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NOTE

Age structure of aspen forests on the Uncompahgre Plateau, Colorado

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Abstract: Aspen forests are one of the most dynamic forest types in western North America, responding to chronic factors of competition for resources, as well as episodes of intense herbivory, drought, and fires. The interactions of these driving factors lead to varying age structures of aspen across landscapes and through time. We characterized the age structure of aspen trees on the Uncompahgre Plateau in western Colorado, USA, to inform collaborative efforts of landscape-scale forest restoration. Over 1000 cores from 51 locations showed few aspen older than 140 years (<0.5% for aspen numbers, <2.5% of aspen basal area). Heavy recruitment in the late 1800s (following the last major fires) led to cohorts from 100 to 140 years of age that account for 15% of current aspen numbers and 40% of current aspen basal area. Perhaps the most important character of the current age structure is a relatively low number of aspen younger than 50 years; normal rates of tree survivorship in coming decades will lead to a substantial decline in aspen on the Plateau as these cohorts progress into older age classes. Patterns of aspen ages on the Uncompahgre Plateau differ substantially from those on the Kaibab Plateau and in Rocky Mountain National Park, owing the varying importance in space and time of driving factors. Landscape-scale increases in aspen regeneration (from major events such as fire) would be necessary to moderate the long-term decline in aspen on the Uncompahgre Plateau.

Key words: forest age structure, sudden aspen decline, fire regime, landscape-scale forest analysis.

Résumé : Les peupleraies comptent parmi les types forestiers les plus dynamiques de l'ouest de l'Amérique du Nord par leurs réactions à des facteurs chroniques de compétition pour les ressources et à des épisodes intenses de défoliation, de sécheresse et de feu. Les interactions entre ces facteurs déterminants mènent à des structures d'âge variées du peuplier dans le paysage et dans le temps. Nous avons caractérisé la structure d'âge de peupliers sur le Plateau Uncompahgre dans l'ouest du Colorado, aux États-Unis, pour documenter les efforts collaboratifs de restauration forestière à l'échelle du paysage. Plus de 1000 carottes de sondage provenant de 51 peuplements ont montré que peu de peupliers étaient plus âgés que 140 ans (<0,5 % en nombre et <2,5 % en surface terrière). Un fort recrutement à la fin des années 1800 (à la suite des derniers feux importants) a engendré des cohortes de 100 à 140 ans représentant 15 % du nombre actuel de peupliers et 40 % de la surface terrière actuelle du peuplier. La plus importante caractéristique de la structure d'âge actuelle est probablement le nombre relativement faible de peupliers âgés de moins de 50 ans. Ainsi, un taux normal de survie des arbres au cours des prochaines décennies se traduira par un déclin substantiel du peuplier sur le Plateau à mesure que les cohortes progresseront vers les plus vieilles classes d'âge. Le patron d'âge du peuplier sur le Plateau Uncompahgre est substantiellement différent de ceux du Plateau Kaibab et du Parc national des Montagnes Rocheuses en raison de l'importance variable des facteurs déterminants dans l'espace et dans le temps. Une augmentation de la régénération du peuplier à l'échelle du paysage (à la suite d'événements majeurs comme un feu) serait nécessaire pour atténuer le déclin à long terme du peuplier sur le Plateau Uncompahgre. [Traduit par la Rédaction]

Mots-clés : structure d'âge des forêts, déclin soudain du peuplier, régime des feux, analyse forestière à l'échelle du paysage.

Introduction

Forests are very dynamic across scales of space and time, and the study of forest changes over time has been a core focus of forest ecology from its inception. The tree composition of forests changes in response to changes in the abiotic environment, shifting competition among plants, and interactions of plants, animals, and people. Long-term patterns of change often show the legacies of prior events, and the present condition of any forest is strongly determined by the forest's history (Egler 1977). Active forest management typically seeks to create trajectories of forest development that lead to predictable desired outcomes such as high growth rates of a desired species and a uniform distribution of age classes of forests across a landscape (Puettmann et al. 2008). Many forest landscapes develop in response to human activities that may not be designed for particular goals. For example, grazing may lead to a reduction of fine fuels that carry frequent fires, and the change in fire frequency resonates into major changes in forest structure and composition (e.g., Fulé et al. 2003). The current structure and composition of a forest carries a large legacy of historical factors that typically constrain future development of the forest across the landscape.

