



Mixed Conifer and Spruce-Fir Forests of Grand Canyon National Park

A Literature Review

Natural Resource Report NPS/GRCA/NRR—2019/2004



ON THE COVER

Photopoint in Southern Colorado Plateau Network mixed conifer monitoring plot in Grand Canyon National Park
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Natural Resource Report NPS/GRCA/NRR—2019/2004

James K. DeCoster

National Park Service
Southern Colorado Plateau Network
Flagstaff, Arizona

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Abstract

This literature review provides an ecological background and context to the long-term vegetation and soils monitoring by the Southern Colorado Plateau Network. This review summarizes vegetation and soils research and other studies conducted in the mixed conifer and spruce-fir forests of Grand Canyon National Park. Other studies from across Southwestern United States are also discussed to fill in data gaps and to provide a regional context. This review includes discussions of the physical environment (climate, geology and soils), vegetation history (from paleo-history through Euro-American settlement), and the spatio-temporal patterns of the structure and composition of the vegetation. The effects of natural and human disturbances on vegetation and soils are also examined. These include fire regime alteration, grazing and browsing, insects and pathogens, nonnative species, and drought. Drought is examined in the context of how these ecosystems may respond to future climates. The goal of this review is to provide background information that will help develop hypotheses for analyzing trends in long-term vegetation and soils monitoring data.

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1 Introduction

At Grand Canyon National Park, the Southern Colorado Plateau Inventory and Monitoring Network (SCPN) monitors the high elevation forests of the North Rim for the Integrated Upland monitoring project. The sampling frame for this ecosystem includes both mixed conifer forests as well as spruce-fir forests. Seven species of trees dominate the vegetation of this site: *Pinus ponderosa* (ponderosa pine), *Abies concolor* (white fir), *Picea engelmannii* (Engelmann's spruce), *Pseudotsuga menziesii* (Douglas fir), *Populus tremuloides* (aspen), *Picea pungens* (blue spruce) and *Abies lasiocarpa* (subalpine fir). These forests occupy the highest elevations of the North Rim of the park that range from approximately 2300 to 2800 m (7600 to 9186 ft.) in elevation. The review will critically examine the plant ecology and related studies that have been conducted in the mixed conifer and spruce-fir forests of Grand Canyon National Park (GRCA), and relevant ecological literature for these systems in other sites in Northern Arizona and the Southwestern United States. The goal of this review is to help inform SCPN's monitoring of these ecosystems at GRCA. The review will focus on factors that are critical drivers and stressors for these ecosystems. This information may help in the development of hypotheses for analyzing trends in the long-term monitoring data. In addition, comparison of data from these studies and SCPN studies may provide insight into trends in the structure and composition of these forests.

Across the southwestern United States, mixed conifer forests occupy approximately 13,000 km² and spruce-fir forests occupy 8,900 km² (Vankat 2013). These figures do not include aspen stands, which occupy an additional 8,100 km² across the Southwest (Vankat 2013). These are generally considered components of mixed conifer and spruce-fir forests, and often contain conifer species.

The spruce-fir forest represents the southern extension of the boreal forest (Peet 1998), and is composed of *Picea engelmannii*, *Abies lasiocarpa*, *Picea pungens*, and *Populus tremuloides* (White and Vankat 1993, Peet 1998, Vankat 2013). While this forest type has been well studied across the Rocky Mountains, Vankat (2013) suggests that spruce-forests of the Southwest may function differently as a result of genetic differences of the component species, as well as climate differences, including the timing of precipitation. In the Southern Rocky Mountains, spruce-fir forests are bordered on their upper elevations by treeline and alpine tundra.

Mixed conifer forest occupies the zone between spruce-fir forest and ponderosa pine forest and includes *Pinus ponderosa*, *Pseudotsuga menziesii* and *Abies concolor*, along with the tree species found in spruce-fir forests. Both spruce-fir and mixed conifer forests are broken up by sub-alpine montane grasslands, which typically occur in valley bottoms on the North Rim, but elsewhere they also may occur on xeric steep slopes (Vankat 2013). In other areas of the Southwest, *Pinus flexilis* (limber pine) and *Pinus strobiformis* (southwestern white pine) may occur in these forests.

SCPN generally bases its sampling frames on ecological sites created by the Natural Resources Conservation Service (NRCS). These are landscape divisions whose classification is based on soil survey data which remain relatively static over relatively long periods of time, have characteristic plant communities, hydrology and disturbance regimes (Butler et al. 2003). For monitoring the forests on the North Rim of Grand Canyon National Park, SCPN used two ecological sites: Loamy

Hills and Loamy Hills Cold. SCPN uses the term “mixed conifer” to refer to the sampling frame which is comprised of both mixed conifer and spruce-fir forests (Figure 1). These two ecological sites comprise the study area.

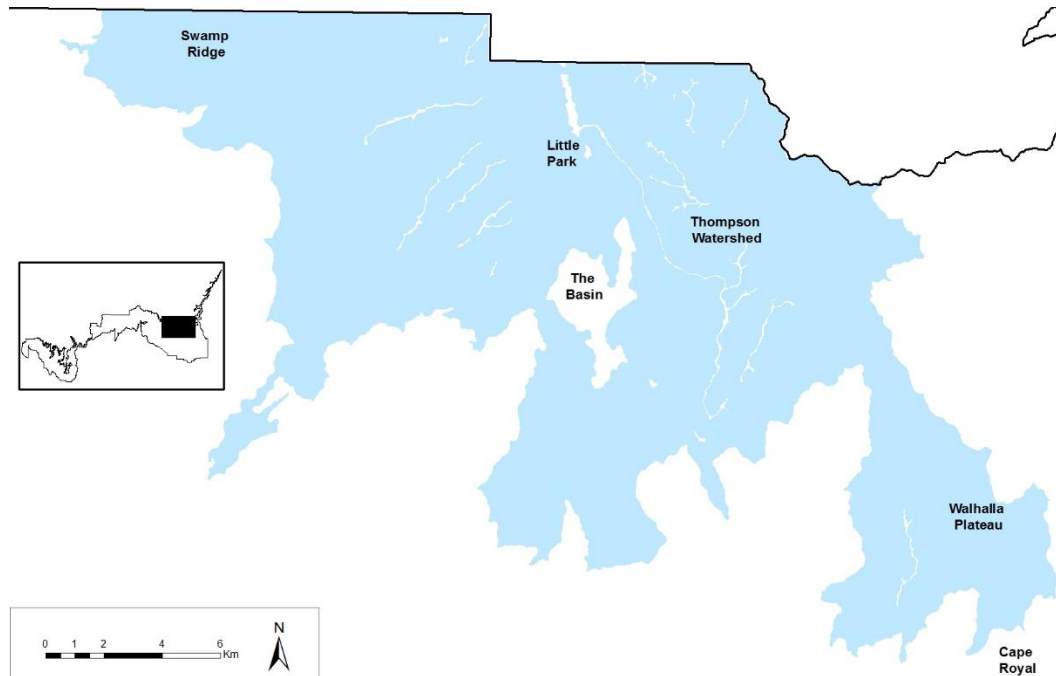


Figure 1. Map of the study area on the North Rim of Grand Canyon National Park. The blue represents the ecological sites that define SCPN’s mixed conifer sampling frame. The inset shows the location of the study area in the park. Various sites mentioned in this report are identified.

2 Physical environment: Geology, soils and climate

Geology is the most conspicuous feature of the Grand Canyon. The oldest exposed rocks are Precambrian Vishnu Basement Rocks, a combination of metamorphic and igneous rocks that were formed between 1750 to 1680 million years ago (Mathis and Bowman 2007). The majority of the exposed rock in the canyon was deposited in a series of layers of sandstone, shale and limestone in the Paleozoic Era between 525 and 270 million years ago. The primary formations in this group include (from oldest to youngest) Tapeats Sandstone, Bright Angel Shale, Muav Limestone, Redwall Sandstone, Supai Group, Hermit Formation, Coconino Sandstone, Toroweap formation and the Kaibab Formation. Subsequent layers of relatively soft sandstone were deposited on top of the Kaibab Formation, but these have since eroded away. During the Cenozoic, over the last 66 million years, cutting by the Colorado River, facilitated by the uplift of the Colorado Plateau, resulted in the formation of the canyon (Baars 2000).

The Kaibab Plateau ranges from 2286 to 2804 meters (7500 to 9200 feet) in elevation (Merkle 1954), of which the southern portion comprises the North Rim of Grand Canyon National Park. The Kaibab Formation, the underlying bedrock of the Kaibab Plateau, is comprised of limestone that was formed from shallow marine deposits. The limestone layer ranges from 90 to 120 meters (295 to 394 feet; Hopkins 1990) thick, and is porous, which limits the formation of rivers and lakes (Merkle 1954).

The most recent soils map of the Grand Canyon (NRCS 2003) delineates four soil map units on the North Rim that are associated with mixed conifer and spruce-fir forests. Due to the coarse scale of the map, soil map units are typically comprised of more than one soil component, in addition to having inclusions of unidentified soils. The soil map is comprised of four soil map units, which are in turn comprised of three main soil components: Kaiparowits, Kanabownits, and Kippers (Table 1). Kippers soils are associated with slopes from 2 to 15%, while the other two soils are associated with slopes from 15 to 40%. All three soils are described as occurring on summits and side slopes of low hills and slopes, and range from 40 to 60 inches (102 to 152 cm) in depth. Vankat (2013) notes that soils tend to be deeper at the lower elevations. The soil map units are Kaiparowits gravelly fine sandy loam, 15 to 40 percent slopes; Kanabownits fine sandy loam, 15 to 40 percent slopes; Kanabownits-Kippers-Kaiparowits complex, 2 to 15 percent slopes; and Kanabownits-Kippers-Kaiparowits complex, cool, 2 to 15 percent slopes (Figure 2).

Table 1. Typical profiles of the three soil components that are associated with the mixed conifer forests of the North Rim of Grand Canyon National Park. Profiles indicate soil textures with soil depth.

Soil Layer	Kaiparowits	Kanabownits	Kippers
1	Oi – 0-1", slightly decomposed conifer and aspen litter	Oi – 0-1", slightly decomposed conifer and grass litter	Oi – 0-1", slightly decomposed mixed conifer litter
2	A – 1 -5"; gravelly sandy loam	A – 1 -5" ; fine sandy loam	A – 1 -5"; sandy clay loam
3	E – 5-15"; very gravelly fine sandy loam	AE – 5-11"; fine sandy loam	Bt – 5-10"; clay

Table 1 (continued). Typical profiles of the three soil components that are associated with the mixed conifer forests of the North Rim of Grand Canyon National Park. Profiles indicate soil textures with soil depth.

Soil Layer	Kaiparowits	Kanabownits	Kippers
4	Bt/E – 15-24"; very cobbly sandy loam	E1 – 11-20"; fine sandy loam	Btss1 – 10-26"; clay
5	Bt1 – 24-36"; cobbly clay	E2 – 20-28"; very cobbly fine sandy loam	Btss2 – 26-35"; clay
6	Bt2- 36-44"; cobbly clay	E3- 28-57"; very gravelly fine sandy loam	C/Bt - 35-46"; sandy loam
7	Bt3 44-58"; very flaggy clay	R – 57"; sandstone bedrock	R – 46"; weathered sandstone bedrock
8	R – 58"; cherty sandstone bedrock	–	–

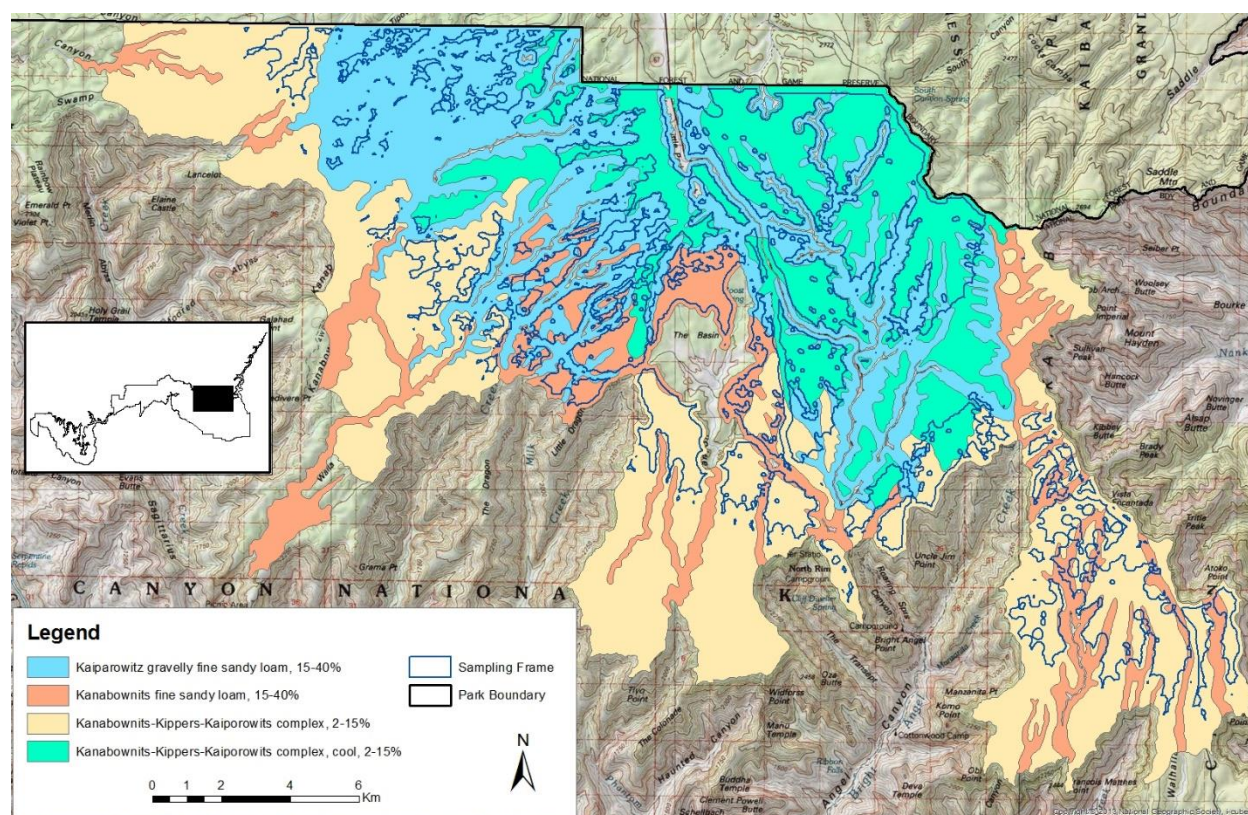


Figure 2. Soil map units associated with the mixed conifer forests of Grand Canyon National Park. Inset map shows location of North Rim study area in the park.

These three soil components comprise two ecological sites: the Kanabownits fine sandy loam and Kanabownits-Kippers-Kaiparowits complex soil map units comprise the Loamy Hills ecological site,

while the Kaiparowits gravelly fine sandy loam and the Kanabownits-Kippers-Kaiparowits complex, cool, 2 to 15 percent slopes soil map units comprise the Loamy Hills Cold ecological site (Table 2). Both ecological sites occur in the 25-33" precipitation zone (p.z.; 64-84 cm). The full names of these ecological sites are Loamy Hills (ABCO, PIPO, POTR5), 25-33" p.z. (F035XI902AZ); and Loamy Hills, Cold (ABLA, PIEN) 25-33" p.z. (F035XI903AZ). (These names include acronyms for the dominant trees: ABCO = *Abies concolor*, PIPO = *Pinus ponderosa*, POTR5 = *Populus tremuloides*, ABLA = *Abies lasiocarpa*, PIEN = *Picea engelmannii*). The Loamy Hills Cold ecological site corresponds to spruce-fir forests; the Loamy Hills ecological site corresponds to mixed conifer forests, but also extends into ponderosa pine forests. In an effort to exclude ponderosa pine forests, SCPN restricted the sampling frame to elevations above 2500 m (8202 ft). While the soil profiles in Table 1 describe the Oi layer as being comprised of 1 inch (2.5 cm) of litter, Hurst (1977) described mean litter depth in North Rim mixed conifer forests as being 7.5 cm.

Table 2. Ecological sites and corresponding soil map units for mixed conifer and spruce-fir forests of North Rim of Grand Canyon National Park.

Ecological sites	Vegetation	Soil map units
Loamy Hills (ABCO, PIPO, POTR5), 25-33" p.z.	Mixed conifer forest and ponderosa pine forest	Kanabownits fine sandy loam, 15 to 40 percent slopes
	Mixed conifer forest and ponderosa pine forest	Kanabownits-Kippers-Kaiparowits complex 2 to 15 percent slopes
Loamy Hills Cold (ABLA, PIEN) 25-33" p.z.	Spruce-fir forest	Kaiparowits gravelly fine sandy loam, 15 to 40 percent slopes
	Spruce-fir forest	Kanabownits-Kippers-Kaiparowits complex, cool, 2 to 15 percent slopes

The Bright Angel Weather Station on the North Rim recorded a mean annual precipitation of 62.4 cm between 1925 and 2018, with a minimum of 35.4 cm and a maximum of 114.4 cm. These data only include the 31 years where there are 12 months of data. This station is located a 2438 m in elevation, which is below the mixed-conifer forest, and, hence, is an underestimation of precipitation for the mixed conifer and spruce fir forests of the North Rim. There is a bimodal pattern of precipitation with monsoon rainfall between July and September, and snowfall in December and March (Figure 3, Climate Analyzer 2019).

