



Natural variability in forests of the Grand Canyon, USA

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Abstract

Aim Compare contemporary with pre-fire-disruption forest structures, assessing the influence of factors that caused ecological change and evaluating remote sites as relatively natural areas.

Location Grand Canyon National Park contains the largest never-harvested and long-term ungrazed forest ecosystem in Arizona, providing valuable sites for measuring natural variability. However, anthropogenic disruption of natural fire regimes since Euro-American settlement *c.* 1880 has led to changes in forest structure.

Methods We compared species composition, tree structure, regeneration, and canopy cover on large (135–603 ha) ponderosa pine-dominated study sites: (1) isolated points on the North Rim where some surface fires continued after 1880, (2) a higher-elevation North Rim site where fire has been excluded and (3) a South Rim site, also without recent fire, with a paired Kaibab National Forest site. Forest tree structure prior to fire-regime disruption was reconstructed with dendroecological techniques.

Results Before fire exclusion, all sites had relatively low tree density (140–246 trees ha⁻¹) dominated by large trees (basal area 9.1–28.5 m² ha⁻¹), primarily ponderosa pine or pine/Gambel oak on the South Rim. Currently all sites are relatively dense (389–955 trees ha⁻¹, 14.1–41.3 m² ha⁻¹) but patterns of species composition and regeneration differed substantially with fire regime and elevation. Regeneration at continued-fire sites was primarily through sprouting species, Gambel oak and New Mexican locust, forming a shrubby midstorey under a relatively open pine canopy. In contrast, all fire-excluded sites were dense with seed-reproducing conifer species.

Main conclusions Comparison of change caused by climate fluctuation, tree cutting, fire exclusion, livestock herbivory, and wildlife herbivory, suggests that fire regime alteration appears to have played the greatest role. The remote North Rim sites provide a close analogue to conditions prior to fire regime disruption, a contemporary example of the forest characteristics that might have been extant had recent human-caused disruption of disturbance regimes and heavy resource extraction not occurred. They merit broader study of natural variability on a range of ecological variables in ponderosa pine ecosystems.

Keywords

Forest structure, fire, Arizona, ponderosa pine, mixed-conifer, aspen, reference conditions.

INTRODUCTION

Aldo Leopold's (1941) seemingly straightforward concept of an ecological 'base datum' has expanded into a complex debate over the role of natural variability in developing conservation strategies. Natural variability [also: 'natural range of variability', 'historical range of variability,' or 'reference conditions,' (Landres *et al.*, 1999)] is most commonly defined in terms of past conditions. For instance, in western North America, Stephenson (1999, p. 1253) defined reference conditions as 'the spectrum of ecosystem conditions ... within a defined area over a specified time period preceding Euro-American settlement.' Recent human-caused change is the root cause of the world's major environmental problems, from extinctions to climate change. Given the pervasive impacts of modern industrial society on global ecosystems, there are clear advantages in studying the relatively unfettered past patterns of ecological structure, function, and disturbance, as mediated by resource management practices of non-industrial societies (e.g. Denevan, 1992; Anderson & Moratto, 1996). Past conditions are extraordinarily important for understanding the evolutionary environment (Millar & Wolfenden, 1999; Moore *et al.*, 1999) and measuring ecological degradation. But the past is also problematic. The accuracy of reconstructed conditions can be uncertain (Stephenson, 1999; Tiedemann *et al.*, 2000). Climate change, species extirpations or introductions, and different social priorities may reduce the modern relevance of historical data (Millar & Wolfenden, 1999). Finally, stochastic, historically contingent, or non-equilibrium events in the past may have created unique and unrepeatable conditions (Swetnam *et al.*, 1999). Stephenson's (1999, pp. 1254–1256) definition of 'natural' linked past with contemporary conditions: 'the (dynamic) conditions that would exist if the dominant Euro-American culture had never arrived, but Native Americans had continued to use the landscape.'

South-western ponderosa pine forests (scientific names of species are given in Table 1) provide examples of alternative approaches to characterize natural variability. Forest structures and frequent-fire disturbance regimes were disrupted after Euro-American settlement throughout the south-west, leading to increasingly large and intense wildfires (Leopold,

1937; Weaver, 1951; Cooper, 1960; Covington & Moore, 1994; Swetnam & Baisan, 1996; Swetnam & Betancourt, 1998). Retrospective analyses of ecological change in ponderosa pine forests have included fire-scar reconstruction of fire regimes (Swetnam & Baisan, 1996), pre-disruption forest structure (Covington & Moore, 1994; Fulé *et al.*, 1997), regeneration (White, 1985; Savage *et al.*, 1996; Mast *et al.*, 1999), and historical evidence from photos, early twentieth century inventories, or early forest plots (Minnich *et al.*, 1995; Moore *et al.*, 1999). At least four complementary approaches are being used to increase the resolution of understanding of natural variability in south-western ponderosa pine forests:

- 1 Reconstruct past conditions through dendroecological, palaeoecological, or historical ecology techniques.
- 2 Measure relatively undisturbed contemporary sites to compare with reconstructed data and to explore the effects of altered modern conditions such as high CO₂ levels. For example, fire regime and/or forest characteristics have been measured at relict sites in Zion National Park, UT (Madany & West, 1983), northern Mexico (Fulé & Covington, 1997) and El Malpais National Monument, NM (Grissino-Mayer & Swetnam, 1997).
- 3 Draw inferences from ecological relationships observed in disturbed sites. For example, Ganey *et al.* (1999) drew inferences about past ecosystems based on observations of modern habitat use by Mexican spotted owls.
- 4 Restore natural ecological conditions as a modern model for observing ecosystem function (Leopold, 1941; Covington *et al.*, 1997).

Grand Canyon National Park contains the largest never-harvested forest in Arizona, with 8600 ha subalpine (spruce-fir) forest, 1230 ha Douglas-fir forest, 37,179 ha ponderosa pine/mixed conifer forest, 55 ha aspen forest, and 1787 ha montane meadows (Warren *et al.*, 1982). The apparently minimal effects of industrial human society in places such as national parks, wilderness areas, research natural areas, and relict sites isolated by geography or ownership, should not be confused with a blanket assumption of pristine conditions in these places. At Grand Canyon, fire regimes have been disrupted across most of the park (Duhnkrack, 1982; White & VanKat, 1993; Wolf & Mast, 1998; Fulé *et al.*, in review)

Table 1 Tree species found on sampling plots at Grand Canyon study sites

Species	Common name	Code
<i>Abies lasiocarpa</i> (Hook.) Nutt.	Subalpine fir	ABLA
<i>Abies concolor</i> (Gordon & Glendinning) Hoopes.	White fir	ABCO
<i>Juniperus osteosperma</i> (Torr.) Little	Utah juniper	JUOS
<i>Picea engelmannii</i> Parry ex Engelm.	Engelmann spruce	PIEN
<i>Pinus ponderosa</i> var. <i>scopulorum</i> P. & C. Lawson	Ponderosa pine	PIPO
<i>Pinus edulis</i> Engelm.	Rocky Mountain pinyon	PIED
<i>Populus tremuloides</i> Michx.	Quaking aspen	POTR
<i>Pseudotsuga menziesii</i> (Mirb.) Franco var. <i>glauca</i> (Beissn.) Franco	Rocky Mountain Douglas-fir	PSME
<i>Quercus gambellii</i> Nutt.	Gambel oak	QUGA
<i>Robinia neomexicana</i> Gray	New Mexican locust	RONE

because of herbivory from livestock grazing (c. 1880–1940) and irrupting deer populations, as well as fire suppression (Mitchell & Freeman, 1993). Anomalous tree regeneration has been linked with regional climatic events in the twentieth century (Savage *et al.*, 1996).

Nonetheless, the absence of tree harvesting makes the park a valuable place to study natural variability using any of the approaches listed above. For the present study, we used the first two approaches to ask whether forest structures have changed following disruption of the frequent fire regime at low- and high-elevation sites. We measured forest density, basal area, canopy cover, age structure, species composition, and regeneration, applying dendroecological methods to reconstruct past forest structure.

Then we compared these measurements with evidence compiled from climate research, forest regeneration studies, historical data on timber harvest, an extensive body of knowledge on the Kaibab deer herd (one of the world's best-studied and most influential examples of wildlife management), and cultural sources of information on livestock grazing practices. This information was interpreted in light of our forest structural findings to address two additional questions: to what extent can the individual influences of fire disturbance, livestock grazing, deer herbivory, tree cutting, and climate be assessed? Finally, has natural forest structure been maintained at remote sites where fire regimes were not completely disrupted?