Aspen (*Populus tremuloides* Michx.) trees and stands are particularly important across the western US as aspen provides for higher diversity of associated vegetation, major wildlife habitat, and relatively moderate behavior of wildfires. Aspen forests may be among the most dynamic across western North America, responding to major events such as fires and droughts, episodic or chronic impacts of herbivory (by livestock, wildlife, and insects), and chronic competition for resources with other plants (Rogers et al. 2013). The outcome of these multiple interacting factors can be quite different for aspen forests in different landscapes (Shinneman et al. 2013), and an understanding of historical aspen dynamics at

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appropriate scales (Kulakowski et al. 2013) is a fundamental starting point for active engagement in shaping the future of forests within particular landscapes.

The forests of the Uncompahgre Plateau in western Colorado cover about 300 000 ha, with aspen trees mixed with a variety of conifer species across elevational gradients from warm, dry environments dominated by ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) to cool, wet forests of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). The Uncompahgre Plateau is the focus of a major collaborative forest restoration project that seeks to restore forest structure to historical conditions that reduce risks of high severity fire and enhance ecosystem services. In this project, we sought to understand potential future trajectories of aspen on the Uncompahgre Plateau by characterizing the age structure across the Plateau. Our specific objectives were to estimate the decade of establishment, the likely drivers of patterns in the age structure, and implications for the future development of these forests. We also compare the Uncompahgre Plateau age structure with other aspen forests to see how generalizable results might be a regional scale.

Methods

The Uncompahgre Plateau is a broad, gently rising landscape of sedimentary formations on the eastern edge of the Colorado Plateau province (Hughes et al. 1995), rising 1000 m above the surrounding valleys. The broad top of the Plateau is composed primarily of Cretaceous Dakota sandstone and Jurassic Morrison shale (U.S. Geological Survey 1975). Forests with aspen occur from the upper elevations of the broad plateau from about 3000 m down gentle slopes to about 2500 m. The winter monthly temperatures at Columbine Pass (2900 m, 38°25′N, 108°23′W, SNOTEL site number 409, http://www.wcc.nrcs.usda.gov/nwcc/site?sitenum=409&state=co) average about –3 to –6 °C, and summer months average 12 to 14 °C. Precipitation (about 850 mm·year^{-1}) falls mostly as snow, with only 20% falling during the growing season. At the lower limit of the distribution of most aspen, the winter months average –2 to –4 °C, and the summer months average 16 to 18 °C, with 550 mm·year^{-1} of precipitation (with 25% falling during the growing season; Sanborn Park RAWS site, 2450 m, 38°11′N, 108°13′W, http://www.raws.dri.edu/cgi-bin/rawMAIN.pl?coCSAN).

Field data for this study were collected during the summer of 2010 as a part of the Uncompahgre Plateau Collaborative Landscape Restoration Project, a collaboration with the USDA Forest Service, Uncompahgre Partnership, and Colorado State University. The portion of the Plateau within the mapped range of aspen was gridded at 2 × 2 km, and a random subset of 63 grid points was chosen for sampling. Fifty-one of the 63 random locations had at least one aspen tree encountered with our sampling design (Fig. 1A), but our extrapolations representing the mapped range of aspen on the Plateau are based on the total sample size of 63.

At each location, nine points were sampled in a triangular design (Fig. 1B) at 50 m intervals. The determination of age structure of a forest at a landscape scale is problematic. All trees may be cored and aged in fixed-area plots, but this approach may capture large numbers of small trees and few large trees. Forestry measurements often use variable radius (prism) plots to provide better representation of larger (and likely older) trees. The documentation of age structure at landscape scales may be more efficient with sampling schemes that do not underemphasize large trees (for an example, see Binkley et al. 2006). For this reason, we used a prism-based sampling scheme rather than fixed-plot-area design.

At each sampling point, a prism (1.15 m^2·ha^{-1} for most plots, or 2.30 m^2·ha^{-1} for high density locations) was used to determine aspen sample trees. All trees included by the prism were cored (at 1.4 m height, similar to other studies) to determine year of recruitment (defined as reaching 1.4 m in height). Six trees were too small to core (<3 cm diameter), and these trees were assigned to the youngest cohort (2000–2010). Conifer basal area was also estimated for each plot with a 4.59 m^2·ha^{-1} prism. The number of small (<1.4 m tall) aspen suckers was measured at each triangle

Fig. 1. (A) Sixty-three random locations were sampled across the range of aspen on the Uncompahgre Plateau. (B) Sampling design. Within the mapped range of aspen, 51 locations had at least one aspen tree encountered in one or more of the nine sample points (arranged in a regular triangle at 50 m intervals.