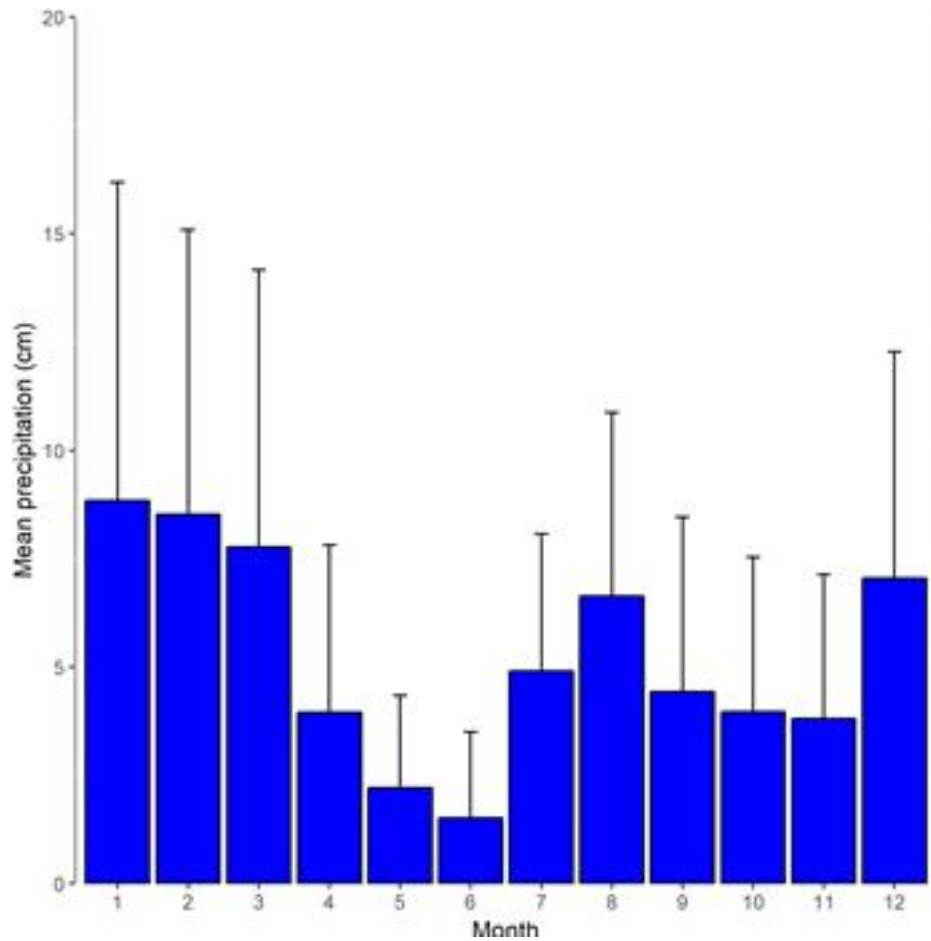


Figure 3. Mean monthly precipitation between 1925 and 2018 at Bright Angel weather station on North Rim of Grand Canyon National Park (from Climate Analyzer 2019). Error bars represent one standard deviation.

3 Vegetation history and human influences

The climate of the Southwestern United States over the past 12,000 years has shown an overall trend of becoming warmer and drier. Vegetation correspondingly changed with species migrating to higher elevations with the warming climate. Weng and Jackson (1999) documented vegetation changes in the Late Wisconsin and Early Holocene on the Kaibab Plateau in a palynology study that examined pollen in sediment cores at several sites. Located several kilometers north of the park boundary, the Bear Lake site is at 2778 m (9,114 ft) in elevation, and is currently surrounded by mixed conifer forest. The earliest pollen records of 13,500 years before present (BP) indicate that the site was alpine tundra. As the climate became warmer and drier, *Picea engelmannii* and *Abies lasiocarpa* migrated up in elevation, reaching the site around 12,900 years BP. *Pinus ponderosa* arrived around 9730 years BP; presence of charcoal suggests that fire may have helped it become established. Around 8000 years BP the forest was composed of *Abies lasiocarpa*, *Pinus ponderosa*, *Pseudotsuga menziesii* and *Picea* (mostly *Picea pungens*). *Picea engelmannii* expanded after 4000 BP. Cole's (1990) packrat midden study showed that between 14,900 and 14,200 BP, a number of mixed conifer tree species, including *Abies concolor*, *Pinus flexilis* and *Picea* spp. were present at 2050 m (6,726 ft) in the eastern portion of the Grand Canyon. He suggests that *Pinus ponderosa* must have been distributed between 1450 and 2050 m (4,757 to 6,726 ft), and migrated upward between 14,000 and 11,000 years BP.

Native Americans occupied the Grand Canyon region for millennia. Corn was introduced into the region from Mexico around 200 BCE (Before Common Era or BC; or 2200 years BP) which caused a change from a nomadic to a more sedentary lifestyle (Anderson 1998). Their populations were concentrated in the inner canyon and canyon rim. Populations increased beginning 900 CE (Common Era or AD), and by 1075 stone dwellings replaced thatched structures. Population declines occurred around 1200, possibly as a result of overpopulation, soil depletion and/or droughts. Paiutes arrived in the area around 1100 CE, and Navajos came to the area from the east around 1500. All indications suggest that these people only used the forests of the North Rim seasonally for hunting (Anderson 1998). Impacts to vegetation were likely negligible, unless these people used fire to improve wildlife habitat, which is uncertain.

The first European to arrive at the Grand Canyon was Garcia López de Cárdenas in 1540, a member of Francisco Vazquez de Coronado's expedition. Over the next 300 years, a series of Europeans passed through the region including conquistadors, trappers and missionaries. The year 1848 was a turning point: the Mexican-American War gave control of the land from Spain to the United States, and gold was discovered in California. A large influx of Euro-Americans subsequently came to the region, including homesteaders, ranchers, miners, tourists and government surveyors. In 1869 John Wesley Powell passed close to the North Rim but did not provide information on the area (Anderson 1998).

Development on the North Rim progressed at a much slower pace than on the South Rim, due to its relative inaccessibility, distance from railroads, and harsh winters. The first permanent European-Americans in the area were Mormons who settled on the northern portions of the Arizona Strip and

Kaibab Plateau beginning in the 1850s. While they engaged in mining, lumbering and agriculture, ranching was their primary occupation (Hurst 1977, Anderson 1998). In 1870 Mormon cooperatives acquired existing ranches, and ranching of cattle, sheep and goats became more extensive (Hurst 1977), although grazing did not occur within the current park boundaries until 1879 (Anderson 1998). In the last decades of the 19th century and first decade of the 20th century, grazing occurred throughout much of the North Rim, extending down to Cape Royal. At the peak of ranching, in 1887, there were 20,000 cattle and 20,000 sheep on the Kaibab Plateau (Merkle 1962). Ranchers built roads, which were later used by early tourists. Tourism slowly developed, primarily in the form of hunting for deer and other game.

The US government began managing the land when it established the Grand Canyon Forest Reserve in 1893, and the Grand Canyon Game Preserve in 1906, which was managed by the US Forest Service. At this point hunting was prohibited (Anderson 1998), wildland fires began to be suppressed (Vankat 2011b), and government hunters began killing predators, including mountain lions, wolves, coyotes and bobcats (Hurst 1977). Timber harvesting began in 1915 on the Kaibab Plateau, but did not occur within the current park boundaries, other than localized cutting of trees for structures, fuel and insect control (Vankat 2011b). In 1917, development on the rim began with the establishment of the North Rim Camp. In 1919, the park was established and management was transferred to the National Park Service. Primary impacts to the vegetation during this era were the result of predator control, fire suppression and livestock grazing. (See Section 5).

4 Vegetation

4.1 Vegetation classification

Research on the North Rim of the Grand Canyon and on the Kaibab Plateau began in 1910, with various researchers conducting vegetation studies that provided descriptions of the forests. As the ecological understanding of these forests developed, and sampling and analytical techniques became more sophisticated, classification of the different forest types became more precise with more complete quantitative descriptions (Table 3). (See Section 4.3).

Table 3. Major research studies that describe mixed conifer forests and spruce-fir forests of Kaibab Plateau and North Rim of Grand Canyon. See tables 4 and 5 for classification from Vankat (2013) and Kearsley et al. (2015).

Author (Year)	Mixed conifer forest	Spruce-fir forest	Notes
Lang and Stewart (1910)	"Mixed type"	"Spruce-balsam"	Conducted outside of park. Did not measure <i>Populus tremuloides</i> .
Rasmussen (1941)	Above 2500 m	–	Did not separate mixed conifer and spruce, but describes some variation in composition based on aspect and elevation
Merkle (1954, 1962)	"Ponderosa pine-white fir"	"Engelmann spruce- alpine fir"	Provided quantitative data for both forest types.
Hurst (1977)	First use of "mixed conifer forest"	–	Only examined mixed conifer forest, and identified indicator species.
White and Vankat (1993)	Classified 4 mixed conifer types	Identified 1 spruce-fir types	Developed classification for forest types in Thomson Watershed
Fulé et al. 2002	–	–	Sampled mixed conifer forests across elevational gradient
Vankat (2011b)	–	–	Resampled 1935 plots and plots from White and Vankat (1993) in both forest types
Vankat 2013	Classified 3 mixed conifer types	Classified 3 spruce-fir types	Developed regional classification
Kearsley et al. (2015)	Classified 8 mixed conifer associations in three map units	Classified 2 spruce-fir associations in one map unit	Detailed vegetation classification and map. Also classified 6 <i>Populus</i> associations in 5 map units.

Table 4. Vankat's (2013) regional classification of mixed conifer and spruce-fir forests.

Forest Type	Component Species
Upper elevation spruce-fir forest	<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>
Lower elevation spruce-fir forest	<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i> , <i>Populus tremuloides</i> , <i>Pseudotsuga menziesii</i> , <i>Abies concolor</i> , <i>Pinus ponderosa</i> , <i>Picea pungens</i>
Quaking aspen forest (spruce-fir)	<i>Populus tremuloides</i>
Moist-mesic mixed conifer forest	<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i> , <i>Populus tremuloides</i> , <i>Pinus ponderosa</i> , <i>Picea pungens</i>
Dry-mesic mixed conifer forest	<i>Pinus ponderosa</i> , <i>Pseudotsuga menziesii</i> , <i>Abies concolor</i> , <i>Picea engelmannii</i> , <i>Populus tremuloides</i>
Quaking aspen Forest (mixed conifer)	<i>Populus tremuloides</i>

Table 5. Crosswalk between vegetation map units and vegetation associations for the vegetation map and classification for Grand Canyon National Park (from Kearsley et al. 2015)

Map unit	Associations	Common name for associations
<i>Abies concolor</i> - <i>Pseudotsuga menziesii</i> Dry Forest Alliance	<i>Abies concolor</i> - <i>Pseudotsuga menziesii</i> / <i>Carex</i> spp. Forest	White Fir-Douglas fir / Sedge Forest
	<i>Abies concolor</i> - <i>Pseudotsuga menziesii</i> / <i>Robinia neomexicana</i> Woodland	White fir – Douglas fir / New Mexico Locust Woodland
	<i>Abies concolor</i> / <i>Cercocarpus ledifolius</i> Woodland	White Fir / Curl-Leaf Mountain Mahogany Woodland
	<i>Abies concolor</i> / <i>Juniperus communis</i> Forest	White Fir / Common Juniper Forest
	<i>Abies concolor</i> / <i>Mahonia repens</i> Forest	White Fir / Creeping Barberry Forest
<i>Abies concolor</i> - <i>Pseudotsuga menziesii</i> Moist Forest Alliance	<i>Abies concolor</i> / <i>Symphoricarpos oreophilus</i> Forest	White Fir / Mountain Snowberry Forest
	<i>Pseudotsuga menziesii</i> / <i>Symphoricarpos oreophilus</i> Forest	Douglas Fir / Mountain Snowberry Forest
<i>Abies lasiocarpa</i> - <i>Picea engelmannii</i> Southern Rocky Mountain Dry Forest Alliance	<i>Abies lasiocarpa</i> - <i>Picea engelmannii</i> / <i>Carex siccata</i> Forest	Subalpine Fir – Engelmann Spruce / Dry-Spike Sedge Forest
	<i>Abies lasiocarpa</i> - <i>Picea engelmannii</i> / <i>Juniperus communis</i> Woodland	Subalpine Fir – Engelmann Spruce / Common Juniper Woodland

Table 5 (continued). Crosswalk between vegetation map units and vegetation associations for the vegetation map and classification for Grand Canyon National Park (from Kearsley et al. 2015)

Map unit	Associations	Common name for associations
<i>Picea pungens</i> / <i>Carex siccata</i> Forest	<i>Picea pungens</i> / <i>Carex siccata</i> Forest	Blue Spruce / Dry-Spike Sedge Forest
<i>Populus tremuloides</i> - <i>Ceanothus fendleri</i> / <i>Carex</i> spp. Shrubland	<i>Populus tremuloides</i> - <i>Ceanothus fendleri</i> / <i>Carex</i> spp. Shrubland	Aspen- Fendler's Ceanothus / Sedge Shrubland
<i>Populus tremuloides</i> / <i>Amelanchier</i> - <i>Symphoricarpos</i> Mesic Forest Alliance	<i>Populus tremuloides</i> / <i>Juniperus communis</i> Forest	Aspen / Common Juniper Forest
	<i>Populus tremuloides</i> / <i>Pteridium aquilinum</i> Forest	Aspen / Western Bracken Fern Forest
<i>Populus tremuloides</i> / <i>Carex siccata</i> Forest	<i>Populus tremuloides</i> / <i>Carex siccata</i> Forest	Aspen / Dry-Spike Sedge Forest
<i>Populus tremuloides</i> / <i>Robinia neomexicana</i> Shrubland	<i>Populus tremuloides</i> / <i>Robinia neomexicana</i> Woodland	Aspen/ New Mexico Locust Woodland
<i>Populus tremuloides</i> Dry Forest Alliance	<i>Populus tremuloides</i> / <i>Muhlenbergia montana</i> Woodland [Park Special]	Aspen / Mountain Muhly Woodland

The first quantitative description of forests in area was a forest survey conducted by Lang and Stewart conducted in 1910 (described in Fulé et al. 2003a and Vankat 2013). The area sampled was on the Kaibab Plateau, north of the current park boundary. They described “spruce-balsam” and mixed-type” forests, referring to spruce-fir and mixed conifer forests respectively. They found *Pinus ponderosa* to be species with the highest density, followed by followed by *Abies* spp., *Picea engelmannii* and *Pseudotsuga menziesii*. *Populus tremuloides* was not measured (Fulé et al. 2003a). Rasmussen (1941) provided the first quantitative description of the high elevation forests within the park as part of a description of biotic communities on the Kaibab Plateau. He described these forests as the *Picea-Abies-Sciurus fremonti* association (spruce-fir-red squirrel), and being composed of seven tree species: *Pinus ponderosa*, *Abies concolor*, *Picea engelmannii*, *Pseudotsuga menziesii*, *Populus tremuloides*, *Picea pungens* and *Abies lasiocarpa*. He suggests that forest composition changed based on elevation and aspect, but does not provide detail. Merkle (1954, 1962) distinguished the ponderosa pine-white fir forests (i.e. mixed conifer forest) from the Engelmann spruce- alpine fir forests. The spruce-fir community is described as being comprised of all seven species and the ponderosa pine white fir community is described as being composed of *Abies concolor*, *Pinus ponderosa*, *Pseudotsuga menziesii* and *Populus tremuloides*. Hurst (1977) described mixed conifer forests as occurring between ponderosa pine forests and spruce-fir forests, and included the following indicator species: *Abies concolor*, *Lotus wrightii* (deer vetch) and *Poa fendleriana* (muttongrass). In his study of mixed conifer forests on the North Rim, Vankat (2011a, 2011b) delineated ponderosa pine from mixed conifer forests as those stands with *Pinus ponderosa* having at least 80% basal area. In contrast, Hurst (1977) delineated North Rim ponderosa pine forests from mixed conifer forests as having greater than 50% density of mature *Pinus ponderosa*. (She did not provide a definition for mature trees).