METHODS

Study area

The study sites formed a geographical gradient (island → peninsula → mainland) on the North Rim, including three remote sites that have maintained the most nearly undisrupted fire regime documented in Arizona (Table 2). Elevation increased along the gradient from 2256 m (ponderosa pine/Gambel oak forest) to 2537 m (mixed conifer forest). To distinguish geographical from elevational effects, we also selected a low-elevation (2264 m) pine/oak mainland site on the South Rim and adjacent Kaibab National Forest. The study sites totaled 1755 ha (Table 2, Fig. 1), all within Grand Canyon National Park except a 207-ha Kaibab National Forest site (southern twenty-three plots in Fig. 1). Soils at the North Rim sites are predominantly of the Soldier series, derived from Kaibab limestone (Bennett, 1974). Soils at the Grandview (South Rim) site are classified as fine, smectitic, mesic, Vertic Paleustalfs and Haplustalfs, clay soils weathered from calcareous sandstone parent material (B. Lindsay, National Resource Conservation Service, personal communication, 2000). Average annual precipitation at the North Rim ranger station (elevation 2542 m) is 58.4 cm, with an average annual snowfall of 328 cm. Temperatures range from an average July maximum of 26 °C to an average January minimum of -2 °C. At the South Rim (elevation 2125 m), average annual precipitation is 36.8 cm with an average annual snowfall of 177.5 cm; average July maximum temperature is 29 °C and average

Table 2 Study site characteristics, listed from lowest to highest elevation. The Kaibab Forest and Grandview sites are located on the South Rim. The following four sites form a geographical and elevational transect from west to east on the North Rim. Fire regime data from Fulé *et al.* (in review)

Study site	Code	Area (ha)	No. plots	Elevation (m)	Geographic position	Average slope (%)	Vegetation type	WMPI _{25%} *	Fire regime disruption†
Kaibab Forest	KF	207	23	2244–2284	South Rim, mainland	11.5	Ponderosa pine/Gambel oak	8.94	1887
Grandview	GV	603	67	2250–2274	South Rim, mainland	11.5	Ponderosa pine/Gambel oak	8.94	1887, then prescribed burns in some portions in 1980s
Powell Plateau	PP	315	36	2256–2336	North Rim, island	11.5	Ponderosa pine/Gambel oak	8.56	1879, then fires in 1892, 1924 and 1987
Fire Point	FP	135	15	2308–2368	North Rim, peninsula	9.9	Ponderosa pine/Gambel oak	6.25	1879, then fires over western 1/3 of site in 1923 and 1989
Rainbow Plateau	RP	225	25	2305–2335	North Rim, peninsula	23.2	Ponderosa pine/Gambel oak	7.53	1879, then fires in 1900, 1985, and 1993
Swamp Ridge	SR	270	30	2427–2537	North Rim, mainland	13.3	Mixed conifer: ponderosa pine, white fir, Douglas-fir	8.70	1879

*WMPI_{25%} = Weibull Median Probability Interval, a probabilistic measure of central tendency in a Weibull distribution fit to fire interval data (Swetnam & Baisan, 1996) for fires scarring 25% or more of the sample trees. These fires are presumably relatively large, crossing much or all of each study site. At each site, the WMPI is calculated from c. 1700 to the fire regime disruption date listed in the last column.

†Disruption date of the frequent fire regime which prevailed prior to European settlement.

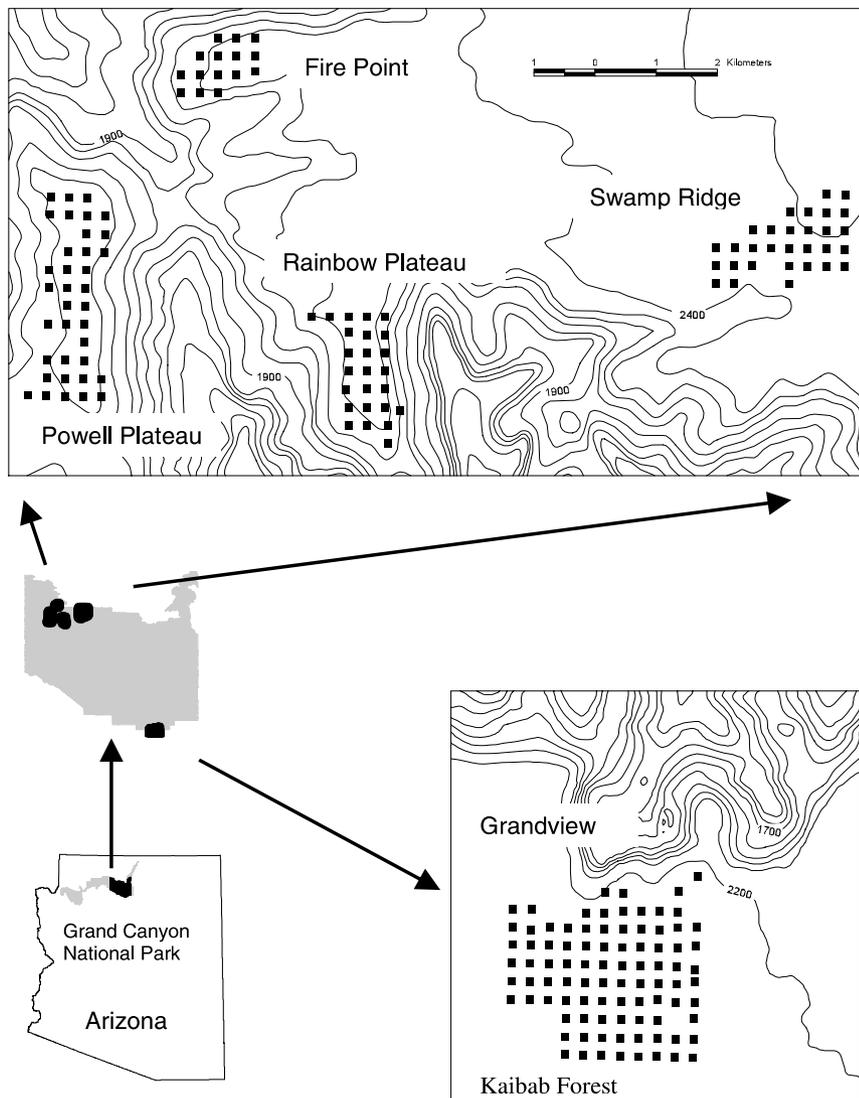


Figure 1 Study sites on the North and South Rims of Grand Canyon National Park and adjacent Kaibab National Forest on the South Rim. A biogeographical and elevational gradient is formed from the western point/plateau sites – Powell Plateau, Fire Point, and Rainbow Plateau – to the ‘mainland’ Swamp Ridge site. The South Rim ‘mainland’ sites – Grandview and Kaibab Forest – are similar in elevation to the western point/plateau sites but differ in the recent fire disturbance regime. Dark squares are locations of sampling plots.

January minimum temperature is -1°C (Bennett, 1974; Sellers & Hill, 1974; GCNP, 1992; White & Vankat, 1993). All sites were used by native Americans for resource use; all but the SR site were occupied at least seasonally for farming (Altschul & Fairley, 1989). Resource use by European settlers – livestock grazing, tree cutting, mining and tourism – began around 1870 on the North Rim, 1887 on the South Rim (Verkamp, 1940; Altschul & Fairley, 1989). All the study sites had frequent fire regimes prior to European settlement, but fires ceased at the ‘mainland’ sites SR and GV/KF after 1879 and 1887, respectively. Fire regimes were also altered after 1879 at the isolated point/plateau sites but each of these sites had two or three large surface fires since 1879 (Table 2).

Field methods

Permanent plots based on the National Park Service’s Fire Monitoring protocol (NPS, 1992; Reeberg, 1995) were used

to measure current conditions of vegetation and fuels, and to collect dendroecological data for reconstruction of past forest structure. The forest sampling type was defined as at least 10% ponderosa pine forest cover prior to European settlement, based on the presence of pre-1880 era trees, snags, stumps, or logs. In mixed species stands, ponderosa pine must have been a dominant tree in the stand with old individuals (or remnants) present. Sampling plot origins were located from a systematic 300 m grid placed over each sampling site. When a gridpoint fell in an unsuitable location (e.g. archaeological site), the points 50 m N, E, W, and S were checked for suitability. If none were acceptable, the gridpoint was discarded.

