THESIS

ASPEN AND CONIFER INTERACTIONS OVER A TWENTY-YEAR PERIOD ON THE UNCOMPAHGRE PLATEAU, COLORADO

Submitted by

Amy E. Smith

Department of Forest, Rangeland, and Watershed Stewardship

In partial fulfillment of the requirements

for the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2004

COLORADO STATE UNIVERSITY

June 9, 2004

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY AMY E. SMITH ENTITLED ASPEN AND CONIFER INTERACTIONS OVER A TWENTY-YEAR PERIOD ON THE UNCOMPAHGRE PLATEAU, COLORADO BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

Committee on Graduate Work

William R Jacobi

William H. Romme

Wayne D. Shepperd

Frederick W Smith
Advisor

E. F. Redente
Department Head

ABSTRACT OF THESIS

ASPEN AND CONIFER INTERACTIONS OVER A TWENTY-YEAR PERIOD ON THE UNCOMPAHGRE PLATEAU, COLORADO

Reports of decreasing aspen cover in western forests have caused concern about the long-term persistence of aspen on landscape scales. In the summer of 2001, fifty-three stands on the Uncompahgre Plateau in western Colorado, originally inventoried from 1979-1983, were resampled to quantify changes in overstory dominance. All types of forested stands were sampled, including pure aspen, pure conifer, and mixed aspen/conifer stands. Patterns in overstory dominance and regeneration were analyzed, along with the landscape-scale distribution of forest community types.

Mixed aspen and conifer stands cover 62 percent of the forested landscape on the Uncompahgre Plateau, and pure aspen stands comprise another 16 percent. Since some aspen can be found on over three-quarters of the forest, it is highly unlikely that aspen will be extirpated from the area for many centuries. Pure aspen stands were extremely stable over the twenty-year study period, with high amounts of regeneration and without conifer invasion. Yet a significant increase in conifer dominance in mixed stands indicates that these stands are experiencing a progressive shift from aspen to conifer cover. Current age distributions indicate that aspen and conifers primarily established together after a large regional fire year in the late 1800’s, but differential height-growth

patterns in mixed stands resulted in aspen dominance for about a century followed by rapid increases in conifer dominance in the last twenty years.

The fate of aspen in mixed species stands on the Uncompahgre Plateau is dependent on a disturbance regime that removes the overstory conifers, providing a favorable environment for the shade-intolerant aspen to regenerate. Since individual aspen stems can persist for over a century, it is likely that the clonal root systems of aspen will be able to regenerate for some time. This coupled with the relatively high frequency of pure aspen stands on the Uncompahgre Plateau ensures that aspen is not currently in danger of decline.

Amy E. Smith
Department of Forest, Rangeland, and Watershed Stewarship
Colorado State University
Fort Collins, Colorado 80523
Summer 2004

AKNOWLEDGEMENTS

I would like to thank Amy Williams for gathering the 2001 field data and for GIS mapping of forest covertypes. The 1979-1984 field data was collected and provided by the USDA Forest Service, as well as the GIS layers and associated data tables for vegetation cover on the Uncompahgre National Forest. Thanks to Dr. Skip Smith, my advisor, for invaluable advice on organizational structure of the manuscript. Thanks to my committee members, Dr. William Jacobi, Dr. Bill Romme, and Dr. Wayne Shepperd for editorial comments and suggestions.

INTRODUCTION

As the only deciduous canopy species amid expansive conifer forests (Peet 1981), quaking aspen (*Populus tremuloides*) is highly valued as a critical component of ecosystem diversity (DeByle and Winokur 1985, White et al. 1998). Often cited as the most widely distributed tree species in North America, most aspen forests are in Canada and the Lake States (Fowells 1965). In Colorado aspen is the dominant forest cover on 17% of the nearly 8.5 million hectares of forested land, second only to spruce (Benson and Green 1987). Aspen forests also provide scenic beauty (Johnson et al. 1985, White et al. 1998), support a productive and diverse herbaceous community (Peet 1981, Korb and Ranker 2001), and function as an important habitat type for birds and mammals (DeByle 1985). Recent literature has been concerned that current stocking of aspen in the west has suffered from the cumulative affects of 20th century human land-use practices and management (Mueggler 1989, Baker et al. 1997, Kay 1997, Bartos 2001).

The ecology of aspen regeneration and stand dynamics is critical to the long-term persistence of aspen, both at local and regional scales. In western forests, aspen is a clonal species that regenerates from root suckering following a disturbance to the canopy (Schier et al. 1985). A clone is composed of genetically identical stems that originally arose from a seedling. Aspen is a prolific seed producer yet establishment is difficult (Barnes 1966); however, regeneration from seed has been recorded after severe fires in Yellowstone (Stevens et al. 1999) and southeast Arizona (Quinn and Wu 2001). Once a clone is established the even-aged cohort grows larger until intraspecific competition or disturbance leads to mortality of suppressed stems and a pulse of regeneration in the canopy gaps (Betters and Woods 1981, Mueggler 1989). This multi-cohort, uneven-aged pattern is often persistent until a disturbance agent disrupts growth (Shepperd 1982). If the clone and root system are healthy new suckers will be produced, but a weak root system may not regenerate. Inadequate carbohydrate reserves (Shepperd and Smith 1993), damage from borers, tent caterpillars, and other insects (Jones et al. 1985), diseases such as cankers and fungal rots (Baker 1925, Hinds 1985, Jacobi et al. 1998), and abiotic conditions such as drought and climate (Romme et al. 1995, Baker et al. 1997, Jacobi et al. 1998) could all limit the suckering response in addition to killing mature trees. Additionally, heavy browsing by herbivores can prevent suckers from maturing into the overstory (Romme et al. 1995, Baker et al. 1997, Kay 1997, Ripple and Larsen 2000). Aspen regeneration failure on previously occupied sites could result in conversion to other covertypes including meadow, shrubland or conifer forest (Jones and DeByle 1985, Bartos 2001).

Conversion of pure aspen stands to conifer forest may lead to a decrease of aspen cover over the landscape. Mixed stands primarily occur when aspen and conifers establish on the same site after disturbance (McKenzie 2001, Shepperd et al. 2001, Kaye 2002). Differential height-growth patterns favor quick growth of aspen for about 100-150 years following disturbance and the suppression of the shade-tolerant conifers in the understory (Mueggler 1989, McKenzie 2001). As the overstory aspen die or are harvested, the conifers fill in and dominate the canopy while shading the intolerant aspen (Baker 1925, Shepperd and Jones 1985). This successional model can be reset by a frequent disturbance regime, primarily fire, which removes the conifers while aspen is still present on the site and able to regenerate successfully (Romme et al. 2001).

Fire history evidence suggests that a disturbance regime marked by frequent, patchy, fires did exist in the aspen zone of Western Colorado in the pre-settlement period (pre-1880). Brown and Shepperd (unpublished) gathered fire scar data from the Uncompahgre Plateau, Colorado and found a median fire return interval of 8-17 years. In the nearby San Juan mountains Romme and others (2001) found that fires occurred somewhere in the region every decade, but it took 140 years for the entire area to burn. This fire rotation time coincides with the maturation age of aspen stands potentially resulting in long-term persistence of aspen over landscape or regional scales; however, climate and browsing pressure also interact with disturbance regime to set up favorable or hostile conditions for aspen regeneration (Romme et al. 1995, Baker et al. 1997, Hessl and Graumlich 2002). Additionally, disturbances are rarely uniform in size or intensity resulting in a mosaic of landscape patches of varying age structure and species composition (Baker 1925, Romme et al. 1995). This patchy structure may be important to sustained aspen dominance over long time scales and across landscapes by providing unforested stands into which aspen can invade (Manier and Laven 2002).

Aspen cover may be decreasing in western forests due to fire suppression and lack of management coupled with the dependence of aspen on stand-replacing disturbance (Kay 1997, Bartos 2001). Stands in Utah were found to be undergoing an increase in conifer density coupled with a corresponding decrease in aspen basal area (Shepperd et al. 2001). In areas where aspen is only a small component of the landscape, such as the southwestern United States (Baker 1925, O'Brien 2002) and the Northwest Great Basin of Oregon, California, and Nevada (Wall et al. 2001), a decrease in aspen cover is alarming and cause for concern; however, there is evidence in the Rocky Mountains indicating that aspen cover is stable on a landscape-scale (Crawford et al. 1998, Suzuki et al. 1999, Barnett and Stohlgren 2001, Kaye 2002) or increasing over longer time scales (Manier and Laven 2001, Kulakowski et al. in press).

In order to determine if aspen was at risk of losing dominance on the forested landscape of the Uncompahgre Plateau in western Colorado, I investigated stand structure in all community types including pure aspen, pure conifer and mixed aspen/conifer. I compared field data from 2001 to inventories collected from 1979-1983 to quantify changes in aspen distribution and to answer the following questions: (1) what portion of the forested landscape on the Uncomphagre Plateau is in pure aspen and mixed aspen/conifer stands?; (2) how has overstory dominance changed from 1979-2001?; and (3) in which types of stands are aspen and conifers regenerating? I hypothesized that pure aspen stands would be stable over the twenty-year period, without conifer invasion and with aspen regeneration. Conversely, mixed aspen/conifer stands were expected to show a decrease in aspen dominance, an increase in conifer dominance, and a lack of aspen regeneration.

