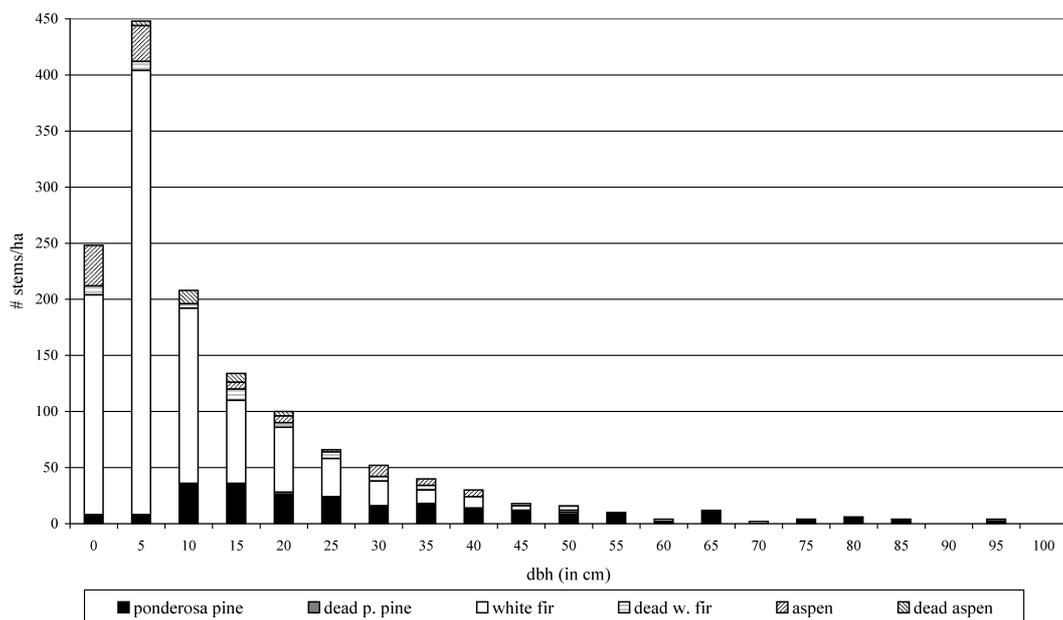


Figure 2. Size structure by species and condition (live vs. dead), by 5 cm dbh classes, in mean number of stems per hectare.

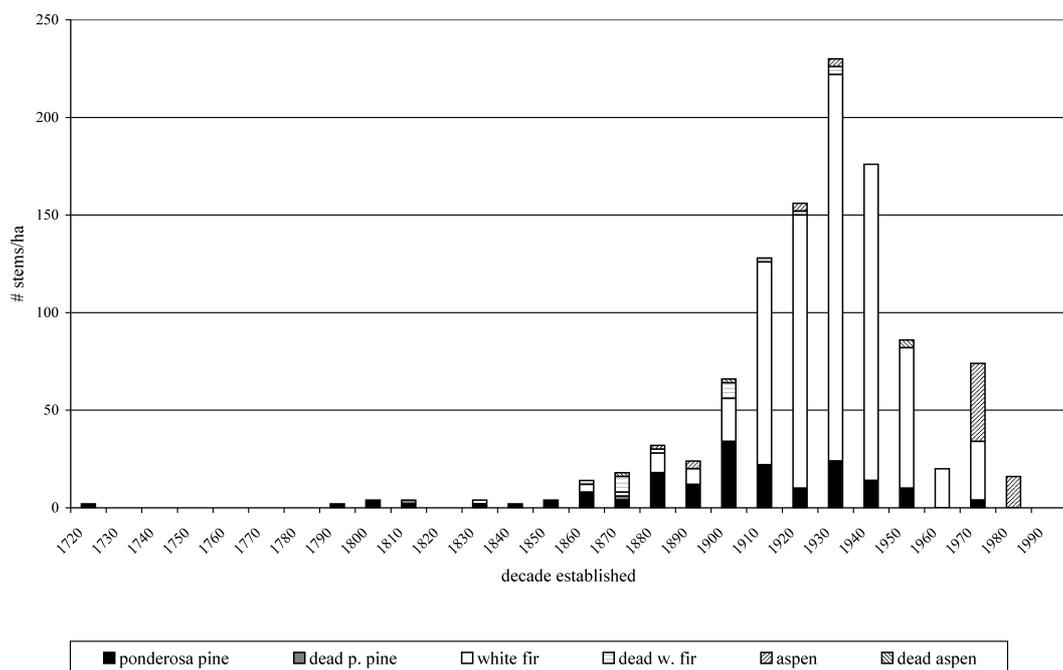


Figure 3. Age structure by species and condition (live vs. dead), by 10 year establishment classes, in mean number of stems per hectare.

has occurred since the 1930s (Figure 3). Aspen trees that established in 1880s-1890s coincide with highest frequency of fire during the Euro-American settlement period, although most aspen trees in the plots date from 1970s and 1980s (oldest dated to 1828). In

contrast, white fir establishment peak (65%) occurred from 1920-1949. Overall, there has been a compositional shift to higher amounts of white fir establishment, with 81% of white fir establishing since the 1920s.

