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Tree Encroachment on Meadows of the North Rim, Grand Canyon National Park, Arizona, U.S.A.

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Abstract

We analyzed attributes of tree encroachment on montane meadows and subalpine grasslands on the North Rim of Grand Canyon National Park. Species composition, age, density, height, diameter, condition class, and patterns of tree establishment were examined on belt transects at 12 meadow sites. Of the 3481 live and dead trees sampled, 52% of all trees were *Populus tremuloides*, 20% were *Picea* spp., 11% were *Abies lasiocarpa*, 10% were *Abies concolor*, and 7% were *Pinus ponderosa*. Tree densities averaged 4703 trees ha^{-1}. Sixty-two percent of the trees sampled were less than 20 yr of age, although some species established in the early and mid-1800s. Ninety-one percent of all trees, however, established after the mid-1930s, with the greatest establishment occurring after the early 1970s. Of this 91%, *Populus tremuloides* composed the majority (90%) of recent tree recruitment, with a mean establishment date of 1983–1984. A general pattern of progressively younger trees from the closed forest toward the meadow interiors was detected for some species, and together with little evidence of historical tree occurrence (e.g., large standing dead, downed logs, etc.) on the transects, indicated that trees had been encroaching on these meadows since the 1800s. These trends suggest a loss of important meadow habitat and landscape biodiversity within Grand Canyon National Park during the past century.

Introduction

Montane meadows and subalpine grasslands are important components in many western forest ecosystems. On the North Rim of Grand Canyon National Park (GCNP), meadows and subalpine grasslands are critical vegetation types, yet they cover less than 2% of the land area (Warren et al., 1982). Plant community composition and structure in meadows are often dramatically different than in the surrounding forests, and these meadows provide important habitat for wildlife, as well as aesthetics and biological diversity. A meadow opening, for example, will generate four to five times the herbaceous production and plant richness of the nearby forest interior (Moore and Deiter, 1992; Brown, 1994). During the past century, it appears that conifers and *Populus tremuloides* (Michx.) species have encroached upon the meadows and subalpine grasslands in GCNP and throughout the Southwest, eliminating or reducing the extent of these critical landscape elements (Brown, 1994). GCNP personnel observed, "Encroachment appears to be occurring on all meadowlands; however, in some areas it seems to be occurring at a faster rate" (NPS-RFP, 1990).

Recent tree encroachment into montane and subalpine meadows of western North America is widely reported from the Pacific Northwest (Franklin et al., 1971; Rochefort and Peterson, 1996; Miller and Halpern, 1998) to Utah (Ostler et al., 1982) (see also Rochefort et al., 1994, for review). In contrast to the numerous studies documented in the Pacific Northwest and northern Rocky Mountains, few studies in the Southwest have been reported (Allen, 1984, 1989; Dyer and Moffett, 1999). We suggest in this study that Arizona's unique monsoonal climate, relatively recent EuroAmerican settlement, and large controversial deer herds from the early 1900s (Leopold, 1943; Russo, 1964) may yield some interesting tree encroachment patterns.

Casual observations of meadow habitat in northern Arizona suggest that some meadows may be relatively stable while others are converting to forest. Several researchers commented on the small trees near meadow borders while conducting other studies on the Kaibab Plateau in the 1930s and 1940s (Mead, 1930; McHenry, 1933; Rasmussen, 1941; Merkle, 1962). For example, Mead (1930) stated, ". . . in many cases seedlings of *Picea pungens* occur along the edge of the meadow in the open. This apparently does not signify encroachment since usually no trees of intermediate size are found between the seedling and the mature tree. These seedlings are stunted and short for their ages." "In a good many cases [however] it appears that *Populus aurea* [now *P. tremuloides*] advances into the meadow making way for *Picea pungens* seedlings. These seedlings are apparently more healthy and in some cases grow to maturity." Merkle (1962) noted, ". . . no isolated young trees are found out in the meadows, but invasion is suggested by the presence of small trees along the margin." Pearson (1913) was the first to investigate possible tree invasion of *Pinus ponderosa* into "parks" near Flagstaff, AZ, and he concluded that the microclimate in the parks was too severe for tree establishment and survival. No quantitative study has been conducted on tree encroachment into meadows in Arizona.

We initiated this study to describe species composition, structure, and temporal patterns of tree encroachment on the montane meadows and subalpine grasslands of the North Rim of GCNP. Quantitative information concerning patterns of encroachment in GCNP will help park ecologists and natural resource managers formulate management strategies to conserve meadow habitat that contributes to species and landscape diversity. Further, such information adds to our scientific understanding of an apparently widespread phenomenon in the western United States.

Study Area

PHYSICAL SETTING

The study was conducted on the North Rim of GCNP, Arizona (36°10′N to 36°28′N, 111°45′W to 112°10′W) (Fig. 1). The North Rim is situated between the northern edge of GCNP and the southern edge of a series of plateaus (primarily the Kaibab and Walhalla), which eventually drop down to the Colorado River. The Kaibab Plateau is the