METHODS

1. Study Area

The Uncompahgre Plateau covers 344,000 hectares on the western slope of the Colorado Rocky Mountains (Fig.1). Running northwest to southeast, the plateau ranges in elevation from about 1700 meters at valley bottoms to uplands at 3000 meters (Hughes 1995). Major forest covertypes include: aspen (*Populus tremuloides* Michx.), spruce/fir (*Picea engelmannii* and *Abies lasiocarpa*), and ponderosa pine/mixed conifer (*Pinus ponderosa* and *Pseudotsuga menziesii*) (USDA Forest Service 1983). Pinyon/juniper woodlands, meadows and riparian areas are also found on the Plateau, but were not a part of this study. Soils include Argiborolls, Cryoborolls, and Cryoboralfs (Hughes 1995). These soils are generally fine-textured with organic layers.

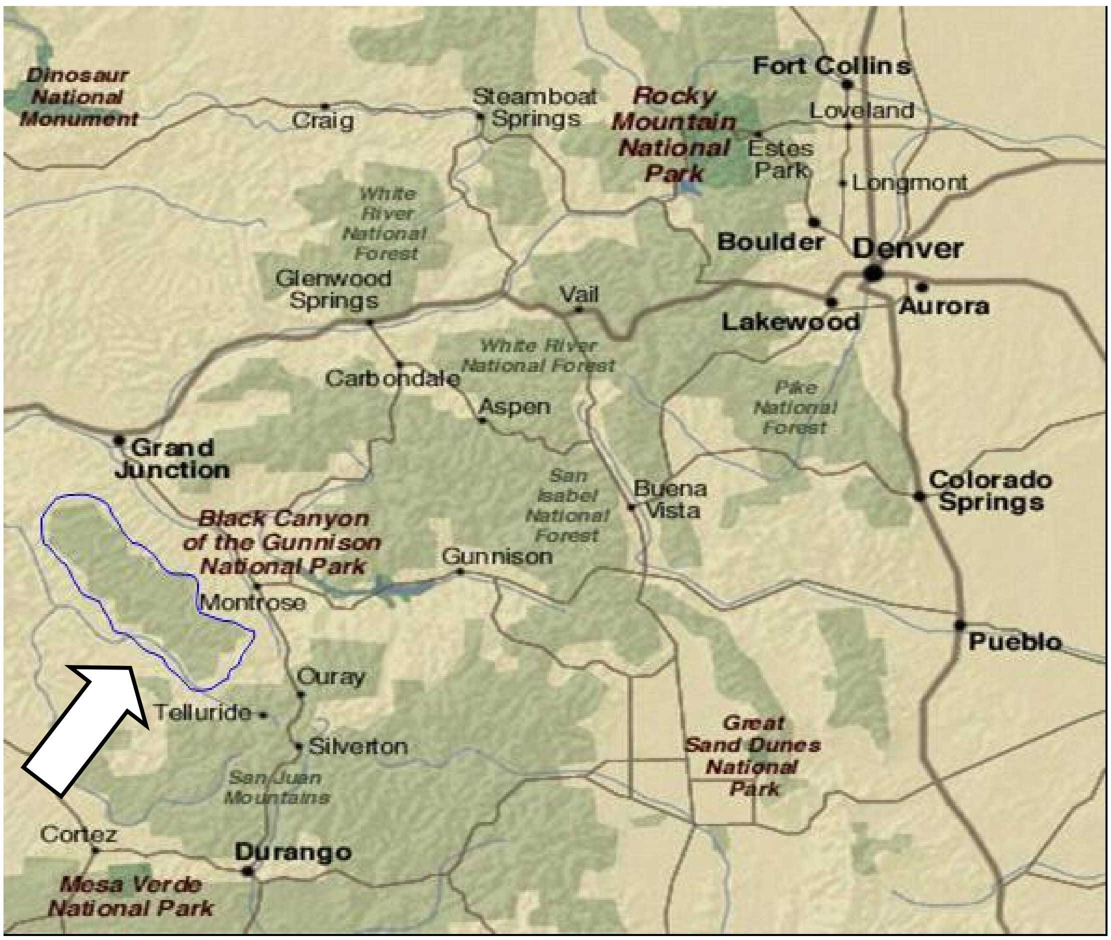

Figure 1: Map of Colorado with the Uncompahre Plateau outlined (A. Williams).

2. Existing data

Forest inventories were conducted by the USDA Forest Service from 1979-1983 on the Uncompahgre National Forest which covers most of the Uncomaphgre Plateau. Measurements were taken for stem diameter at breast height (DBH), height, height to live crown, damage and age for selected trees. Regeneration was also tallied. In 1998, aerial photos were taken of the Plateau and the data entered into a Geographical Information System (GIS) which was employed to classify and analyze vegetation cover along with the existing inventory database of stand structure. By resampling in the same stands as the original inventory, it would be possible to quantify changes in stand structure over time.

3. Forest community types

In order to select stands that would represent all forested vegetation associations on the Uncompahgre Plateau, a classification of the overstory species composition was created and applied to the existing GIS layers (A. Williams, personal communication). Community types were composed of the most common vegetation associations found on the Uncomphagre Plateau and are outlined in Table 1. For example, Engelmann spruce often coexists with subalpine fir (spruce/fir association- SF), while ponderosa pine is commonly the only conifer species in a stand or sometimes found with Douglas-fir on more mesic sites (montane conifer association- MT). Aspen exists in pure stands and is also found in mixed stands with all types of conifers. Pure aspen stands (ASP) contained only aspen in the overstory, while mixed stands were classified as aspen dominant if aspen basal area was greatest of all species present (aspen dominant with spruce/fir- ASF and aspen dominant with montane conifers- AMT). Likewise, mixed stands where

Table 1: Forest Community Types on the Uncompahgre Plateau including number and percent of stands sampled in each category for each year.

Community Type		Number of stands		Percent of stands		Combined Community Type	Number of stands		Percent of stands	
		1979	2001	1979	2001		1979	2001	1979	2001
ASP	Pure aspen, no conifer component	9	7	17.0	13.2	**Aspen**	9	7	17.0	13.2
ASF	Aspen dominant, spruce and/or fir subdominant	12	10	22.6	18.9	**Aspen/Conifer**	19	14	35.8	26.4
AMT	Aspen dominant, montane conifers subdominant	7	4	13.2	7.5					
SFA	Spruce and/or fir dominant, aspen subdominant	7	14	13.2	26.4	**Conifer/Aspen**	15	24	28.3	45.3
MTA	Montane conifers dominant, aspen subdominant	8	10	15.1	18.9					
SF	Spruce and/or fir, no aspen component	2	0	3.8	0.0	**Conifer**	10	8	18.9	15.1
MT	Montane conifers, no aspen component	8	8	15.1	15.1					

Note: Spruce/fir covertype includes: Engelmann spruce- *Picea engelmannii*, subalpine fir- *Abies lasiocarpa*, and blue spruce- *Picea pungens*.

Montane conifers include: Ponderosa pine- *Pinus ponderosa* and Douglas-fir- *Pseudotsuga menziesii*.

Aspen is Quaking aspen only- *Populus tremuloides*.

conifer basal area was greater than aspen were considered conifer dominant and aspen subdominant (spruce/fir dominant with aspen- SFA and montane conifers dominant with aspen- MTA). Pure conifer stands were of either the spruce/fir association (SF) or montane conifer association (MT). Ten stands in each of the seven categories were selected for resampling, fifty-three of which were remeasured in 2001 (Fig. 2).

Since GIS mapping from aerial photos is not an exact representation of actual ground conditions, some of the resampled stands had a different vegetative association than was expected. Additionally, if signs of harvest activity were noted in a stand once in the field, that stand was removed from the sample. Resulting small sample sizes for some community types after the 2001 field inventories prompted me to combine conifer species into one category; therefore, most results are analyzed within the following broad community classification: 1) pure aspen (aspen), 2) aspen dominant and conifer subdominant (aspen/conifer), 3) conifer dominant and aspen subdominant (conifer/aspen), and 4) pure conifer (conifer) (Table 1).

4. Survey methods

Identical methods were used for the 1979-1983 sampling and for the 2001 sampling following the USDA Forest Service *Standard Specifications for Stand Exam* (1993). Before entering the field, six randomly selected plots were identified for sampling in each stand. The 1998 aerial photos along with hard copy maps of the forest on the Uncompahgre Plateau were used to locate the stands on the ground. Geographical positioning system (GPS) was then employed to locate and map the six plots in each stand. The distribution of sampled stands by community type is given in Table 1.