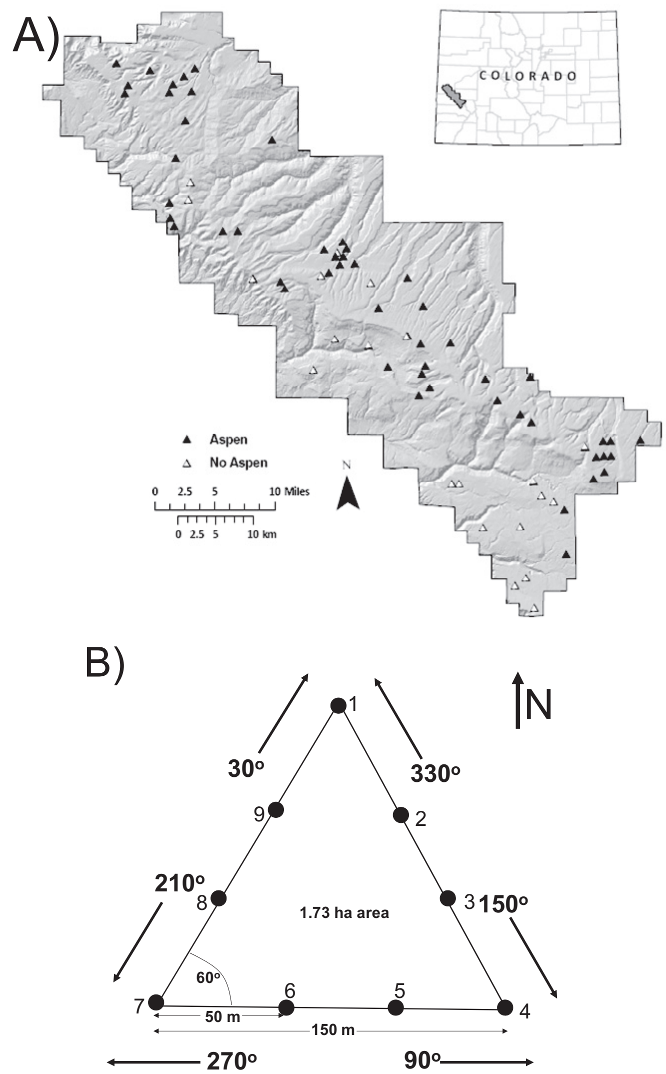
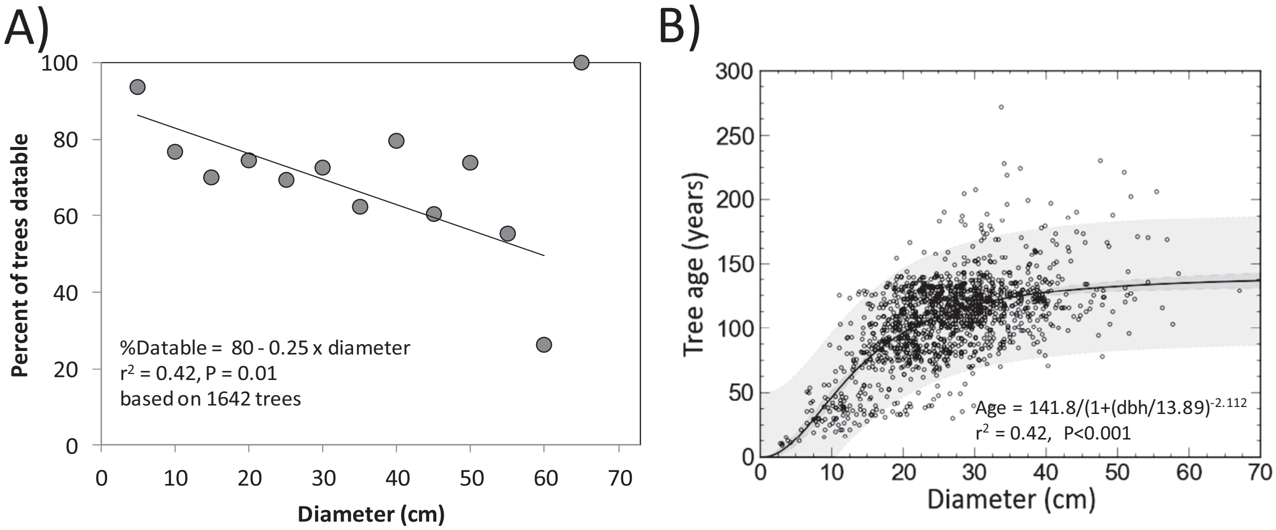


Table 1. Aspen was the most frequently occurring species and contributed the largest portion of stand basal area (BA) across the Plateau, though the sum of all conifer species accounted for almost twice the basal area of aspen.

