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Twenty-year change in aspen dominance in pure aspen and mixed aspen/conifer stands on the Uncompahgre Plateau, Colorado, USA

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Abstract

Reports of decreasing quaking aspen (*Populus tremuloides*) cover in forests of the western USA have caused concern about the long-term persistence of aspen on landscape scales. We assessed changes in overstory aspen dominance on the Uncompahgre Plateau in western Colorado over a 20 year period. We measured stand density, species composition and regeneration in 53 undisturbed, mature pure aspen, pure conifer, and mixed aspen/conifer stands originally inventoried between 1979 and 1983. Ages of overstory and understory trees were used to evaluate long-term change in regeneration and overstory development.

While pure aspen stands occupy 16% of the study area, mixed aspen and conifer stands cover 62% of the forested landscape on the Uncompahgre Plateau. Pure aspen stands were self-thinning, but stable over the twenty-year study period, with high amounts of regeneration and without conifer invasion. Mixed stands of aspen and conifer had undergone significant change. In aspen dominated mixed species stands, conifer basal area increased from 10 to 23 $m^2\ ha^{-1}$ in the last 20 years, while aspen basal area decreased. In conifer dominated mixed species stands, conifer basal area increased from 18 to 24 $m^2\ ha^{-1}$. Most overstory aspen in pure aspen stands were between 80 and 120 years old. Substantial aspen suckering was occurring, but all suckers were <20 years old, indicating lack of current growth into the overstory. Aspen suckering was occurring in mixed species stands, but again, most suckers were <20 years old, and few overstory trees were <100 years old. In contrast, understory and overstory conifers spanned ages from <20 to over 250 years old.

Aspen dominance is decreasing in the forested communities of the study area. Pure stands are likely to persist without decline for a considerable time. Mixed stands are likely to continue to experience a decrease in overstory aspen canopy dominance. These changes are probably within the historic range of variability, but restoration of aspen canopy cover consistent with an early- to mid-seral landscape condition would require disturbances such as fire or cutting to create canopy gaps to permit growth of suckers into the overstory of mixed species stands.
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Keywords: Aspen; *Populus tremuloides* Colorado; Vegetation change; Aspen decline

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1. Introduction

Quaking aspen (*Populus tremuloides* Michx.) is an important component of forests of western Colorado, but there has been concern that it is declining during the 20th century. Aspen is the primary deciduous canopy species amid expansive conifer forests (Peet, 1981), and is highly valued as a critical component of ecosystem diversity (DeByle and Winokur, 1985; White et al., 1998). In Colorado, aspen is the dominant forest cover on 17% of the nearly 8.5 million hectares of forested land, second only to Engelmann spruce (*Picea engelmannii* (Parry) Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) (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). Aspen is a shade-intolerant disturbance dependent species, and which some observers argue is in decline because of fire suppression and increased herbivory (Romme et al., 1995; Kay, 1997; Bartos, 2001). However, others have observed no decline in aspen in western Colorado, and argue that changes in aspen communities are within the historic range of variability (Manier and Laven, 2002; Kulakowski et al., 2004). We assess changes in aspen dominance of pure aspen, pure conifer and mixed aspen/conifer stands on the Uncompahgre Plateau in western Colorado using 20-year remeasurements of pure aspen and mixed aspen and conifer stands.

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 Colorado forests, aspen is primarily 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 rare (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 unfavorable climatic conditions 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). Failure of aspen regeneration on previously occupied sites could result in conversion to other cover types 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 (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). 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 stand replacing 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 (2003) found a median fire return interval of 8–17 years at low elevations on the Uncompahgre Plateau and suggest the presence of extensive fire in 1879. In the nearby San Juan mountains Romme et al. (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. 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 canopy cover may be decreasing in western forests of Colorado due to fire suppression and lack of management (Kay, 1997; Bartos, 2001). Stands in Utah were found to be undergoing an increase in conifer basal area coupled with a corresponding decrease in aspen basal area (Shepperd et al., 2001). In the Warner Mountains of California, repeated aerial photography has shown a 24% decline in aspen clones over the last 48 years (Di Orio et al., 2005) 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, 2002; Kulakowski et al., 2004).