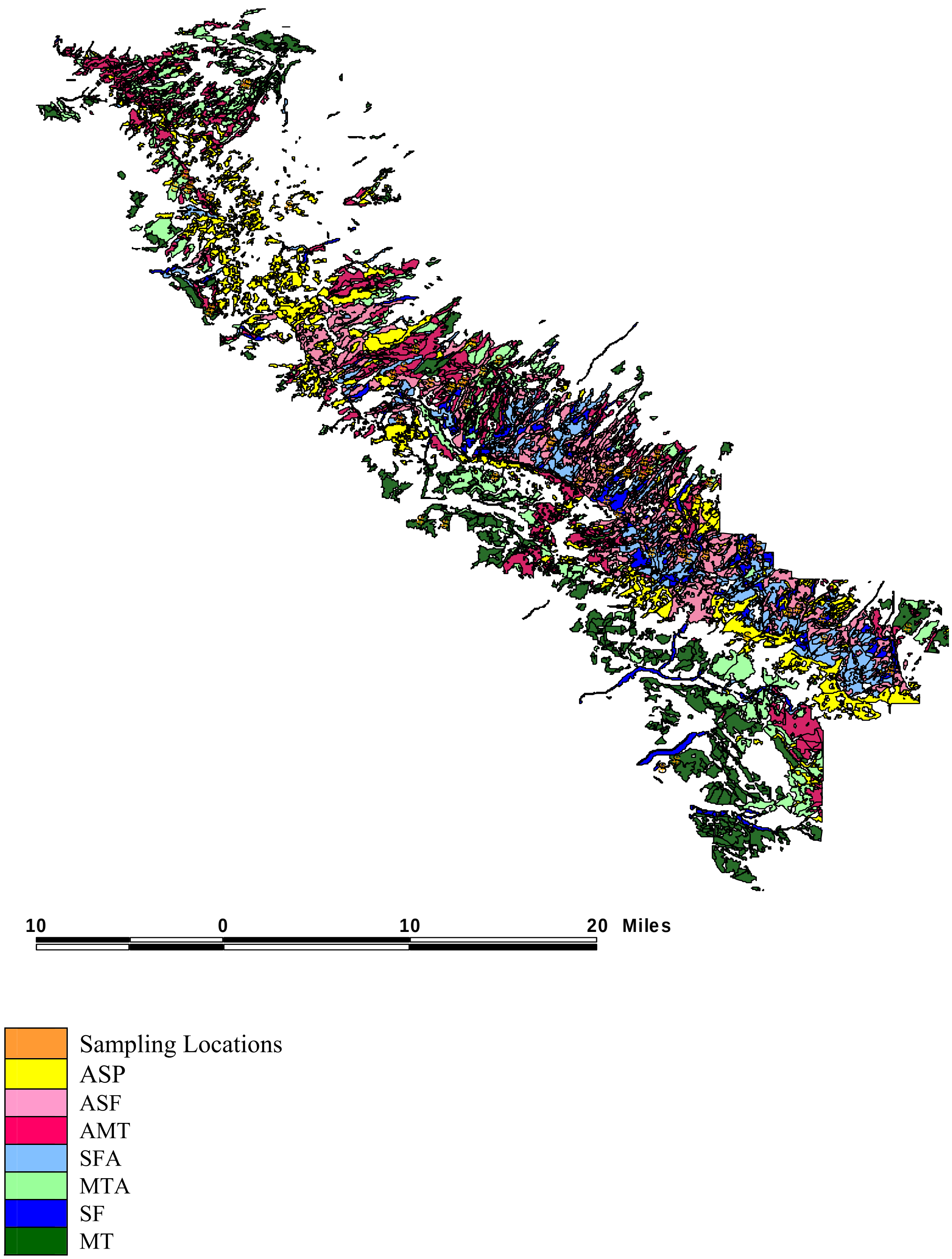

Figure 2: GIS map of forest community types and sampling locations on the Uncompahgre Plateau.

For each plot, the overstory (DBH ≥ 12.7 cm) was sampled on a variable radius prism plot, while the understory (DBH < 12.7 cm) was measured on a fixed radius plot of 0.04 hectares. Species, DBH, height, height to live crown and damage were recorded for every tree on the overstory plot, while species, DBH and height were recorded for all trees in the understory plot between 2.5 and 12.7 cm DBH. Trees less than 12.7 cm DBH were tallied according to species and height class from 0-5 feet by one foot increments.

To determine age structure, increment cores were taken on every other plot from the first tree and from every fourth tree after that. Increment cores were taken at 30 cm above ground from large trees (greater than about 12.7 cm DBH), and small trees were destructively harvested at the ground. A total of 711 increment cores were taken, 107 of which were rotten and not included in the sample. Another 28, mostly aspen, were unreadable and also removed. An additional 495 samples were obtained from harvested trees. Cores were mounted and sanded with progressively finer grit sandpaper until rings were clearly visible. Annual rings were counted using a stereo-microscope. A subsample of 15% of cores taken was crossdated and compared to a master chronology from the Uncompahgre Plateau (P. Brown, personal communication). Errors in ring counts were negligible as most trees are open-grown and rings widths are complacent. Median age at coring height (30 cm) was determined for aspen and conifers separately resulting in an adjustment of 5 years to coring height for aspen and 24 years for conifers. This adjustment was added to all reported ages from increment cores to estimate the true age of the sample.

5. Data analysis

For all analyses, conifer species are grouped and compared to aspen within the four community types (aspen, aspen/conifer, conifer/aspen, and conifer). Basal area and stems per hectare for each stand were grouped by community type and analyzed for differences between years using the Satterthwaite method for unequal variances to calculate p-values. Ages from the 2001 sample were compared between groups using ANOVA.

RESULTS

1. Landscape-scale distribution of aspen and conifers

I examined the distribution of community types on the Uncompaghre Plateau to assess the amount of aspen occurrence and the proportion of area where aspen and conifers occurred together in the overstory of the same stands. The study area was nearly evenly divided between conifer dominated stands (54% of the study area) and aspen dominated stands (46% of the study area) based on 1998 aerial photography analyzed in a GIS (Fig. 2, Table 2). Montane conifers in pure stands or mixed with aspen occurred on 43% of the study area and subalpine conifers (spruce and fir) were present over 41% of the area. While pure conifer stands occurred on 22% of the area and pure aspen stands occurred on 16% of the area, mixed stands of conifer and aspen occurred on 62% of the study area. Thus, a substantial proportion of the study area is in mixed stands of aspen and conifers where species composition of regeneration and shifts in overstory canopy dominance may be having an impact on landscape abundance of aspen.

Table 2: Percent of land area in each community type calculated from 1998 aerial photos analyzed by a GIS.

Community Type		Percent of land area 1998	Combined Community Type	Percent of land area 1998
ASP	Pure aspen, no conifer component	16.1	**Aspen**	16.1
ASF	Aspen dominant, spruce and/or fir subdominant	15.1	**Aspen/Conifer**	29.9
AMT	Aspen dominant, montane conifers subdominant	14.8		
SFA	Spruce and/or fir dominant, aspen subdominant	15.5	**Conifer/Aspen**	31.7
MTA	Montane conifers dominant, aspen subdominant	16.2		
SF	Spruce and/or fir, no aspen component	10.0	**Conifer**	22.3
MT	Montane conifers, no aspen component	12.3		

Note: Spruce/fir covertype includes: Engelmann spruce- *Picea engelmannii*, subalpine fir- *Abies lasiocarpa*, and blue spruce- *Picea pungens*.

Montane conifers include: Ponderosa pine- *Pinus ponderosa* and Douglas-fir- *Pseudotsuga menziesii*.

Aspen is Quaking aspen only- *Populus tremuloides*.

2. Aspen/conifer interactions in the overstory

Change in overstory composition of pure aspen, pure conifer, conifer dominated mixed species stands (conifer/aspen), and aspen dominated mixed species stands (aspen/conifer) between the 1979-1983 (hereafter referred to as 1979 data) and 2001 inventories was calculated based on repeated samples of stands in these types (Table 3). Dominance in mixed species stands was determined from overstory basal area and community types were calculated from the 1979 data.

Table 3: Mean basal area (m^2/hectare) for aspen and conifers in the overstory within community types. Sample size, *N*, is number of stands.

			1979	2001		
Community Type	Species	N	mean ba	mean ba	difference	p-value
Aspen	Aspen	9	34.0	32.1	-1.9	0.7578
	Conifer	9	0	2.5	2.5	0.1543
Aspen/Conifer	Aspen	19	21.2	18.3	-2.9	0.4073
	Conifer	19	10.2	22.8	12.6	0.0003
Conifer/Aspen	Aspen	15	8.3	8.5	0.3	0.8839
	Conifer	15	18.1	23.9	5.9	0.0971
Conifer	Aspen	10	0	4.2	4.2	0.1444
	Conifer	10	19.9	19.9	0.0	0.9973

As reported in previous studies (Shepperd et al. 2001, Kaye 2002), pure aspen stands support the greatest amount of aspen basal area. Basal area for aspen in the overstory (stems $\geq$ 12.7 cm DBH) in pure aspen stands was the greatest of any species in any community type: 34.0 m^2/hectare in 1979 and 32.1 m^2/hectare in 2001. Aspen/conifer stands supported the second highest amount of aspen in both years (Fig. 3). In the aspen dominated aspen/conifer community type, conifer basal area more than doubled from 10.2 m^2/hectare in 1979 to 22.8 m^2/hectare in 2001. The conifer/aspen community type had low basal area for aspen in both 1979 and 2001. Conifers, on the other hand, gained basal area in this covertype from 18.1 to 23.9 m^2/hectare (p=0.0971). Pure conifer stands supported the greatest amount of conifer basal area in 1979 with 19.9 m^2/hectare that remained stable into 2001.