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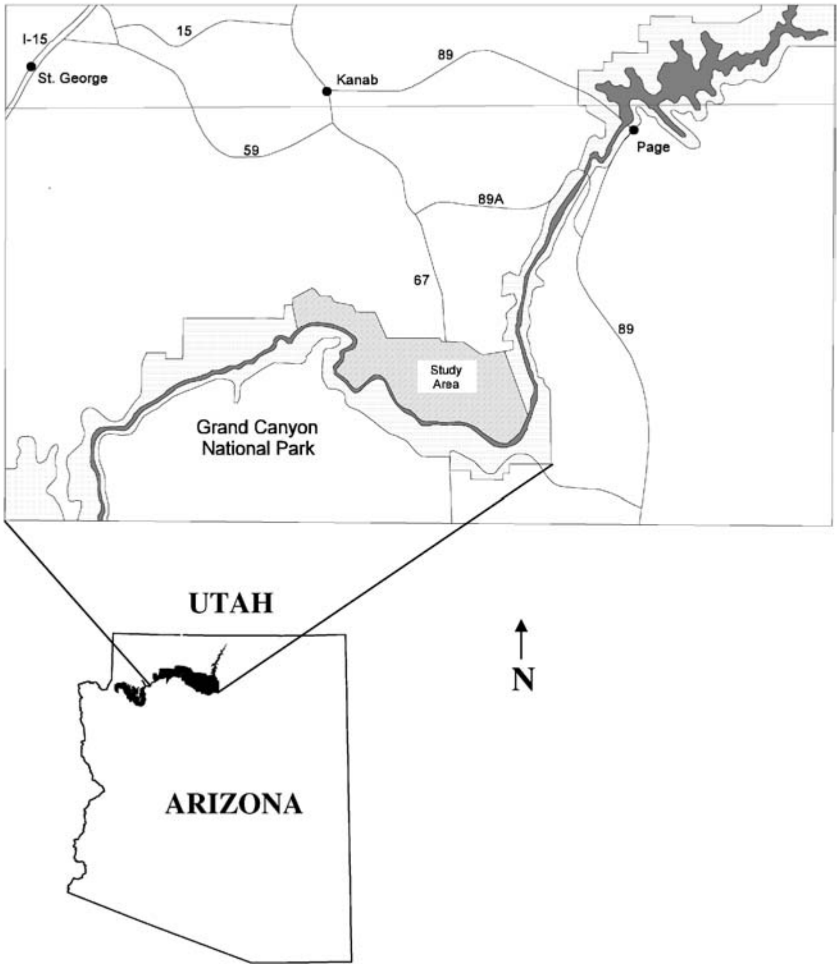

FIGURE 1. Study area on North Rim of Grand Canyon National Park, Arizona.

largest and highest. The North Rim ranges from ca. 2075 to 2800 m in elevation.

The general climate of the North Rim is characterized by cold, snowy winters and mild, moist summers. The only year-round weather records that exist for the Kaibab Plateau are for the Bright Angel Ranger Station, which is located near the southern tip of the plateau in GCNP. Annual precipitation at the Bright Angel Ranger Station (elevation 2560 m) averaged 65 cm, with a range from 35 cm to 114 cm between 1930 and 1995 (National Climatic Data Center, 2004; Arizona Weather, 2004). Precipitation distribution is bimodal, with distinct monsoonal rains from mid-July until September and snowfall can be heavy with 50–60% of the precipitation falling in the winter months (December through March). Temperature averages 17°C in July and –3°C in January (Green and Sellers, 1964; Sellers et al., 1985). The average freeze-free period ranges from 93 to 101 days (from approximately mid-June until mid-September).

A series of elongate topographic depressions and drainage valleys, which generally trend north to south, are located throughout the Kaibab and Walhalla Plateaus (Strahler, 1944). Surface streams are absent and drainage is subsurface, except after snowmelt. These basins and drainage valleys are grassy and often treeless (called "parks" or "meadows"), and contain limestone outcrops and solution sinks. Soils on upper slopes are well-drained, moderately deep to deep gravelly loam to clay loam, and formed in residuum and alluvium from limestone sources—primarily Kaibab and Toroweap Limestone (Robbie, 1980; Brewer et al., 1984). Soils of meadow bottoms are somewhat poorly drained, loam or clay loam (Robbie, 1980; Brewer et al., 1984).

The primary tree species on the forest-meadow boundaries includes *Populus tremuloides* (Michx.), *Picea engelmannii* (Parre), *Picea pungens* (Engelm.), *Pinus ponderosa* (Laws.), *Abies concolor* (Lindl.), and *Abies lasiocarpa* (Nutt.) (Warren et al., 1982, White and Vankat, 1993). Forest understory shrubs include *Juniperus communis* (L.) and *Berberis repens* (Lindl.).

Approximately 1780 ha (between 1% and 2%) of the North Rim's vegetation is classified as meadow (Warren et al., 1982). Hereafter, in this study, we will use the general term "meadow" to collectively represent montane meadows, subalpine grasslands, parks, and woodland parks.

CULTURAL AND HISTORICAL SETTING

A rich prehistory, aboriginal, Mormon, and EuroAmerican history surrounds the Kaibab Plateau and North Rim of GCNP. Early land use and anthropogenic impacts on these forests and meadows undoubtedly played important roles in shaping contemporary plant community structure and dynamics.

Recorded history began with Spanish expeditions in the late 1700s on the Kaibab Plateau, and in the nearby remote region from the Colorado River north to the Utah border known as the Arizona Strip (Altschul and Fairley, 1989). By the mid-1830s Mexican traders were traveling regularly through the Arizona Strip region on the Old Spanish Trail, but did not venture onto the Kaibab Plateau. Altschul and Fairley (1989) stated, "During the mid-1800s, the human impact on the Kaibab Plateau was limited to a declining population of Kaibab Paiutes [due to European diseases and slavery] and possibly some trappers."

Mormon settlers occupied the Arizona Strip in the 1850s and

1860s, but did not begin timber harvesting or livestock grazing (sheep, cattle, and horses) on the Kaibab Plateau until the early and mid-1870s (Verkamp, 1940; Rasmussen, 1941; Altschul and Fairley, 1989). The Kaibab Plateau also experienced additional grazing pressure in the early 1900s (approximately 1915–1930) due to an overabundance of deer (Mann and Locke, 1931; Rasmussen, 1941). Deer population irruption was soon followed by a population crash. This story became a classic (and controversial) story of predator-prey relationships (Leopold, 1943; Caughley, 1970; Young 2002).

The low-intensity surface fires, which were a common occurrence in northern Arizona *Pinus ponderosa* forests and lower elevation mixed conifer forests prior to the 20th century, ceased in the late 1870s and early 1880s. Frequent fire regimes were disrupted in forested highlands of the Arizona Strip as early as 1870 in the Mount Trumbull area (P.Z. Fulé et al., unpublished data), about 85 km west of the Kaibab Plateau, and between 1876 and 1883 near Flagstaff, AZ (Dieterich, 1980; Fulé et al., 1997). Wolf and Mast (1998) and Fulé et al. (2002) report fire regime disruption between 1879 and 1887 at several locations on the North Rim of GCNP.