We investigated stand structure and age distributions in mature stands in pure aspen, pure conifer and mixed aspen/conifer community types to assess potential long-term changes in aspen dominance on the Uncompahgre Plateau in western Colorado. We analyzed the current distribution of cover types to determine what portion of the forested landscape on the Uncompahgre Plateau is in pure aspen and mixed aspen/conifer stands We compared stand species composition by basal area and density measured in 2001 to inventories of species composition of the same stands as collected from 1979 to 1983. We measured current age structures of the overstory and understory of these stands. We used these comparisons and age distributions to assess changes in aspen and conifer dominance over the past 20 years.

2. Methods

2.1. Study area

The Uncompahgre Plateau covers 344,000 ha on the western slope of the Colorado Rocky Mountains. Running northwest to southeast, the plateau ranges in elevation from about 1700 m at valley bottoms to uplands at 3000 m (Hughes et al., 1995). Major forest cover types include: aspen, spruce/fir, and ponderosa pine/mixed conifer (*Pinus ponderosa* Dougl. ex Laws. and *Pseudotsuga menziesii* (Mirb.) Franco) (USDA Forest Service, 1983). 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 et al., 1995). These soils are generally fine-textured with organic layers.

2.2. Existing data

Forest inventories were conducted by the USDA Forest Service from 1979 to 1983 on the Uncompahgre National Forest, which covers most of the Uncompahgre 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 remeasuring the same stands as in the original inventory, it would be possible to quantify changes in stand structure over time.

2.3. Forest community types

In order to select stands that would represent forested vegetation associations on the Uncompahgre Plateau, we classified stands based on overstory species composition. To facilitate the classification, we defined two conifer associations, Engelmann spruce and subalpine fir (spruce/fir association, SF) and ponderosa pine with Douglas-fir (montane conifer association, MT). Pure conifer stands (SF or MT) had >80% of their basal area in a single association or conifer species and were classified as "conifer". Pure aspen stands had >80% of their basal area in aspen (ASP) and were classified as ‘‘aspen’’. Mixed conifer/aspen stands had <80% of their basal area in a single association or species. Mixed stands were classified based on aspen or conifer dominance. Mixed stands where aspen had >50% of the canopy cover or basal area were designated as ‘‘aspen/conifer’’ and where conifers had >50% of the canopy cover or basal area were designated as ‘‘conifer/aspen’’. This classification system was applied to the common vegetation layer (CVU) in the US Forest Service GIS. This layer contained estimates of overstory canopy cover by species based on photo interpretation.

2.4. Survey methods

We randomly selected 70 stands for sampling from stands that were measured in the 1979 forest inventory covering the range of stand types identified in our GIS analysis. About 17% of the sample was pure aspen stands, 19% was pure conifer stands, 36% aspen/conifer and 28% conifer/aspen. Mixed stands included approximately equal representation of aspen mixed with SF and MT conifers.

Fifty-three stands were sampled in 2001. Seventeen stands were rejected based on a field visit if they had been disturbed by logging in the past 20 years or if the CVU classification was in obvious error. The resulting sample frequency was nine pure aspen, 10 pure conifer, 15 aspen/conifer and 19 conifer/aspen stands.

Identical methods were used for the 1979–1983 (hereafter referred to as 1979 data) sampling and for the 2001 sampling following the USDA Forest Service Standard Specifications for Stand Exam (1993). The 1998 aerial photos along with maps of the GIS classification of the forest on the Uncompahgre Plateau were used to locate the stands on the ground. Six sampling points were located in each stand to cover the extent of the stand. For each point, the overstory trees (DBH $\geq$12 cm) were measured on a variable radius, 4.5 $m^2\ ha^{-1}$ factor prism, while the understory trees (DBH <12 cm) were measured on a fixed radius plot of 0.004 ha. Species, DBH, height, height to live crown and damage were recorded for each tree on the overstory plot, while species, DBH and height were recorded for each tree in the understory plot between 2.5 and 12 cm DBH. Trees less than 2.5 cm DBH were tallied by species and height.