Forest dominant species	Percent of locations present	Mean BA (m^2·ha^{-1})	Percent of total stand BA
Aspen	81	6.6	34
Ponderosa pine	41	4.8	25
Douglas fir	15	0.9	5
Blue spruce and Engelmann spruce	30	1.9	10
Subalpine fir	44	3.7	19
Gambel oak	33	1.4	7

Fig. 2. Relationship between diameter and (A) percentage of trees datable and (B) tree age. The proportion of trees with heartrot increased with tree size (A; best-fit line excludes the single 65 cm tree encountered in the sampling), resulting in datable trees declining to about 60% for trees larger than 50 cm. Although the average age increased with diameter, the residual variation was notable (B; very narrow dark-shaded band is the 95% confidence interval for the best-fit regression; the broad, light-shaded band is the 95% prediction interval).



vertex in 5.6 m radius (100 m^2) plots. An aspen sucker was defined as a single root collar with one or more stems.

Tree cores were placed into paper straws for several weeks for air drying. After drying, cores were mounted on wooden blocks and sanded for better definition of the annual rings. Growth rings were dated by using a stereo-microscope and standard dendrochronological procedures (Stokes and Smiley 1968). The pith date for cores that did not capture the pith was calculated by estimating the length of the missing radius and ring width (Duncan 1989). Many aspen had rotten interiors and could not be dated. We estimated the ages of these trees based on the relationship between diameter and age for the datable trees (using CurveExpert Professional 1.6). Some analyses are presented based on all sampled trees, and some use only datable trees (as noted).

We extrapolated the prism sample data and tree ages to obtain a representation of the age structure of aspen across the Plateau following methods similar to those of Binkley (2008). Each tree sampled by the prism was converted to the number of trees that it would represent in a hectare based on the basal area factor of the prism, and each of the extrapolated trees was assumed to have the same age as the sampled tree. For each of the 63 locations, the nine subplots were averaged together, and the Plateau-wide estimate of tree numbers and ages was derived as the average of the 63 locations.

Similar analyses of aspen age structures have been developed for Rocky Mountain National Park (Binkley 2008) and the Kaibab Plateau (Binkley et al. 2006), and we compared patterns across the three sites to see how common and unique factors might influence aspen dynamics in different locations.

Results

Aspen was the dominant tree species across the Uncompahgre Plateau, with an average of 6.6 $m^2 \cdot ha^{-1}$ of basal area (33% of total basal area; Table 1). Datable cores were obtained from 81% (1364) of the trees counted with the prisms. Ten trees were older than 200 years (at breast height), and the oldest aspen reached breast height 272 years before 2010. Heartrot was more common in larger (and likely older) trees; about one-third of the larger trees were undatable (Fig. 2A). As expected, the relationship between tree diameter and age was very significant with very tight confidence intervals around the best-fit curve. The residual variation around the average was substantial with a broad prediction interval (Fig. 2B). Across the population, the relationship between diameter and age was strong, so our extrapolation from sampled trees to the population of aspen on the Plateau should represent the population well.

The Plateau-wide size distribution of aspen stems showed roughly equal numbers of stems in diameter classes up to 25 cm and then fewer larger trees (Fig. 3A). This even distribution of tree numbers across several size classes demonstrates that the aspen population did not develop from consistent rates of recruitment and mortality that would lead to a classic inverse-J curve. The basal area distribution across size classes approached a normal distribution, with mid-sized trees (20 to 35 cm) accounting for the majority of aspen basal area (Fig. 3B).

The age distribution showed that few aspen are older than 140 years, but this might reflect disturbance history more than life span limitations (Fig. 4A). The last substantial fires on the Plateau occurred in 1879, and the large cohorts of aspen date from after 1880. The disparity of numbers of trees older than 140 years and those between 100 and 140 years may simply reflect higher recruitment after 1880 rather than an increase in mortality after 140 years of age. Alternatively, stand-replacing fires in the late 1800s may have created an "age cap", with most aspen regenerating after these events.