Sampling plots were 0.1 ha (20×50 m) in size, orientated with the 50 m sides uphill–downhill to maximize sampling of variability along the elevational gradient and to permit correction of the plot area for slope. Plot corners and centres were marked with 30-cm iron stakes sunk flush to the forest

floor. The distance and bearing from a tagged reference tree to the centre was recorded. Trees greater than 15 cm diameter at breast height (dbh) were measured on the entire plot (1000 m²) and trees between 2.5 and 15 cm dbh were measured on one quarter-plot (250 m²); all trees were tagged. Tree attributes measured were: dbh, crown position (dominant, codominant, intermediate or subcanopy), damage, and tree condition (1. live; 2. declining; 3. recent snag; 4. loose bark snag; 5. clean snag; 6. snag broken above breast height; 7. snag broken below breast height; 8. downed dead tree; and 9. cut stump). The condition categories were derived from snag decomposition studies in dry ponderosa pine/mixed conifer forests in eastside Oregon and Washington (Maser *et al.*, 1979; Thomas *et al.*, 1979) and tested in Arizona (sensitivity analysis described below and in Fulé *et al.*, 1997). Previous research in northern Arizona showed that the pre-1880 status of trees could be conservatively identified in the field: ponderosa pines with dbh > 37.5 cm or ponderosa of any size with yellowed bark (White, 1985; Mast *et al.*, 1999), as well as all oaks, junipers, and pinyon trees > 17 cm (Barger & Ffolliott, 1972). 'Conservative' estimation meant that these criteria included all pre-1880 trees as well as numerous post-1880 trees. Tree status was later corrected in the laboratory using age data. One hundred percent of living trees meeting the field criteria above were considered potentially pre-1880 trees and were cored. Ten percent of all post-1880 live trees were also cored. Coring height was 40 cm above ground level, chosen to meet two objectives: first, to measure tree age, and second, to measure growth between the fire regime disruption date and the present (needed for the forest reconstruction). The two objectives conflict because the best coring height for age is ground level, but the butt swell and irregular growth around the root collar make this an inappropriate height for growth measurement. The 40-cm height is the lowest position on the bole for consistency of tree form, permitting a good measurement of growth. Seedling trees, those below 2.5 cm dbh, were tallied by species, condition, and height class in a 50-m² subplot.

Canopy cover measured by vertical projection (Ganey & Block, 1994) was recorded at 30 cm intervals on two 50-m point intercept transects along the outer plot edges (total of 332 intercept points). Photopoints were established at the corners and quarter-corners of each plot.

Laboratory methods

Plot areas were corrected for slope. Tree increment cores were surfaced and visually crossdated (Stokes & Smiley, 1968) with tree-ring chronologies we developed. Rings were counted on cores that could not be crossdated, especially younger trees. Additional years to the centre were estimated with a pith locator (concentric circles matched to the curvature and density of the inner rings) for cores that missed the pith (Appelquist, 1958). Past forest structure was reconstructed at the time of disruption of the frequent fire regime 1887 at the South Rim sites and 1879 at the North Rim sites, following dendroecological methods described in

detail by Fulé *et al.* (1997). Briefly, size at the time of fire exclusion was reconstructed for all living trees by subtracting the radial growth measured on increment cores since fire exclusion. For dead trees, the date of death was estimated based on tree condition class using diameter-dependent snag decomposition rates (Thomas *et al.*, 1979) or historical harvesting records for stumps. To estimate growth between the fire exclusion date and death date, we developed local species-specific relationships between tree diameter and basal area increment ($r^2 = 0.45\text{--}0.90$). An analogous process of growth estimation was used to estimate the past diameter of the small proportion of living pre-1880 trees for which an intact increment core could not be extracted because of rot.

RESULTS

Contemporary forest structure

Ponderosa pine was the predominant species at each site (Table 3), making up 73–97% of basal area everywhere except the high-elevation SR site (48%). Gambel oak was second in basal area at all the sites but SR, where white fir, quaking aspen, and Douglas-fir followed ponderosa pine in basal area. Other species, especially New Mexican locust and Rocky Mountain pinyon, were found at several sites but never represented more than 0.4 m² ha⁻¹ of basal area. Utah juniper was found only at the South Rim sites, while quaking aspen, Douglas-fir, and New Mexican locust were encountered only on the North Rim. Patterns of tree density (Table 3) often contrasted with basal area: pines were in the minority everywhere except the South Rim GV and KF sites. Oaks accounted for 20–70% of the total trees ha⁻¹ across the sites, except at SR where non-pine species made up 83% of tree density. New Mexican locust constituted 30% of trees at the FP site.

Forest age distributions at each site were uneven-aged and generally dominated by relatively young trees that established after fire regime disruption (Fig. 2). Of a total of 2597 cored trees, 2092 were dated (81%). As all but the KF sites were never harvested, the age distributions represent unusually complete records of old trees. Ponderosa pine trees made up the majority of pre-disruption trees at each site. The oldest trees by species had centre dates of: ponderosa pine 1537, Gambel oak 1650, Utah juniper 1770, white fir 1793, Douglas-fir 1796, aspen 1813, New Mexican locust 1904, and Engelmann spruce 1932. Sprouting species (Gambel oak, quaking aspen) predominated in the early regeneration after fire regime disruption, generally 1880–1920. Exceptions were FP, where very little oak was found, and SR, where pre-1880 white fir establishment equalled or exceeded aspen establishment in nearly every 20-year period. The only areas where ponderosa pine establishment was dominant after settlement were the adjacent GV and KF sites, beginning in the 1921–1940 period.

Regeneration (Table 4) was categorized as trees < 30 cm in height (new seedlings or sprouts), trees between 30 cm and 2 m in height (established seedlings or sprouts), and trees > 2 m in height, up to 2.5 cm dbh (saplings). The

Table 3 Forest structure (trees ≥ 2.5 cm dbh) at Grand Canyon study sites in 1997 or 1998. Species codes are derived from the genus and species (e.g. ABCO = *Abies concolor*). Statistics presented are the mean (standard error), and minimum–maximum

Site	Total	ABCO	JUOS	PIED	PIPO	POTR	PSME	QUGA	RONE
<i>Density (trees ha⁻¹)</i>									
KF	689.3 (242.8)			2.6 (1.9)	540.7 (233.9)			146.0 (53.2)	
	10.0–5481.1			0–40.1	0–5301.1			0–1241.0	
GV	955.1 (147.4)	1.2 (1.2)	9.9 (2.4)	3.9 (1.7)	645.7 (140.7)			292.5 (50.2)	
	120.1–9354.2	0–81.2	0–90.0	0–80.7	20.0–9214.1			0–1893.8	
PP	638.1 (102.5)				249.3 (32.6)			289.4 (89.3)	99.4 (45.4)
	70.1–2944.9				60.1–953.5			0–2811.5	0–1524.9
FP	388.8 (119.3)			0.7 (0.7)	192.8 (24.0)			79.1 (63.6)	116.3 (86.3)
	50.0–1590.1			0–10.3	50.0–340.6			0–946.1	0–1272.0
RP	935.8 (180.0)	6.4 (6.4)		0.4 (0.4)	208.8 (35.6)	7.3 (7.3)		653.2 (175.1)	59.5 (26.1)
	100.3–2707.1	0–160.5		0–10.1	10.4–583.5	0–183.4		0–2661.7	0–567.0
SR	940.7 (104.3)	466.5 (62.3)			156.6 (22.9)	255.8 (59.8)	56.3 (19.9)		5.6 (5.6)
	309.2–2417.7	0–1132.5			20.2–524.4	0–1411.1	0–475.3		0–168.0
<i>Basal area (m² ha⁻¹)</i>									
KF	14.1 (2.1)		0.03 (0.03)	0.02 (0.02)	10.3 (1.9)			3.8 (0.8)	
	2.1–34.9		0–0.8	0–0.5	0–33.1			0–13.6	
GV	22.9 (1.0)	0.002 (0.002)	0.5 (0.2)	0.02 (0.01)	16.8 (1.0)			5.5 (0.7)	
	6.4–48.4	0–0.1	0–7.0	0–0.7	1.0–44.1			0–26.5	
PP	26.3 (1.7)				24.4 (1.5)			1.7 (0.6)	0.3 (0.12)
	8.4–51.9				8.4–50.0			0–19.0	0–3.7
FP	31.4 (3.2)			0.01 (0.01)	30.5 (3.2)			0.7 (0.5)	0.2 (0.1)
	11.2–56.7			0–0.2	11.2–56.7			0–7.0	0–1.3
RP	27.2 (2.5)	0.06 (0.06)		0.01 (0.01)	21.8 (2.7)	0.007 (0.007)		5.0 (1.2)	0.4 (0.2)
	2.7–53.1	0–1.5		0–0.3	0.8–52.8	0–0.2		0–21.4	0–5.2
SR	41.3 (1.9)	14.5 (1.2)			19.9 (1.9)	5.3 (1.0)	1.6 (0.6)		0.004 (0.004)
	18.5–62.2	0–26.8			1.6–39.8	0–19.7	0–10.0		0–0.1