Repeated sampling of the same stands allows for quantification of change within community types. The only significant change in basal area was the tremendous increase in conifer cover in aspen/conifer stands (gain of 12.6 m^2/hectare, p=0.0003; Fig. 4). Conifers also gained basal area in conifer/aspen stands. Aspen basal areas were fairly stable with no significant changes over the 20 year period.

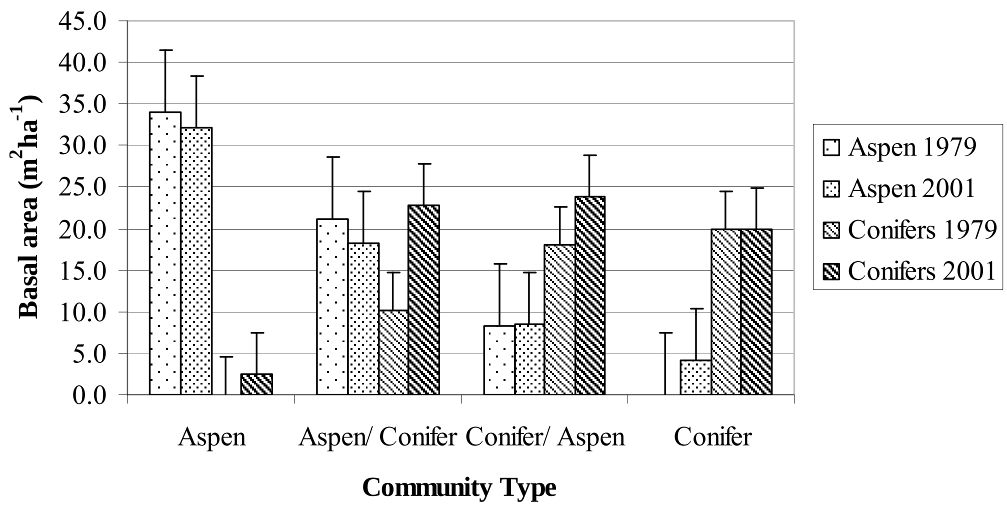

Figure 3: Mean basal area for aspen and conifers in the overstory within community types for 1979 and 2001.

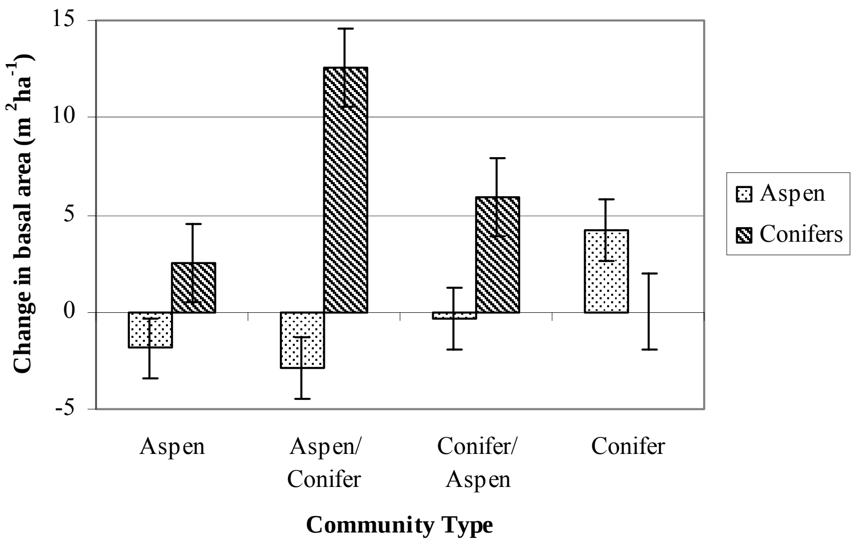

Figure 4: Change in basal area between 1979 and 2001 for aspen and conifers within community types.

Trends in overstory tree density generally followed those of basal area. The greatest density of aspen was found in pure aspen stands; however, in 2001 there were significantly ($p=0.0388$) fewer stems per hectare than in 1979 (Table 4). Aspen/conifer stands also supported greater densities of aspen than community types where aspen is not dominant, and conifer densities were low in 1979 (Fig. 5).

Table 4: Mean stems per hectare for aspen and conifers in the overstory within community types. Sample size, *N*, is number of stands.

Community Type	Species	N	1979 mean	2001 mean	difference	p-value
Aspen	Aspen	9	823	548	-275	0.0388
	Conifer	9	0	89	89	0.2391
Aspen/Conifer	Aspen	19	594	405	-190	0.0856
	Conifer	19	141	383	242	0.0003
Conifer/Aspen	Aspen	15	204	197	-7	0.8751
	Conifer	15	320	341	21	0.7893
Conifer	Aspen	10	0	126	126	0.1631
	Conifer	10	283	246	-37	0.6599

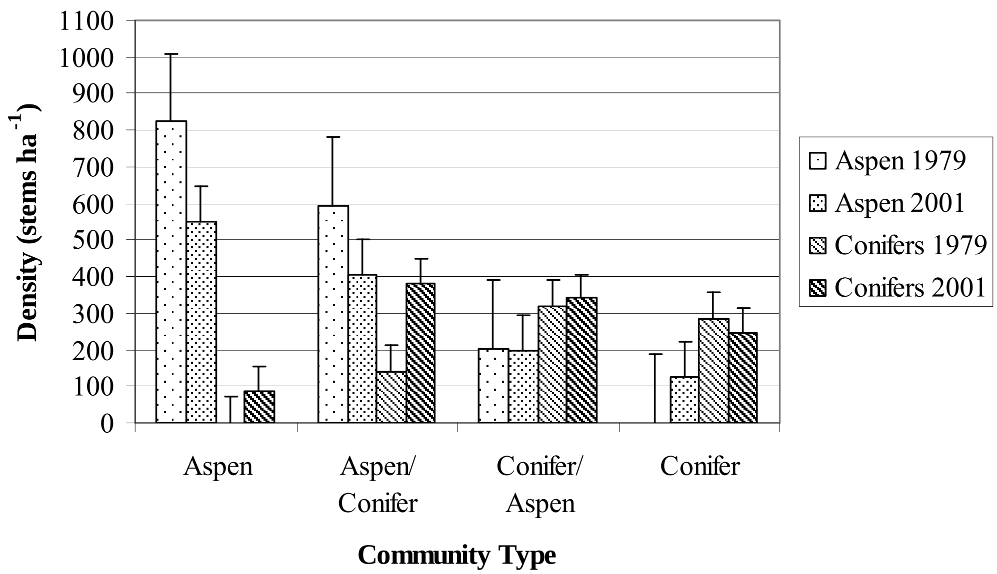

Figure 5: Mean stems per hectare for aspen and conifers in the overstory within community types for 1979 and 2001.

In the aspen/conifer community type conifer density increased dramatically from 141 to 383 stems per hectare over the 20-year period (p=0.0003), while in conifer/aspen stands densities of aspen were low and densities of conifers were high in both years. Conifer densities in pure conifer stands were slightly lower and not different from conifer densities in other community types. Aspen lost an average of 275 stems per hectare in pure aspen stands (p=0.0388), and slightly decreased in density in aspen/conifer stands (p=0.0856; Fig. 6). Conifers gained the most stems per hectare in aspen/conifer stands, increasing from 141 to 383 stems per hectare (p=0.0003). The conifer/aspen community type did not experience significant net changes in tree densities for either aspen or conifers.

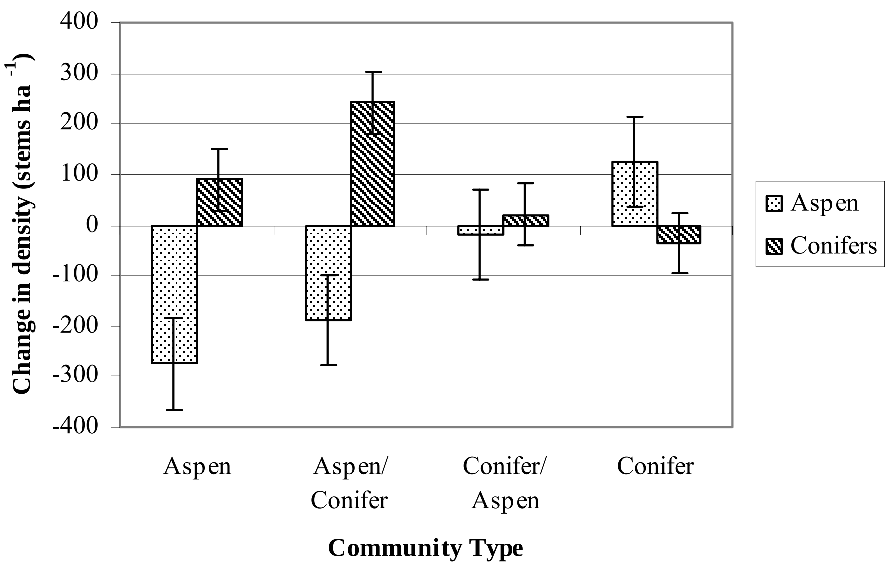

Figure 6: Change in stems per hectare between 1979 and 2001 for aspen and conifers within community types.