Methods

FIELD PROCEDURES

The meadow sites studied varied by size, forest type surrounding the site, landform, and topographic position (Table 1). Landform or topographic positions were based on McHenry (1933), who observed that the North Rim meadows occupied three distinct locations over the landscape, including the flat floor of broad shallow valleys, intermediate stream drainages, and south-facing slopes of drainage valleys. The intermediate stream drainages (ISD) are relatively abundant, while the south facing slopes (SFS) and the broad and shallow valleys (BSV) are few in total number but often large in extent.

We used a 1967 1:62,500 U.S. Geological Survey topographic quadrangle map to stratify the North Rim of GCNP by elevation from 2400 to 2700 m, which is the elevation range of the meadows. We identified 32 ISD, 16 SFS, and 2 BSV. We numbered the meadows within each category and visited these meadows in the field. Over 60% of the ISD and SFS categories had paved roads, unimproved dirt roads, or old livestock runways running through the middle of them resulting in erosion and disturbances that impeded natural tree encroachment. From the few relatively undisturbed ISD and SFS, we randomly selected 10 meadow sites to represent the western, central, and eastern portions of the North Rim. We sampled all meadows from the BSV category, since there were only two in GCNP (Table 1). The 12 meadow sites were sampled in the summers of 1992 and 1993.

Transect placement was systematically determined and based off northern and southern points we identified for each meadow using maps and photographs. We relocated these points in the field and used a 50-, 100-, or 150-m random start to establish the first transect along the forest-meadow margin. Thereafter, we established transects every 250 m along the margin until we had sampled the entire meadow perimeter. Transects were then categorized by general aspect, according to their location along the meadow perimeter: southwest-facing (45°), northwest-facing (135°), northeast-facing (225°), or southeast-facing (315°). The number of transects established per meadow, therefore, varied with meadow site, shape, and size; at least two transects were established in the narrow or very small (≤ 1 ha) meadows and up to 15 transects were established in large (>24 ha) meadows. Sixty-two belt transects were sampled in total.

After the location of each belt transect was determined, the starting point was anchored at the tree (mature, sapling, seedling, or sucker) that was farthest into the meadow interior. Each transect was then established from meadow interior toward the closed forest for 50 m perpendicular to the forest-meadow edge (Vale, 1981). All transects reached the forest edge, and some transects extended beyond into the closed forest. Each transect length was corrected for slope, if necessary. The belt transect was 2 m wide. The corners of each plot were permanently staked with rebar.

TABLE 1

General characteristics[1] of the 12 meadow sites sampled on the North Rim, Grand Canyon National Park, Arizona, U.S.A.

Site name	Area[1] (ha)	Perimeter[1] (m)	Elevation[1]	Forest type[2]	Landform, topographic position[3]
1—Milk Creek	1.1	407	2500	MC	ISD
2—The Basin	191	42,237	2500	MC	BSV
3—Tipover Springs #1	0.91	485	2465	MC	ISD
4—Tipover Springs #2	3.6	1415	2465	MC	ISD
5—Tipover #1	1.0	561	2465	MC	ISD
6—Tipover #2	6.9	1364	2440	MC	SFS-sinkhole
7—Walhalla Plateau #1	5.6	2139	2480	PP/MC	ISD
8—Walhalla Plateau #2	14.6	6928	2440	PP	SFS
9—Walhalla Plateau #3	0.5	374	2530	PP/MC	ISD
10—Walhalla Plateau #4	0.6	298	2500	PP	ISD
11—Fuller Canyon	24.5	4592	2545	SF/MC	SFS
12—Upper Little Park	60	7964	2680	SF	BSV

[1] The area and perimeter were obtained from 1988 U.S. Geological Survey $7.5'$ quadrangle maps and do not account for areas "filled in" by encroaching trees; it is the approximate meadow perimeter where transects were located. Elevation is an average elevation for entire meadow.

[2] Forest type surrounding meadow: PP = *Pinus ponderosa*; PP/MC = *Pinus ponderosa* dominated, with other conifers in understory; MC = mixed confer = a relatively even mix of conifer species; SF/MC = *Picea* spp. and *Abies lasiocarpa* (spruce-fir) dominated, with other conifers possible; SF = *Picea* spp. and *Abies lasiocarpa* (spruce-fir).

[3] Landform or topographic position as described by McHenry (1933): ISD = intermediate stream drainage, BSV = broad and shallow valley, SFS = south-facing slope.

All trees encountered within the 50 m × 2 m belt transects were measured. Data recorded for each tree included location (x, y; recorded to the nearest 0.10 m), species, age, condition class (sensu Maser et al., 1979), total height, and diameter. For this study, we combined the two *Picea* species because of the difficulty in correctly identifying them in the seedling stage (up to 1 m tall) (Jones and Bernard, 1977). Diameters were measured at ground level for seedlings, suckers, and smaller saplings (≤ 5 cm in diameter at ground level). Diameters of larger saplings (>5 cm in diameter at ground level) and mature trees were measured at 30 cm.

The ages of trees ≤ 5 cm in diameter were indeterminate or questionable in the field and, therefore, were cut with a handsaw at ground level, and a cross-section was brought to the lab to determine total age using a binocular microscope. Peters et al. (2002) reported that ground-level ring counts in young (<10 yr) stands are a reliable way to identify initial regeneration patterns.