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 711 large trees (>12 cm DBH) and mounted in the field, and small trees were harvested at the ground line. In the lab, 135 cores were either too rotten or discolored to be aged, and were not included in the sample. We aged 315 seedlings and suckers (<12 cm DBH) collected as the first two small trees encountered on each inventory plot. These were cut at the ground line. 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. Errors in ring counts were negligible as most trees as ring widths were readily visible. We estimated total tree age by adding time to reach coring height. Time to coring height was determined for a harvested sample of suckers or seedlings. Median age at coring height (30 cm) for aspen was 5 years ($n = 131$) and for conifers was 24 years ($n = 131$).

2.5. Data analysis

Conifer species were grouped and compared to aspen within the four community types (aspen, aspen/conifer, conifer/aspen, and conifer). We used a paired *t*-test to test for differences in basal area and tree density between 1979 and 2001 by community type. The Satterthwaite method (Steel et al., 1997) was used to estimate degress of freedom due to unequal variances.

3. Results

3.1. Distribution of aspen and conifers

We examined the distribution of community types on the Uncompahgre 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

Table 1
Distribution of aspen, conifer and mixed species forest community types on the Uncompahgre Plateau determined based on overstory canopy cover from 1998 aerial photographs

Community type		Percent of land area	Combined community type 1998	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		

(Table 1). Pure stands were a minority of the landscape, and only 16% were pure aspen. The majority (62%) of the landscape was composed of mixed stands including both aspen and conifers. This was more or less evenly divided between stands where aspen was the dominant species (~30%) and stands where conifers were the dominant species (~32%).

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.

3.2. Aspen and conifer change 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 and 2001 inventories was calculated based on repeated measurement of these stands (Table 2). Pure stands of aspen and pure stands of conifer showed little change in basal area between 1979 and 2001. Basal area for aspen in the overstory (stems $\geq$12 cm DBH) in pure aspen stands was the greatest of any species in any community type at 34.0 $m^2\,ha^{-1}$ in 1979. There was no significant change in aspen basal area between the 1979 and 2001 measurements. Pure conifer stands supported 19.9 $m^2\,ha^{-1}$ of basal area in 1979 and remained stable until 2001.

Aspen/conifer stands supported the second highest amount of aspen in both years (Table 2). In the aspen-dominated aspen/conifer community type, conifer basal area significantly increased ($p = 0.0003$) more than doubling from 10.2 $m^2\,ha^{-1}$ in 1979 to 22.8 $m^2\,ha^{-1}$ in 2001 (Table 2). Aspen basal area slightly declined in this time. The conifer-dominated, conifer/aspen community type had low basal area for aspen in both 1979 and 2001 at about 8 $m^2\,ha^{-1}$. There was no significant change in basal area of aspen in the 20 years between measurements. Conifers, on the other hand, gained basal area in this cover type, increasing from 18.1 in 1979 to 23.9 $m^2\,ha^{-1}$ in 2001 ($p = 0.0971$).

Changes 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 fewer stems per hectare ($p = 0.0388$) than in 1979 (Table 2). Aspen lost an average of 275 stems/ha in pure aspen stands, accounting for the lack of significant increase in basal area. In aspen/conifer stands, aspen stems density decreased ($p = 0.0856$) by about 200 stems/ha while conifer stems increased by about 240 stems/ha ($p = 0.0003$). In conifer/aspen stands, stems densities of aspen and conifers did not change in the 20 years between measurements.

3.3. Age structure of overstory aspen and conifers

The age distribution of overstory aspen in pure aspen stands from the 2001 measurement indicated that nearly 70% of sampled aspen stems were between 80 and 120 years old, establishing from 1880 to 1920 (Fig. 1a). This regeneration coincides with a major fire year recorded on the Uncompahgre Plateau in 1879 (Brown and Shepperd, 2003). No overstory aspen in pure aspen stands were found to be less than 60 years or greater than 140 years old. In contrast, over 20% of conifers in pure conifer stands were greater than 140

Table 2
Comparison of average basal area and tree density for aspen and conifers in the overstory (=12 cm DBH) in aspen, aspen/conifer, conifer/aspen and conifer community types between 1979 and 2001 on the Uncompahgre Plateau, Colorado