species that reproduce primarily by sprouting, Gambel oak, New Mexican locust, and quaking aspen, dominated regeneration density at all sites except SR. Conifers had substantially lower densities, except for new white fir seedlings at SR. Regeneration was highly variable: minimum per-plot regeneration density was zero at all sites and standard errors were high relative to means.

Canopy cover ranged from 36.4% at KF (the only site where trees had been harvested) to 63.2% at SR (Table 5). The other four sites were within 5% of each other in average canopy cover. Although the means were similar, per-plot extremes ranged widely. The RP site had the greatest range, from the lowest minimum of any site (0.3%) to the highest maximum (85.5%). Overall variability was greatest at GV, where the standard error as a proportion of the mean (17.9%) was over four times greater than that of the next closest site, RP (4.3%). Canopy cover was correlated with basal area ($r = 0.65$) with a predictive relationship explaining 42% (adjusted r^2) of the variation.

Changes since fire-regime disruption

Although a consistent methodology was used at all sites to estimate past forest structure, differences in environmental conditions, species characteristics, and management history can influence the accuracy of reconstruction and interpretation of results. Limitations and interpretations

are discussed in ‘Assessment of reconstruction data’, below.

Increases in total tree density since fire regime disruption (1887 South Rim, 1879 North Rim) were statistically significant at every site except FP (paired t -test, $P < 0.05$); density increases ranged from 155 (FP) to 581% (GV) (Table 6). Even without including New Mexican locust, a small-stature and short-lived species that is poorly suited for dendroecological reconstruction techniques, the range of increase in tree density was high: 78% (FP) to 582% (GV). Presently dead trees (i.e. trees dead in the current inventory but reconstructed as living at the time of fire regime disruption) comprised the following proportion of reconstructed density: 43 (KF), 32 (GV), 27 (PP), 37 (FP), 29 (RP), and 58% (SR). Total basal area increases were statistically significant at every site except KF; basal area increases ranged from 12 (KF) to 152% (GV). Presently dead trees comprised the following proportion of reconstructed basal area: 86 (KF), 43 (GV), 31 (PP), 40 (FP), 37 (RP), and 69% (SR). The reconstructions were relatively insensitive to changes in decomposition rates. Comparing the twentyfifth and seventyfifth decomposition percentiles with the fiftieth percentile, reconstructed tree densities varied by 1.9% (range 0–8.8%) and basal areas varied by 4.8% (range 2.3–15.0%).

Ponderosa pine dominated all the study sites at the time of disruption. Ponderosa pine density was higher in the

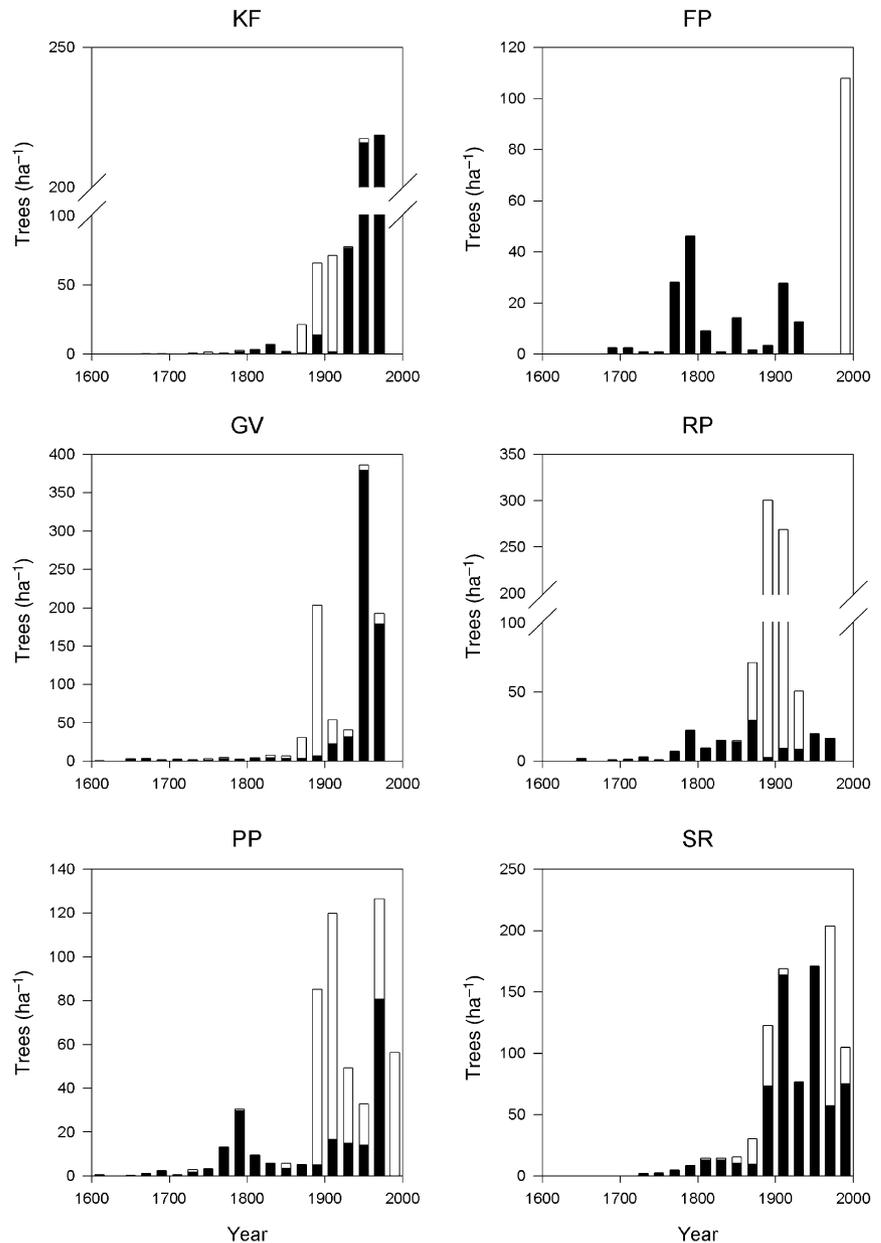


Figure 2 Tree age distributions (centre date at increment coring height of 40 cm). Black bars are coniferous species, all obligate seeders. White bars are deciduous species, all strong sprouters.

contemporary forest at all sites, but the increase was significant only at sites GV and PP (paired *t*-test, $P < 0.05$). Ponderosa basal area increased significantly at all but the KF, RP and SR sites. At KF, the contemporary pine basal area might have been expected to be similar to that of the adjacent GV site except for the harvesting of 12.5 m² ha⁻¹ of large ponderosa trees.

Tree density changes as disruption differed by mode of regeneration, seeding vs. sprouting (Fig. 3). Since disruption, seed-reproducing pine populations increased substantially (743–993%) at the two South Rim sites and mesic conifer species, especially white fir, increased nearly 1500% at SR. On the western North Rim, however, where post-settlement

fire regimes were the least disrupted (see Table 2 for the dates of post-1879 fires), the densities of pines increased only slightly to moderately: 65% at PP, 27% at FP, and 34% at RP. Sprouting species (Gambel oak at all sites but SR, quaking aspen at SR) increased substantially in basal area and density at all sites, but the greatest proportional increase occurred on the western North Rim where oaks rose from 1 to 6% of the pre-disruption tree density to 20–70% of contemporary density. The proportion of oak basal area increased much less, as most of the oaks were small in diameter.