Mortality of overstory trees varied by species and between years, although differential stump longevity between species makes comparisons difficult. In 1979 22% of aspen stems were dead and in 2001 mortality increased to 30%. Aspen had the greatest amount of dead stems per hectare in both surveys, but also the most live stems per hectare (Table 5). Subalpine fir, on the other hand, had the greatest percent dead in 2001 and the second greatest in 1979 at 36% and 40% respectively. Dead aspen stems were found in all community types, while dead subalpine fir was almost equally distributed between aspen/conifer and conifer/aspen. The only species with more dead stems was Douglas-fir in 1979 where 43% of the stems were dead, all in the pure conifer community type. The stands where Douglas-fir was found dead are the same as those where aspen gained dominance in the pure conifer covertype. One of these stands experienced a wind event between the 1979 and 2001 samples, resulting in the removal of the overstory conifer species and a resulting pulse of aspen regeneration.

Table 5: Mean live and dead stems per hectare by species in 2001.

1979	Aspen	Subalpine-fir	Engelmann Spruce	Ponderosa Pine	Blue Spruce	Douglas-fir
Mean live stems per hectare	361	71	123	49	38	92
Mean dead stems per hectare	80	29	8	13	11	40
Percent dead	22	40	7	26	29	43
2001	Aspen	Subalpine-fir	Engelmann Spruce	Ponderosa Pine	Blue Spruce	Douglas-fir
Mean live stems per hectare	300	102	84	59	56	50
Mean dead stems per hectare	91	37	17	4	11	9
Percent dead	30	36	20	6	20	18

3. Overstory age structure

The age distribution of overstory aspen from the 2001 survey indicates that the peak age of aspen cohorts established from 1880-1920 (Fig. 7A). This coincides with regeneration after a major fire recorded on the Uncompahgre Plateau in 1879 (Brown and Shepperd, unpublished). The oldest aspen recorded aspen tree was 266 years found in a conifer/aspen stand (Table 6). Trends in aspen age structure did not vary between community types (Fig 7B-D). In all community types with aspen present the majority of trees became established between 1880 and 1920 with fewer young trees in the overstory. Similar age ranges and means for aspen and conifers are a strong indication that overstory stems for both established at the same time. In aspen/conifer stands, most overstory conifers were established between 1901 and 1940 (Fig. 8A). In conifer/aspen stands, establishment of conifers that grew into the overstory was continuous for the last century. The oldest conifer was a 254 year-old ponderosa pine in a pure conifer stand. Conifers in pure conifer stands are significantly older than those in either type of mixed stand.

Table 6: Mean ages for overstory trees within community types, 2001 age data. Sample size, *N*, is number of trees.

	Aspen-2001			**Conifers-2001**		
Community Type	**Mean**	**Range**	**N**	**Mean**	**Range**	**N**
Aspen	101	36-156	44	n/a		
Aspen/ Conifer	108	40-241	67	110	56-221	108
Conifer/ Aspen	108	65-271	51	113	57-251	165
Conifer	n/a			137	67-278	58

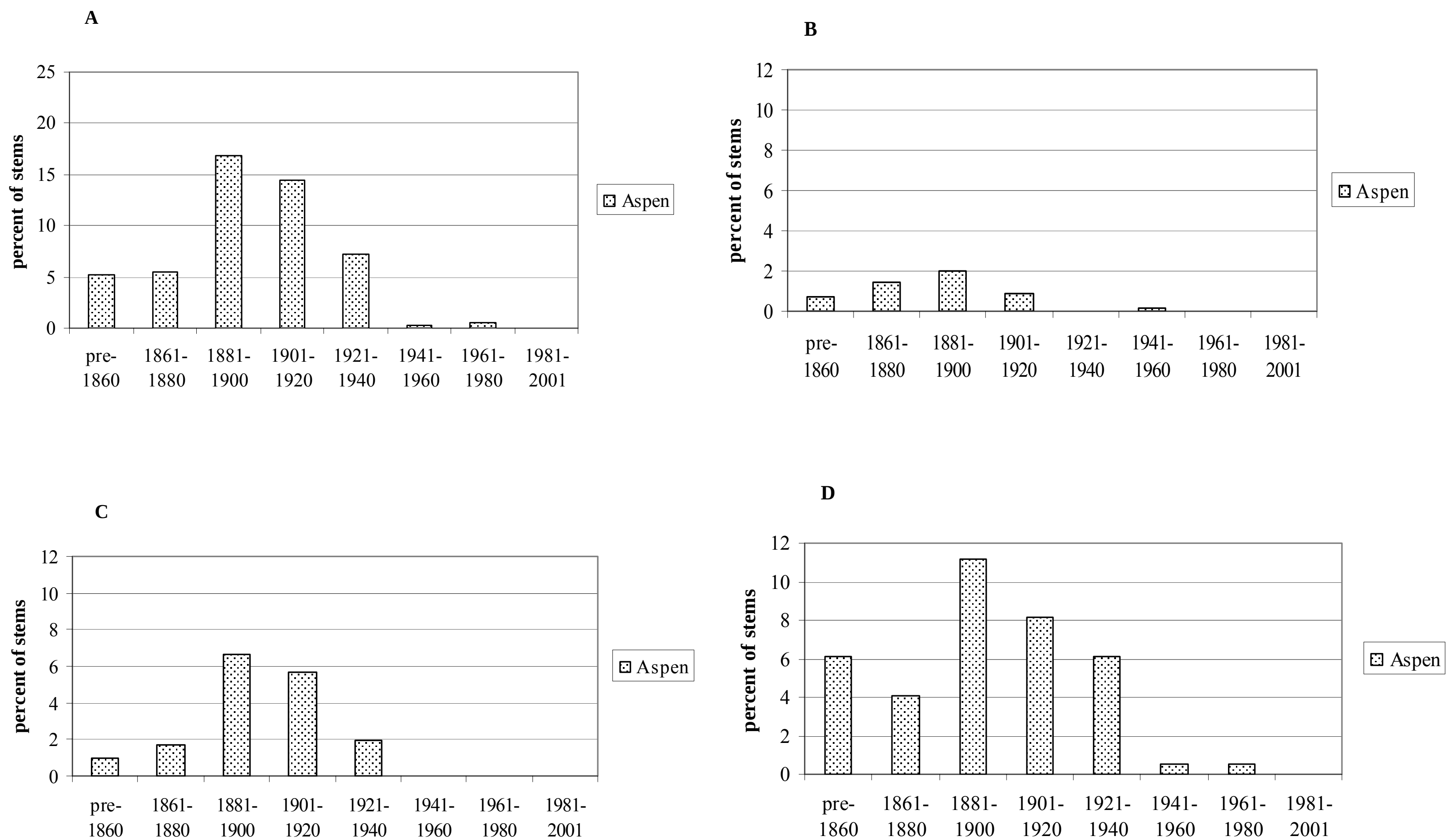

Figure 7: Age distribution of overstory aspen (DBH >5"). A) Establishment dates for all aspen sampled in 2001. B) Overstory aspen in pure aspen stands. C) Overstory aspen in aspen/conifer stands. D) Overstory aspen in conifer/aspen stands.