Community type	Species	Basal area ($m^2\ ha^{-1}$) (S.E.)		*p*-Value	Tree density (ha^{-1}) (S.E.)		*p*-Value
		1979	2001		1979	2001	
Aspen (*n* = 9)	Aspen	34.0 (4.4)	32.1 (4.0)	0.7578	823 (104)	548 (58)	0.0388
	Conifer	0.0 (0.0)	0.5 (0.4)	0.1543	0.0 (0.0)	20 (14)	0.1853
Aspen/conifer (*n* = 19)	Aspen	21.2 (2.6)	18.3 (2.2)	0.4073	594 (89)	405 (58)	0.0856
	Conifer	10.2 (1.9)	22.8 (2.5)	0.0003	141 (30)	383 (51)	0.0003
Conifer/aspen (*n* = 15)	Aspen	8.3 (1.3)	8.0 (1.2)	0.8839	204 (39)	184 (27)	0.6677
	Conifer	18.1 (2.0)	23.9 (2.8)	0.0971	320 (63)	341 (47)	0.7893
Conifer (*n* = 10)	Aspen	0.0 (0.0)	1.7 (1.1)	0.1476	0 (0.0)	51 (38)	0.2123
	Conifer	19.9 (4.5)	19.9 (2.8)	0.9973	283 (68)	246 (47)	0.6599

years old, and conifer ages on sampled trees were evenly distributed from 60 to over 140 years old (Fig. 1b).

Ages of aspen in aspen-dominated aspen/conifer stands were similar to the distribution of ages in pure aspen stands (Fig. 1c). Over 70% of the aspen stems aged in the aspen/conifer stands were between 80 and 120 years old, and only 15% of stems were older than 120 years. Conifers in aspen/conifer stands were younger than conifers in pure conifer stands, with over 70% of the stems <100 years old. In conifer/aspen stands, aspen ages were more uniformly distributed than in pure aspen or aspen/conifer stands. Only ~50% of aspen stems were between 80 and 120 years old, while nearly 30% of aspen stems were >120 years old (Fig. 1d). In these conifer/aspen stands, conifer ages were nearly evenly distributed between 60 and over 140 years old. More than 20% of conifer ages were >140 years old.

3.4. Aspen and conifers in the understory

Aspen regeneration (defined as trees with DBH <2.5 cm) was found in ~90% of stands in 2001.

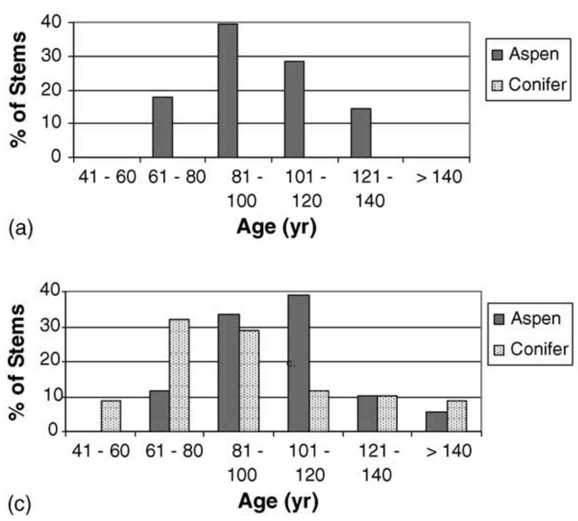

Fig. 1. Age distribution of overstory aspen and conifer stems (>12 cm DBH) in 2001 expressed as a percentage of stems sampled by species in pure and mixed aspen/conifer community types on the Uncompahgre Plateau, Colorado. (a) Aspen stems (*n* = 28) in pure aspen stands, (b) conifer stems (*n* = 57) in pure conifer stands, (c) aspen stems (*n* = 69) and conifer stems (*n* = 69) in aspen/conifer stands and (d) aspen stems (*n* = 71) and conifer stems (*n* = 228) in conifer/aspen stands.