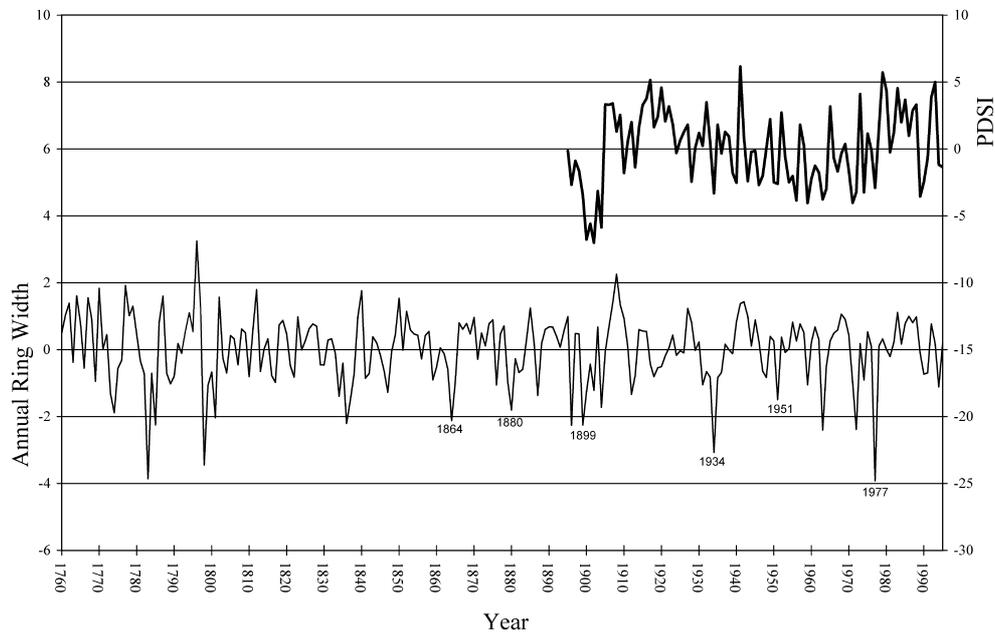


Figure 4. Combined graph of master chronology with Palmer Drought Severity Index.

Master chronology and Palmer Drought Severity Index results

The lower ecotone chronology had a high average mean sensitivity (or variation in annual ring index marker years). Over 78% of the variance (from the mean of annual ring width index values) was due to autoregression, meaning that a high level of confidence may be assumed from the standardized values. The signal-to-noise ratio (effect of large-scale exogenous disturbances in ring series) was 16.833, indicating a high enough ratio value for cross-dating. Variance in the first eigenvector (which represents the first expected coordinates) was 61.98, due to sensitive annual ring widths. In analyzing the standardized annual ring index, ponderosa pine ring widths were more compact for the most recent 70 years, beginning 11 years after the start of active fire suppression in 1919 (Figure 4). In regards to specific marker years during the key time period of interest (mid-1800s to mid-1900s), narrow rings occurred in 1864, 1879-1882, 1896, 1899, 1904, 1934, and 1951. Marker years (narrow rings) in the chronology also corresponded with a low PDSI for 1899 to 1904 and 1934.

Univariate spatial patterns

Overall spatial pattern by species was analyzed using the univariate spatial statistic Ripley's $K(t)$ for both the "tree" and the "pole" size classes (Table 2). Ponderosa pine trees displayed a random distribution from 0.5 to 3.5 m patch radius and a clumped distribution from 4.0 to 10.0 m patch radius. Similarly, tree-sized white fir showed random spatial distribution from 0.5 to 7.0 m and a clumped pattern from 7.5 to 10.0 m patch radius. In contrast, pole-sized white fir displayed clumped distributions at most distances from 0.5 to 10.0 m patch radius. There were too few pole sized ponderosa pine (< 30 poles per plot) to run the $K(t)$ test.

Bivariate spatial associations

Bivariate spatial association tested with Ripley's $K_{12}(t)$ compared: (1) ponderosa pine trees *versus* white fir trees; and (2) ponderosa pine trees *versus* white fir poles (Table 2). In the first analysis, a pattern of positive spatial association (i.e., attraction) between tree-sized ponderosa pine and tree-sized white fir occurred at 1.5 to 3.0 m and at 6.5 to 7.5 m. For the second analysis, no spatial association (i.e., independence) existed between ponderosa pine trees and white fir poles for all distances analyzed.