More recently, studies have described various forest types or plant communities within the mixed-conifer and spruce-fir forests. Vankat (2013) created a classification based on forests across Southwestern United States. He describes three broad groups of spruce fir forests, and three broad groups of mixed conifer forests (Table 4). As suggested by their names, two spruce-forest types are primarily determined by elevation. The upper elevation spruce-fir forest is composed primarily of two species: *Picea engelmannii* and *Abies lasiocarpa*. The lower elevation spruce-fir forest is dominated by these two species, with low abundances of *Pinus ponderosa*, *Abies concolor*, *Pseudotsuga menziesii*, *Populus tremuloides* and *Picea pungens*. Two of the mixed conifer types are distinguished by the moisture/topographic gradient. Moist-mesic mixed conifer forests occur on north and eastern slopes and on valley bottoms, while the dry-mesic mixed conifer forests occur on south and western aspects and ridgetops. There are two quaking aspen forests in this classification: one associated with the mixed conifer forest and one associated with the spruce-fir forest. These are early successional forests that establish following severe wildland fires. As the stands develop, *Picea* spp. and *Abies* spp. become established under the canopies.

In their study of the Thompson watershed in the park, White and Vankat (1993) identified five vegetation types based on tree composition: *Pinus ponderosa*-*Pseudotsuga menziesii*, *Pinus ponderosa*-*Abies concolor*, *Picea pungens*-*Pseudotsuga menziesii*, *Abies concolor*-*Pinus ponderosa*-*Pseudotsuga menziesii* and *Picea engelmannii*-*Abies lasiocarpa*. The *Picea engelmannii*-*Abies lasiocarpa* type represented the spruce-fir forest, while the other four represent mixed conifer forest with varying abundances of the component species.

Warren et al. (1982) and Kearsley et al. (2015) created vegetation maps and classifications of Grand Canyon National Park that provided detail for the descriptions of the mixed conifer and spruce-fir forest communities, including the shrub/herbaceous layers. The most recent vegetation map (Kearsley et al. 2015) identifies nine map units associated with mixed conifer and spruce-fir forests (Figure 4, Table 5). One map unit represents spruce-fir forests, three map units represent mixed-conifer, and five map units represent aspen forests. This classification follows National Vegetation Classification Standard (NVCS), and is based on tree, shrub and herbaceous layers. The *Abies lasiocarpa* – *Picea engelmannii* Dry Forest Alliance occupies a large portion of the eastern side of the study area, which comprises the highest elevations in the park, which corresponds to spruce-fir forests. The *Abies concolor* – *Pseudotsuga menziesii* Dry Forest Alliance occupies portions of the western side of the study area. The *Picea pungens* – *Carex siccata* Forest (blue spruce – dry-spike sedge forest) surrounds The Basin, a montane grassland, and has small patches distributed across the study area. The *Abies concolor*- *Pseudotsuga menziesii* Moist Forest Alliance and the *Populus tremuloides* Forests have small patches distributed across the study area. There are two large areas of the *Populus tremuloides* shrublands, which are early successional communities associated with the burned areas of the 2000 Outlet fire and the 2003 Poplar fire. (See Section 5.2.3). The associations that comprise each of the map units are shown in Table 5. Note that the original map units for *Populus tremuloides* forests and *Populus tremuloides* shrublands have been grouped in Figure 4 for greater legibility.

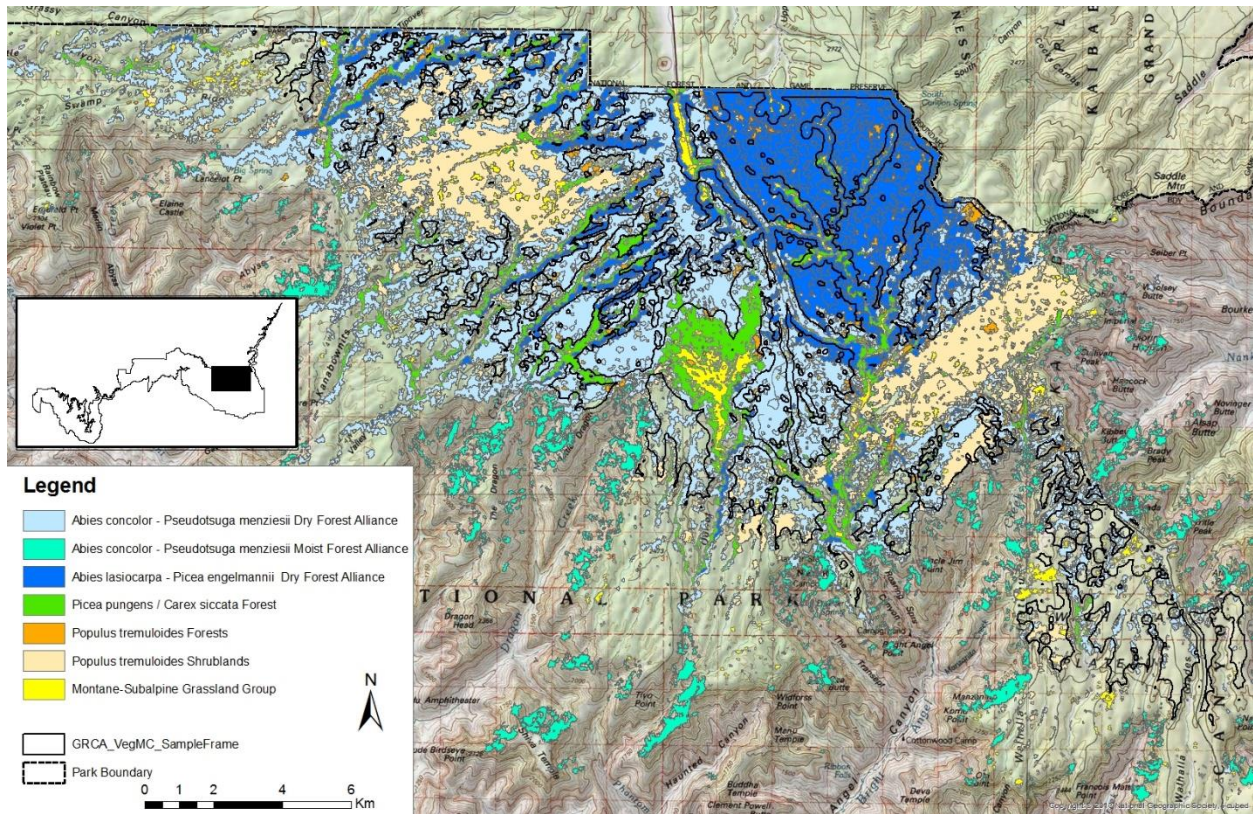


Figure 4. Mixed conifer forest communities delineated in the recent vegetation map of Grand Canyon National Park (Kearsley et al. 2015). Map units for *Populus tremuloides* forests and *Populus tremuloides* shrublands have been grouped for greater legibility. See Table 4. Inset map shows location of North Rim study area in the park.

While the classifications have similarities, there are differences that in part result from their spatial scales: Vankat's (2013) classification covers the Southwestern United States, Kearsley et al. 2015 covers the park, and White and Vankat (1993) covers a watershed within the park. Moreover, Vankat (2013) and White and Vankat's (1993) classifications were based on tree composition and structure, while Kearsley et al.'s (2015) classification included tree, shrub and herbaceous layers. White and Vankat (1993) describe one spruce-fir forest type; Vankat (2013) describe two based on elevation and tree composition, and Kearsley et al. (2015) describe two associations based on shrub/herbaceous layers. For the mixed-conifer forests, Vankat (2013) describes two types: a moist-mesic and a dry mesic. Kearsley *et al.* (2015) similarly describe a Dry Forest and a Moist Forest Alliance, comprised of five and two associations, respectively. They also describe a *Picea pungens* forest. White and Vankat (1993) describe four mixed conifer types based on the relative abundance of tree species, including a *Picea pungens* type. Vankat describes two aspen forest types, one associated with spruce-fir forests and one with mixed-conifer. Kearsley et al. (2015) described five *Populus tremuloides* map units that are comprised of six associations. White and Vankat (1993) did not sample aspen stands.

4.2 Environmental gradients

The major forest types of the Southern Rockies and mountains and plateaus of the Southwest are arranged on two main environmental gradients – an elevational gradient and a topographic-moisture gradient. The elevational gradient is the primary gradient, and represents a combination of environmental factors including temperature, precipitation, solar radiation (including ultraviolet radiation), snow depth and duration, and wind (Peet 1988). Studies of the North Rim forests have noted the zonation of forests along this elevational gradient (Merkle 1954, Merkle 1962, Halvorson 1972, White and Vankat 1993, Vankat 2011a, Vankat 2011b; Figure 5). Merkle (1954, 1962), Halvorson (1972), and White and Vankat (1993) describe the elevational boundary between spruce-fir and mixed conifer forests at about 2650 m. While Merkle (1954, 1962) and Halvorson (1972) describe the boundary between mixed conifer and ponderosa pine forests at slightly above 2500 m (8202 ft), White and Vankat (1993) describe a lower boundary of 2450 m (8038 ft), and note the presence of *Abies concolor* in the ponderosa pine forests. Vankat's (2011a, 2011b) zonation is more complex by providing broad transitional zones between the forest types.

	Merkle (1954,1962)	Halvorson (1972)	White & Vankat (1993)	Vankat (2011a,b)	
2800				Spruce >2750 m	2800
2700	Englemann spruce – alpine fir >2650 m	Spruce-fir <2652 m	<i>Picea engelmannii/ Abies lasiocarpa</i> >2650 m	Mixed conifer and Spruce 2600–2750m	2700
2600	Ponderosa – white fir 2515–2650m	Ponderosa/ white fir 2525–2652 m	<i>Abies concolor</i> and <i>Pinus ponderosa</i> with <i>Pseudotsuga</i> and <i>Picea pungens</i> 2450–2650 m	Mixed conifer 2550–2600 m	2600
2500				Mixed conifer and Ponderosa pine 2350–2550 m	2500
2400	Ponderosa <2515 m	Ponderosa <2525 m	<i>Pinus ponderosa</i> with <i>Abies concolor</i> <2450 m	Ponderosa <2350 m	2400
2300					2300
2200					2200

Figure 5. Elevational zonation of forest types on the North Rim of Grand Canyon National Park as described by four researchers.

While vegetation is often described as discrete bands along the elevational gradient (e.g. ponderosa pine forest, mixed conifer forest, and spruce-fir forests) vegetation generally varies continuously along the gradient with broad transitions among the major forest types (Peet 1988). Moreover, topography causes variation in forest composition, with southern and western aspects and ridge tops being more xeric, while northern and eastern aspects and valley bottoms are more mesic (White and Vankat 1993, Peet 1998, Vankat 2013). Topography is particularly important on the Kaibab Plateau, where the plateau is dissected by drainages producing diverse topography over a relatively small area. Disturbance history can result in further. While the influence of soils on the composition of

these forests has not been well studied, Peet (1988) notes that limestone soils, such as those found on the North Rim tend to be more xeric than granitic soils.

When elevation and topography are combined, much of the variation in vegetation is explained. A graph of the two gradients results in diagonal bands (Figure 6a). At the lower elevations of their distributions, the vegetation types occur in the most mesic sites, while at the higher elevations the vegetation types occur in the most xeric sites. This results in a patchy transition between forest types. For example, at the lower elevations of the study area mixed conifer forests are restricted to northern aspects and valley bottoms (Rasmussen 1941, Merkle 1954, Vankat 2013). Similarly, at the higher elevations mixed conifer forests are restricted to ridge tops and southern slopes (Merkle 1962). In the mid-elevations, there is a mosaic of varying species combinations based on aspect, topographic position and slope (White and Vankat 1993, Vankat 2005 Vankat 2013; Figure 6b). White and Vankat (1993) used Detrended Correspondence Analysis (DCA) to identify where their identified communities were located on the landscape in terms of topography and elevation. (See Section 4.1). For example, *Pinus ponderosa*-*Pseudotsuga menziesii* sites were located on xeric ridgetops and steep southern slopes up to 2600 meters (8530 ft); *Picea engelmannii*-*Abies lasiocarpa* sites were located on cool, moist slope at low and mid elevations and all topography above 2700 meters (8858 ft).

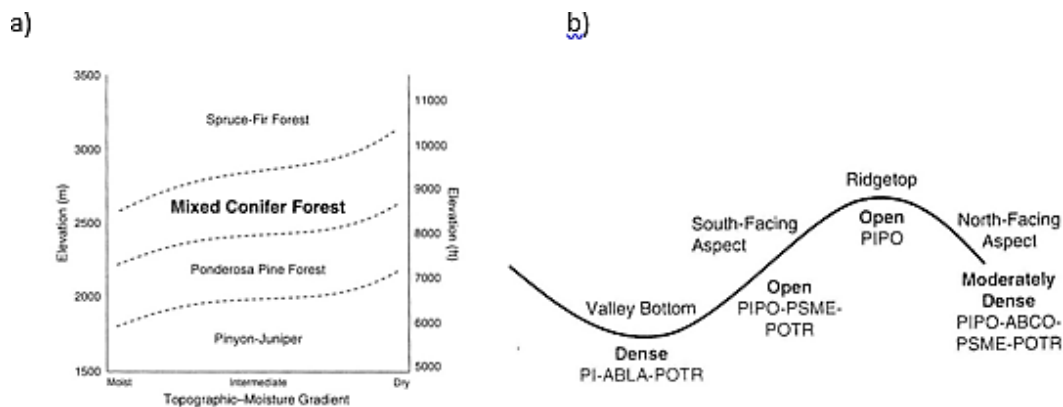


Figure 6. Influence of elevation and topography on vegetation in mixed conifer forests of the Southwestern United States (from Vankat 2013). a. Diagram showing where mixed conifer and spruce-fir forests are generally located on elevational and topographic gradients. b) Schematic of topographic landscape showing how forests differ in terms of composition and structure. Species code names are use: ABCO=*Abies concolor*, ABLA= *Abies lasiocarpa*, PI=*Picea* spp. PIPO = *Pinus ponderosa*, PSME=*Pseudotsuga menziesii*, POTR= *Populus tremuloides*.

While researchers have often described mixed conifer forests as generally occurring above 2500 meters (8202 ft; Rasmussen 1941, Merkle 1962), the park's vegetation map shows ponderosa pine forests extending as high as 2600 meters (8558 ft) on the Walhalla Plateau, and *Abies concolor* – *Pseudotsuga menziesii* forests occurring as low 2,250 meters (7382 ft) in side canyons (Kearsley et al. 2015). This is largely the result of microclimates, such as rising heat from the canyon that affects sites close to the canyon rim, and a cool, mesic environment on north facing aspects in side canyons.

The presence and abundance of species at a given site is dependent on a large number of factors. White and Vankat (1993) rank the tree species not only in terms of drought tolerance, but also in terms of shade tolerance and fire tolerance (Table 6). Drought tolerance explains where the species occur on the elevational- topographic gradient. Shade tolerance helps explains species abundance in terms of stand age, and relative position within the canopy. Shade intolerant species can colonize following disturbance, and can regenerate only in open stands. Shade tolerant species can regenerate only under a tree canopy, and will become a canopy species in old stands. Fire tolerance explains the ability of trees to survive low-severity ground fires. (See Section 5.2).

Table 6. Drought, shade, and fire tolerance rankings of tree species of the mixed conifer and spruce-fir forests of Grand Canyon National Park, where 1 is most tolerant and 7 is least tolerant (from White and Vankat 1993).

Species	Drought tolerance	Shade tolerance	Fire tolerance
<i>Abies concolor</i>	3-4	2	4
<i>Abies lasiocarpa</i>	6	1	7
<i>Picea engelmannii</i>	7	3	5
<i>Picea pungens</i>	3-4	4-5	3
<i>Pinus ponderosa</i>	1	6	1
<i>Populus tremuloides</i> ¹	5	7	6*
<i>Pseudotsuga menziesii</i>	2	4-5	2

¹*Populus tremuloides* is fire intolerant, but can sprout from roots following fire.

4.3 Forest composition, structure and dynamics

A number of studies of the forests on the North Rim of the Grand Canyon have quantified forest structure in terms of tree basal area and tree density (Merkle 1954, Merkle 1962, Hurst 1977, Vankat 2011b, Fulé et al. 2002; Table 7). Several caveats must be considered when comparing these data. First, the studies encompass different areas, with different forest types. Merkle (1954) focuses on spruce-fir stands, Vankat (2011b) includes mixed conifer and spruce-fir stands, while Merkle (1962) and Fulé *et al.* (2002) focus on mixed conifer stands. This explains the lack of *Picea* spp. and *Abies lasiocarpa* in Merkle (1962) and Fulé et al. (2002), and explains differences in the other species' metrics. Second, the studies were published over a 57-year span of time, during which changes in forest structure and composition likely occurred as a result of succession and disturbances, such as drought, and insect infestations. Third, the authors of these studies used different tree size classes in the calculations of basal area and density that often are not indicated. Sampling that includes trees greater than 15 cm diameter will provide very different estimates, especially for density, than sampling of all trees greater than 1 cm diameter.

Table 7. Basal area and density by species from various studies of mixed conifer and spruce-fir forests on the North Rim of Grand Canyon National Park. Some of the variation can be explained by the fact that researchers sampled different sizes of the trees sampled, which were not always stated. Merkle (1954) and Hurst (1977) did not report tree densities. Vankat (2011b) only shows data from 1935 plots, and *Picea pungens* was grouped with *Picea engelmannii*.