Table 3
Aspen and conifer regeneration density by community type in 1979 and 2001

Community Type	Aspen sucker density (ha^{-1}) (S.E.)		Conifer seedling density (ha^{-1}) (S.E.)	
	1979	2001	1979	2001
Aspen (*n* = 9)	1617 (714)	3299 (1485)	110 (110)	201 (167)
Aspen/conifer (*n* = 15)	818 (193)	1907 (373)	831 (224)	2626 (456)
Conifer/aspen (*n* = 19)	721 (206)	1351 (294)	1462 (436)	2725 (591)
Conifer (*n* = 10)	334 (224)	906 (403)	205 (113)	708 (408)

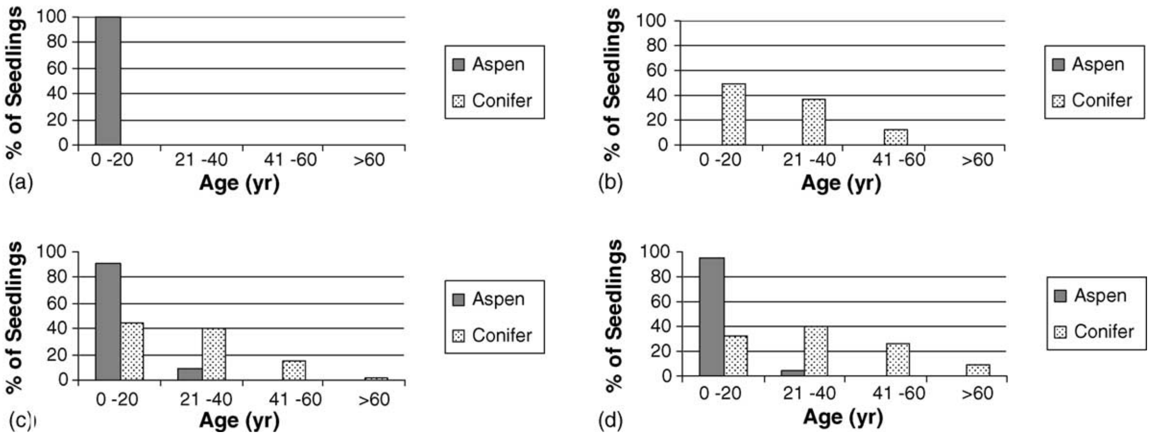

Fig. 2. Age distribution of aspen suckers and conifer seedlings expressed as a percentage of small stems (<12 cm DBH) sampled by aspen and conifer in pure and mixed aspen/conifer community types. (a) Aspen suckers (*n* = 18) in pure aspen stands, (b) conifer seedlings (*n* = 16) in pure conifer stands, (c) aspen suckers (*n* = 24) and conifer seedlings (*n* = 70) in aspen/conifer stands and (d) aspen suckers (*n* = 47) and conifer seedlings (*n* = 135) in conifer/aspen stands.

Suckers were present in all community types, even pure conifer in 1979 and 2001 (Table 3). Pure aspen stands averaged ~1600 suckers/ha in 1979 and ~3300 aspen suckers/ha in 2001. Aspen/conifer, conifer/aspen and pure conifer stands had similar amounts of aspen regeneration, with 700–800 suckers/ha in 1979 and 1350–2000 suckers/ha in 2001. Conifer regeneration was the highest in mixed stands, with aspen/conifer and conifer/aspen stands having ~2600 conifer seedlings/ha in 2001.

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.

Aspen sucker ages in pure aspen stands were all less than 20 years (Fig. 2a). No small aspen stems were >20 years old. Conifer seedling ages in pure conifer stands ranged from 0 to 60 years old. In mixed stands, (aspen/conifer and conifer/aspen stands), >90% of aspen sucker ages were <20 years old. In contrast, conifer seedling ages ranged from 0 to 60 years old in both aspen/conifer and conifer/aspen stands, with about 20–40% of seedlings sampled in each of these age classes (Fig. 2b and c).

4. Discussion

We ask if aspen is persisting on the Uncompahgre Plateau and if aspen is maintaining overstory dominance following ~120 years without significant stand initiating disturbance. The forested landscape of the Uncompahgre Plateau contains significant amounts of aspen, even after a century without significant disturbances. Aspen is found as a component of the overstory on 78% of the forested area and occurs in two types of stand structures—pure aspen on 16% of the landscape where there is no significant presence of overstory conifers, and mixed stands on 62% of the landscape where the aspen and conifer occur together in the overstory at varying proportions.