Spatial autocorrelation for age

When analyzed by species, significant positive spatial autocorrelation occurred for older ponderosa pine at smaller distances (2.5 m and 3.5 m), indicating even-aged patches, with no significant spatial autocorrelation at greater distances (Table 2). Older white fir similarly trees showed positive spatial autocorrelation (1.5 m, 2.5 m, and 7.5 m). By analyzing older and younger white fir together, positive spatial autocorrelation occurred at smaller patch distances (1.0 to 4.5 m), representing small even-aged patches. Negative spatial autocorrelation existed at larger patch distances (5 to 10 m), indicating mixed-aged patches of older white fir mixing with younger white fir.

When older ponderosa pine and older white fir were combined, negative spatial autocorrelation occurred at 1 m and 8 m, indicating younger white fir trees overlapping with older ponderosa pine trees. When ponderosa pine and white fir trees and poles were analyzed together, positive spatial autocorrelation for age occurred at smaller distances (0.5 to 5.0 m), signifying small patches of similarly aged trees. In contrast, negative spatial autocorrelation for age occurred at a larger distance (8 m), representing larger patch of mixed-age ponderosa pine and white fir.

Discussion and conclusions

Patch development along the lower mixed-conifer ecotone on the North Rim of Grand Canyon National Park has shifted from ponderosa pine forest (white fir absent or uncommon) to mixed-conifer forest in the twentieth century. Ponderosa pine trees occurred up to the 95 cm dbh size class but few individuals occur in the pole size class. In comparison, the smaller pole size classes comprised the majority of white fir. Periods of peak establishment also contrasted between the two conifer species, with little ponderosa pine establishment in the last 40 years. Ponderosa pine establishment peak (42%) occurred in the 1880 to 1919, while 81% of white fir established since the 1920s. According to the master chronology, ponderosa pine ring widths became generally narrower for the most recent 70 years, representing increased competition and stress from white fir. Thus, we would argue that invasion of white fir was at the expense of ponderosa pine establishment. Fire histories, determined from crossdated fire-scars (Wolf and Mast 1998), show these five plots experienced fires in the period 1732-

1938. Following years of drought in the late 1896-1904 (PDSI), the age structure indicates establishment of both ponderosa pine and white fir between 1910s (during high PDSI values) and 1940s, but at the ratio of one ponderosa pine to nine white firs. Although climatic variability has the over-riding influence on the patterns of tree establishment, the cessation of periodic fires resulted in increases in the density and distribution of shade-tolerant fire-intolerant white fir, and the subsequent decrease in growth and establishment of shade-intolerant fire-adapted ponderosa pine.

Univariate spatial statistics indicated random distribution of ponderosa pine in the tree size class at smaller distances, likely due to shade intolerance and competitive thinning of initially even-sized small patches, but clumped at larger distances. This spatial analysis of ponderosa pine is consistent with the interpretation of stand development as consisting of episodic tree establishment in groups (Peet 1981). When combined with the age structure results showing white fir was rare or absent in these stands prior to the late 1800s, our interpretation is that ponderosa pine trees initially established in monospecific stands, with individual ponderosa pine trees spaced far enough apart to avoid shading and competition for water and nutrients with other ponderosa pine. Tree-sized white fir was randomly distributed at smaller distances, likely due to competition causing density dependent mortality. In contrast, pole-sized white fir was clumped at all patch sizes, as expected with an invading shade-tolerant understory that had not experienced significant competitive or fire-caused thinning.

As indicated by the bivariate spatial statistics, white fir establishment initially occurred under the shade of mature ponderosa pine (positive spatial association between ponderosa pine and white fir in the tree size class), with subsequent white fir establishment occurring throughout the understory in the shadier conditions following fire suppression (no spatial association between ponderosa pine trees and white fire poles). Given that the age structure data support the hypothesis that the study area was primarily a ponderosa pine forest prior to the start of fire suppression, our interpretation is that the shade-tolerant white fir seedlings that initially invaded the ponderosa pine forest would have better chance of survival under the partial shade of larger ponderosa pine (due to increased moisture and shelter). In contrast, as the forest grew denser, the shadier conditions

avored white fir seedling establishment throughout the understory, not just under the partial shade of large ponderosa pine.

In the interpretation of spatial autocorrelation analyses for size (Moran's I statistic), four types of patches separated by large distances (> 5 m) occurred: (1) mixed-sized ponderosa pine patches for tree size class only, similar to White's (1985) patches of mixed-sized groups of ponderosa pine in ponderosa pine forests near Flagstaff Arizona, (2) mixed-sized ponderosa pine patches for tree and pole size classes combined, (3) mixed-sized white fir patches for tree size class only, and (4) mixed-sized combined species patches. In the first case, patches of mixed-sized ponderosa pine trees may represent a size hierarchy that developed when one or a few of the shade-intolerant ponderosa pine attained size dominance in a patch due to competition for sunlight. In the second patch type, mixed-sized patches formed from ponderosa pine trees mixing with smaller pole-sized ponderosa pine. The third type indicates patches of mixed-sized white fir trees, probably representing a size hierarchy that developed when one (or a few) white fir attained size dominance in a patch. Finally, for both species combined, the mixed-sizes of trees likely represent overstory ponderosa pine trees mixed with understory white fir poles.