	Merkle (1954) Spruce-fir	Hurst (1977) Mixed conifer	Merkle (1962) Ponderosa pine - white fir		Fulé et al. (2002) Mixed conifer		Vankat (2011b) Mixed-conifer		Merkle (1962) Ponderosa pine - white fir	
Species	Basal area (m ² /ha)	Basal area (m ² /ha)	Basal area (m ² /ha)	Density (#/ha)	Basal area (m ² /ha)	Density (#/ha)	Basal area (m ² /ha)	Density (#/ha)	Basal area (m ² /ha)	Density (#/ha)
<i>Abies concolor</i>	6.0	14.0	13.4	160.6	14.5	466.5	8.4	135.8	0.3	5.0
<i>Abies lasiocarpa</i>	9.2	4.1	0	0	0	0	0.3	11.3	5.3	100.0
<i>Picea engelmannii</i>	10.1	9.6	0	0	0	0	3.3	49.8	15.9	290.0
<i>Picea pungens</i>	1.4	2.8	0	0	0	0	n/a	n/a	n/a	n/a
<i>Pinus ponderosa</i>	7.6	30.3	11.8	103.8	19.9	156.6	17.3	97.1	0	0
<i>Populus tremuloides</i>	9.4	14.9	6.7	197.7	5.3	255.8	3.3	61.1	2.7	30.0
<i>Pseudotsuga menziesii</i>	11.5	1.4	7.8	47.0	1.6	56.3	3.0	26.7	0	0
All species	55.2	77.1	39.7	509.1	41.3	935.2	35.6	382.7	24.2	425.0

Given these caveats, there are some similarities among the studies. Merkle (1962), Fulé *et al.* (2002) and Vankat (2011b) report similar basal areas, ranging from 35.6 to 41.3 m²/ha. Merkle (1954) and Hurst (1977) reported higher basal areas: 55.2 and 77.1 m²/ha, respectively. Density estimates were much more variable but this would be expected, as studies that have included a smaller diameter threshold will inevitably have higher tree densities. The studies generally showed that *Pinus ponderosa* and *Abies concolor* were the most abundant species. Merkle (1962), Vankat (2011b) and Fulé *et al.* (2002) reported *Pinus ponderosa* and *Abies concolor* as the two species with the greatest basal area, and Vankat (2011b) reported them as the two species with the greatest densities. The reported densities of *Populus tremuloides* and *Abies concolor* were particularly variable. *Abies concolor* density ranged from 135.8 to 466.5 stems/ha, and *Populus tremuloides* density ranged from 61.1 to 255.8 stems/ha across the five studies in Table 6. This may be the result of large numbers of stems in small size classes, changes in forest structure between the times sampled and/or high spatial variability. Forests on the San Francisco Peaks – the closest high-elevation forests to the North Rim–demonstrated densities and basal areas on the upper end of those measured on the North Rim. Cocke *et al.* (2005) reported a total tree density of 820.8 stems/ha for mixed conifer stands, and 840.3 stems/ha for spruce-fir stands. Total basal area for these stands were 45.3 m²/ha and 57.8 m²/ha in the mixed conifer and spruce fir stands, respectively.

In their sampling of mixed conifer forests in their Little Park site, Fulé *et al.* (2003a) found that mean canopy cover ranged from 51.6% in spruce-fir stands, to 55.3% in mixed conifer stands, and 60.9% in aspen stands. White and Vankat (1993) found a greater range of canopy cover, from 25% in *Picea engelmannii*-*Abies lasiocarpa* forest type to 55% in the *Picea pungens*-*Pinus ponderosa* type.

Fulé *et al.* (2003a, 2003b) cored and dated trees in their mid-elevation Little Park site and low elevation Swamp Ridge site (Figure 1). The oldest trees at Little Park, by species, were a *Pinus ponderosa* from 1618, a *Pseudotsuga menziesii* from 1693 and an *Abies concolor* from 1735. In their Swamp Ridge site, 63% of the trees predated 1800, but only 3% predated 1700.

Regeneration varies among species. *Abies concolor*, is shade-tolerant, and can form dense understories in smaller size classes (Merkle 1954, White and Vankat 1993, Kearsley *et al.* 2015). On the other extreme, seedlings and saplings of *Pinus ponderosa* and *Pseudotsuga menziesii* are uncommon, and only occur in open areas (Merkle 1954). Because mortality rates for seedlings and saplings in these forests are unknown, it is unclear if the forest understory is an indication of future composition. Dense understories of shade tolerant *Abies concolor* may suggest that successional processes may cause these species to increase in their abundance over time. Alternatively, if seedling and sapling mortality rates were moderately high, it would suggest that these forests are in a quasi-steady state. (See Section 4.6). Disturbance, on the other hand, can move forests to early successional states. (See Section 5).

Populus tremuloides is considered a seral species, forming even-aged stands from root sprouts following severe wildland fires, but also appears as an understory or mid-story tree in mixed conifer stands (Peet 1988, Vankat 2013). While this species formed dense early successional shrublands and woodlands on the North Rim following the severe fires of the early 21st century, there are few large stands of mature *Populus tremuloides* on the North Rim (Laughlin *et al.* 2005, Vankat 2005, Vankat

2011b, Kearsley et al. 2015). Instead, this species tends to grow as a subdominant (Kearsley et al. 2015), in small patches (Hurst 1977, Vankat 2005, Vankat 2011b, Kearsley et al. 2015) and along the edges of montane meadows (Rasmussen 1941, Hurst 1977, Moore 1994). Vankat (2005) noted that in the 1936 vegetation map for the park, aspen patches had a mean size of 10 ha. In mature stands, *Picea* spp. and *Abies* spp. become established in the understory (Rasmussen 1941, Merkle 1954). Over time, the conifers can become co-dominant, and possible dominants.

Within the mixed conifer forests on the North Rim are montane meadows that generally occur in elongate, anticlinal valleys which occur between 2377 and 2774 meters (7799 and 9101 ft; Moore 1994, Moore and Huffman 2004). Across the Southwest, montane meadows are generally controlled by edaphic factors, occurring in extreme xeric and wet sites, but they may also be controlled by disturbances, such as fire (Vankat 2013). *Picea pungens* and *Populus tremuloides* are abundant in the forests surrounding meadows (Rasmussen 1941, Hurst 1977, White and Vankat 1993, Kearsley et al. 2015). Moore and Huffman (2004) documented the invasion of trees into the meadows, and found that approximately half (52%) of the invaders were *Populus tremuloides*, but other tree species were also present: *Picea* spp. (20%), *Abies lasiocarpa* (11%), *Abies concolor* (10%), and *Pinus ponderosa* (7%). The majority of the trees had established in the 1980s, but tree establishment had been occurring since the early 1880s. Between 1940 and 1990, there was a mean encroachment of 17 meters, suggesting an encroachment rate 0.34 cm/ year (Moore 1994). Shade intolerant species invaded first, followed by more shade tolerant species. It is unclear what factors historically prevented tree encroachment in meadows, and/or are facilitating recent trends tree encroachment. Possible mechanisms include fire, deer browsing and climate. A recruitment pulse in the 1940s coincided with a reduction in the deer herd, and a pulse in the 1980s coincided with a wetter climate (Moore 1994, Moore and Huffman 2004).

4.4 Shrub/ herbaceous layer

The relatively few studies of the shrub/herbaceous layer of the mixed conifer forest of the North Rim suggest that it is variable and patchy. White and Vankat (1993) found that the various forest types ranged in mean shrub/herbaceous cover from 27 to 55%, with cover in individual plots ranging from 15% to 60%. Merkle (1954, 1962) and Hurst (1977) quantitatively sampled the shrub and herbaceous layer, providing cover estimates for each species; White and Vankat (1993) and Kearsley et al. (2015) listed species by community type. Abundant species are listed in Table 8. More detailed species lists by study and vegetation type are provided in the Appendix. It is important to note that these studies differed in the areas that they sampled. White and Vankat (1993) restricted their study to a single watershed. Merkle (1962) focused on spruce-fir forests, while Merkle (1954) and Hurst (1977) focused on mixed conifer forests. The timing of the studies may also explain some variation. The various studies occurred over a period of 60 years, during which change inevitably occurred due to succession, climate and disturbances. In their study on the North Rim, Laughlin et al. (2005) used non-metric multi-dimensional scaling to determine indicator species for mixed conifer and spruce-fir forests (Table 8).

Table 8. Abundant shrub and herbaceous species of the mixed conifer and spruce-fir forests of Grand Canyon National Park. “A” indicates high abundance, “M” indicates indicator for mixed conifer forests, “S” indicates indicator for spruce-fir forest (Abundant species determined by Merkle (1954, 1962), Hurst (1977), White and Vankat (1993). Indicators from Laughlin et al. (2005). See Appendix for more complete species list.

Scientific name	Common name	Growth form	Abundance/ Indicator
<i>Achillea millefolium</i>	western yarrow	forb	A
<i>Androsace septentrionalis</i>	pygmyflower rockjasmine	forb	S
<i>Arenaria fendleri</i>	Fendler's sandwort	forb	S
<i>Bromus ciliatus</i>	fringed brome	perennial grass	A
<i>Carex rossii</i>	Ross' sedge	graminoid	A
<i>Carex siccata</i>	dry-spike sedge	graminoid	A
<i>Chamerion angustifolia</i>	fireweed	forb	M
<i>Elymus elymoides</i>	squirreltail	perennial grass	A
<i>Erigeron</i> spp.	Fleabane	forb	M
<i>Fragaria virginiana</i>	Virginia strawberry	forb	A M
<i>Goodyear oblongifolia</i>	western rattlesnake plantain	forb	A M
<i>Hieracium fendleri</i>	yellow hawkweed	forb	M
<i>Hymenoxys subintegra</i>	Arizona rubberweed	forb	S
<i>Juniperus communis</i>	common juniper	shrub	A M
<i>Ligusticum porteri</i>	Porter's licorice root	forb	A
<i>Lotus utahensis</i>	Utah' Bird's-foot trefoil	forb	A
<i>Mahonia repens</i>	creeping barberry	shrub	A
<i>Muhlenbergia montana</i>	mountain muhly	perennial grass	S
<i>Pedicularis centranthera</i>	dwarf lousewort	forb	M
<i>Penstemon virgatus</i>	upright blue penstemon	forb	S
<i>Potentilla hippiana</i>	wooly cinquefoil	forb	S
<i>Pteridium aquilinum</i>	western bracken fern	fern	A
<i>Pyrola chlorantha</i>	green flowered wintergreen	forb	A M

The factors that influence the structure of the shrub/herbaceous layers in mixed conifer forests have not been well studied. There is thought to be greater shrub/herbaceous cover in forests with low canopy cover where there is greater light availability. Researchers have noted herbaceous plants were more common in forest openings, and suggested that there was a negative relationship between tree

density and herbaceous cover (Rasmussen 1941, Merkle 1954, Hurst 1977), and between tree density and shrub cover (Hurst 1977). Laughlin et al. (2005) found that basal area of *Abies lasiocarpa* was negatively correlated with shrub/herbaceous cover but, surprisingly, basal area of *Picea engelmannii* was positively correlated with shrub/herbaceous cover. They also found that coarse woody debris (including dead and down trees) and duff were negatively correlated with shrub/herbaceous cover. There are undoubtedly complex interactions occurring. Low tree density may, on one hand, allow for abundant light for the herbaceous layer; on the other hand, low tree density may be the result of a past tree mortality event that resulted in large amounts of dead and down wood that limit the abundance of herbaceous species.

The diversity of the shrub/herbaceous layer is closely linked to its cover. Species richness in the shrub/herbaceous layer has been shown to be correlated to shrub/herbaceous cover (Laughlin et al. 2005, Laughlin and Fulé 2008). Laughlin et al. (2005) found species richness was higher on southern aspects, largely the result of a greater number of perennial forbs. They also found that species richness was lower in the mixed conifer stands than spruce-fir forest, but that Shannon diversity was lower in the spruce-fir forest. Hurst (1977) found a positive correlation between tree diversity and herbaceous cover within the mixed-conifer forest.

4.5 Rare species

There are several rare species in the mixed conifer and spruce-fir forests of the North Rim, which is expected given the relatively small area that these forests occupy in the region. No Threatened and Endangered species have been identified in these forests, however. *Hymenoxys subintegra* (Arizona rubberweed) is endemic to the Kaibab Plateau North Rim and a few other sites in Arizona (Kearsley et al. 2015, Southwestern Environmental Information Network [SEINET] 2017). It has been given a G4 ranking, indicating that it is “Apparently Secure.” There are two species in the mixed conifer forests of the North Rim identified in the vegetation map (Kearsley et al. 2015) that are ranked G3G4, which indicates that they may be vulnerable. *Ligusticum porteri* was identified in five vegetation associations in mixed conifer and spruce-fir forests. *Shepherdia rotundifolia* (roundleaf buffaloberry) was identified in the *Abies concolor* / *Cercocarpus ledifolius* Woodland, which is associated with rimrock environments. *Cystopteris reevesiana* (Reeves’ bladderfern) was given a G4? Ranking, indicating apparently secure with some uncertainty due to insufficient data. This species was found in the *Abies concolor* / *Juniperus communis* association (Kearsley et al. 2015). The vegetation classification also lists a number of “noteworthy” species, all of which are ranked G5, indicating that they are secure but uncommon in the region. A number of species are restricted to one or two vegetation associations (Table 9).

Table 9. Rare plant species found in mixed conifer and spruce-fir forest communities in Grand Canyon National Park (Kearsley et al. 2015), with conservation status and whether they are restricted to 1 or 2 vegetation associations. Plants with G5 rankings were listed as noteworthy by Kearsley et al. (2015).

Scientific name	Common name	Status	Restricted to 1 or 2 associations
<i>Hymenoxys subintegra</i>	Arizona rubberweed	G4, Endemic	no
<i>Ligusticum porteri</i>	Porter's licorice root	G3G4	no
<i>Shepherdia rotundifolia</i>	roundleaf buffaloberry	G3G4	yes
<i>Cystopteris reevesiana</i>	Reeve's bladderfern	G4?	yes
<i>Campanula rotundifolia</i>	bluebell bellflower	G5	yes
<i>Chamerion angustifolium</i>	fireweed	G5	yes
<i>Chimaphila umbellata</i>	common pipsissewa	G5	yes
<i>Corallorhiza maculata</i>	spotted coralroot	G5	yes
<i>Packera werneriiifolia</i>	hoary groundsel	G5	yes
<i>Pterospora andromedea</i>	woodland pinedrops	G5	yes
<i>Ribes viscosissimum</i>	sticky currant	G5	yes
<i>Zigadenus elegans</i>	mountain deathcamas	G5	yes
<i>Goodyera oblongifolia</i>	western rattlesnake plantain	G5	no
<i>Orthilia secunda</i>	sidebells wintergreen	G5	no
<i>Pyrola chlorantha</i>	green flowered wintergreen	G5	no
<i>Pyrola picta</i>	white veined wintergreen	G5	no

4.6 Pre-Euro-American settlement forest structure composition and changes through 20th century

The presettlement structure and composition of the mixed conifer and spruce-fir forests on the North Rim of the Grand Canyon can be assessed through two types of inquiries: examining historical records and forest reconstruction. Comparisons of historic and contemporary forest structure and composition demonstrate how forests have changed since Euro-American settlement.

A forest survey conducted by Lang and Stewart in 1910 describes “spruce-balsam” and “mixed type” forests (*i.e.* spruce fir and mixed conifer forests) that were less dense than contemporary forests (described in Fulé *et al.* 2003a and Vankat 2013). While this study took place three decades after grazing commenced, it provides an approximation of pre-settlement conditions for forest structure and composition. They estimated total tree density at 360 stems/ha for trees ≥ 0.9 m in height (Vankat 2013) and 117.4 stems/ha for trees ≥ 15 cm dbh (Fulé *et al.* 2003a). Densities of species for stems ≥ 15 cm (stems/ha) are as follows: *Pinus ponderosa* 45.7, *Abies* spp. 30.5, *Picea engelmannii* 21.0 and

Pseudotsuga menziesii 19.3 (cited in Fulé et al. 2003a). Despite the quantitative nature of these data, Vankat (2013) points out that these data are probably underestimates because *Populus tremuloides* was not measured and that areas of montane meadows may have been included in the samples.