Stumps provided evidence of past tree cutting at the KF site, averaging 141.2 trees ha⁻¹ (SEM = 34.8, range

Table 4 Regeneration density (trees ha⁻¹) at Grand Canyon study sites in 1997 or 1998. Statistics presented are the mean (standard error), and minimum–maximum

Site	Total	ABCO	JUOS	PIED	PIPO	POTR	PSME	QUGA	RONE
<i>Regeneration 0–30 cm in height</i>									
KF	506.0 (202.1)				17.4 (12.0)			488.5 (200.5)	
	0–3630.3				0–200.1			0–3630.3	
GV	3084.4 (496.1)		6.0 (4.2)	3.0 (3.0)	122.9 (35.5)			2952.6 (495.0)	
	0–23204.6		0–202.9	0–200.4	0–1411.8			0–23204.6	
PP	2596.3 (822.0)				44.9 (21.5)			2238.0 (803.0)	313.4 (106.6)
	0–25061.2				0–600.8			0–25061.2	0–3231.2
FP	1757.6 (1035.9)				228.2 (146.1)			905.0 (905.0)	624.4 (312.5)
	0–15014.6				0–2204.0			0–13,574.8	0–3509.1
RP	3094.5 (795.1)				158.0 (98.0)			1980.2 (669.3)	956.3 (304.1)
	0–13572.4				0–2345.8			0–12361.6	0–5220.2
SR	5304.4 (1032.7)	2397.0 (691.1)			54.1 (25.6)	2185.5 (628.9)	27.0 (21.1)	640.9 (346.8)	
	0–26833.5	0–13126.8			0–602.4	0–16020.0	0–606.7		0–9011.2
<i>Regeneration 30 cm to 2 m in height</i>									
KF	985.9 (457.2)				43.7 (35.7)			942.1 (458.1)	
	0–7806.2				0–805.7			0–7806.2	
GV	700.6 (255.5)	3.0 (3.0)	23.9 (13.8)	9.0 (6.7)	110.7 (57.9)			553.9 (252.2)	
	0–15203.0	0–202.9	0–800.0	0–400.1	0–3601.6			0–15203.0	
PP	2661.4 (547.1)				61.4 (30.8)			1425.5 (480.0)	1174.5 (306.4)
	0–13574.8				0–1005.0			0–13574.8	0–3821.7
FP	1659.8 (678.5)				721.0 (380.5)			575.9 (575.9)	362.8 (179.1)
	0–8844.2				0–5409.7			0–8638.5	
RP	3749.3 (1212.7)				65.2 (43.2)	9.2 (9.2)		1457.5 (845.9)	2217.3 (699.8)
	0–27390.5				0–1001.8	0–229.2		0–20542.9	0–13242.2
SR	3411.3 (796.3)	1653.2 (441.6)			40.8 (18.0)	1362.9 (503.4)	6.7 (6.7)	347.7 (197.8)	
	0–19563.2	0–9479.1			0–406.4	0–10084.1	0–202.2		0–4619.8
<i>Regeneration greater than 2 m in height</i>									
KF	69.6 (61.1)				8.8 (8.8)			60.9 (60.9)	
	0–1400.3				0–201.4			0–1400.3	
GV	66.2 (27.1)		6.0 (6.0)		32.9 (21.5)			27.3 (16.5)	
	0–1400.1		0–400.1		0–1400.1			0–1000.2	
PP	559.5 (232.1)							386.5 (201.5)	173.0 (79.2)
	0–6010.8							0–5080.4	0–2407.7
FP	333.0 (150.9)				174.9 (91.5)			41.1 (41.1)	117.0 (117.0)
	0–1973.9				0–1202.2			0–617.0	0–1754.5
RP	151.9 (84.8)					9.2 (9.2)		41.8 (41.8)	101.0 (49.0)
	0–1879.3					0–229.2		0–1044.0	0–835.2
SR	148.3 (70.4)	60.6 (36.4)				74.2 (39.3)	13.4 (9.3)		
	0–2016.8	0–1008.4				0–1008.4	0–202.2		

Table 5 Canopy cover (measured by vertical projection) at Grand Canyon study sites in 1997 or 1998

Study site	N (no. of plots)	Minimum (%)	Maximum (%)	Mean (%)	SEM (%)
KF	23	6.7	66.6	36.4	3.2
GV	67	11.4	84.6	47.1	17.9
PP	36	15.4	79.2	49.7	2.1
FP	15	8.7	82.8	51.7	4.2
RP	25	0.3	85.5	48.3	4.3
SR	30	31.6	84.9	63.2	2.2

0–540 trees ha⁻¹). Eighty-nine percent of the cut trees were ponderosa pine; the remainder was Gambel oak. Trees less than 40 cm dbh, probably cut in thinning treatments or for firewood collection, made up 81.9 pines ha⁻¹ and 14.5 oaks ha⁻¹. Trees over 40 cm dbh, predominantly pines cut for lumber production, averaged 43.5 pines ha⁻¹ and 1.7 oaks ha⁻¹. The total basal area removed in all cutting was 12.6 m² ha⁻¹, 98% of which was ponderosa pine > 40 cm dbh. Within Grand Canyon National Park, tree cutting at the Grandview site averaged 6.5 trees ha⁻¹ (SEM = 1.7, range 0–60 trees ha⁻¹). On the North Rim, the FP site averaged 2.0 cut trees ha⁻¹ (SEM = 1.5, range 0–20 trees ha⁻¹) and the SR site averaged 0.7 cut trees ha⁻¹ (SEM = 0.7, range 0–20.1 trees ha⁻¹). No cut trees were encountered on plots at the PP and RP sites, but infrequently we observed stumps off plots.

DISCUSSION

Changes in Grand Canyon forests: assessment of reconstruction data

We reconstructed past forest conditions on the same sites where we measured contemporary conditions. Age and past growth were measured directly on increment cores from living trees of pre-1880 origin. However, many trees alive at the time of fire regime disruption have died. Dendroecological reconstruction of past south-western forest conditions is based on the persistence of dead woody material such as snags, logs, and stumps from 1879 to present (Covington & Moore, 1994; Fulé *et al.*, 1997). These methods have recently been tested quantitatively in northern Arizona. Mast *et al.* (1999) demonstrated that ponderosa pine wood persisted since at least 1876 at the Gus Pearson

Table 6 Reconstructed forest structure (trees ≥ 2.5 cm dbh) at Grand Canyon study sites at the date of the final fire of the pre-European settlement frequent fire regime 1887 at the South Rim sites (KF and GV) or 1879 at the North Rim sites. Species codes are derived from the genus and species (e.g. ABCO = *Abies concolor*). Statistics presented are the mean (standard error), and minimum-maximum

Site	Total	ABCO	JUOS	PIED	PIPO	POTR	PSME	QUGA	RONE
<i>Density (trees ha⁻¹)</i>									
KF	144.9 (31.1) 20.0–560.3		0.4 (0.4) 0–10.0		72.3 (15.8) 20.0–390.1			72.2 (28.3) 0–489.7	
GV	140.2 (14.0) 10.1–610.1		8.2 (3.2) 0–170.1	0.1 (0.1) 0–10.0	65.0 (6.5) 0–287.3			66.9 (13.3) 0–600.1	
PP	157.1 (23.3) 20.2–646.2		0.3 (0.3) 0–10.3		151.5 (23.5) 20.2–646.2			5.4 (2.8) 0–92.3	
FP	152.6 (20.3) 40.0–310.2				151.1 (20.4) 40.0–310.2			1.5 (1.5) 0–21.9	
RP	159.7 (25.6) 20.0–562.2	0.9 (0.9) 0–22.9			155.7 (26.1) 20.0–562.2			3.1 (2.2) 0–45.8	
SR	245.7 (12.9) 90.1–373.6	31.8 (5.2) 0–90.1			131.5 (10.7) 20.2–261.6	67.9 (14.1) 0–250.3	14.6 (4.5) 0–80.9		
<i>Basal area (m² ha⁻¹)</i>									
KF	12.6 (1.5) 3.3–30.4		0.01 (0.01) 0–0.2		11.5 (1.4) 3.1–30.4			1.1 (0.3) 0–5.4	
GV	9.1 (0.6) 0.3–22.8		0.3 (0.1) 0–4.7	0.0004 (0.0003) 0–0.02	7.9 (0.6) 0–22.1			0.8 (0.2) 0–8.2	
PP	17.9 (2.5) 4.7–77.3		0.02 (0.02) 0–0.7		17.8 (2.5) 4.6–77.3			0.1 (0.05) 0–1.5	
FP	20.5 (2.1) 6.5–30.2				20.5 (2.1) 6.5–30.2			0.01 (0.01) 0–0.2	
RP	17.0 (2.9) 4.4–64.5	0.2 (0.2) 0–4.7			16.8 (2.9) 4.4–64.5			0.02 (0.01) 0–0.2	
SR	28.5 (1.8) 15.1–54.0	3.4 (0.6) 0–12.0			21.3 (2.0) 5.5–49.7	1.1 (0.3) 0–6.1	2.7 (0.8) 0–15.2		