The Uncompahgre Plateau had as many stems in the 90 to 130 year age classes as in the <40 year age classes, again indicating that recruitment and mortality have not been consistent across decades. Trees older than 100 years accounted for about two-thirds of aspen basal area (Fig. 4B).

The density of aspen suckers (trees < 1.4 m tall) was high across most of the Plateau (Fig. 5), averaging 555 suckers$\cdot ha^{-1}$ compared with an average of 170 aspen trees$\cdot ha^{-1}$ across all size classes. Only one of the 51 sampling locations that had adult aspen failed to have aspen suckers. This sucker density is notably lower than Mueggler (1989) reported for aspen-dominated forests in Utah, Idaho, and Wyoming; the median number of suckers was about 1800$\cdot ha^{-1}$. Mueggler (1989) did not define if multiple stems from one root collar would be one sucker or multiple suckers. We suspect the major difference is that his stands all had a minimum of 50% of basal area comprised of aspen, and our samples averaged 34% aspen (Table 1), so the difference is not unexpected.

Fig. 3. Relationship between diameter at 1.4 m and (A) number of aspen trees per hectare and (B) aspen basal area. The number of trees declined with size class (A), whereas the majority of aspen basal area occurred in trees 20–35 cm in diameter (B).

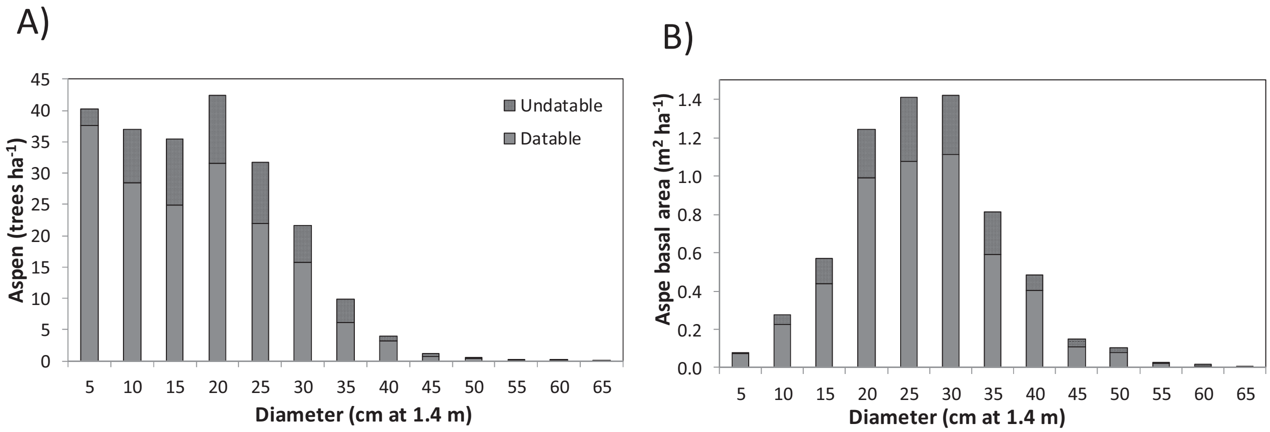


Fig. 4. Relationship between age in 2010 at 1.4 m height and decade reaching 1.4 m height and (A) number of aspen trees per hectare and (B) aspen basal area. A large proportion of aspen date from the late 1800s and early 1900s (A), with relatively few of the current trees dating to the mid-1900s. In B, it is apparent that basal area is dominated by the cohorts from the late 1800s and early 1900s.