Larger saplings and mature trees were cored at 30 cm above ground level. Although we recognize the advantages of coring at ground level, the butt swell and irregular growth at the base of older trees, and the GCNP personnel concerns about destructive sampling of

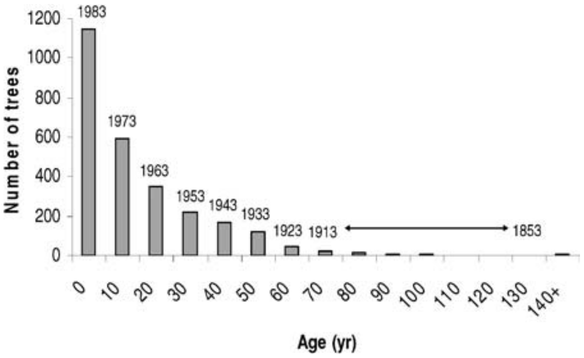

FIGURE 2. *Total number of live trees by 10-yr age classes for all 50 m × 2 m transects and species pooled. Dates above bars correspond to beginning of 10-yr establishment periods shown.*

older trees, made sampling at ground level an unreasonable choice. The 30 cm coring height was the lowest position on the tree stem we could use for consistency in aging, given the circumstances. Age-to-coring height (years to reach 30 cm in this study) was obtained by taking the average age of seedlings, suckers, or saplings in the 2.54 cm to 61 cm height category by species, and then adding this estimate to the total age. Estimates by species were 2, 13, 3, 9, and 19 yr to reach 30 cm for *P. tremuloides*, *Picea* spp., *P. ponderosa*, *A. concolor*, and *A. lasiocarpa*, respectively. Peters et al. (2002) suggested a 3- to 6-yr underestimate in age of older (ca. 20–40 yr) stands, even if sampled at ground level, and especially for shade-tolerant species such as *Abies* and some *Picea* species. To compensate for this problem, our data were examined for decade-scale patterns of tree establishment by species.

Of the 3481 trees sampled on all belt transects, 766 were dead, had rotten centers, or had unreadable cores. Therefore, age statistics were from a sample size of 2715 live trees. Tree density statistics were from a sample of 2916 live trees.

DATA ANALYSES

Our data analyses were divided into two general parts: (1) general trends, intended to determine if trees were encroaching upon the meadows on the North Rim of GCNP, and (2) individual species patterns, a more specific examination of species' structural attributes and temporal patterns of establishment.

To examine the general trends, we used percentage and descriptive statistics for a pooled-view of the trees at the forest-meadow borders. We also divided the 50 m transects into thirds (0–16.6 m, 16.7–33.3 m, and 33.4–50 m) for analysis of spatial patterns of tree establishment along transects from meadow interiors toward the closed forest. We used one-way analysis of variance (ANOVA) to test for main effects ($p \leq 0.05$) of transect distance on maximum tree age, mean tree density, maximum tree diameter, and overall mean density of dead woody material (e.g., standing dead, downed logs, etc.). When main effects were found, Tukey's post-hoc test ($p \leq 0.05$) was used to examine differences among group means. Chi-squared goodness-of-fit tests, for individual species and for all species combined, were used to test for significant differences ($p \leq 0.10$) in number of trees among aspects.

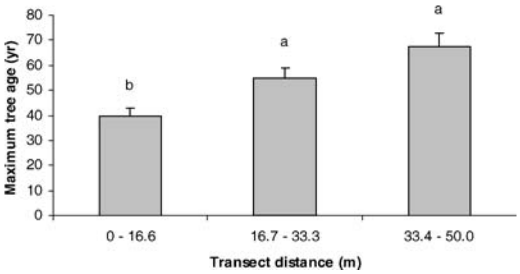

FIGURE 3. *Effect of transect distance on maximum tree age, all species combined. Values are means and standard errors. Significant differences (Tukey post-hoc;* p < *0.001–0.02) were detected among distances.*

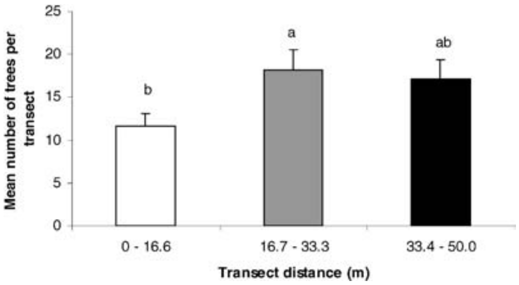

FIGURE 4. *Effect of transect distance on mean tree density, all species combined. Values are means and standard errors. Significant differences (Tukey post-hoc;* p *= 0.05) were detected among distances.*

The data were examined further to determine differences in individual tree species' structural attributes and temporal patterns of encroachment. These analyses also used percentages and descriptive statistics. We used ANOVA to test for main effects ($p \leq 0.05$) of distance on individual species' ages or species' densities or a combination of species' age and density. When main effects were found, Tukey's post-hoc test ($p \leq 0.05$) was used to examine differences among group means. For all analyses, data were natural-log or square root transformed to normalize distributions or to obtain homogeneity of variance when necessary.

Results

GENERAL TRENDS

The majority of trees on the forest-meadow margins were young and small when data for all species were pooled. Mean tree age was 20 yr (in 1993), and 62% of the trees sampled were less than 20 yr of age (Fig. 2). Less than 8% of the trees sampled were greater than 53 yr of age, while only 23 trees (<1%) were greater than 90 yr of age. When trees were grouped into 10-year age classes, the establishment distribution had a distinct period between the mid-1800s and 1903 where only 23 trees (ca. 1%) established on the plots (Fig. 2). The period from 1968 to 1993 had the greatest tree establishment; 71% of the trees in our study plots established during this period, and of those, the majority (60%) established during the 1980s (Fig. 2). In addition, more than 80% of the trees were less than 3 m in height and nearly 90% were less than 15 cm in basal diameter.

Tree age, density, and size varied with distance along belt transect. For all species combined, there was a significant effect ($p < 0.001$) of transect distance on the maximum age of trees (Fig. 3). Trees that were the farthest into the meadow were significantly ($p < 0.001$) younger than trees closer to the forest and the middle one-third ($p = 0.02$) of all transects. Likewise, there was a significant ($p = 0.04$) effect of transect distance on the mean number of trees (Fig. 4), where fewer trees were established farthest into the meadow, and the greatest number of trees were established in the middle one-third. Tree density closest to the forest edge was not significantly different from the other two distances. Lastly, for all species combined, there was no significant effect of transect distance on mean tree size (Fig. 5).