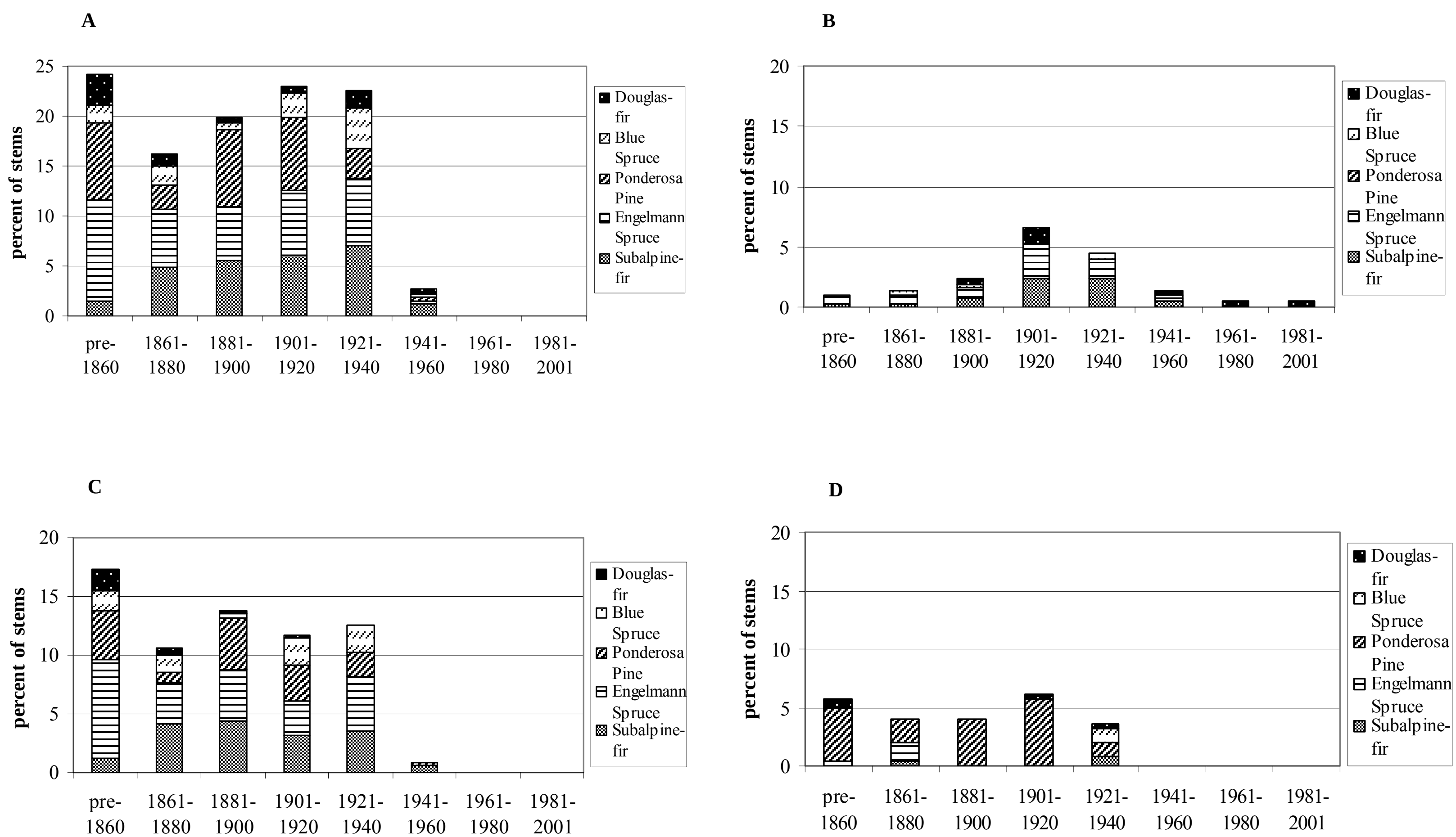

Figure 8: Age distribution of overstory conifers (DBH >5"). A) Establishment dates for all conifers sampled in 2001. B) Overstory conifers in aspen/conifer stands. C) Overstory conifers in conifer/aspen stands. D) Overstory conifers in pure conifer stands.

4. Aspen and conifers in the understory: Regeneration

Aspen regeneration (defined as trees with DBH < 2.5 cm) was found in 37 stands in 1979 (70%) and in 47 stands in 2001 (89%). Suckers were present in all community types, even pure conifer, in both years (Table 7). Of the stands with no aspen regeneration in 1979, nearly half were in the pure conifer community type and the other half were in mixed stands. Two of these mixed stands without aspen regeneration shifted from aspen dominated to conifer dominated over the 20-year period. Two pure aspen stands had no aspen suckers recorded in 1979, yet these stands did not experience conifer invasion and did record suckers in 2001. Stands without aspen regeneration in 2001 were pure conifer stands dominated by ponderosa pine. Not only did these stands lack aspen regeneration, but half had no conifer seedlings or aspen suckers at all.

Table 7: Mean stems per hectare for aspen suckers and conifer seedlings within community types.

Community Type	Species	N	1979 mean	2001 mean	difference	p-value
Aspen	Aspen	9	2079	3299	1220	0.4885
	Conifer	9	988	604	-384	0.7188
Aspen/Conifer	Aspen	19	1036	1907	871	0.0516
	Conifer	19	1053	2626	1573	0.0055
Conifer/Aspen	Aspen	15	902	1447	545	0.1604
	Conifer	15	1566	2725	1159	0.1323
Conifer	Aspen	10	1112	1812	700	0.4197
	Conifer	10	410	1012	602	0.3353

The greatest densities of seedlings or suckers (any tree with DBH < 2.5 cm) were of aspen in pure aspen stands in 1979 and 2001 (Fig. 9). A high density of conifer seedlings in pure aspen in 1979 was located in a stand that shifted from pure aspen to aspen/conifer mixed in 2001. When remeasured in 2001 the conifers in this stand (Engelmann spruce and subalpine fir) were 30-40 years old indicating that the conifer invasion was sustained for the 20-year period. Indeed, conifer seedlings can be over 60 years old in the understory, while aspen suckers were primarily twenty years old or less (Fig. 10). High densities of aspen in pure conifer stands were associated with two stands that shifted from pure conifer to conifer/aspen in 2001. Both of these stands retained aspen into the next size class in 2001. One of these stands experienced a blowdown event that eliminated most mature conifers (Douglas-fir) and allowed the aspen understory to grow. One pure conifer stand with aspen suckers in 1979 remained pure conifer in 2001, but aspen suckers were again recorded in the second survey. In this stand no aspen were recorded in the next size class indicating that the aspen is regenerating but not surviving.

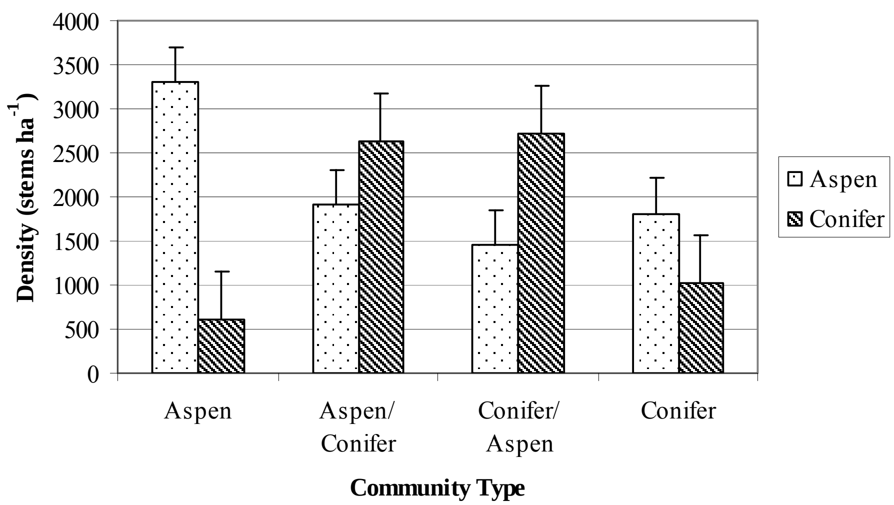

Figure 9: Stems per hectare for conifer seedlings and aspen suckers (DBH < 2.5 cm) in 2001 within community types.