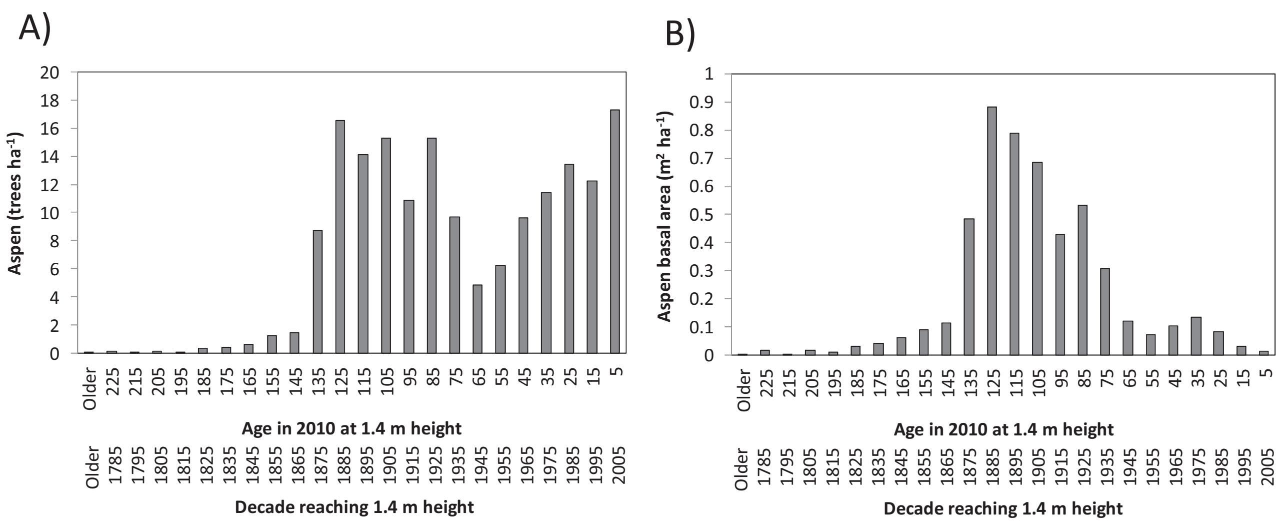
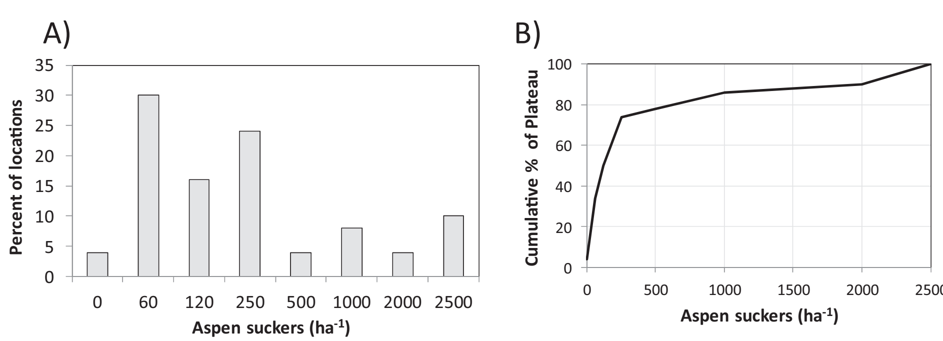


Fig. 5. Relationship between number of aspen suckers per hectare and (A) percentage of locations and (B) cumulative percentage of Plateau. Aspen suckers (shoots < 1.4 m tall) were generally abundant across the Plateau (A), with about two-thirds of the Plateau sustaining >100 suckers·ha⁻¹ (B).



Discussion

Livestock grazing coincided with the cessation of fire in the late 1800s, and the large cohorts of aspen from this time indicate that the absence of fire may have been more beneficial to aspen recruitment than any impairment by livestock browsing. The large increase in cohorts after about 1880 is consistent with the pattern on the Kaibab Plateau in northern Arizona, where aspen recruitment increased greatly when the regime of frequent fires stopped (Fulé et al. 2003; Binkley et al. 2006). As noted above, stand-replacing fires may have killed most aspen trees across the Plateau in the late

Fig. 6. Relationship between estimated age at 1.4 m and (A) cumulative percentage of aspen trees and (B) cumulative percentage of aspen basal area. The size structure of aspen differed substantially on the Uncompahgre Plateau (UP) compared with the Kaibab Plateau (KP) in northern Arizona and with Rocky Mountain National Park (RMNP). About 90% of aspen on the Kaibab Plateau were younger than 30 years, compared with less than 40% for the other two areas (based on data from this study and from Binkley et al. (2006) and Binkley (2008)).