Ecologists have also tried to estimate pre-settlement composition and structure through dendrochronological forest reconstructions. Fulé et al. (2003a) found that the mixed conifer forest at their Little Park site had lower density and lower basal area in 1880 than the contemporary forest. Contemporary densities ranged from 150 to 337 trees/ha and basal areas ranged from 10-18 m²/ha. Total tree density for 1880 was estimated to be 107.0 stems/ha (for trees ≥ 15 cm) with the following densities by species (in stems/ha): *Pinus ponderosa*- 34.2, *Abies* spp.- 29.8, *Picea engelmannii*- 22.2, and *Pseudotsuga menziesii*- 20.8. Similar values between their study and Lang and Stewart's 1910 data may validate their data (Fulé et al. 2003a), but it may also suggest that forest reconstruction methods may also underestimate tree densities, particularly for stems in smaller size classes (Fulé et al. 2003a, Vankat 2013). In a comparable study in the nearby San Francisco Peaks, Cocke et al. (2005) estimated 1876 densities for mixed conifer and spruce-fir stands to be 160.9 and 262.9 stems/ha, respectively. They found basal area for these two forest types to be 17.9 m²/ha and 15.5 m²/ha, respectively.

In addition to changes in forest structure, there have been changes in species composition. Fulé et al. (2003a) found that *Abies lasiocarpa* and *Picea engelmannii* had much lower basal areas in 1870 than in contemporary forests. Mast and Wolf (2006) used dendrochronology to determine when cohorts of trees established in mixed conifer stands. They found that there was a large establishment pulse of both *Pinus ponderosa* and *Abies concolor* between 1880 and 1919, but little establishment of *Pinus ponderosa* since. In a mid-elevation mixed conifer site near The Basin, they found that *Picea engelmannii* and *Pseudotsuga menziesii* began increasing in density in the 1920s, and that there were pulses of establishment for *Populus tremuloides* in the 1890's, the 1920's, and 1980's. These studies indicate that tree density and basal area in the mixed conifer forests on the North Rim have increased since 1880, with shade-tolerant species showing the largest increases. A combination of grazing and fire suppression has promoted successional processes, causing the allowed the forests to increase in density. (See Sections 5.1 and 5.2).

Post-settlement changes in the structure and composition of mixed conifer forests suggest that there were changes in the transition between mixed conifer forests and the ponderosa pine forests. Mast and Wolf (2004) conducted a dendrochronological study in lower elevation mixed conifer forests on the North Rim between 2100 and 2500 meters. *Abies concolor* was rare or absent in 1880, but experienced pulses of establishment between 1920 and 1949. By the beginning of the 21st century, its density increased to 968 stems/ha. In contrast, *Pinus ponderosa* had experience pulses of establishment between 1880 and 1919, and little establishment since the 1930's. Their data suggests that historically these were *Pinus ponderosa* stands that were subsequently invaded by *Abies concolor*. Vankat (2011a) noted similar trends in his resampled plots that were established in 1935 in the ponderosa pine forests. In the Moist Ponderosa Pine Forest type, i.e. forests adjacent to mixed conifer forests on the elevation/topography gradient, he found that between 1935 and 2004, *Abies concolor* density increased in density, while *Pinus ponderosa* density showed nominal changes.

These two studies suggest that the transition between ponderosa pine and mixed conifer forests have been moving downslope. This is further supported by more recent studies of White and Vankat (1993) and Vankat (2011a, 2011b) describing this transition occurring at lower elevations than the earlier studies of Merkle 1954, 1962), and Halvorson (1972; Figure 5).

Vankat (2011b) conducted a study on the North Rim that resampled plots that were originally established in 1935 and resampled in 2004 (hereafter “1935 plots”), and plots that were established in 1984 by White and Vankat (1993) and were resampled in 2005 (hereafter “1984 plots”). This study found that there was an overall decrease in tree density and tree basal area in mixed conifer forests between 1935 and 2004 (Table 10). Density of trees >10 cm dbh decreased from 586.7 stem/ha to 386.0 stems/ha in the 1935 plots, and from 582.3 to 386.5 in the 1984 plots. Similarly, there were decreases in total basal area, from 65.0 m²/ha to 35.6 m²/ha in the 1935 plots and from 41.8 m²/ha to 33.1 m²/ha in the 1984 plots. There was also a significant increase in saplings in the 1984 plots (data not shown). In the 1935 plots, all tree species showed decreases in basal area, and *Pinus ponderosa*, *Populus tremuloides* and *Pseudotsuga menziesii* demonstrated decreases in density. *Populus tremuloides* demonstrated the greatest changes: its density decreased from 227.3 stems/ha to 61.1 stems/ha and its basal area decreased from 12.4 m²/ha to 3.3 m²/ha.

Table 10. Changes in tree density and basal area in mixed conifer plots between 1935 and 2004, and between 1984 and 2005 from Vankat’s (2011b) study of forests of Grand Canyon National Park.

Species	Tree density (stems/ha)				Tree basal area (m ² /ha)			
	1935	2004	1984	2005	1935	2004	1984	2005
<i>Abies concolor</i>	127.9	177.4	138.5	81.9	15.2	8.4	9.7	5.7
<i>Abies lasiocarpa</i>	7.7	11.3	43.5	23.8	1.1	0.3	1.9	0.9
<i>Picea</i> spp.	40.6	49.8	87.3	100.8	5.7	3.3	5.0	6.4
<i>Pinus ponderosa</i>	135.9	97.1	73.8	66.9	24.9	17.3	11.7	11.8
<i>Populus tremuloides</i>	227.3	61.1	186.9	72.3	12.4	3.3	8.3	4.7
<i>Pseudotsuga menziesii</i>	47.2	26.7	52.3	40.8	5.6	3.0	5.3	3.6
Total	586.7	386.0	582.3	386.5	65.0	35.6	41.8	33.1

For the spruce-fir forest, Vankat (2011b) found similar decreases in tree density and basal area (Table 11) and increases in saplings (data not shown). Total tree density decreased from 994.5 stems/ha to 425.0 stems/ha in the 1935 plots, and from 738.8 stems/ha to 421.3 stems/ha in the 1984 plots. Similarly, total basal area decreased from 90.1 m²/ha to 24.2 in the 1935 plots, and from 42.3 m²/ha to 27.2 m²/ha in the 1984 plots. The largest decreases were seen in *Picea* spp. and *Populus tremuloides*. *Abies concolor* showed increases in both density and basal area in both sets of plots, while *Abies lasiocarpa* showed increases in both metrics in the 1935 plots. Aspen stands in the 1935 plots showed similar decreases in density and basal area, as a result of the dominance of *Populus tremuloides* (data not shown).

Table 11. Changes in tree density and basal area in spruce-fir plots for 1935–2004, and for 1984–2005 from Vankat's (2011b) study of Grand Canyon National Park.

Species	Tree density (stems/ha)				Tree basal area (m ² /ha)			
	1935	2004	1984	2005	1935	2004	1984	2005
<i>Abies concolor</i>	0.0	5.0	6.3	12.5	0.0	0.3	0.2	0.4
<i>Abies lasiocarpa</i>	37.1	100.0	208.8	95.0	4.5	5.3	9.9	5.2
<i>Picea</i> spp.	531.3	290.0	270.0	195.0	52.3	15.9	18.6	14.1
<i>Pinus ponderosa</i>	0.0	0.0	11.3	5.0	0.0	0.0	0.4	0.3
<i>Populus tremuloides</i>	426.3	30.0	223.8	97.5	33.4	2.7	11.9	6.1
<i>Pseudotsuga menziesii</i>	0.0	0.0	18.8	16.3	0.0	0.0	1.3	1.0
Total	994.5	425.0	738.8	421.3	90.1	24.2	42.3	27.2

The forest reconstructions by Fulé *et al.* (2003a) and Mast and Wolf (2006) suggest that between 1880 and the first years of the 21st century, there was an overall trend of increasing tree density and basal area, with shade tolerant trees becoming more abundant. These changes in forest structure and composition were thought to be the result of the removal of fire from the ecosystem, but other disturbances also likely played a part. (See Section 5). Vankat (2011b) resampling of historic plots from 1935, found some increases in abundance of shade intolerant species, particularly within the sapling layer, but also some suggestions of changes towards greater shade intolerance: *Pinus ponderosa* increased in basal area and *Populus tremuloides* decreased in density. More importantly and in contrast to forest reconstruction studies, Vankat (2011b) found that between 1935 and 2004, there was an overall decrease in tree density and basal area. While these results appear contradictory, it is critical to consider the time periods for the studies and the changes that occurred between 1880 and 1935. Vankat (2011b) suggests that tree density and basal area may have increased through the first half of the 20th century, reach a maximum at some point in the middle of the century, and then began to decrease. The decreases in density and basal area were likely the result of a combination of factors including density dependent self-thinning, drought, insects and pathogens, herbivory, prescribed fires, Sudden Aspen Decline (SAD) and elevated ozone levels. (See Section 5). Vankat (2013) also suggests that both Lang and Stewart's 1910 study, and the forest reconstruction studies (Fulé 2003a, Mast and Wolf 2006), likely underestimated tree densities. Lang and Stewart did not include *Populus tremuloides* in their estimates, and may have included meadows. Forest reconstruction studies likely underestimate tree densities, due to loss of dead trees from combustion and decomposition. This suggests that the increases in tree density during the 20th century reported in these forest reconstruction studies are exaggerated.

5 Disturbance

5.1 Grazing and browsing

Livestock grazing on the North Rim began around 1879, and lasted through the first decades of the 20th century. (See Section 3). With the establishment of the park in 1919, grazing officially ended, but trespass grazing continued until fencing was completed in 1930 (Fulé et al. 2002). The greatest impact to the mixed conifer and spruce-fir forests was the removal of herbaceous vegetation, thus limiting the spread of surface fires. In combination with the suppression of fires, this removal of fine fuel from the system disrupted the natural fire regime, allowing for increased establishment of trees (Fulé et al. 2002; see Section 5.2). Removal of the herbaceous layer may have also promoted increased tree generation, by reducing competition between tree seedlings and herbaceous plants. Forest reconstructions from the North Rim (Fulé *et al.* 2003a, Mast and Wolf 2004) showed that there was an increase in tree density beginning around 1879, the same time that livestock grazing was introduced in the region. Similar trends were seen for mixed conifer forests on the San Francisco Peaks (Cocke *et al.* 2005).

Browsing and grazing by native deer also affected the vegetation composition and structure of the mixed conifer and spruce-fir forests of the North Rim. The greatest impact has been the browsing on seedlings and saplings of *Populus tremuloides*, but deer also browse/graze on *Pinus ponderosa* and *Abies concolor*, shrubs and herbaceous species (Rasmussen 1941). Vegetation impacts from deer inevitably vary with fluctuations in the deer population. Shortly after the establishment of the game preserve in 1906, federal land managers began a predator control program. Government hunters began killing predators, including mountain lions, wolves, coyotes and bobcats (Hurst 1977). As a result, the size of the deer herd increased from 4,000 in 1906 to 100,000 in 1924 (Rasmussen 1941). The predator killing ceased in 1939, after which deer populations began to decrease. Merkle (1954) noted a lack of *Populus tremuloides* in intermediate size classes that corresponded to tree regeneration in the 1920's and 1930's, but abundant young stems that corresponded to the 1940s. An increase in the deer population increased again in the 1950 similarly caused a large reduction in the regeneration of *Populus tremuloides* (Merkle 1962). In their forest reconstruction, Fulé *et al.* (2002) found that there was little regeneration of *Populus tremuloides* between 1900 and 1960 on their Swamp Ridge site. Browsing by deer may partially explain Vankat's (2011b) finding of a decrease in *Populus tremuloides* density between 1935 and 2004.

Bison also potentially impact the mixed conifer and spruce-fir forests through grazing, and more importantly through trampling of vegetation. While bison may have historically been present on the Kaibab Plateau, they were likely at the edge of their geographic range and present in small numbers (Plumb et al. 2016). The herd was brought to the Kaibab Plateau in 1906 with the establishment of the Grand Canyon Game Preserve, on the Kaibab National Forest, north of the park boundary. They were hybridized with cattle, and currently they retain "relatively higher cattle introgression amongst public conservation herds" (Plumb et al. 2016). By the 1990s, the herd began using large areas of the park. By 2014 the population size of the herd ranged between 400 and 600 animals (NPS 2017), much higher than would have historically occurred (Plumb et al. 2016). According to the Initial Bison Herd Environmental Assessment (NPS 2017), the bison primarily use the montane meadows,

springs, and shrublands, but use the forests to travel between their preferred habitats. There is evidence, however, that the bison use recently burned areas of prescribed fires in ponderosa pine forests and mixed conifer forests, apparently attracted to the flush of perennial grass growth following the fires (pers. comm. Li Brannfors). Grazing preference for recently burned area has been cited in other ecosystems (Shaw and Carter 1990, Pearson et al. 1995). Impacts to the forests include trailing, soil disturbance from wallowing (depressions caused by rolling on the ground), and spread of nonnative species. Bison impacts are described in the Environmental Assessment (EA) as “not noticeable”. It is unclear how these impacts were assessed in the EA, and how they could be present but “not noticeable”.

The introduction of non-native ungulates can cause large changes in ecosystem structure and processes. At Bandelier National Monument, the introduction of nonnative ungulates (cattle, sheep and burros) caused a cascading series of effects on the woodland ecosystems that included removal of herbaceous vegetation, elimination of surface fires, increased soil erosion, and increased tree establishment (Sydoriak et al. 2000, Jacobs et al. 2002). Increased erosion and alteration of fire regimes are potentially occurring in the forests of the North Rim. On the Channel Islands off the California coast, nonnative bison were found to be vectors for nonnative plant species, both through seeds attached to their fur that were deposited in the wallows, and through digested seeds deposited in their dung (Constible et al. 2005). Due to their preference for burned areas over unburned, and their ability to spread nonnative species, there is a potential for bison to cause an increase in nonnative species in burned areas of mixed conifer forests of Grand Canyon National Park.

5.2 Fire

5.2.1 Fire regimes

Prior to human settlement, fires regularly burned in the mixed-conifer and spruce-fir forests of the North Rim. In the 1909 forest survey, Lang and Stewart noted evidence of “light ground fires” and areas denuded by fires across the Kaibab Plateau (cited in Fulé et al. 2003a). Vankat (2013) suggests, however that these denuded areas may have just been montane grasslands. It is unclear to what extent the ignition sources for fires prior to the 20th century were lightning or caused by Native Peoples. There were 71 lightning caused fires between 1933 and 1996 in the 4400 ha area of the Little Park region on the North Rim (Fulé et al. 2003a), suggesting that natural sources may have sufficient for maintaining the fire regime. The natural fire regimes were disrupted with the advent of settlement by European-Americans. Livestock grazing removed the fine fuels that allowed surface fire to carry. This change in fire regimes is evident with a sudden decrease in fires in the dendrochronological record beginning around 1879 (Fulé et al. 2003a, Fulé et al. 2003b). The decrease in fire was exacerbated by suppression of wildland fires, which began in 1905 (Vankat 2011b)

Fulé et al. (2003a, 2003b) conducted the most thorough fire history study on the North Rim. In a study at Swamp Ridge, a low elevation mixed conifer site (ranging from 2427 to 2537 m, or 7963 to 8323 ft), Fulé et al (2003b) found a mean fire interval (MFI) was 5.1 years between 1721 and 1879. The MFI for large fires, that is those scarring 25% of the trees on the site, was 8.7 years. In a study of the mixed conifer forest at Little Park, Fulé et al. (2003a) found that the MFI for the mid-elevation mixed conifer forest at Little Park (elevation range from 2550 to 2650 m (8366 to 8694 ft))

was 6.7 years. The fire return interval increased with elevation: above 2750 m (9022 ft), the MFI was 15.9 years. In a comparable study, Mast and Wolf (2006) found fire return intervals to range from 8.41 years on low elevational sites on the Walhalla Plateau (2200-2500 m, or 7218 to 8202 ft) to 10.33 years on high elevation sites near The Basin (2600 to 2830 m, or 8530 to 9285 ft). Fulé et al. (2003a) found that the MFI varied with stand type and aspect. South aspects had a MFI of 5.5 years, while north aspects had an MFI of 13.1 years. Aspen forests had the shortest MFI with 5.7, followed by ponderosa pine forest with 7.4 years, mixed conifer forests and spruce-fir forests with 8.7 years. This suggests that fires help to maintain stand types in particular topographic locations. *Pinus ponderosa* occurs on southern aspects and ridgetops, due to their relatively xeric conditions, but also due to the fact that they are adapted to the surface fires associated with these sites (White and Vankat 1993, Fulé et al. 2003a, Vankat 2013). Fulé et al. (2003a) found evidence that presettlement fires may have been very large, and that many stands had been initiated following fires.

The dendrochronological record shows a correlation between large fires and drought years, particularly dry years that follow wet years (Fulé et al. 2003a, 2003b, Wolf and Mast 2006). This is likely the result of an increase in herbaceous biomass during the wet years, creating a greater and more continuous fine fuel load that allows for the spread of fire in the following year. The occurrence of fires among spatially separated sites may be the result of multiple fires occurring during the same dry season, or even from multiple lightning starts on a single day (Fulé et al. 2003b). Alternatively, it may also may be the result of very large fires. Fulé et al. (2003b) suggest that fires may have started in the lower, drier forests, and spread to the higher elevation forests. The Walhalla Plateau have had a higher MFI due to its relative isolation.