The pure aspen stands that we sampled were mature stands, with most trees between 80 and 120 years old. These stands appeared to be self-thinning, maintaining high basal area over the last 20 years, while experiencing a decline in stem numbers. Aspen suckering was occurring in most of these stands, and at high numbers. We observed over 2000 suckers/ha in 1979 and in 2001 in pure aspen stands and the presence of conifer regeneration in some clones. Aspen regeneration is occurring, but is not growing into the overstory under current conditions of high basal area and self-thinning. The understory aspen that we sampled were mostly <20 years old and few overstory aspen were less than 80 years old. If aspen suckers were surviving and growing into the overstory, suckers present in 1979 would now be between 20 and 40 years old. We did not find aspen suckers in this age class. Pure aspen stands are exhibiting prolific suckering, and as overstory mortality creates canopy gaps, stable, uneven-aged aspen stands are likely to persist.

Mixed stands of aspen and conifer are undergoing change where overstory aspen basal area is declining and overstory conifer basal area is increasing. This change has been rapid in stands that were characterized as aspen-dominated aspen/conifer stands. In the past 20 years, conifer basal area has doubled in these stands and aspen basal area has declined. As a result, the proportion of aspen basal area in these stands has declined from 68 to 44% in the past 20 years. In conifer-dominated mixed stands, conifer basal area has increased by about a third in the past 20 years, resulting in a decrease in the proportion of aspen basal area from 31 to 26%.

The rapid change in aspen cover is consistent with dynamics of mature, mixed aspen/conifer stands in Utah where aspen were competitively dominant in early stand development, and conifers became competitively dominant at about 100 years of growth (Shepperd et al., 2001). After this change in dominance, aspen growth rates and vigor declined relative to aspen of the same age in pure stands. Aspen/conifer stands where a majority of the basal area was in aspen had a higher proportion of conifers in trees <100 years old than conifer/aspen stands, where a majority of the basal area was conifer (Fig. 1). McKenzie (2001) observed a similar change in western Colorado where conifer gained height dominance after about 100 years of growth.

The conifer dominated mixed stands may have undergone the change in competitive dominance between aspen and conifer sooner, and their current structure reflects this. Conifer/aspen stands have about the same amount of conifer overstory basal area as aspen/conifer stands, but have only half of the aspen basal area (Table 2). Decreasing dominance by aspen is likely to continue in these mixed stands. Aspen suckering is occurring, with over 700 suckers/ha observed in 1979 and 1300–1900 suckers observed in 2001; however, ages of small aspen are mostly limited to <20 years old. This suggests that few aspen suckers are growing into the overstory under current stand conditions. Conifer regeneration is prolific and regeneration has been continuous for the past century given the presence of conifer trees of all ages. Even under current stand condition, conifers are persisting and are growing into the overstory.

Our results suggest that aspen will persist across the Uncompahgre Plateau in pure and mixed species stands. Many pure aspen stands appear to be stable, self-replacing stands (Shepperd et al., 2001). They are currently mature, vigorous, self-thinning stands with a viable root system capable of producing high amounts of suckers. Aspen trees in mixed stands are declining in numbers and in basal area, but are likely to persist. We observed individual stems >250 year old, as have other studies in western Colorado (McKenzie, 2001; Kulakowski et al., 2004). The majority of aspen in these stands are ~100 years old. As in the past, it is likely that some of these individuals will live for more than another century. These individuals can maintain a root system sufficient to ensure the persistence of aspen in these mixed stands (Shepperd et al., 2001).

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 to 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 et al., 2004).

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 areas. In Yellowstone National Park, 10% of pure aspen stands originated before 1871, 85% between 1871 and 1920, and 5% from 1921 to 1998 (Ripple and Larsen, 2000). 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 (Hessl and Graumlich, 2002). In Yoho and Kootenay National Parks, the majority of aspen stands regenerated from 1816 to 1935, also a period of frequent fires (Kay, 1997).

Aspen is likely to maintain dominance in pure aspen stands on the Uncompahgre Plateau. However, in mixed stands of aspen and conifers, aspen canopy dominance has decreased, and is likely to continue to decrease in the future. The limited age range of aspen relative to the broad range of conifers is 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, such as fire or cutting, will be required to reestablish and maintain the level of aspen dominance characteristic of early to mid-seral landscapes, particularly in mixed stands.

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