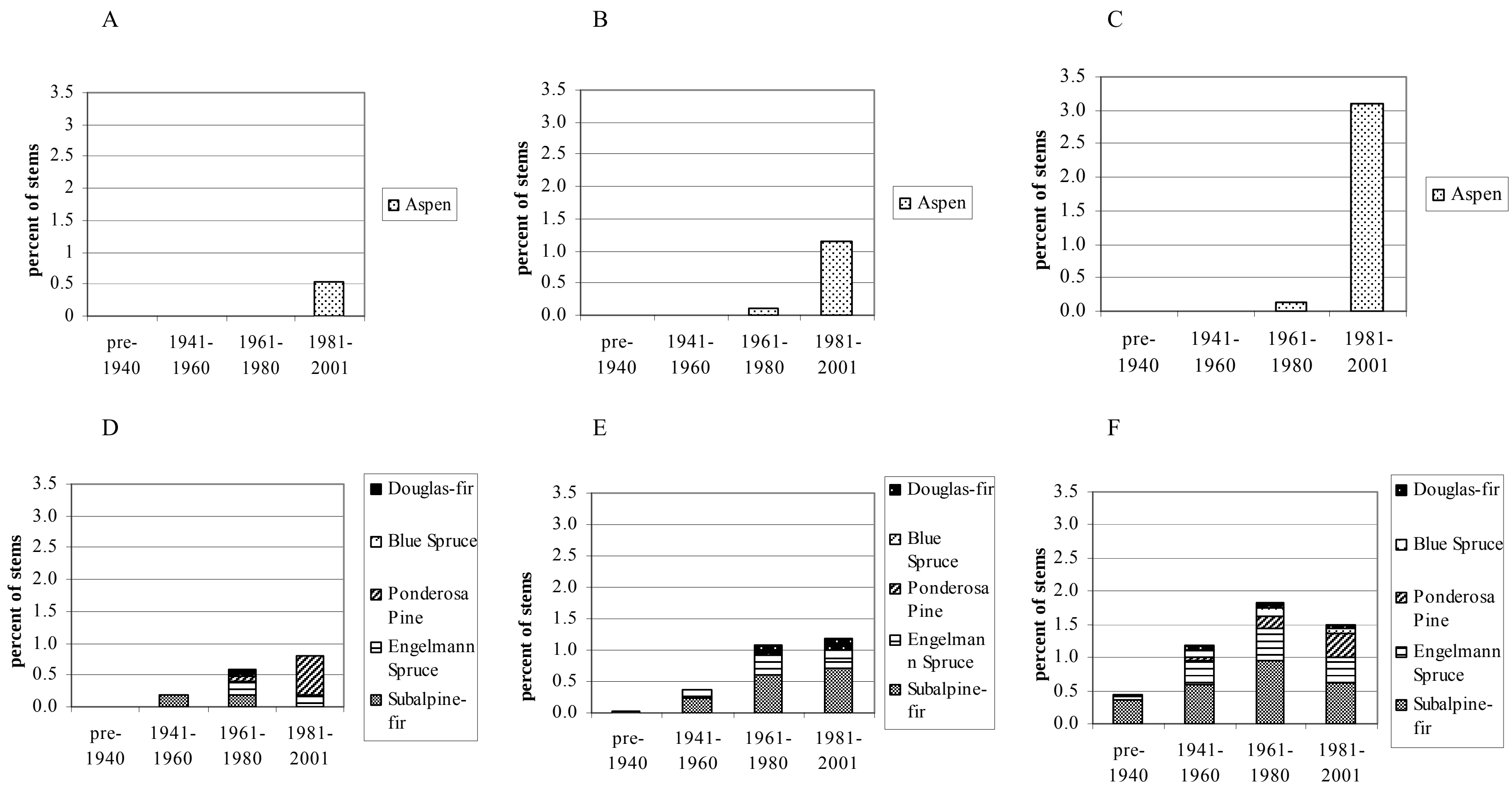

Figure 10: Age distribution of aspen suckers and conifer seedlings. A) Aspen suckers in pure aspen stands. B) Aspen suckers in aspen/conifer stands. C) Aspen suckers in conifer/aspen stands. D) Conifer seedlings in pure conifer stands. E) Conifer seedlings in aspen/conifer stands. F) Conifer seedlings in conifer/aspen stands.

DISCUSSION

The forested landscape of the Uncompahgre Plateau is highly variable and patchy. Remote photography and GIS analysis of the region indicate a high degree of spatial heterogeneity in forest covertypes (Fig. 2). Mixed species stands with both aspen and conifers occur on over 60 percent of the study area, and another 16 percent of the forested landscape is in pure aspen stands. The high frequency of mixed stands and proximity to conifer seed sources could indicate that aspen on the Plateau is at risk of losing dominance in the absence of disturbance, but because some aspen can be found on over three quarters of the forested landscape, the extirpation of aspen is highly unlikely.

In particular, there is ample evidence that pure aspen stands on the Uncompahgre Plateau are stable and will be for some time. These stands supported the greatest amount of aspen basal area of any community type, and the modest decline in overstory density is most likely due to natural thinning as stems mature. The mean age of aspen in pure aspen stands is 101 years; however, the age distribution reveals aspen in every age class (Fig. 7B). Prolific regeneration, an average of nearly 3300 suckers per hectare, is well over the 2500 suckers per hectare suggested by Mueggler (1989) for persistence. As mature stems senesce and gaps in the canopy open, this new cohort will be recruited to the overstory resulting in a stable, multi-aged structure. Additionally, conifer regeneration was minimal and only two of nine pure aspen stands experienced any conifer invasion.

While aspen dominance remained stable in pure aspen stands, overstory dominance in mixed species stands is shifting. The oldest aspen and conifer components of mixed stands are the same age, indicating that both established at the same time following disturbance (McKenzie 2001, Kaye 2002). A large regional fire year on the

Uncompahgre Plateau in 1879 (Brown and Shepperd unpublished) resulted in a strong pulse of regeneration from 1880 and 1920 (Figs. 7 and 8). The aspen/conifer component of mixed stands cover one-third of the Uncompahgre landscape. Aspen dominance in this community type declined significantly from 68 to 45 percent over the twenty-year study period (Table 3). Conifer/aspen stands compose another third of the forest but were less dynamic; conifer dominance increased slightly from 70 to 74 percent. Regeneration data provides further evidence of the successional nature of mixed stands. Conifers have regenerated continuously in mixed stands over the last century (Figs. 8 and 10) and current seedling densities are over 2500 stems per hectare (Table 7). Aspen regeneration in mixed stands is ephemeral and suckers are not recruited into the overstory (Figs. 7 and 10). Densities of aspen suckers in mixed stands are currently too low to be considered adequate for aspen persistence (Schier 1975, Muegller 1989).

Mixed stands on the Uncompahgre Plateau are experiencing a progressive increase in overstory dominance of conifers relative to aspen. In particular, the recent shift in aspen/conifer stands has been rapid. Continuous regeneration of conifers and short-lived regeneration of shade-intolerant aspen has exacerbated this trend. Yet aspen stems remain in the overstory and will for some time, as individual stems can persist for over a century or two. These stems support an interconnected clonal root system from which aspen suckers could be produced following a stand-replacing disturbance (Shepperd et al. 2001). Evidence of this was found in the pure conifer stand that shifted to aspen/conifer following a wind event that caused high mortality for the conifer species and resulting in a pulse of aspen suckering.

In the absence of disturbance, the rapid changes to conifer dominance measured in the last 20 years will continue in both aspen/conifer and conifer/aspen stands, leading to the reduction of aspen basal area through mortality and a lack of recruitment into the overstory. Recent studies of aspen dynamics over centuries-long time scales suggest that the rapid changes measured from 1979-2001 on the Uncompahgre Plateau may be simply a stage in the shifting dominance patterns between aspen and conifers (Crawford et al. 1998, Romme et al. 2001, Manier and Laven 2002, Kulakowski and Veblen in press). Due to rapid initial growth of aspen and slow growth of conifers, the canopy of mixed stands would have been dominated by aspen for many years. Within a century of stand establishment conifer height growth will equal or exceed that of aspen. The current shift in conifer dominance in mixed stands is likely to be the result of this change in competitive superiority from aspen to conifer stems (McKenzie 2001, Shepperd et al. 2001, Kaye 2002). Since the last major fire events on the Plateau were recorded in 1879, the shifts in dominance measured 100 years later appear to be consistent with natural historic variation in vegetation cover for aspen forests in the Western Rocky Mountains. Further, the successional cycle of aspen to conifers followed by stand-replacing fires is likely perpetuated by the nature of the fuels. Aspen stands are less flammable than conifer stands, often surviving episodic fire events as the fire moves to the surface in the aspen (Jones and DeByle 1985). After conifers gain dominance on the site flammability and the probability of stand-replacing fires increases, followed by aspen suckering and the perpetuation of the successional cycle.

The age distribution of aspen on the Uncompahgre Plateau is similar to that reported for other Rocky Mountain aspen. In Yellowstone National Park, Ripple and Larsen

(2000) report that 10% of pure aspen stands originated before 1871, 85% between 1871 and 1920, and 5% from 1921 to 1998. Hessl and Graumlich (2002) note that aspen regeneration was high from 1840 to 1879 and coincided with high fire frequencies for the Greater Yellowstone area resulting in age structures similar to the Uncompahgre Plateau but further influenced by elk browsing. In Yoho and Kootenay National Parks Kay (1997) found the majority of aspen stands regenerated from 1816 to 1935, also a period of frequent fires.

The limited age range of aspen relative to the broad range of conifers is compelling evidence for accelerated change on a landscape scale. While conifers in mixed species stands are successfully regenerating and recruiting mature stems into the overstory, aspen is not. Most stands are capable of producing aspen suckers, but some level of disturbance to the existing canopy will be required to create a successful new cohort of aspen that can grow into the canopy, particularly in mixed stands. The dramatic changes I have measured indicate that landscape patterns are dynamic, but not unpredictable. Aspen persistence relies on a combination of factors including levels and frequency of disturbance, proximity to conifer seed sources, climate, and the overall health of the aspen clone. The GIS analysis and mapping of the Uncompahgre Plateau indicate a high level of landscape heterogeneity. Even over the relatively short time span of this study, changes in landscape patterns were measurable and predictable. All mixed stands are likely to lose aspen dominance in the absence of disturbance. Pure aspen stands are relatively stable when regeneration is present. Future study and management action should focus on pure aspen stands where new conifer encroachment has occurred or where regeneration is absent. Stands currently dominated by conifers with aspen in the understory are candidates for manipulation that removes the existing canopy to stimulate aspen regeneration and recruitment, mimicking the historic disturbance regime.

REFERENCES

Baker, F. S. 1925. Aspen in the central Rocky Mountain Region. USDA Department Bulletin, Number 1291.