The age data were divided into 30-yr age classes and tree density by age class as a function of transect distance yielded some interesting

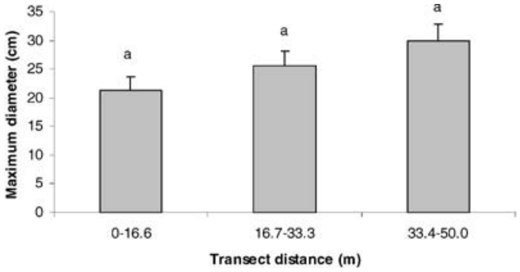

FIGURE 5. Effect of transect distance on maximum tree diameter, all species combined. Values are means and standard errors. No significant effect of distance (ANOVA; $p > 0.05$*) was detected.*

results (Fig. 6). As expected, the older age classes (61–90 yr and 90+ yr) had a greater tree density toward the forested end of the transects, and gradually tapered off out into the meadow. Tree densities for the younger age classes (1–30 yr and 31–60 yr), however, did not differ with transect distance.

Sixty-seven percent of trees sampled were live and in the healthy condition class. However, many of the younger trees appeared stressed from seasonal drought, disease, browsing, and fossorial animals (Moore, personal observation), which Moir et al. (1999) suggest are local controls on tree encroachment. This observation is supported further by our data. Approximately 33% of the tree seedlings and suckers were either declining or dead. The amount of smaller standing dead material ($\leq$5 cm; seedlings, young suckers, small saplings) was significantly greater ($p = 0.04$) than that of larger standing or downed material at all three transect distances (Fig. 7). Of the 3481 total trees (live and dead) sampled, 35 (ca. 1%) were classified as dead and down logs. Nearly half (17) of these logs were found on 3 of the 62 transects, while the majority (68%) of transects were completely devoid of large down woody material (Fig. 7).

The majority (62%) of encroaching trees occurred on the north-facing aspects (Table 2), although tree density by aspect was not statistically significant. More specifically, 22% of all trees occurred on SW-facing aspects (45°), 35% occurred on NW-facing aspects (135°), 27% occurred on NE-facing aspects (225°), and 16% occurred on SE-facing aspects (315°). This general trend is consistent with other studies that found greater tree encroachment (and greater tree densities) on northerly aspects, and is attributed to a longer retention of snow and greater soil moisture (Rochefort et al., 1994; Moir et al., 1999).

These results, in combination with age data and analysis of dead structures, indicate that the contemporary meadow edges on the North Rim were essentially devoid of trees in the late 1800s and early 1900s. By the 1940s, however, an average of 300 trees ha^{-1} established, and by 1993 there were an average of 4703 trees ha^{-1}. A large proportion of the trees established in 1992–1993 were aspen suckers, and, many of these will not likely survive to maturity because seedling and sucker mortality is typically high (Schier et al., 1985).

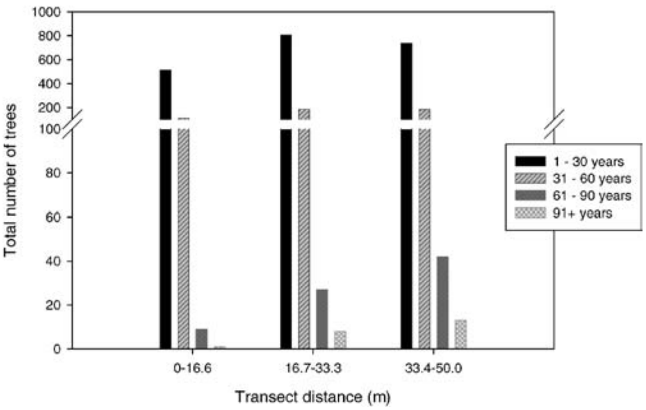

FIGURE 6. Total number of live trees by transect distance and age class (all species pooled).

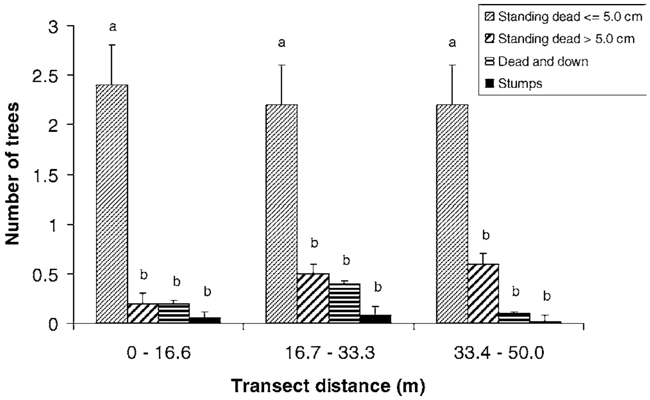

FIGURE 7. Effect of transect distance on all dead woody material. Values are means and standard errors. Similar letters within distance classes denote statistically similar means (Tukey post-hoc; $p > 0.05$*). Significant differences (Tukey post-hoc;* $p < 0.001$*) between mean dead seedlings/suckers and means of other dead structures within each distance class were found. No significant difference existed between seedlings/suckers across distance classes; however, mean standing dead >5.0 cm diameter in distance classes 16.7–33.3 m and 33.4–50.0 m were significantly greater (ANOVA;* $p = 0.04$ *main effect of distance) than mean standing dead >5.0 cm in distance class 0–16.6 m (Tukey post-hoc,* $p < 0.05$*). Similarly, mean dead and down in distance class 16.7–33.3 m was significantly greater (ANOVA;* $p = 0.01$ *main effect of distance) than dead and down means in 0–16.6 m and 33.4–50 m, both of which were similar (Tukey post-hoc,* $p < 0.05$*). Mean stump density was similar across distance classes.*

INDIVIDUAL TREE SPECIES PATTERNS

Of the 3481 live and dead trees sampled, 52% of all trees on the transects were *Populus tremuloides*, 20% were *Picea* spp., 7% were *Pinus ponderosa*, 10% were *Abies concolor*, and 11% were *Abies lasiocarpa*.