Spatial autocorrelation analyses for age show different results from the size analyses. Both older ponderosa pine and older white fir were found in even-aged patches (positive spatial autocorrelation for age), similar to Cooper's (1960, 1961) description of a mosaic of even-aged ponderosa pine groups in ponderosa pine forests in the White Mountains of Arizona. By analyzing older and younger white fir together, smaller even-aged patches existed with mixed-aged patches occurring at greater distances. When older ponderosa pine and older white fir were combined, relatively younger white fir trees were shown to overlap in patches with relatively older ponderosa pine trees (negative spatial autocorrelation for age).

According to our hypothesis, internal patch structure should change as single cohort patches age due to self-thinning and only a few trees may attain dominance within a small patch (Kenkel 1988; Szwagrzyk 1992). Spatial autocorrelation results for the size *versus* the age for tree-sized ponderosa pine and tree-sized white fir indicated patches of mixed-sized (negative spatial autocorrelation for size) but not mixed-aged trees at the 5 to 10 m distance. Hence, as initially patches aged, a size hierarchy developed

with one or a few trees attain size dominance in a patch. In contrast for white fir trees and poles combined, both size and age analysis showed even-aged patches at smaller distances. This pattern resulted from fire suppression permitting seedling establishment for patches of shade-tolerant white fir seedlings and subsequent lack of competitive thinning. As a result, even-aged "dog-hair" thickets of white fir occurred in the understory, with no individual(s) from the post-1920 age cohorts reaching size dominance to canopy height.

An alternative hypothesis to our conclusions could be that white fir was abundant in the early 1800s as it is today, but simply had a faster turnover rate than ponderosa pine (i.e., shorter-lived species). Yet no dead white fir exist that date from before Euro-American settlement in the 1870s in the plots, even though the climate of this region is conducive to preserving snags and logs (Mast et al. 1999). In addition, although white fir has a shorter longevity compared to ponderosa pine, this species can still produce cones at well over 300 years old (Burns and Honkala, 1990). Hence, if white fir were co-dominant in these forests before the 1970s, then some establishment record should still exist in the age structure. Moreover, mixed conifer forests that naturally include white fir in the Southwest exist where ponderosa pine is minor (or absent) and/or where the disturbance regime consists of stand-replacing fires (Moir et al. 1997). The fact that white fir is fire intolerant, especially in its early years, limited their establishment due to high fire frequency until c. 1920.

Information on altered stand structures, modified species compositions, spatial patterns, and shifted successional patterns along mixed-conifer gradients will help in developing forest management plans that conserve natural patch mosaics and landscapes. With fire suppression and prohibition of cattle grazing after 1919, the lower mixed-conifer ecotone is altered in both species composition and densities, reflecting the impacts of human land use on this forest ecotone. Future restoration plans for these forests need to integrate the natural spatial patterns and patch structure. Our study now continues into the upper-most elevations of mixed-conifer forests that form ecotonal communities with spruce and fir forests on the North Rim of Grand Canyon National Park.

In regards to adaptive management recommendation based on our findings, we advocate restoring the ponderosa pine forest by removing the white fir from the understory. In addition, we recommend that land

managers conduct prescribed fires to re-establish the natural disturbance regime and forest structure. With the shift in species dominance from ponderosa pine to white fir, the potential for stand-replacing crown fires on a large scale is greatly increased. One prescribed burn will not restore the forest species composition and structure, needing instead decades of restoration treatments with secondary and tertiary prescribed burning and if feasible some mechanical treatment to reduce white fir. Given the forest condition and fuel load from the exclusion of fire over the last 80 years, as well as increased recreational use, prescribed fire would also need to be conducted under carefully developed conditions to maximize control of the prescribed burns. Ideally, the use of prescribed fires with white fir thinning will assist park managers in returning the disturbance regime to one of frequent low-intensity surface fires.

Acknowledgements

This research was supported by the U.S. National Park Service and Northern Arizona University's Organized Research Program. We wish to thank Jesse Duhnkrack for assistance with the initial research proposal, and Carl Helquist, Amy Bess, Kelley Corbett, Barbara Kent, Mike Lewelling, Elizabeth Miller, Sean Molina, Andy Thorstenson, Stacey Wickland, and Brenda Zimpel for assistance with field work. The paper benefited from the editorial comments of William Romme, Melissa Savage, and one anonymous reviewer.

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