Baker, W. L., J. A. Munroe, and A. E. Hessl. 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 20:155-165.

Barnes, B. V. 1966. The clonal growth habit of American aspens. Ecology 47:439-447.

Barnett, D. T. and T. J. Stohlgren. 2001. Aspen persistence near the National Elk Refuge and Gros Ventre Valley elk feedgrounds of Wyoming, USA. Lanscape Ecology 16:569-580.

Bartos, D. L. 2001. Landscape dynamics of aspen and conifer forests. In: W. D. Shepperd, D. Binkley, D. L. Bartos, T. J. Stohlgren, and L. G. Eskew, eds. Sustaining aspen in western landscapes: Symposium proceedings; 13-15 June 2000; Grand Junction, CO. USDA, Forest Service, Proceedings RMRS-P-18. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO:5-14.

Benson, R. E. and A. W. Green. 1987. Colorado's Timber Resources. USDA Forest Service, Res. Bull. INT-48. Intermountain Research Station, Ogden, UT: 53p.

Betters, D. R. and R. F. Woods. 1981. Uneven- aged stand structure and growth of Rocky Mountain aspen. Journal of Forestry 79: 673-676.

Crawford, J. L., S. P. McNulty, and J. B. Sowell. 1998. Changes in aspen communities over 30 years in Gunnison County, Colorado. The American Midland Naturalist

140:197-205.

DeByle, N. V. 1985. Wildlife. In: N. V. DeByle, and R. P. Winokur, eds. Aspen: ecology and management in the Western United States. USDA, Forest Service, Gen. Tech. Rep. RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO:135-152.

DeByle, N. V., and R. P. Winokur. 1985. Introduction. In: N. V. DeByle, and R. P. Winokur, eds. Aspen: ecology and management in the Western United States. USDA, Forest Service, Gen. Tech. Rep. RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO:1.

Fowells, H. A. 1965. Silvics of forest trees of the United States. USDA Handbook Number 271.

Hessl, A. E. and L. J. Graumlich. 2002. Interactive effects of human activities, herbivory and fire on quaking aspen (*Populus tremuloides*) age structures in western Wyoming. Journal of Biogeography 29:889-902.

Hinds, T. E. 1985. Diseases. In: N. V. DeByle, and R. P. Winokur, eds. Aspen: ecology and management in the Western United States. USDA, Forest Service, Gen. Tech. Rep. RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO:87-106.

Hughes, T., Kingston, R., and B. Cencich. 1995. Soil survey of Uncompahgre National Forest Area, Colorado, parts of Mesa, Montrose, Ouray, and San Miguel counties. USDA Forest Service and Soil Conservation Service, in corporation with the Colorado Agricultural Experiment Station. Fort Collins, CO. 122pp.

Jacobi, W. R., E. F. Kelly, C. A. Troendle, P. A. Angwin, and C. A. Wettstein. 1998. Environmental conditions and aspen regeneration failure. USDA Forest Service, Tech. Rep. R2-60. Rocky Mountain Region, Renewable Resources, Forest Health Management, Golden, CO:24p.

Jones, J. R. and N. V. DeByle. 1985. Fire. In: N. V. DeByle, and R. P. Winokur, eds. Aspen: ecology and management in the Western United States. USDA, Forest Service, Gen. Tech. Rep. RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO:77-81.

Jones, J. R., N. V. DeByle, and D. M. Bowers. 1985. Insects and other invertebrates. In: N. V. DeByle, and R. P. Winokur, eds. Aspen: ecology and management in the Western United States. USDA, Forest Service, Gen. Tech. Rep. RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO:107-114.

Johnson, C. W., T. C. Brown, M. L. Timmons. 1985. Esthetics and landscaping. In: N. V. DeByle, and R. P. Winokur, eds. Aspen: ecology and management in the Western United States. USDA, Forest Service, Gen. Tech. Rep. RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO:185-188.

Kay, C. E. 1997. Is aspen doomed? Journal of Forestry 95:4-11.

Kaye, M. W. 2002. Forest ecology of quaking aspen in Rocky Mountain National Park: A landscape survey, a reconstruction, and a predictive model. Master’s Thesis, Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523. 103pp.

Korb, J. E. and T. A. Ranker. 2001. Changes in stand compostition and structure between 1981 and 1996 in four Front Range plant communities in Colorado. Plant Ecology

157:1-11.

Kulakowski, D., T. T. Veblen, and S. Drinkwater. The persistence of quaking aspen (*Populus tremuloides)* in the Grand Mesa area, Colorado. In press, Ecological Applications.

Manier, D. J. and R. D. Laven. 2002. Changes in landscape patterns associated with the persistence of aspen (*Populus tremuloides* Michx.) on the western slope of the Rocky Mountains, Colorado. Forest Ecology and Management 167:263-284.

McKenzie, C. 2001. Establishment patterns and height growth rates of aspen and conifer species growing on the Gunnison National Forest in Western Colorado. Master's Thesis, Department of Forest Sciences, Colorado State University, Fort Collins, CO 80523. 30pp.

Mueggler, W. 1989. Age distribution and reproduction of intermountain aspen stands. Western Journal of Applied Forestry 4:41-45.

O'Brien, R. A. 2002. Arizona's Forest Resources, 1999. USDA Forest Service, Res. Bull. RMRS-RB-2, Rocky Mountain Research Station, Ogden, UT:116p.

Peet, R. K. 1981. Forest vegetation of the Colorado Front Range: Composition and dynamics. Vegetatio 45:3-75.

Quinn, R. D. and L. Wu. 2001. Quaking aspen reproduce from seed after wildfire in the mountains of southeastern Arizona. In: W. D. Shepperd, D. Binkley, D. L. Bartos, T. J. Stohlgren, and L. G. Eskew, eds. Sustaining aspen in western landscapes: Symposium proceedings; 13-15 June 2000; Grand Junction, CO. USDA, Forest Service, Proceedings RMRS-P-18. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO:369-376.

Ripple, W. J. and E. J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biological Conservation 95: 361-370.

Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk, and fire in Northern Yellowstone National Park. Ecology 76:2097-2106.

Romme, W. H., L. Floyd-Hanna, D. D. Hanna, and E. Bartlett. 2001. Aspen's ecological role in the west. In: W. D. Shepperd, D. Binkley, D. L. Bartos, T. J. Stohlgren, and G. Eskew, eds. Sustaining aspen in western landscapes: Symposium proceedings; 13 15 June 2000; Grand Junction, CO. USDA, Forest Service, Proceedings RMRS-P-18. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO:243-259.

Schier, G. A. 1975. Deterioration of aspen clones in the middle Rocky Mountains. USDA Forest Service, Research Paper INT-170. Intermountain Forest and Range Experiment Station, Ogden, Utah: 14pp.

Schier, G. A., J. R. Jones, and R. P. Winokur. 1985. Vegetative regeneration. In: N. V. DeByle, and R. P. Winokur, eds. Aspen: ecology and management in the Western United States. USDA, Forest Service, Gen. Tech. Rep. RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO:29-33.

Shepperd, W. D. 1982. Stand characteristes of Rocky Mountain aspen. In: N. V. DeByle, ed. Situation management of two intermountain species: Aspen and coyotes. Symposium proceedings. Volume I, Aspen:22-30.

Shepperd, W. D. and F. W. Smith. 1993. The role of near-surface lateral roots in the life cycle of aspen in the central Rocky Mountains. Forest Ecology and Management 61: 157-170.

Shepperd, W. D. and J. R. Jones. 1985. Nurse Crop. In: N. V. DeByle, and R. P. Winokur, eds. Aspen: ecology and management in the Western United States. USDA, Forest Service, Gen. Tech. Rep. RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO:181-184.

Shepperd, W. D., D. L. Bartos, and S. A. Mata. 2001. Above- and below-ground effects of aspen clonal regeneration and succession to conifers. Canadian Journal of Forest Research 31:739-745.

Stevens, M. T., M. G. Turner, G. A. Tuskan, W. H. Romme, L. E. Gunter, and D. M. Waller. 1999. Genetic variation in postfire aspen seedlings in Yellowstone National Park. Molecular Ecology 8:1769-1780.

Suzuki, K., H. Suzuki, D. Binkley, and T. J. Stohlgren. 1999. Aspen regeneration in the Colorado Front Range: differences at local and landscape scales. Landscape Ecology 14:231-237.

USDA Forest Service. 1983. Final environmental impact statement for Grand Mesa, Uncomphagre, and Gunnison National Forests: Land and resource management plan. Delta, CO: Rocky Mountain Region.

USDA Forest Service.1993. Standard specifications for stand exam. Rocky Mountain Region, Southwest Region, Intermountain Region:154p.

Wall, T. G., R. F. Miller, and T. J. Svejcar. 2001. Juniper encroachment into aspen in the Northwest Great Basin. Journal of Range Management 54:691-698.

White, C. A., C. E. Olmsted, and C. K. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. Wildlife Society Bulletin 26:449-462.