The few number of fires that occurred following Euro-American human settlement makes it difficult to quantify fire return intervals accurately. After 1879, only two fires were recorded at the Little Park Site, creating an MFI of 31.0 years (Fulé et al. 2003a). At the Swamp Ridge site, the fire free periods since 1879 were approximately 5.5 times longer than presettlement intervals. Wolf and Mast (1998) found that fire return intervals were shorter during the settlement period: they found that the MFI changed from 4.85–10.3 years before 1870 to 4.88–6.40 between 1870 and 1920. A possible explanation for this is an increase in human-caused fires. Their study sites on the Walhalla Plateau and near The Basin may have received more human use than the study sites of Fulé et al. (2003a). After 1920, Wolf and Mast (1998) found the fire returned interval ranged from 18.75 to 75 years.

The disruption of fire regimes caused dramatic changes in forest composition. Understory seedlings and saplings that were typically susceptible to fire were allowed to regenerate, resulting in an increase in density of mesic, shade-tolerant, species such as *Abies* spp., *Picea* spp. and *Pseudotsuga menziesii* (Merkle 1962, White and Vankat 1993, Fulé et al. 2004b, Vankat 2005, Mast and Wolf 2006), and little regeneration of shade-intolerant *Pinus ponderosa*. Mixed conifer forests, particularly on the xeric south-facing slopes, likely became invaded by more mesic species such as *Abies concolor* (White and Vankat 1993, Vankat 2005). The disruption of fire regimes has also caused *Abies concolor* to invade ponderosa forests thus causing the ecotone between mixed conifer and ponderosa forests to become lower in elevation. Low elevation mixed conifer forest used to be ponderosa pine forest prior to settlement, but has subsequently been invaded by *Abies concolor* (Mast

and Wolf 2004, Vankat 2011a; see Section 4-6). The evidence of increasing tree density and fuel loads, however may not have occurred linearly since 1879 to the present. Vankat (2011b) found that there has been decreasing tree density and basal area since 1935, suggesting that these metrics may reach their maxima in the latter half of the 20th century. (See Section 4.6).

There is a growing consensus that the fire regimes of the mixed conifer forests on the North Rim were mixed-severity (Fulé et al. 2003b, Vankat 2004, Vankat 2005, Mast and Wolf 2006), with frequent, low-severity surface fires occurring on the south facing slopes and ridges, and infrequent, high-severity crown fires occurring on the north slopes and valley bottoms. Vankat (2004) found that crown fires were restricted to patches of less than 40 ha. Fulé et al. (2004b) modeled fuel loads between 1920 and 2040, and found steady increases in canopy fuel loads, allowing surface fires to become crown fires at increasingly lower wind speeds. (Vankat's mixed-conifer study suggests, however, that tree density, and hence fuel loads, have decreased since the mid-20th century).

White and Vankat (1993) suggested that the disruption of fire regimes have caused the vegetation to become more homogenous across the landscape. A consequence of this that the fuels have become more homogenous, thus increasing the likelihood of larger high-severity fires. These theories were born out with the large number of wildfires occurring in the first decade of the 21st century, although drought conditions also were responsible (Table 12, Figure 7). The homogenizing effect on the landscape is further demonstrated by the large severely burned areas supporting early successional forest stands (Vankat 2005). While there clearly have been changes in the fire regimes, there is insufficient data to determine the extent to which the contemporary fire regimes, and consequently the vegetation, fall within the historic range of variability.

Table 12. Wildland fires between 1960 and 2012 and greater than 800 ha that impacted the mixed conifer and spruce-fir forests in Grand Canyon National Park.

Name	Year	Size (ha)
Saddle Mt	1960	3876
NR Complex	1998	1594
Outlet	2000	4976
Vista	2001	1463
Poplar	2003	4756
Rose	2003	1393
Dragon	2005	3205
Roosevelt	2007	2096
Aspen	2009	4279

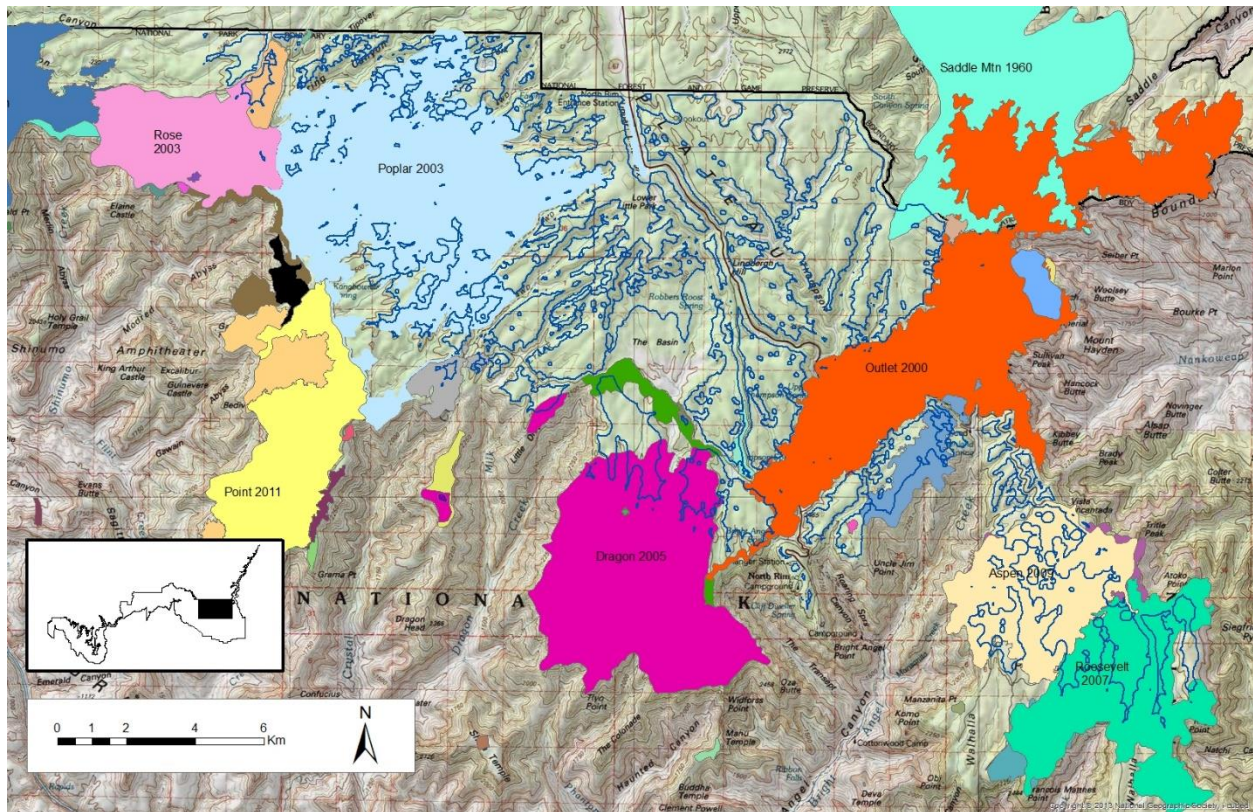


Figure 7. Wildland fires on the North Rim of Grand Canyon National Park between 1960 and 2011, including escaped prescribed fires. The names and dates of the larger fires are noted. Inset map shows location of North Rim study area in the park.

5.2.2 Prescribed fire and fire management activities

In 1980, the Fire Management Program at Grand Canyon National Park began using prescribed fire to reduce hazard fuel loads and to restore forested ecosystems (Vankat 2011b; Figure 8). While these fires targeted ponderosa pine forests, they sometimes burned into areas of low elevation mixed conifer forests. In 1999, fire managers began using prescribed fire in the mixed conifer forest, and managing lightning-ignited fires, allowing fires to burn within ranges of certain weather prescriptions. The largest of these was the Poplar Fire, which burned 4756 ha in 2003. Due to heavy fuel loads, and a historic mixed-severity fire regime, prescribed and lightning fire proved challenging to manage. For example, the Outlet Fire of 1999 was a prescribed fire escaped, burning 5034 ha. In contrast, the Range Fire and Thompson Fire of 2012 burned 1873 ha, the majority of which was low burn severity. The Thompson fire burned some of the highest elevations in the park that are comprised of spruce-fir forests. In 2014, Grand Canyon Fire Management began conducting prescribed fires in the fall and spring, using aerial ignition and hand ignition to target southern slopes and ridges of mixed conifer forests (pers. comm. Li Brannfors), xeric stands that historically had more frequent fire regime. Grand Canyon Fire Management has also been conducting mechanical thinning of trees in the mixed conifer forests along roads, and developed areas.

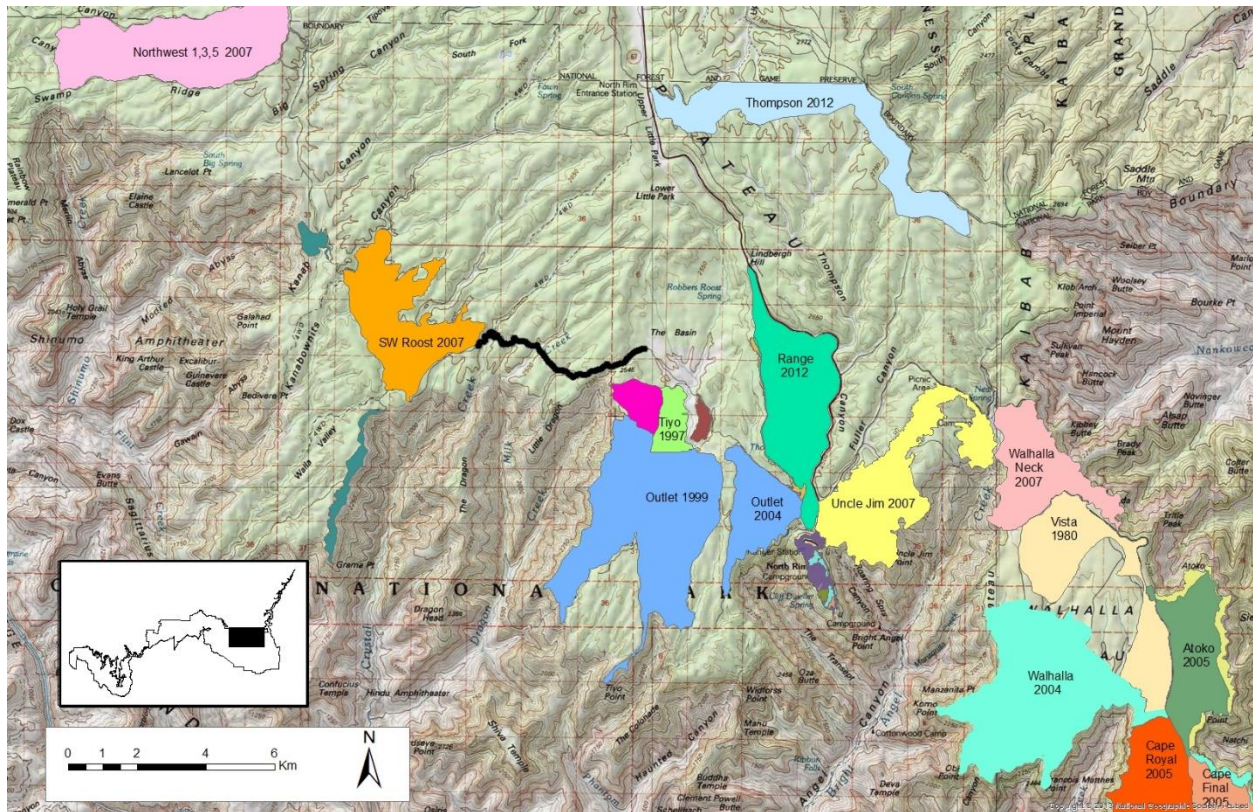


Figure 8. Prescribed fires between 1980 and 2012 on the North Rim of Grand Canyon National Park. Escaped prescribed fires were not included. The names and dates of the larger fires are noted. Inset map shows location of North Rim study area in the park.

5.2.3 Fire effects –forest structure

Forest structure is impacted through fires causing tree mortality, thus decreasing their density, basal area and canopy cover, at least in the short term. Fulé et al. (2004a) found that in the Northwest III prescribed fire on the Swamp Ridge area, a low-elevation mixed conifer forest dominated by *Pinus ponderosa* and *Abies concolor*, *Abies concolor* sustained the greatest mortality, causing a shift towards greater dominance of *Pinus ponderosa*. Comparing the burned area with an adjacent unburned area, tree density was 33%, basal area was 69% and canopy cover was 42% that of the unburned forest. In this fire, tree density in the burned area was reduced to 331 stems/ha which is slightly higher than the pre-Euro American tree density of 246 stems/ha. Basal area of was reduced to 28.5 m²/ha which matched the pre-European-American basal area. This suggests that fire has restored the forest structure of this ponderosa pine stand that had been invaded by *Abies concolor* to pre-settlement densities.

Low-severity fires kill the most susceptible species, namely smaller individuals and species that are not fire adapted. A prescribed fire in a ponderosa pine forest with *Abies concolor* encroachment caused 98% mortality of all conifer trees less than 15 cm in diameter (NPS 2012). Similarly, Fulé and Laughlin (2007) found that 83% and 79% of tree mortality was confined to trees less than 20 cm dbh in a mid-elevation and high elevation sites, respectively. *Pinus ponderosa* is the tree species that is most fire tolerant followed by *Pseudotsuga menziesii* (Table 5). *Populus tremuloides* is sensitive to

fire, but sprouts vigorously following fire. In a study of fires of varying severities across an elevational gradient on the North Rim, Fulé and Laughlin (2007) found that large trees (greater than 37.5 cm dbh) experienced differential mortality by species as follows: *Abies lasiocarpa* -29%, *Picea engelmannii* - 16%, *Abies concolor* - 15%, *Populus tremuloides* - 14%, *Pinus ponderosa* - 7%, and *Pseudotsuga menziesii* - 0%.

In the Poplar fire, Fulé and Laughlin (2007) found a 57% decrease in tree density and a 39% decrease in basal area, driven mostly by *Picea engelmannii* and *Abies lasiocarpa*. They also found evidence of delayed tree mortality: mortality between 1 and 2 years post-fire accounted for 15.6 and 11.2% of the trees dying in mid and high elevation sites, respectively. Fire intensity and burn severity inevitably vary within a single fire, resulting in a heterogeneous post-fire landscape. In this fire, large aspen and other old-growth trees were killed in some areas while tree mortality was minimal in other areas, creating greater spatial variability in the forest structure. High-intensity fire can occur with high fuel loads, high wind speeds and drought conditions, that result in high burn severity burns with 100% mortality of trees. For example, the Outlet Fire of 2000 a prescribed fire that escaped, and the Poplar Fire of 2003, a lightning fire that was managed, burning 4976 ha and 4811 ha, respectively, with a large areas of complete tree mortality.

The factors that influence tree regeneration are paramount in determining the future composition and structure of forests in severely burned areas. The increase in light from canopy removal, in addition to the removal of the duff and litter layers, allows for the regeneration of shade intolerant species such as *Pinus ponderosa* and *Pseudotsuga menziesii*. More shade tolerant species may become established once a canopy is formed. *Populus tremuloides* can establish in the years following fires, often regenerating from root sprouts. For examples, large areas that were severely burned by the Outlet and Poplar fires are dominated by *Populus tremuloides*. In the vegetation map, these areas are classified as *Populus tremuloides* shrublands, and consist of two associations: *Populus tremuloides* - *Ceanothus fendleri* / *Carex* spp. Shrubland, and *Populus tremuloides* / *Robinia neomexicana* Woodland (Kearsley et al. 2015).

5.2.4 Fire effects – shrub-herbaceous layer and soil surface

Fires affect the herbaceous and shrub layers through a variety of means, including mortality, stimulation of seed germination, increased nutrient availability and increased light availability from reduced canopy cover (Huisinga et al. 2005). In a low elevation mixed conifer stand on Swamp Ridge, Huisinga et al. (2005) found large differences in the shrub/herbaceous layer six years following a fire: relative to unburned areas, burned areas had twice as much shrub/herbaceous cover, greater abundance of annual and biennial species, greater species richness and higher Shannon diversity. In contrast, Laughlin and Fulé (2008) found no difference in species richness between burned and unburned spruce-fir forest stands six years following a fire. Differences between these two studies may be a result of different forest types. In her post-fire survey, Crawford (2005) found that high severity sites had the lowest Shannon diversity, while low severity sites and sites of moderate severity with patches of high severity had the highest Shannon diversity. The increases in annual and biennial species in burned areas may be offset by a loss of shade tolerant species, such as *Pyrola secunda* (Laughlin et al. 2005). Laughlin et al. (2005) speculated that increased species

richness in burned sites might be the result of removal of dead and down trees, as well as removal of duff and litter and increased light availability. A number of herbaceous species have been identified as indicators of burned mixed conifer forests (Huisinga et al. 2005, Laughlin and Fulé 2008; Table 13). Three of these species are nonnative: *Bromus tectorum* (cheatgrass), *Poa pratensis* (Kentucky bluegrass) and *Taraxacum officinale* (common dandelion). This demonstrates that fires can create environments that promote the spread of invasive species. (See Section 5.3). Crawford (2005) found that the most abundant species growing in areas severely burned in the Outlet fire were *Sambucus nigra* (American black elderberry), *Carex rossii* and *Ceanothus fendleri*. There are also herbaceous species that are sensitive to fire, and are indicators of unburned areas: these include *Goodyera oblongifolia*, *Mahonia repens*, *Solidago velutina* (threenerve goldenrod), *Pteridium aquilinum*, *Eriogonum racemosum* (redroot buckwheat), *Pyrola* spp. and *Kelloggia galioides* (milk kelloggia; Huisinga et al. 2005).