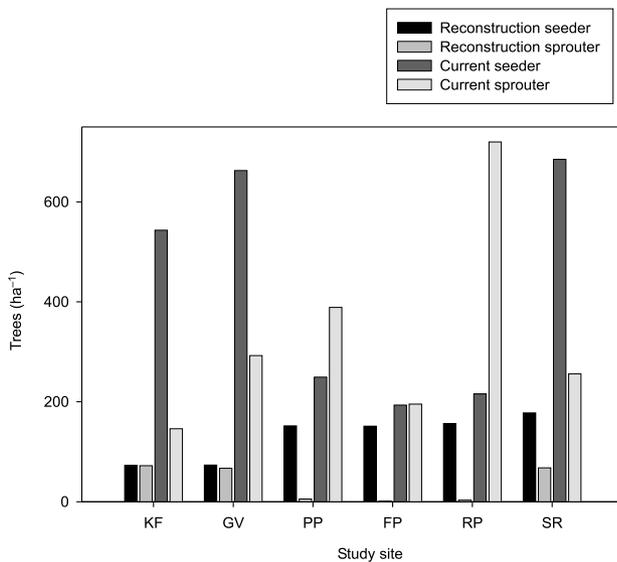


Figure 3 Relative dominance by seed-reproducing species and sprouting species in reconstructed 1887 (South Rim) or 1879 (North Rim) forest and in current forest conditions. Fire-excluded sites KF, GV, and SR show large increases in seed-reproducing conifer species. Seeders remained relatively constant while sprouters increased at PP, FP, and RP, where either two or three large spreading surface fires occurred after 1879.

Natural Area (about 75 km south of the GV study site) and could be reliably identified in the field as to pre-1880 vs. post-1880 origin. On adjacent sites, Huffman *et al.* (2001) reconstructed ponderosa pine densities on 90-year-old-historically measured plots (trees ≥ 10.2 cm in 1909), finding that errors caused by missed evidence of dead trees averaged only 3.2 trees ha^{-1} , less than 6% of local historic tree density.

Applying this method in a nearby mixed-species forest, however, Fulé *et al.* (1997) suggested that it had limited applicability for New Mexican locust, a small in diameter, short-lived species. The absence of pre-1880 locust evidence was interpreted as more likely to have been caused by decay than to increased locust density in contemporary forests (Fulé *et al.*, 1997) – although there is evidence from elsewhere in northern Arizona that dense locust sprouting is associated with overstory tree harvesting and fire exclusion (Gottfried, 1980). Other species have intermediate characteristics: trees such as Gambel oak, quaking aspen, white fir, and the other species encountered at Grand Canyon are capable of reaching large size and multicentury lifespans. But these species lack the decay-resistant chemical structure of ponderosa pine and may have more rapid decay rates, especially white fir (Laacke, 1990) and Gambel oak, which are susceptible to heart rots that often initiate the wood decay process even before tree death.

Site and disturbance factors also influence reconstruction accuracy. Decay rates are likely to be less limited by moisture at the high-elevation SR site. Post-1880 surface

fires at PP, FP and RP, and prescribed burning of part of the GV site may have consumed evidence of some trees of pre-1880 origin. The effect of missing evidence would be to widen the gap between pre-disruption and current forest densities. As these sites actually had the greatest agreement between 1879 and current forest structures for seed-reproducing species, the conclusions of relatively little change at these sites are strengthened. Utilization of wood resources and treatment of logging residues have been limited or non-existent at the park sites but could have affected pre-1880 evidence at the KF site. Contemporary and pre-disruption basal area values within sites were significantly correlated ($P < 0.05$) at the unharvested park sites GV, PP, FP and RP ($r = 0.60$ – 0.68), but correlations were much lower at the SR site (0.47) and non-significant at the harvested KF site ($r = 0.24$). In sum, reconstructions should be considered most accurate for sites with the least disturbance and for species with the greatest resistance to decay (ponderosa pine, Utah juniper, Rocky Mountain pinyon and Douglas-fir).

Multiple lines of evidence

Historical evidence from a variety of sources supports the trend of changes found at the study sites. On the South Rim, Woolsey (1911) reported a mean of twenty-six pines over 15.2 cm dbh per hectare on ‘average’ stands in timber-sale areas on the Tusayan National Forest (including the present-day KF site but also forests to the south around Williams, AZ) and a mean density of eighty-five pines over 10.2 cm dbh ha^{-1} on ‘maximum’ stands in the adjacent Coconino National Forest. Reconstructed pine densities at the GV site were 59.4 pines > 15.2 cm dbh ha^{-1} and 61.7 pines > 10.2 cm dbh ha^{-1} ; the KF site had 67.1 pines > 15.2 cm dbh ha^{-1} and 71.4 pines > 10.2 cm dbh ha^{-1} . A 1909 photograph ‘south of Grand View’ shows an open and apparently unharvested forest structure of large trees (Fig. 4).

On the Kaibab Plateau, the Lang & Stewart (1910) survey reported stand averages over a 202-ha area in the ponderosa pine type of 128.1 pines > 15.2 cm dbh ha^{-1} . For comparison, the PP, FP, and RP sites averaged 141.4, 136.4 and 124.8 pines > 15.2 cm dbh ha^{-1} in the 1879 reconstruction and 141.2, 148.5, and 147.8 pines > 15.2 cm dbh ha^{-1} in the contemporary forest – nearly no change in pine density over *c.* 120 years. An example of the PP forest structure is shown in Fig. 5. In mixed conifer, Lang & Stewart (1910) reported density averages for trees > 15.2 cm dbh of: ponderosa pine 45.7 trees ha^{-1} , Douglas-fir 16.8 trees ha^{-1} , ‘balsam’ [white] fir 30.5 trees ha^{-1} , and spruce 115 trees ha^{-1} . At the SR site, trees > 15.2 cm dbh in the 1879 reconstruction averaged: ponderosa pine 122.1 trees ha^{-1} , Douglas-fir 14.2 trees ha^{-1} , white fir 28.1 trees ha^{-1} , and no spruce. The higher pine density and absence of spruce at SR suggests that Lang & Stewart’s (1910) sampling site was at higher elevation than SR. Other structural studies on the Kaibab Plateau found 99–111 pines ha^{-1} (Rasmussen, 1941) and an average of 138 pines ha^{-1} in a dendroecological reconstruction of 1880 conditions (Covington & Moore,



Figure 4 1909 photograph by G.A. Pearson: 'Tusayan National Forest ... showing typical group arrangement of age classes. South of Grand View.' USDA Forest Service, Rocky Mountain Research Station, Historical Archives, Flagstaff, AZ.

1992). Moore *et al.* (1999) noted that pre-1880 ponderosa pine densities on the coarse-textured limestone soils of the Kaibab Plateau were about twice as high as on fine-textured basalt soils elsewhere in northern Arizona.

Lang & Stewart (1910, p. 8) noted that 'the pine occurs mostly in open stand [sic] park-like or even isolated in character... all age classes in varying density and proportions, but nowhere fully stocked.' They emphasized that 'forest fires have been the cause of incalculable losses... Vast denuded areas, charred stubs and fallen trunks and the general prevalence of blackened poles [illustrate] their frequency and severity long before this country was explored by white men... Evidence indicates light ground fires over practically the whole forest, some of the finest

stands of yellow pine show only slight charring of the bark and very little damage to poles and undergrowth' (Lang & Stewart, 1910, pp. 18–19). Dutton (1882, p. 136) observed that 'the trees are large and noble in aspect and stand widely apart, except in the highest parts of the plateau where the spruces predominate. Instead of dense thickets where we are shut in by impenetrable foliage, we can look far beyond and see the tree trunks vanishing away like an infinite colonnade.' B. Vaughn, a cowboy with the Grand Canyon Cattle Company, recalled being able to 'see a cow a half mile (0.8 km) in ponderosa country (c. 1924), but now brush has grown up... Fires started on the points and burned through needles and small growth but didn't do much damage to larger trees...