We also examined the maximum tree age (Fig. 8) and the mean tree density (Fig. 9) along each transect by individual tree species. *Pinus ponderosa* and *Picea* species both demonstrated a significant effect (ANOVA; $p < 0.05$) of transect distance on the maximum age. *Pinus* and *Picea* trees that were the farthest into the meadow were significantly (Tukey post-hoc; $p = 0.008–0.02$) younger than trees closer to the forest. The middle one-third of all transects were not significantly different from the meadow or forested ends for either species, suggesting a gradual progression of these tree species into the meadow. *Populus tremuloides*, *Abies concolor*, and *Abies lasiocarpa*, however, did not demonstrate a significant effect of transect on maximum age. There was no significant effect ($p > 0.05$) of transect distance on the mean number of trees (Fig. 9) for any species.

When number of trees was plotted against establishment date for individual species, details of regeneration and stand structure patterns became apparent (Fig. 10). *Populus tremuloides* age structure was a distinct "inverse-J" shaped curve, which is indicative of an uneven-aged distribution dominated by young trees (Nyland, 1996). *P. tremuloides* established on some transects as early as 1850 (Fig. 10), and the mean establishment date was 1983–1984. The majority (90%) of *P. tremuloides* regeneration occurred relatively recently between

TABLE 2

*Total number of live trees sampled by species and aspect. Chi-squared goodness-of-fit tests for individual species and all species combined showed no significant (*p *> 0.10) difference in number of trees among aspects*

	Aspect (°)				
Species	45	135	225	315	Sum
Populus tremuloides	289	409	385	282	1365
Picea spp.	127	216	236	68	647
Pinus ponderosa	52	50	24	94	220
Abies concolor	55	184	90	25	354
Abies lasiocarpa	127	150	53	0	330
Sum	650	1009	788	469	2916

1973 and 1993. Substantial mortality may eventually occur on the sites, however, because over 50% of the *P. tremuloides* suckers in our study were classified in a "declining" condition. Schier et al. (1985) noted that *P. tremuloides* is an early successional species and can produce abundant vegetative suckers from roots, yet many of these die within the first 5 yr.

Picea species established as early as 1859 (Fig. 10) with a mean establishment date of 1960–1961. The *Picea* species' age distribution, and therefore establishment, was rather consistent in the last 80 yr (1913–1993).

Pinus ponderosa represented the oldest trees on the forest-meadow borders (10 older than 113 yr; Fig. 10), with a mean establishment date of 1948–1949. This species established as early as 1780, with scattered individuals establishing on the drier and generally lower elevation meadows (primarily Walhalla Plateau site) or southwest-facing aspects (primarily the Basin site), almost every decade until the early 1880s. Maximum age observed for *P. ponderosa* was 78, 164, and 180 yr of age on transect thirds from meadow interior toward closed forest, respectively. These older trees, located 25 m to 50 m or more from the contemporary meadow edge, may be useful indicators of the forest-meadow boundary that existed in the late 1800s and early 1900s (McHenry, 1933). Since the early 1900s, there has been an increase in *P. ponderosa* establishment, with a peak between 1943 and 1953. We did not see, however, the large 1919 *P. ponderosa* regeneration event described by Savage et al. (1996) for other parts of Arizona. *P. ponderosa* establishment was minimal on these meadows from 1963 until 1993.

Abies concolor first established on these transects around 1925, and gradually increased until 1993 (Fig. 10). The mean establishment date was 1975–1976. *A. concolor* tree density nearly doubled from 1973 to 1993. *A. lasiocarpa* initially established on the mesic and higher elevation transects around 1902 (Fig. 10) with a mean date of establishment 1967–1968. In general, *A. lasiocarpa* numbers increased, with a noticeable pulse of establishment between 1933 and 1943, and then a more recent pulse between 1963 and 1983. *A. lasiocarpa* establishment slowed between 1983 and 1993.

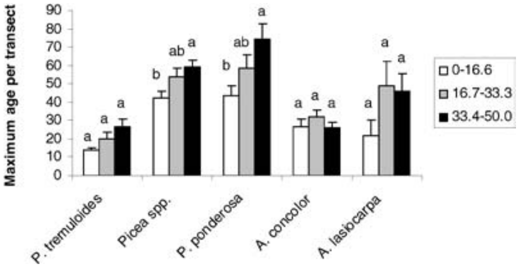

FIGURE 8. Maximum tree age by distance for individual species. Age is significantly different (Tukey post-hoc, p *= 0.008–0.02) for* Pinus ponderosa *and* Picea *spp. for 0–16.6 m (near meadow interior) and 33.4–50 m (toward closed forest) distances.*

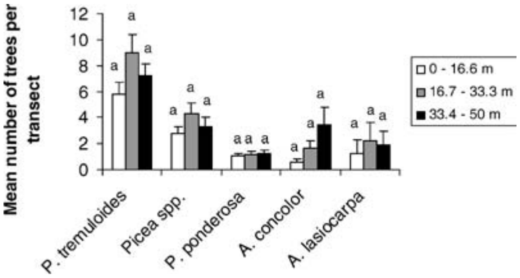

FIGURE 9. Mean tree density by distance for individual species. No main effect (ANOVA, p *> 0.05) of distance on tree density was found.*

DISCUSSION

During the past century, conifers and *Populus tremuloides* (Michx.) have invaded montane meadows and subalpine grasslands within the North Rim of GCNP. The tree age structure and general pattern of progressively younger trees from the closed forest toward the meadow interiors, together with little evidence of historical tree occurrence (e.g., large standing dead, downed logs, etc.) on the transects, indicate that trees have been encroaching on these meadows since the early 1900s. Tree encroachment and increased tree density of contemporary forest-meadow boundaries occurred to some extent since the mid-1800s, however, the encroachment has increased steadily since the 1930s and 1940s, with the greatest numbers of trees occurring during the 1980s. These results confirm the casual observations of early scientists who commented on the presence of small trees (*Picea pungens* and *Populus tremuloides* in particular) along the North Rim meadow margins in the 1930s through the 1950s (Mead, 1930; McHenry, 1933; Rasmussen, 1941; Merkle, 1962; see also photo pair in Fig. 11 located 1.8 km north of the Upper Little Park study site). Further, our data suggest that the meadow-forest boundaries are dynamic and may change over relatively short or long time periods (Rochefort et al., 1994; Miller and Halpern, 1998). And, finally the recent tree encroachment we describe for the meadows of GCNP is consistent with a widespread phenomenon observed in meadow areas across the western United States (Franklin et al., 1971; Ostler et al., 1982; Rochefort et al., 1994; Rochefort and Peterson, 1996; Miller and Halpern, 1998).