Table 13. Herbaceous species that are indicators of burned mixed-conifer forest of Grand Canyon National Park (from Huisinga et al. 2005, Laughlin and Fulé 2008).

Scientific name	Common name
<i>Androsace septentrionalis</i>	pygmyflower rockjasmine
<i>Bromus tectorum</i>	cheatgrass
<i>Ceanothus fendleri</i>	Fendler's ceanothus
<i>Chamerion angustifolium</i> .	fireweed
<i>Chenopodium</i> spp.	goosefoot
<i>Cirsium wheeleri</i>	Wheeler's thistle
<i>Gayophytum diffusum</i>	spreading groundsmoke
<i>Houstonia wrightii</i>	pygmy bluet
<i>Phacelia egea</i>	Kaweah River phacelia
<i>Poa pratensis</i>	Kentucky bluegrass
<i>Polygonum douglasii</i>	Douglas' knotweed
<i>Pseudognaphalium macounii</i>	Macoun's cudweed
<i>Rubus idaeus</i>	American red raspberry
<i>Taraxacum officinale</i>	common dandelion

Erosion following wildland fires can be severe. Few studies of soil erosion following wildland fires have been conducted on the North Rim. In post-fire survey of the Outlet Fire, Crawford and Straka (2004) observed large amount of bare ground in the first year following the fire, but it gradually decreased over a five-year period. At Bandelier National Monument, the Las Conchas fire of 2011

caused extensive erosional deposition in the riparian areas of the monument (White et al. 2012), the majority of the erosion likely attributable to burned areas in mixed conifer forests.

5.3 Nonnative species

Non-native plant species are not a large problem for the mixed conifer forests on the North Rim, compared to other ecosystems on the Colorado Plateau. The low abundance of nonnative species is likely the result of relatively low levels of human disturbance that has occurred in the park (Laughlin *et al.* 2005). The park's vegetation map and classification (Kearsley et al. 2015) listed the nonnative species found in mixed conifer forest and spruce-fir forest associations with their relative abundance (Table 14). Park management has identified four species for high priority management: *Bromus tectorum*, *Bromus inermis*, *Poa pratensis* and *Rumex acetosella* (common sheep sorrel). *Verbascum thapsus* (common mullein) was also identified as a species of concern (NPS 2017).

Table 14. Nonnative species listed Grand Canyon National Park's vegetation map and classification for mixed conifer and spruce-fir communities (from Kearsley et al. 2015).

Scientific name	Common name
<i>Bromus inermis</i>	smooth brome
<i>Bromus tectorum</i>	cheatgrass
<i>Dactylis glomeratus</i>	orchardgrass
<i>Phleum pratense</i>	timothy
<i>Poa pratensis</i>	Kentucky bluegrass
<i>Tragopogon dubius</i>	yellow salsify
<i>Conyza canadensis</i>	Canadian horseweed
<i>Lactuca serriola</i>	prickly lettuce
<i>Polygonum aviculare</i>	prostate knotweed
<i>Sisymbrium altissimum</i>	tall tumbled mustard
<i>Taraxacum officinale</i>	common dandelion

The only areas where nonnative species occur in moderate to high abundance are areas that burned in high severity fires. (See Section 5.2). In the recent vegetation map and classification for the park, the *Populus tremuloides* / *Ceanothus fendleri* / *Carex* spp. Shrubland and the *Populus tremuloides* / *Robinia neomexicana* Woodland, which grow in areas that experience high-severity crown fires, contain a number of nonnative species (Kearsley et al. 2015). A number of nonnative species were also identified during post-burn surveys of the Outlet fire, including *Malva neglecta* (common mallow), *Medicago lupulina* (black medick), *Polygonum aviculare* (prostate knotweed), *Rumex acetosella* (garden sorrel) and *Tragopogon dubius* (yellow salsify; Crawford 2005, Crawford and Straka 2004). Huisinga et al. (2005) identified four nonnative species in areas that had been burned in low severity prescribed fires: *Bromus tectorum*, *Tragopogon dubius*, *Cirsium vulgare* (bull thistle)

and *Taraxacum officinale*. Their cover, however, never exceeded 1% cover. Nonnative species are also found in areas that have experienced other types of disturbance: for example, *Verbascum thapsus* and other nonnative species are commonly found in bison wallows (NPS 2017). Preferential use of recently burned areas by bison may also be furthering the spread of nonnative species (pers. comm. Li Brannfors).

5.4 Insects, pathogens and parasites

There are a wide variety of insects, pathogens and parasites that impact the trees of the mixed conifer and spruce-fir forests of the North Rim. Some are generalists that affect multiple species, while others are species specific. Most of these act to weaken individuals, causing reduced growth, dieback, and increased susceptibility to other agents. The ultimate cause of mortality for the majority of trees is fungal infections, but these generally occur following the weakening of trees and bark damage from insects. Insects generally target weakened trees, but will attack healthy trees during epidemics (Lynch et al. 2008). A wide variety of environmental factors can weaken trees and act in conjunction with these agents, including drought, competition, lightning, structural damage, poor site quality, presence of dead and down trees and frosts (Hurst 1977, Lynch et al. 2008).

Spruce budworm (*Choristoneura occidentalis*) is the insect with the greatest impact to the mixed conifer and spruce-fir forests of the North Rim, causing defoliation that is focused on new growth (Hurst 1977, Lynch et al. 2008). While its primary host is *Picea engelmannii*, it also affects other conifer species to varying degrees. This insect experiences periodic population eruptions that last from several years to several decades. In some cases, spruce budworm can cause direct mortality, but other agents such as bark beetles and fungi are often involved. It prefers moist conditions, and shade tolerant species in forests with several canopy layers. Spruce budworm populations have increased on the North Rim since in the 1950s (Lynch et al. 2008). Increases in tree density through the 20th century (Fulé et al. 2003a, Mast and Wolf 2006), may have promoted spruce budworm outbreaks. Tree mortality from these outbreaks may have been partially responsible to the declines in tree density that Vankat (2011b) reported.

There are large varieties of other insects that use *Picea* spp., *Abies* spp. and *Pseudotsuga menziesii* as hosts. They act in conjunction with other agents, but generally have lower impact than spruce budworm (Lynch et al. 2008). The western balsam bark beetle (*Dryocoetes confusus*), fir engraver (*Scolytus ventralis*), tip moths (*Rhyacionia* spp.) and white fir needleminer (*Epinotia meritana*) attack stressed *Abies* spp. trees, but populations have generally remained at low densities. The species-specific Douglas fir beetle (*Dendroctonus pseudotsugae*) attacks large trees with mistletoe (*Arceuthobium douglasii*), root disease and structural damage. Damage from this species increases in drought – outbreaks coincided with droughts from in the 1950's and from the recent drought between 2002 to 2006. Spruce beetles (*Dendroctonus rufipennis*), specific to *Picea* spp., prefer dense stands of large diameter spruces, with large amounts of dead and down trees. While the nonnative spruce aphid (*Elatobium abietinum*) has not been found on the North Rim, it occurs in the San Francisco Peaks, and has the potential to cause significant damage if it is introduced.

Populus tremuloides is affected by a number of agents; foremost is the western tent caterpillar (*Malacosoma californicum*). It causes defoliations, which can lead to mortality if defoliations occur

in several consecutive years. It often works in conjunction with large aspen tortix (*Choristoneura conflictana*), melampsora rust and black leaf spot. In the last quarter of the 20th century, stands on the North Rim were damaged by a combination of these agents (Hurst 1977, Lynch et al. 2008). Recent mortality events of *Populus tremuloides* have been described as Sudden Aspen Decline (SAD), which appears to be the result of a combination of factors: drought, high temperatures, insects, pathogens and late frosts when the trees had leafed out (Fairweather et al. 2007, Morelli and Carr 2011). In the San Francisco Peaks, the cause of the *Populus tremuloides* mortality was attributed primarily to a late frost in 1999 followed by a severe drought, with western tent caterpillar, *Cytospora* canker, bronze poplar borer (*Agilus liragus*), aspen bark beetles (*Trypophloeus populi* and *Procryphalus mucronatus*) and clearwing moth (*Paranthrene robinae*) acting as contributing agents (Fairweather et al. 2007). The influence of drought is evident with lower elevation stands generally being more severely impacted than high elevation stands (Gitlin et al. 2006, Fairweather et al. 2007). Gitlin et al. (2006) found that stands below 2600 m sustained mortality levels of 18.3%, while stands above 2900 m sustained mortality levels of 9.5%.

Pinus ponderosa hosts a large variety of insects (Lynch et al. 2008). The most damaging are species of *Ips* and *Dendroctonus* bark beetles. Factors that lower trees' resistance to the beetle include poor site quality, high tree density, drought, injury and disease (Lynch et al. 2008). While *Dendroctonus*, which attacks larger trees, was more abundant in the 1950s, *Ips*, which attacks smaller trees, has become common in the subsequent decades. These bark beetles are kept in check with cold temperatures. *Pinus ponderosa* is also impacted by defoliating insects such as sawflies (*Neodiprion* spp. and *Zadiprion* spp.), tiger moths (*Lophocampa ingens* and others), the western pine shoot borer (*Eucosma sonomana*) and the Southwestern pine tip moth (*Rhyacionia neomexicana*), as well as beetles such pine engravers (*Ips pini*), the western pine beetle (*Dendroctonus brevicomis*), the mountain pine beetle (*Dendroctonus ponderosae*) and the round head pine beetle (*Dendroctonus adjunus*). These beetles are favored by droughts, as evidenced by infestations during in the droughts from 2002 to 2004. Damaged trees are unable to produce oleoresins to fend off beetles due to their lowered photosynthetic rates (Peterman et al. 2012). These insects have a greater impact on pure stands of *Pinus ponderosa* than trees in mixed conifer forest.

Another suite of pathogens includes fungi and bacteria. These include witches brooms, cankers, rusts, trunk swellings, root rot and galls. Cankers cause breakage of stems in wind and snow. Rusts are a group of fungi that starve trees through strangulation, and rely on alternate hosts to complete their lifecycle. For example, *Picea* spp. is infected by broom rust, which uses *Arctostaphylos* spp. as an alternate host; black rust (*Melampsorella caryophyllacearum*) uses *Pseudostellaria jamesiana* as an alternate host (Hurst 1977). Broom rust causes tree dieback beginning in the crown and working its way downwards. There are a number of root fungi including Armillaria (*Armillaria* spp.), Annosus (unknown species), Tomentosus (*Inonotus tomentosus*) and Schweinitzii (*Phaeolus schweintzii*) root rots. *Armillaria* spp. is prevalent in *Pinus ponderosa* in Arizona and *Picea* spp. *Abies* spp. and *Pseudotsuga* spp. across western United States (Lynch et al. 2008). Fungi tend to prefer moist conditions, hence are more prevalent in more mesic forests (Hurst 1977).

Mistletoes are plant parasites that include a number of species that are generally specific to host species. Southwestern dwarf mistletoe (*Arceuthobium vaginatum* spp. *cryptodum*) infects *Pinus ponderosa*; Douglas fir dwarf mistletoe (*Arceuthobium douglasii*) infects *Pseudotsuga menziesii*, but sometimes *Abies* spp.; western spruce dwarf mistletoe (*Arceuthobium microcarpum*) infects *Picea* spp. They weaken their hosts by depleting them of water and nutrients, generally increasing their susceptibility to other agents (Lynch et al. 2008).

5.5 Drought and climate change

Climate variability inevitably impacts forest composition and structure in the mixed conifer and spruce-fir forests of the North Rim. Historic droughts are recorded in the dendrochronological records of trees in these North Rim forests. Mast and Wolf (2006) identified nine drought years in the 19th century and five drought years in the 20th century on both low elevation and mid-elevation mixed conifer sites. Drought inevitably reduces tree growth, and can have indirect impacts by increasing insect outbreaks, increasing fire frequency and severity, and reducing deer populations (See Sections 5.1, 5.2 and 5.4).

Droughts in Southwestern US are a cyclical phenomenon influenced by ocean and atmospheric patterns at different time scales. The El Niño Southern Oscillation (ENSO) is characterized by periodic variations from sea surface temperatures in the Pacific Ocean that operate on the scale of years. Warmer sea surface temperatures in the eastern Pacific Ocean (the El Niño phase) generally bring increased variability in warm season precipitation and above normal cool season precipitation; in contrast, cooler sea surface temperatures (La Niña phase) bring lower variability in warm season precipitation, and below normal cool season precipitation (Hereford et al. 2002). There are two climatic phenomena that act on the scale of decades that influence climate patterns of the Colorado Plateau: the Pacific Decadal Oscillation (PDO) reflects variations in sea surface temperatures in the North Pacific Ocean, and the Atlantic Multidecadal Oscillation (AMO) reflects sea surface temperatures in the North Atlantic Ocean. The negative, cool phase of the PDO is associated with decreased precipitation in the Southwestern US, while the positive, warm phase is associated with increased precipitation. Hereford et al. (2002) described warm-wet phases of the PDO as occurring from 1905 to 1941 and from 1978 to 1998, and cool-dry phases occurring from 1942 to 1977, and beginning in 1999. Gray et al. (2003) describes similar periodicities: warm-wet phases of the PDO occurring from 1925 to 1946 and from 1977 to 1998, and cool- dry phases occurring from 1890 to 1924 and from 1947 to 1976. Gray et al. (2003) also described phases of the AMO with warm-dry phases occurring from 1860 to 1890 and 1930 to 1960, and cool-wet phases occurring from 1905 to 1925 and from 1970 to 1990. The coupling of the cool phase of the PDO and the warm phase of the AMO has the potential to create severe droughts, such as droughts of the 1950's.

Droughts can directly cause tree mortality, but tree mortality often results with drought interacting with other agents such as bark beetle and other insects and pathogens. (See Section 5.4). Vankat (2011b) suggests that droughts between 1942 and 1977 may have been responsible for decreases in tree densities. The drought between 1999 and 2003 similarly was responsible for increased mortality rates in mixed conifer and spruce-fir forests. *Populus tremuloides* appears to be particularly susceptible to drought. In a study in the San Francisco Peaks, Gitlin et al. (2006) found that tree

mortality was negatively correlated with elevation. Sites above 2900 meters experienced 9.5% mortality, mid-elevation sites at 2600 to 2900 m experienced 16.5% mortality, and sites below 2600 m experienced 18.35% mortality.

Critical to the management of the mixed conifer forests and spruce-fir of the North Rim of Grand Canyon is how these systems will change in the next century, and specifically how climate change will impact these systems. There is a general agreement among climate models that the southwestern United States will become hotter and drier as a result of climate change. Specifically, the following changes are predicted (Garfin et al. 2013):

- Hotter and longer summers with hotter heat waves
- Greater precipitation extremes in winter
- Decrease in late-season snowpack
- Decrease in soil moisture
- Hotter, more severe and more frequent droughts
- Decrease in average winter precipitation in the southern southwest and perhaps an increase in winter precipitation the northern Southwest.

These six predictions are all expressed with high to medium- high confidence with the exception of the last one, which was cited, with medium to low confidence. The ensemble mean of numerous climate models indicate that by 2050 projected droughts will more severe than any drought since 1000 CE (Williams et al. 2013).

Analysis of climate data at Grand Canyon National Park between 1901 and 2012 suggests that climatic conditions have moved outside the range of historical range of variability. Monahan and Fisichelli (2014) used 10, 20 and 30 year windows to compare recent temperatures and precipitation variables to historical records, and found that 5 temperature variables exceeded the 95th percentile of the their historical range. Maximum temperature of the warmest month, annual mean temperature, mean temperature of the warmest quarter, mean temperature of the coldest quarter and mean minimum temperature of the coldest month all showed recent values that exceeded the 95th percentile indicating “extreme warm”. In contrast, no precipitation variables were found to be extreme, *i.e.* all values fell between the 5th and the 95 percentiles.

Longer summers with hotter, more severe and more frequent droughts suggest that the impacts evident in current droughts will become more pervasive. Tree mortality through direct effects of drought would be predicted, particularly on *Populus tremuloides* and the more drought-sensitive species – *Picea engelmannii* and *Abies lasiocarpa*. Tree mortality would be expected to be greatest at the lower elevations and more xeric areas of species’ ranges, causing overall shifts in species composition to more drought tolerant species, such as *Pinus ponderosa*, *Pseudotsuga menziesii* and *Abies concolor*. This suggests a reversal of the successional trend towards denser forests with more mesic species. Vankat (2011b) suggests that this reversal has already begun. Increased drought may reduce the prevalence of fungal agents of mortality, but would increase the frequency and severity of insect infestations, such as bark beetles and affecting *Pinus ponderosa* and *Pseudotsuga menziesii*

and increased prevalence of SAD. This suggests that all tree species could be negatively impacted by increased droughts, making it difficult to identify the winners and losers.