Figure 5 1997 photograph in the Powell Plateau (PP) study site. Sporadic surface fires occurred at Powell Plateau after 1879. The site is characterized by groups of large trees, productive understory communities, and crownfire-resistant fuel complexes.

Indians burned areas near the rim when they were gathering piñon nuts to make the gathering easier' (Fossey, 1974). C. Wagner, a forester with the Park Service in 1935, described seeing through the pine forest for 'three-eighths of a mile (0.6 km)... unobstructed. There was no amount of undergrowth at all. At that time they had the heavy deer population on the North Rim. No young oak or aspen or anything' (Winchester, 1994).

The ponderosa pine age distribution on the North Rim was unusually young for this species and region (Fig. 2). Few trees predated 1650 and 95.5% of the pre-1880 tree population was less than 300 year old-in 1998. The oldest tree encountered had a centre date of 1537 (site PP). In contrast, trees up to 540-year-old were encountered at the unharvested Gus Pearson Natural Area (Mast *et al.*, 1999) and at Mt Logan, about 70 km west of the North Rim sites (Waltz & Fulé, 1998). Two hypotheses could explain the short age distributions found on the North Rim: first, forests could have been affected by a stand-replacing disturbance, such as severe fire, before 1700. In central Colorado, Brown *et al.* (1999) suggested that a 'stand-destroying event' could explain the relatively young trees on an unharvested study site. However, the fire history reconstructed by Brown *et al.* (1999) included fire-free gaps up to 128 years long, allowing for increases in dead and living fuels to support such a fire. The North Rim fire histories, although temporally limited by the relatively young ages of sampled trees, show steady, frequent fires from the early 1700s through 1879, with no indication of extended gaps (Fulé *et al.*, in review). A second hypothesis is that North Rim ponderosa pines, growing on coarse-textured limestone soils, may have shorter lifespans than their counterparts on fine-textured basalt soils. Wind-thrown trees were commonly observed on the study sites.

The early increase in populations of sprouting species, coinciding with the exclusion of fire, is consistent with the continual reproductive capability of oaks and aspen. Under the frequent fire regime oaks may have maintained relatively dense sprouts but few would survive repeated surface fires. Once fires stopped, however, thickets of young ramets would be well-positioned to become sapling and pole thickets. At Camp Navajo, concurrent ponderosa pine harvesting may have facilitated oak dominance by removing pine seed sources (Fulé *et al.*, 1997). But at the Grand Canyon sites, pine harvesting occurred only after oak regeneration at KF and early oak reproduction was extensive even at the unharvested GV, PP, and RP sites.

Interacting factors of change

Climate

The spread of ponderosa pine forests across the Colorado Plateau was associated with warming of climate since the latest Wisconsin period, *c.* 11,000–14,000 years BP (Anderson, 1989; Weng & Jackson, 1999). Over much shorter time periods, climatic fluctuation has been associated with tree establishment in south-western ponderosa pine (Savage *et al.*, 1996). However, an analogous climate-regener-

ation pattern was not observed in the present study. Grand Canyon tree establishment dates were not concentrated in the early twentieth century, in contrast to the pattern of high regeneration in 1919 and other favourable moisture years elsewhere in northern Arizona and the south-west (Schubert, 1974; Savage *et al.*, 1996; Grissino-Mayer & Swetnam, 2000). Regeneration of sprouting oak and aspen species began right after fire exclusion and the seed-reproducing species, ponderosa pine, white fir and Douglas-fir, regenerated at a relatively consistent rate through most of the post-settlement period (Fig. 2). Tree centre dates by species were not significantly correlated with the 20-year running average of Palmer Drought Severity Index (PDSI) reconstructed from dendrochronological data by Cook *et al.* (1996) for 1710–1950. We compared all dated trees with those where the estimated rings to pith were five or less. There were differences in the absolute numbers, because *c.* 50% of the trees had an estimate > 5 years to centre, but there was no difference in the pattern.

In discussing the exceptional ponderosa pine regeneration of 1919, Savage *et al.* (1996) recognized the novel circumstances of livestock grazing and fire exclusion which permitted dense seedling patches to flourish, but they speculated that the 1919 climate event might have caused a significant pine regeneration pulse even had these human-caused disruptions not occurred. This hypothesis is not supported by the Grand Canyon data: large increases in seed-reproducing species occurred only at the fire-excluded sites (KF, GV and SR), not at the sites where at least a few surface fires occurred after 1879 (PP, RP and ±FP). Pine density did increase significantly at PP, but statistical significance may not equate with ecological significance: the magnitude of the increase was small (98.2 trees ha⁻¹, a 65% increase) in comparison with increases in fire-excluded forests [hundreds to thousands of percent (Covington & Moore, 1992; Covington *et al.*, 1997; Fulé *et al.*, 1997)]. These patterns suggest that recent climatic factors were less influential in affecting forest structure, especially as compared with the human-caused factors described below.

Tree cutting

The Tusayan Ranger District (KF site) was one of the last forests in northern Arizona south of the Colorado River to be logged, because of its remoteness from the transcontinental railroad (Putt, 1995). The KF site was probably first logged between 1929 and 1931; a section of logging railroad crossed the south-eastern corner of the study site (Stein, 1993; Putt, 1995). Within Grand Canyon National Park, old stumps in the GV site date from a sawmill operated on the Berry/Hearst (Grandview Hotel) property to supply mine timbers (Sutphen, 1991). Trees were also cut in the Grandview site in dwarf mistletoe treatments (Lightle & Hawksworth, 1973), road and utility corridors, and 'insect treatments' on both rims, as well as cutting 1600 trees for telephone poles on the South Rim and lumber for the lodge at Bright Angel Point on the North Rim (Annual Superintendent's Reports, 1933 and 1936, on file at Grand

Canyon National Park). Pyne (1989) described snag cutting during fire suppression in the park.

Two implications arise from the tree cutting history. First, the unharvested park sites retain a legacy of old-growth trees that are missing from KF (Fig. 2). Second, tree cutting has long lasting effects. Approximately 60 years after timber harvest, pine density at KF was roughly equal to that of the unharvested GV site, 541 vs. 646 trees ha⁻¹ (Table 3). But basal area at KF was only 62% that of GV, 14.1 vs. 22.9 m² ha⁻¹, mostly because of a 6.5-m² ha⁻¹ difference in pine basal area (Table 3).

Fire exclusion and herbivory

Domestic and wild mammalian herbivores affected forests in at least three ways: disrupting frequent-fire regimes by removing fine fuels, facilitating tree regeneration by eliminating competing herbaceous plants, and direct herbivory of young trees. Belsky & Blumenthal (1997) suggested that focus on the effects of fire suppression and logging in the interior West has led to underestimation of the role of livestock grazing in causing ecological degradation. No understatement is evident in the south-west, where heavy livestock grazing by early European settlers has been consistently linked by numerous authors with the removal of fine fuels and interruption of frequent fire regimes throughout the south-west (e.g. Leopold, 1924; Cooper, 1960; Swetnam & Baisan, 1996). Heavy livestock grazing also coincided with fire regime disruption at both earlier and later dates than the typical 1870–1890 dates of European settlement of the south-west, indicating that grazing itself and not some coincidental factor was responsible for initiating fire exclusion. For example, grazing in the Rio Grande valley had local effects on fire regimes prior to 1800 (Baisan & Swetnam, 1997), Navajo sheep grazing led to fire cessation in north-eastern Arizona as early as 1830 (Savage & Swetnam, 1990), and increased grazing in northern Mexico resulted in fire regime disruptions as late as 1930–50 (Fulé & Covington, 1997, 1999).