The pattern of tree encroachment on the North Rim differed with species. Trees establishing in the 1800s on the forest-meadow borders were *Pinus ponderosa* in the lower elevation sites and drier south-facing aspects of the higher elevations, *Picea* species in the higher elevation sites and mesic north-facing aspects of lower sites, and *Populus tremuloides* on all sites. *Pinus* and *Picea* species steadily invaded the North Rim meadows beginning approximately 1900, but in low numbers. *Populus tremuloides* exhibited low recruitment from the early 1900s until the 1950s, and then over a more recent 20–25 yr period (1968–1993) has made substantial advances into neighboring meadow habitat and contributed disproportionately to increasing tree densities relative to the other species. *Abies concolor* and *A. lasiocarpa* occurred on the meadow edges in the 1930s, but not in great numbers until more recently. Abies spp. increased gradually from 1943 to 1993.

Pinus ponderosa and *Picea* species appeared to follow a more "linear" model of tree encroachment, with older trees in or near the closed forest and younger trees farther out into the meadow interior. In contrast, *Populus tremuloides* and *Abies* spp. did not invade in a linear fashion, but contributed to tree encroachment by increasing tree

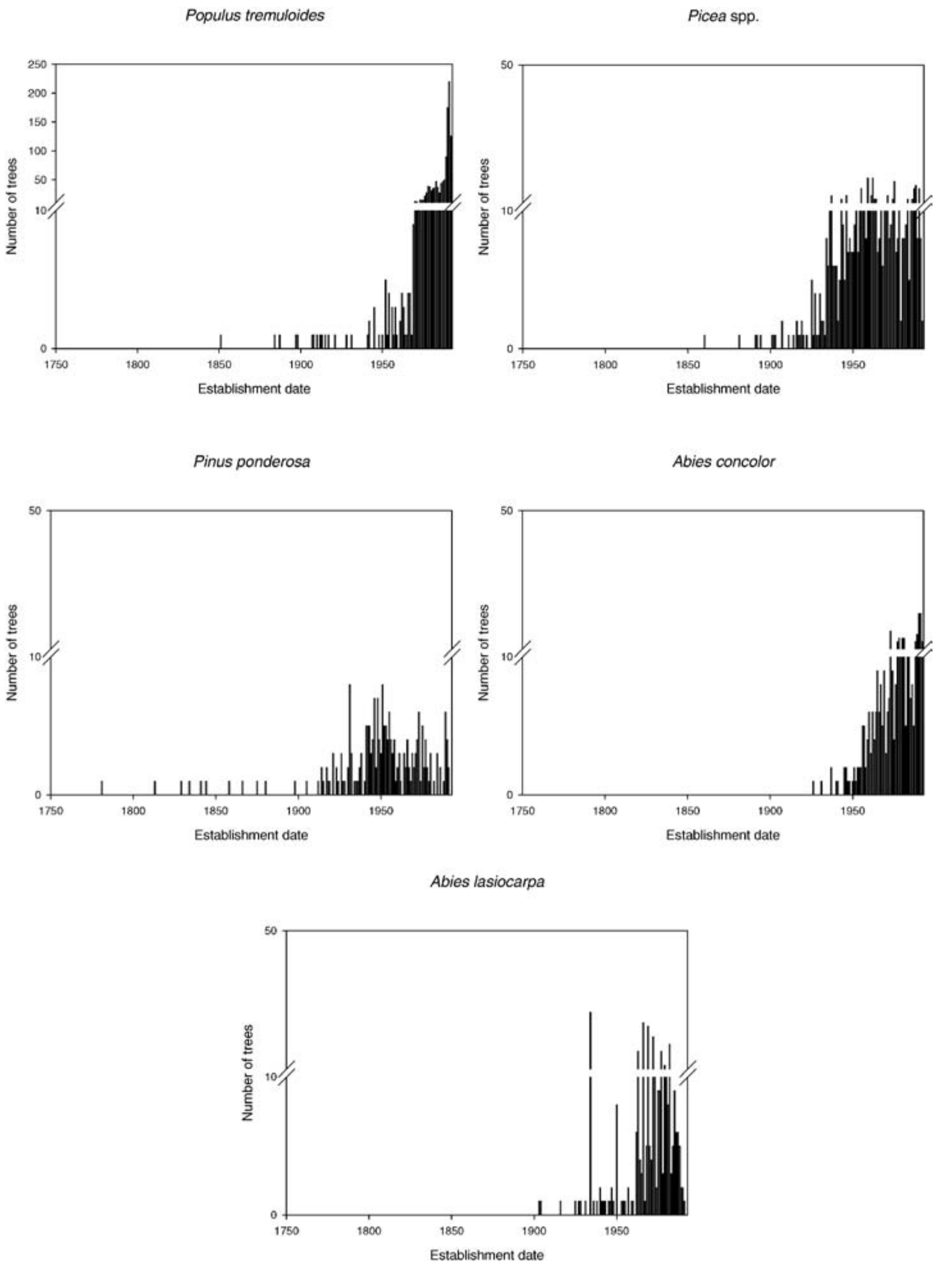

FIGURE 10. Number of trees by species and establishment date, all sites combined.

densities and filling in space around existing trees, a pattern noted by other researchers (Franklin et al., 1971; Rochefort and Peterson, 1996). White and Vankat (1993) suggested that *Pinus ponderosa* and *Picea* species create favorable microsite conditions for the shade-tolerant *Abies concolor* and *Abies lasiocarpa* to establish.