While the dynamics of the shrub/herbaceous layer of the mixed conifer and spruce-fir forest have not been well studied, there would likely be shifts in the composition towards more xeric species. The mesic species would be restricted to the most mesic habitats, and could be possibly extirpated.

The greatest impact to the mixed conifer and spruce-fir forests is the likelihood of an increase in wildland fires, thus reversing the trend of the previous century of a decreasing fire frequency. While this may be misinterpreted as having the potential to restore the forests to pre-settlement densities and composition, there is a greater potential particularly under drought conditions, for large, intense fires, such as those that have occurred in the first decade of the 21st century. These high-severity fires result in large areas high tree mortality, and lead to the conversion to large areas of early successional communities. These areas would likely result in high soil erosion and would be colonized by nonnative species.

5.6 Other natural and human disturbances

Blowdowns from windstorms has not been well studied in mixed conifer and spruce-fir forests (White and Vankat 1993, Vankat 2014). Wind tends to damage trees whose stability has been compromised by fungal and other types of pathogens. However, high-speed winds can potentially cause healthy trees to snap or uproot.

Air pollution has the potential to stress and reduce growth of plants through a variety of mechanisms. This stress on trees causes them to become more susceptible to insects and pathogens (Vankat 2013). Acid deposition alters soil pH. Nitrogen deposition can provide nutrient enrichment to ecosystems. Ozone pollution can damage plant tissue. All have the potential to cause changes in vegetation composition. Herbaceous vegetation and tree seedlings may be most sensitive. Areas with high precipitation tend not to be sensitive to nutrient enrichment, but tend to be sensitive to acid deposition through the leaching of base cations, and ozone (Sullivan 2016).

In his assessment of atmospheric deposition on SCPN park units, Sullivan (2016) described the estimated acid pollutant exposure as low for Grand Canyon, and impacts resulting from nutrient enrichment were very low. In 2011, total sulfur average 0.75 kg/ha/yr and total nitrogen average 2.91 kg/ha/yr. The overall risk to plants in the park was considered low; however, this is based on the predominantly arid conditions across much of the park. The higher precipitation on the North Rim suggests that acid deposition risk may be greater in the mixed conifer and spruce-fir forests than other ecosystems in the park. Ozone exposure indices were high at Grand Canyon, compared with other park units across the country. The W126 indicator was 17.78 ppm-hr and the Sum06 indicator was 26.62 ppm-hr for the years 2005-2009. Moderate values range from 7 to 13 ppm-hr for the W126 indicator and from 8 to 15 ppm-hr for the Sum06 indicator. Morelli and Carr (2011) suggest that ozone is one of numerous interacting environmental factors that could be influencing SAD.

6 Conclusions and Impacts of Climate Change

The mixed conifer and spruce-fir forests of the North Rim of Grand Canyon National Park are dynamic. Their composition and structure has shown dramatic changes over the past century. Broadly speaking, the changes in the forests are the result of succession on one hand, which is characterized by an increase in tree density and a change towards more mesic species composition, and disturbance, which tend to result in less dense stands with less mesic composition. Ecological research in these forests has produced contradictory evidence on the nature of the changes in structure and composition of these forests since European-American settlement. Forest reconstructions of Fulé et al. (2003a) and Mast and Wolf (2006) describe the changes as that of increasing tree density and basal area with increasing abundance of shade tolerant species. In contrast, Vankat's (2011b) resampling of permanent plots indicates that tree density and basal have decreased since 1935.

There are a number of natural and human disturbances that are affecting mixed conifer and spruce-fir forests at Grand Canyon National Park, including fire, drought, nonnative species and pathogens. It is important to understand that these disturbances interact with each other. For example, drought conditions accompanied by spruce budworm epidemic can cause extensive tree mortality, which can increase fuel loads and therefore may increase fire frequency and severity. This in turn may cause increases in soil erosion and the spread of nonnative species. The interaction of these disturbances also can cause positive feedbacks, thus accelerating ecosystem responses (Allen 2007). While disturbances such as fire, droughts and insects may be considered natural disturbance regimes, anthropogenic climate change may cause deviations from their natural range of variability. Deviations from the natural range of variability of fire and climate regimes cause a “blurring” of the distinction between natural and human disturbances.

The mixed conifer forests of Grand Canyon National Park comprise a unique ecosystem that faces a number of significant threats. Paramount among these threats are changing fire regimes and expected droughts from climate change. Predictions of a hotter, drier climate suggests greater mortality rates of trees, and shifts in forest structure and community composition in both the tree and shrub/herbaceous layers.

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Appendix A

Table A-1. Shrub and graminoid species identified in various North Rim studies. The first 3 column represent individual studies. Abundant species are indicated with “X”, less abundant species are indicated with “+”, and not detected species are indicated with a “–”. For Hurst (1977) abundant species were defined as cover ≥1, while Merkle (1954) abundant species were species with measurable cover. Merkle (1962) and White and Vankat (1993) did not provide cover values. Merkle (1962) and Hurst (1977) excluded spruce-fir stands, and Merkle (1954) only sampled spruce-fir stands. The next 5 columns list species identified in the 5 forest types identified by White and Vankat (1993). The last 10 columns represent species identified for selected association in Kearsley et al. 2015). The following species codes are used: ABCO = *Abies concolor*, ABLA= *Abies lasiocarpa*, CARO=*Carex rossii*, CASI=*Carex siccata*, JUCO=*Juniperus communis*, PIEN=*Picea engelmannii*, PIPO=*Pinus ponderosa*, PIPU=*Picea pungens*, POTR=*Populus tremuloides*, PSME=*Pseudotsuga menziesii*, RONE=*Robinia neomexicana*, SYOR=*Symphoricarpos oreophilus*.

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Shrubs	<i>Amelanchier utahensis</i>	Utah serviceberry	+	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Arctostaphylos patula</i>	greenleaf manzanita	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Ceanothus fendleri</i>	Fendler’s ceanothus	–	X	+	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–
	<i>Ceanothus martini</i>	Martin’s ceanothus	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Juniperus communis</i>	common juniper	X	–	X	–	–	–	X	X	X	X	–	X	–	X		X	X	–
	<i>Mahonia repens</i>	Creeping barberry	+	X	+	X	X	–	X	X	X	–	–	–	X	X	X	–	X	–
	<i>Quercus gambelii</i>	Gambel oak	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Ribes viscosissimum</i>	sticky currant	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–
	<i>Robinia neomexicana</i>	New Mexico locust	–	+	X	–	–	–	–	–	–	–	–	–	X	–	X	–	–	–
	<i>Rosa woodsia</i>	Wood’s rose	–	+	+	X	X	X	–	–	–	–	–	X	–	–	–	–	–	–
	<i>Shepherdia canadensis</i>	russet buffaloberry	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–
	<i>Symphoricarpos oreophilus</i>	mountain snowberry	–	–	+	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–
Graminoids	<i>Achnatherum nelsonii</i>	Columbia needlegrass	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Agrostis scabra</i>	rough bentgrass	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Blepharoneuron tricholepis</i>	pine dropseed	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Bromus ciliatus</i>	fringed brome	X	–	X	–	–	–	–	–	X	X	–	X	–	X	–	X	–	X
	<i>Carex spp.</i>	sedge	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Carex occidentalis</i>	western sedge	–	+	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Carex rossii</i>	Ross’ sedge	–	+	X	–	–	–	–	–	X	X	X	–	X	X	X	X	X	–
	<i>Carex siccata</i>	dry-spike sedge	–	+	X	X	X	X	X	–	X	X	X	X	–	X	X	X	–	X
	<i>Elymus elymoides</i>	squirreltail	+	+	X	–	–	–	X	X	–	–	X	X	X	–	–	–	X	–
	<i>Hesperostipa comata</i>	needle and thread	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Table A-1 (continued). Shrub and graminoid species identified in various North Rim studies. The first 3 column represent individual studies. Abundant species are indicated with “X”, less abundant species are indicated with “+”, and not detected species are indicated with a “–”. For Hurst (1977) abundant species were defined as cover ≥1, while Merkle (1954) abundant species were species with measurable cover. Merkle (1962) and White and Vankat (1993) did not provide cover values. Merkle (1962) and Hurst (1977) excluded spruce-fir stands, and Merkle (1954) only sampled spruce-fir stands. The next 5 columns list species identified in the 5 forest types identified by White and Vankat (1993). The last 10 columns represent species identified for selected association in Kearsley et al. 2015). The following species codes are used: ABCO = *Abies concolor*, ABLA= *Abies lasiocarpa*, CARO=*Carex rossii*, CASI=*Carex siccata*, JUCO=*Juniperus communis*, PIEN=*Picea engelmannii*, PIPO=*Pinus ponderosa*, PIPU=*Picea pungens*, POTR=*Populus tremuloides*, PSME=*Pseudotsuga menziesii*, RONE=*Robinia neomexicana*, SYOR=*Symphoricarpos oreophilus*.

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Graminoids (continued)	<i>Koeleria micrantha</i>	prairie Junegrass	–	+	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Muhlenbergia montana</i>	mountain muhly	–	+	+	X	X	X	–	–	–	–	–	–	X	–	X	–	–	–
	<i>Poa fendleriana</i>	Muttongrass	X	+	X	–	–	–	X	–	–	–	–	X	X	X	–	–	–	–
Forbs	<i>Achillea millefolium</i>	western yarrow	–	+	X	X	X	X	X	X	–	–	–	X	–	X	–	–	–	–
	<i>Agoseris aurantiaca</i>	orange agoseris	–	+	+	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–
	<i>Antennaria parviflora</i>	small leaf pussytoes	+	+	X	X	X	–	–	–	–	–	–	X	–	–	–	X	–	–
	<i>Aquilegia coerulea</i>	Colorado blue columbine	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Arenaria fendleri</i>	Fendler's sandwort	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Astragalus castaneiformis</i>	chestnut milkvetch	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Calochortus nuttallii</i>	sego lily	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Campanula rotundifolia</i>	bluebell bellflower	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–
	<i>Castilleja miniata</i>	giant red Indian paintbrush	+	+	+	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Chamerion angustifolia</i>	Fireweed	+	–	–	–	–	–	–	–	X	X	–	–	–	–	–	–	–	–
	<i>Chimaphila umbellata</i>	common pipsissewa	+	–	–	–	–	–	–	–	X	X	–	X	–	–	–	–	–	–
	<i>Chrysopsis fulcrata</i>	rockyscree false goldenaster	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Chrysopsis villosa</i>	hairy false goldenaster	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Cirsium drummondii</i>	dwarf thistle	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Collinsia parviflora</i>	blue-eyed Mary	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Corallorhiza maculata</i>	spotted coralroot	+	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–
	<i>Cryptantha setosissima</i>	bristly cryptantha	–	+	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Delphinium nuttallianum</i>	twolobe larkspur	–	+	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Draba asprella</i>	rough draba	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Erigeron divergens</i>	spreading fleabane	–	+	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Erigeron formosissimus</i>	beautiful fleabane	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

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Forbes (continued)	<i>Erigeron speciosus</i>	aspen fleabane	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–
	<i>Erigeron ursinus</i>	Bear River fleabane	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Eriogonum racemosum</i>	redroot buckwheat	–	+	X	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–
	<i>Erysimum capitatum</i>	sanddune wallflower	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Euphorbia palmeri</i>	woodland spurge	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Fragaria virginiana</i>	Virginia strawberry	+	+	–	X	X	X	–	X	X	–	–	–	–	X	X	X	X	–
	<i>Frasera speciosa</i>	elkweed	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Gayophytum humile</i>	dwarf groundsmoke	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Geranium richardsonii</i>	Richardson’s geranium	+	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Goodyera oblongifolia</i>	western rattlesnake plantain	+	–	–	–	–	–	–	–	X	X	–	X	–	X	X	X	X	–
	<i>Heliomeris multiflora</i>	showy goldeneye	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Hieracium fendleri</i>	yellow hawkweed	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Hymenoxys subintegra</i>	Arizona rubberweed	–	–	X	–	–	–	–	–	X	X	–	–	–	–	–	–	–	–
	<i>Lewisia pygmaea</i>	alpine lewisii	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Ligusticum porteri</i>	Porter’s licorice root	–	–	–	–	–	–	–	X	X	X	–	–	–	X	X	–	X	–
	<i>Lithophragma tenellum</i>	slender woodland-star	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Lomatium bicolor</i>	Wasatch desertparsley	–	+	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Lotus utahensis</i>	Utah bird’s-foot trefoil	–	+	X	X	X	X	–	–	–	–	–	–	–	X	–	X	–	X
	<i>Machaeranthera bigelovii</i>	Bigelow’s tansyaster	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Maianthemum stellatum</i>	starry false lily of the valley	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Mimulus suksdorfii</i>	Suksdorf’s monkeyflower	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Noccaea fendleri</i>	Fendler’s pennycress	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Oreochrysum parryi</i>	Parry’s goldenrod	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–
	<i>Orthilia secunda</i>	sidebells wintergreen	+	–	–	–	–	–	–	–	–	X	–	–	–	–	X	–	–	–

Table A-1 (continued). Shrub and graminoid species identified in various North Rim studies. The first 3 column represent individual studies. Abundant species are indicated with “X”, less abundant species are indicated with “+”, and not detected species are indicated with a “–”. For Hurst (1977) abundant species were defined as cover ≥1, while Merkle (1954) abundant species were species with measurable cover. Merkle (1962) and White and Vankat (1993) did not provide cover values. Merkle (1962) and Hurst (1977) excluded spruce-fir stands, and Merkle (1954) only sampled spruce-fir stands. The next 5 columns list species identified in the 5 forest types identified by White and Vankat (1993). The last 10 columns represent species identified for selected association in Kearsley et al. 2015). The following species codes are used: ABCO = *Abies concolor*, ABLA= *Abies lasiocarpa*, CARO=*Carex rossii*, CASI=*Carex siccata*, JUCO=*Juniperus communis*, PIEN=*Picea engelmannii*, PIPO=*Pinus ponderosa*, PIPU=*Picea pungens*, POTR=*Populus tremuloides*, PSME=*Pseudotsuga menziesii*, RONE=*Robinia neomexicana*, SYOR=*Symphoricarpos oreophilus*.

Category	Scientific name	Common name	Merkle 1954	Merkle 1962	Hurst 1977	PIPO- PSME	PIPO- ABCO	PIPU- PIPO	ABCO- PIPO- PSME	PIEN- ABLA	ABLA- PIEN/ CASI Forest	ABLA- PIEN/ JUCO Wood- land	ABCO / SYOR Forest	PIPU/ CASI Forest	ABCO- PSME/ CARO Forest	ABCO- PSME / CASI Forest	ABCO- PSME / RONE Wood- land	ABCO/ JUCO Forest	POTR / JUCO Forest	POTR / CASI Forest
Forbes (continued)	<i>Packera multilobata</i>	lobeleaf groundsel	+	–	X	–	–	–	–	–	–	–	–	X	–	X	–	–	–	–
	<i>Packera wernerii</i> folia	hoary groundsel	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–
	<i>Pedicularis centranthera</i>	dwarf lousewort	X	+	+	–	–	–	X	–	–	–	–	–	X	X	–	–	–	–
	<i>Penstemon virgatus</i>	upright blue penstemon	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Phacelia egea</i>	Kaweah River phacelia	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Polygonum douglasii</i>	Douglas' knotweed	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Pseudocymopterus montanus</i>	alpine false springparsley	+	+	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Pseudostellaria jamesiana</i>	tuber starwort	–	+	X	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–
	<i>Pteridium aquilinum</i>	western bracken fern	+	+	X	–	–	–	–	–	–	–	X	–	–	X	X	–	X	–
	<i>Pterospora andromedea</i>	woodland pinedrops	+	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–
	<i>Pyrola chlorantha</i>	green flowered wintergreen	+	–	+	–	–	–	X	X	–	X	X	X	–	X	–	–	–	–
	<i>Pyrola picta</i>	white veined wintergreen	+	–	–	–	–	–	–	–	–	X	–	X	X	X	–	–	–	–
	<i>Ranunculus flammula</i>	greater creeping spearwort	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Saxifraga rhomboidea</i>	diamondleaf saxifrage	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Silene scouleri</i>	simple campion	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Solidago nana</i>	baby goldenrod	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Solidago spp.</i>	goldenrod	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	X
	<i>Symphyotrichum ascendens</i>	western aster	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Thalictrum fendleri</i>	meadow-rue	–	X	X	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–
	<i>Zigadenus elegans</i>	mountain deathcamas	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–

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1201 Oakridge Drive, Suite 150
Fort Collins, CO 80525