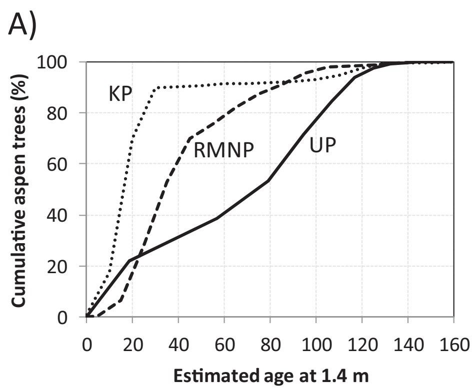
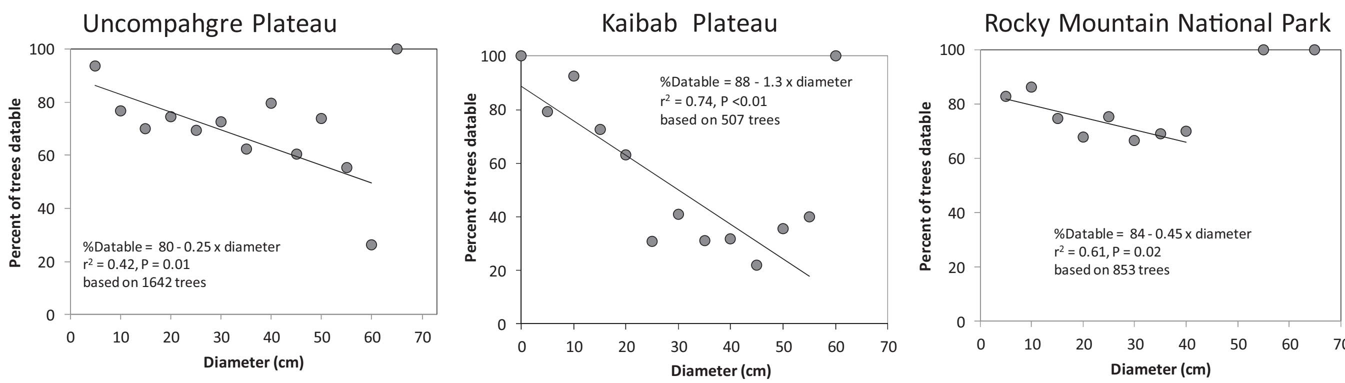


Fig. 7. Relationship between percentage of trees datable and diameter for the Uncompahgre Plateau, the Kaibab Plateau, and Rocky Mountain National Park. Across the three locations, about 85% of <15 cm trees were datable. The datable percentage declined to about 40% for 40 cm trees on the Kaibab Plateau, but remained about 65% for the other two. All three studies found that the largest individual trees were datable, perhaps indicating that only rot-free stems persist to the largest size classes (based on data from this study and from Binkley et al. (2006) and Binkley (2008)).



1800s, followed by a fire-free period that promoted survival of regenerating trees. No such age cap was apparent on the Kaibab Plateau, but an age cap may have been present in Rocky Mountain National Park (Binkley 2008).

The relatively low numbers of young aspen (<100 years old) on the Uncompahgre Plateau indicates that the current age structure cannot provide as many older stems in the next 50 years as are currently on the landscape. Aspen tree survivorship tends to be about 70% to 80% per decade in the absence of major events (Clendenen 1972; Mueggler 1994; Binkley et al. 2006; Binkley 2008), so the younger cohorts currently present will likely fall far short of replacing the current older cohorts. In contrast, if the older cohorts show a consistent 70% to 80% survivorship per decade, the number of very old trees (>150 years) would increase substantially on the Plateau in coming decades as a long-lasting legacy of high recruitment in the late 1800s.

The low rate of aspen recruitment in the past 50 years on the Uncompahgre Plateau may have resulted from the increase in conifer basal area. Smith and Smith (2005) re-measured plots after 20 years and found that conifer basal area increased to over 20 $m^2 \cdot ha^{-1}$ in areas formerly dominated by either aspen or conifers. Kaye et al. (2005) found that aspen regeneration was minimal in mixed stands with more than about 12 $m^2 \cdot ha^{-1}$ of conifer basal area in Rocky Mountain National Park, so aspen recruitment in recent decades may have been impeded by increased conifer dominance. Heavy browsing by wildlife and livestock may also be important; recruitment is higher inside fenced exclosures in some places on the Uncompahgre Plateau (Johnston 2001).

Kaye (2011) found evidence of meso-scale synchrony in the establishment ages of aspen stands. Should we expect the age structure of aspen cohorts to also be similar across locations? The age structures on the Uncompahgre Plateau, the Kaibab Plateau, and Rocky Mountain National Park (in Colorado) show substantially different patterns for each site (Fig. 6). The current stocking of trees differed substantially among the three sites. The Uncompahgre Plateau averaged 170 $trees \cdot ha^{-1}$ and had the highest basal area (6.6 $m^2 \cdot ha^{-1}$). The dominance of young trees on the Kaibab Plateau provided the greatest density of aspen trees (310 $trees \cdot ha^{-1}$) but moderate basal area (2.9 $m^2 \cdot ha^{-1}$ of basal area; Binkley et al. 2006). Rocky Mountain National Park had the fewest aspen (80 $trees \cdot ha^{-1}$) and the lowest basal area (0.5 $m^2 \cdot ha^{-1}$). Aspen on the two plateaus are most often found on relatively flat topography in association with ponderosa pine, Douglas-fir, true firs, and spruces. Aspen in Rocky Mountain National Park occur mostly on slopes and often where lodgepole pines are a major landscape component.