In the Grand Canyon region, grazing of sheep and cattle was heavy on both rims since European settlement until the fencing of Park Service lands in the late 1930s. Ranches were established at Short Creek and Pipe Spring, on the Arizona–Utah border, as early as 1863 but the range was not available for livestock until the settlement of hostilities with Navajos in 1869 (Altschul & Fairley, 1989). The earliest quantified use of the ‘Kaibab mountain’ and surrounding areas was 1885–86, with about 2000 cattle; by 1887–89, use of the west-side ranges increased to 200,000 sheep and 20,000 cattle (Rasmussen, 1941). By 1909, Forest Service permits covered 14,000 head of cattle and horses, plus a band of 5000 sheep on the Kaibab Plateau (Lang & Stewart, 1910). Mace (1990: p. 68) described ‘hundreds’ of wild horses ranging over the Plateau at that time. Near Grandview, Hull cabin was constructed in 1888 as the base for a sheep ranching operation (Anderson, 1998).

Herbivory by wildlife increased substantially in the early twentieth century. Following the designation of the Grand Canyon Game Preserve in 1906, hunting was prohibited

and predator control efforts led to extirpation of the wolf and massive killing of mountain lions, coyotes, and other predators by 1931 (Rasmussen, 1941). The Kaibab deer population irrupted after 1905, reaching an estimated 100,000 head of deer in 1924 before declining because of starvation and government hunting programmes (Rasmussen, 1941; Mitchell & Freeman, 1993). Adams (1925) noted the ‘absence of young aspens caused mainly by overbrowsing by deer and stock’ on the North Rim (Adams, 1925, p. 589). Near Grandview, he observed that the ‘condition of the range in the forest and the park are equally bad, so that you cannot tell by the appearance of the range whether you are in the park or the forest’ (Adams, 1925, p. 585).

Irrupting deer herds have reduced tree recruitment in forests around the world: Japan (Abrams *et al.*, 1999), Patagonia (Veblen *et al.*, 1989) and the eastern USA (Abrams & Orwig, 1996). At Grand Canyon, mammalian herbivory influenced tree survival with long-term effects on forest structure (Rasmussen, 1941; Merkle, 1954, 1962; Mitchell & Freeman, 1993). Direct effects of excessive herbivory appear to be most evident at the SR site. Approximately 49 aspen trees ha⁻¹ survived from establishment in the first decades after fire exclusion (1880–1900), but then a long demographic gap occurred between 1900 and 1960 when less than 5 aspen trees ha⁻¹ established (Fig. 2). Trampling and exposure of bare mineral soil by deer and livestock may also have facilitated conifer regeneration (Mitchell & Freeman, 1993).

The consequences of elimination of approximately 60 years of aspen regeneration at SR may have far-reaching effects. In the absence of aspen regeneration and fire, white fir and Douglas-fir dominated the post-settlement regeneration of the mesic site, leading to a conifer-dominated forest that could support stand-replacing fire because of the dense forest floor, high fuel loading, and low canopy base heights (unpublished data). Intense burning occurred in the 1993 NWIII prescribed fire, adjacent to the SR site (unpublished data). Had excessive deer herbivory not occurred, the fuel structures of an aspen/pine forest would probably be less susceptible to crownfire and more conducive to long-term ponderosa pine survival, although white fir still may have come to predominate in the absence of fire.

Evidence of direct mammalian herbivory of tree species other than aspen is unclear because there are no apparent gaps in recruitment after fire exclusion. Aspen is by far the most palatable of the tree species on the study sites, but Adams (1925) noted grazing on oak and cliffrose as well and Rasmussen (1941, p. 254) photographed a ponderosa pine seedling repeatedly browsed by deer. Insect herbivory may also have played a role. Ponderosa pine defoliation by the pandora moth (*Coloradia pandora*) has been shown to interact with climate and fire regime fluctuations in Oregon (Speer, 1997). The Kaibab Plateau is the southernmost region where large-scale pandora moth outbreaks have occurred (Miller & Wagner, 1989).

Herbivory and fire exclusion are usually so interlinked that the relative importance of their separate influences on

increased tree recruitment is difficult to determine, but comparisons have been made at a few rare study sites (Belsky & Blumenthal, 1997). At Zion National Park (Utah) and on Meeks Table (Washington), dense ungrazed herbaceous plants appeared to have resisted the establishment of dense ponderosa pine seedlings even in the absence of fire (Rummel, 1951; Madany & West, 1983). The Grand Canyon study sites were all grazed by livestock through the 1930s and all sites experienced high deer populations. Although sprouting species established at all the study sites since European settlement, density of seed-reproducing species did not increase substantially at any of the sites with post-settlement surface fires (PP, FP and RP, Tables 3 and 6). But density of seed-reproducing species did increase by as much as several orders of magnitude at all the unburned sites (KF, GV and SR, Tables 3 and 6). The differences in density and species composition between burned and fire-excluded sites support the hypothesis that the thinning effect of surface fires was relatively more important than climate, herbivory, or tree cutting, in regulating seedling or sprout establishment and consequent forest density increases within the park.

Are remote Grand Canyon forests 'reference sites'?

A central theme of this paper is that sites PP, RP, and the western third of FP, are currently in conditions similar to those which prevailed prior to European settlement, so contemporary characteristics of these sites can be used as points of reference of natural variability. Even the fire-disrupted sites, eastern FP, SR and GV, are nonetheless unharvested ('virgin') forests and provide useful comparisons. This information could be helpful for restoration and conservation on the Kaibab Plateau – and, to some extent, broadly over the south-west and through the range of related ecosystems. Is this valid?

There are two general arguments against placing much reliance on concepts of 'natural variability' or 'reference conditions.' First, these conditions may be poorly understood or difficult to reconstruct (e.g. Stephenson, 1999; Tiedemann *et al.*, 2000). Second, even a good understanding of conditions prior to European settlement may be of limited relevance today given continual change: climate, extinctions, invasions, management practices and evolution (e.g. Millar & Wolfenden, 1999). With respect to the first point, a contemporary reference site can be measured for all variables of interest, so knowledge is not limited by the need to reconstruct past conditions. However, clearly even the 'undisrupted' forests have changed in terms of fire regime, herbivory, invasion of exotic species, predator control, native American resource management, etc. The only appropriate option is to present the historical context as completely as possible to permit an informed interpretation of the data. With respect to the second point, we suggest that reference information from contemporary sites is in fact highly relevant. The concept of reference information is not a static condition at a point in time, but rather an understanding of the recent evolutionary environment of

an ecosystem (Moore *et al.*, 1999). Contemporary reference sites are unusually important because they show the variability in ecological conditions under today's climate, atmospheric composition, and so on, corresponding most closely to Stephenson's (1999) definition of 'natural'.

Some have interpreted reference information as implicitly prescriptive, translating directly into management goals (see criticism of this approach in Tiedemann *et al.*, 2000). Of all resource management agencies, this may be most nearly true for the National Park Service, mandated to manage for 'natural' conditions (Stephenson, 1999). In most settings, though, reference information is applied to inform the design of management strategies and selection of alternatives. The natural range of variability may indeed be a useful management goal, but it is rarely likely to be the only goal (Landres *et al.*, 1999).

Cole (2001) drew a helpful distinction between 'wildness' (minimal human manipulation) and 'naturalness' (minimal ecological degradation caused by 'post-aboriginal human influence'). Grand Canyon forests are largely 'wild' but fall along a continuum of 'naturalness.' The fire-excluded forests – especially SR – exemplify the fact that unmanaged areas are not necessarily natural. The National Park Service, Forest Service, and other agencies are faced with contentious management choices that may emphasize minimal manipulation even if systems diverge greatly from the evolutionary environment (wild/not natural), manipulation to restore ecological function and structure (not wild/natural), or a compromise position of intermittent and partial intervention, such as sporadic prescribed burning. Cole (2001) considered compromise the most likely outcome because of the bureaucratic characteristics of resource management agencies and the costs of restoration.

Simply through maintenance of fire disturbance regimes and protection against external degradation, the small but important areas like the points and plateaus of the western North Rim may retain key elements of both wildness and naturalness, as far as possible given their size, atmospheric composition change, and other factors. Remote relict areas, which were least connected to pervasive changes in disturbance regimes, appear to be currently in least disrupted conditions. Now these sites provide valuable opportunities to ask questions about dynamic or transitory ecosystem elements that cannot be adequately studied through retrospective or inferential means. Herbaceous plant communities, wildlife habitat use, soil biogeochemistry and water relations, and invertebrate diversity are examples of studies that can build on the 'base datum' of understanding of North Rim fire regime and forest structure.

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BIOSKETCHES

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