Relationships of tree species' establishment patterns with respect to specific microsite conditions or landscape factors, such as historical and current climatic patterns, fire exclusion, livestock, and native ungulate herbivory has been examined by numerous researchers at other locations in the western United States (Franklin et al., 1971; Dunwiddie, 1977; Jakubos and Romme, 1993; Rochefort et al., 1994; Rochefort and Peterson, 1996; Miller and Halpern, 1998; Moir et al., 1999). Although examination of causal factors was beyond the scope of this study, as with the studies cited above, the factors driving tree encroachment on the meadows of the North Rim of GCNP are likely operating at several scales (White and Vankat, 1993; Miller and Halpern, 1998). Further, the many possible landscape-scale mechanisms such as climate change, fire exclusion, and ungulate herbivory are confounded. For example, the end of the Little Ice Age (ca. 1850), which brought about a warmer and wetter climate in the Rocky Mountains and Southwest (Lamb, 1977), has been cited as the trigger for *Pinus contorta* invasion of meadows in Yellowstone National Park (Jakubos and Romme, 1993), *Picea-Abies* encroachment on forest-tundra ecotone in Colorado (Hessl and Baker, 1997) and subalpine meadows of south central New Mexico (Dyer and Moffett, 1999). In our study, however, the period from the mid 1850s through the early 1900s did not see a large amount of tree encroachment, although it may have contributed to the few *Pinus* and *Picea* individuals that established during that time. On our sites, the period from 1968 to 1993 had the greatest tree establishment (especially *Populus tremuloides*), with a peak during the 1980s. Climate may have been a possible forcing factor in tree invasion during this time, because the period from 1983 to 1988 was an extremely wet one in northern Arizona (Salzar, 2000).

Fire regime disruption occurred around 1879 on the North Rim of GCNP (Wolf and Mast, 1998; Fulé et al., 2002), and our data show some initial establishment of *Pinus ponderosa*, *Picea* species, and *Populus tremuloides* near this time. Similarly, Merkle (1954) and Fulé et al. (2002) suggest that the high-intensity crown fires, which occurred

FIGURE 11. Seventy-four years of tree encroachment on meadow. Top photo was taken in 1930 near the forest-meadow border within a fenced enclosure (25 ft × 25 ft in size), which was erected the same year. Bottom photo was taken from same photo point in 2004. Note: fence corner post in each photo; fence was repaired several times between 1930 and 1945. Spruce in foreground of top photo is now dead, but spruce near corner post survived (arrow points to tree in both photos). The forest-meadow border moved 26–35 m out into the meadow and filled in the area in between over that period. Both photos were taken looking east-northeast into DeMotte Park, which is ca. 1.8 km north of the Little Park study site. (photo credit: 1930, W. Mann; 2004, D. Binkley)

in the higher *Picea-Abies* forest type in the mid-1800s in GCNP, were most likely the origin of *Populus tremuloides* stands that dated to the middle and late 1800s.

Another factor often cited as a trigger in tree encroachment is release from domestic or native ungulate browsing. In the early and mid-1870s, Mormon settlers began using the Kaibab Plateau as summer range for livestock (sheep, cattle, horses), and for 20–30 yr grazing was intense (Mann and Locke, 1931; Rasmussen, 1941; Mitchell and Freeman, 1993). The livestock numbers decreased dramatically at the turn of the 20th century because of a severe 10-yr drought (1894–1904) (D'Arrigo and Jacoby, 1991; Mitchell and Freeman, 1993; Grissino-Mayer and Swetnam 2000; Salzar 2000). Surprisingly, our data do not show a large amount of tree encroachment during the early 1900s as you might expect after release from livestock herbivory, although other studies have shown that livestock, especially sheep, effectively slow tree establishment, and then subsequently cause increases in tree invasion when animals are removed (Dunwiddie, 1977; Vankat and Major, 1978; Vale, 1981; Allen, 1989; Savage and Swetnam, 1990; Miller and Halpern, 1998).

Our data do suggest, however, a release of *Populus tremuloides* in the late 1940s and 1950s. This release appears to coincide with a reduction of large deer herds that occurred on the North Rim between 1915 until the early 1950s (Mann and Locke, 1931; Rasmussen, 1941; Leopold, 1943; Merkle, 1962; Russo, 1964). Deer apparently were rarely seen using the meadows and parks on the Kaibab Plateau until about 1916, when they began to appear in large numbers (Rasmussen, 1941). In 1935, McHenry stated that very few *P. tremuloides* trees were under 20 yr of age in GCNP. Merkle (1962) determined that size distribution was irregular in the *P. tremuloides* of the North Rim with almost complete absence in intermediate sizes (2 to 25 ft), which he assumed was due to the intense browsing by deer that began in the early 1920s and continued into the 1950s. Romme et al. (1995), White et al. (1998), Ripple and Larsen (2000), and Binkley et al. in (in press) also suggest that large ungulate herds, together with alteration of historical fire regimes and predator/prey relationships, have affected successful *P. tremuloides* recruitment in several national parks and other areas in the Rocky Mountains of the western United States.

Conclusions

Tree establishment patterns varied with tree species and size and type of meadow on the North Rim of Grand Canyon National Park during the past century. On meadow sites where the soils are extremely rocky or gravelly (Mead, 1930, McHenry, 1933) or remain saturated during the growing season, or where severe frost pockets exist (Moir et al., 1999), trees will have difficulty establishing. Mead (1930) and Merkle (1962) suggested that the high elevation subalpine meadows will persist indefinitely without invasion of trees from the adjacent forest because the high soil moisture levels in spring cause seeds to rot, while scalding surface temperatures and very dry soil in early summer kill any tree seedlings that manage to germinate. Although these harsh conditions exist on the higher elevation broad valley meadows of the North Rim (McHenry, 1933), our data show significant tree establishment on these sites. In contrast, where meadows are small (≤ 1 ha) or long and narrow in shape, such as the intermediate stream drainages, it is possible that these meadows could be completely replaced by forest vegetation within the next several decades. Meadow size on the North Rim appears to have decreased since the mid-1930s, but most dramatically since the 1970s and 1980s. These results suggest at least a temporary loss of important meadow habitat and landscape biodiversity within Grand Canyon National Park.

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