The age structure on the Uncompahgre Plateau showed generally constant numbers of trees across many age classes (Fig. 6A). The Kaibab Plateau had a very large number of young trees (90% of all aspen were <40 years old) and very few trees between 50 and 100 years old. Rocky Mountain National Park had very few trees less than 20 years old, but older cohorts showed a typical pattern of consistently declining numbers with increasing age. The patterns of basal area (Fig. 6B) amplify the influence of older, larger stems.

Prior to European settlement, fire return intervals on the Kaibab Plateau averaged less than 10 years (based on fire scars occurring on 10% or more of the trees within a stand; Fulé et al 2003). Fire return intervals were longer on the Uncompahgre, about 20 to 25 years (based on fires that scarred 10% of trees within stands; Brown and Shepperd 2003). Fire return intervals of 30 to 100 years (or more) were characteristic for Rocky Mountain National Park (Sibold et al. 2006; Sherriff and Veblen 2007). The Kaibab Plateau had prolonged periods of low recruitment in the early 20th century and very high recruitment in the later 20th century, reflecting early severe browsing by deer and later widespread logging (Binkley et al. 2006). The low recruitment of aspen on the Uncompahgre Plateau in the late 20th century probably results from a lack of major events. Heavy wild ungulate browsing in Rocky Mountain National Park likely impeded aspen recruitment in the late 20th century (Binkley 2008), along with few fires (Sibold et al. 2006) and no logging.

Many aspen stems have heartrot that prevents determination of tree age. The proportion of trees that are datable (rot-free) tends to decrease with increasing stem sizes. This pattern was similar for the Uncompahgre Plateau and Rocky Mountain National Park, but the slope was much steeper for the Kaibab Plateau (Fig. 7). The incidence of heartrot appears to differ among these landscapes, adding another factor that may lead to difference in long-term aspen dynamics.

Overall implications for future aspen in forests in coming decades are that the Uncompahgre Plateau may have a major decline, the Kaibab Plateau may have a major increase in aspen, and Rocky Mountain National Park may show less change. Of course, these likely trends would depend on future recruitment patterns and whether major events (e.g., large fires) change both survivorship and recruitment. At the scale of 100 000 ha, these case studies show that local influences of disturbance (both presence and absence) have a larger influence on aspen age structure than regional factors (for more discussion of meso-scale synchrony issues, see Kaye 2011; Kulakowski et al. 2013).

The future of any forested landscape is uncertain, but the potential influence of some driving factors can provide useful insights. The current age distribution is a legacy of past events and chronic interactions, and on the Uncompahgre Plateau, these will have a legacy that almost certainly will include substantially fewer aspen trees in middle-aged cohorts in the future than at present. The current forest has a potential to lead to more old aspen (>140 years) in the future, as the large recruitment cohorts from the late 1800s move into older age classes. Competition with conifers will reduce aspen densities and heavy browsing by wildlife and livestock will limit aspen regeneration, but the influence of these driving factors will likely remain highly variable across the Plateau. The potentially most important driving factor for future development of aspen cohorts on the Uncompahgre Plateau will be the occurrence, extent, and severity of fires that may remove existing cohorts of aspen and conifers and create opportunities for recruitment of new aspen cohorts.

Acknowledgements

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References

Binkley, D. 2008. Age distribution of aspen in Rocky Mountain National Park, U.S.A. For. Ecol. Manage. **255**: 797–802. doi:10.1016/j.foreco.2007.09.066.

Binkley, D., Moore, M., Romme, W., and Brown, P. 2006. Was Aldo Leopold right about the Kaibab deer herd? Ecosystems, **9**: 227–241. doi:10.1007/s10021-005-0100-z.

Brown, P.M., and Shepperd, W.D. 2003. Preliminary fire history in ponderosa pine forests of the Uncompahgre Plateau. Report, Rocky Mountain Tree-Ring Research, Inc., Fort Collins, Colorado.

Clendenen, GW. 1972. Growth and yield of unmanaged stands of quaking aspen on the upper Navajo River in the Rocky Mountains of southwest Colorado. M.Sc. thesis, Department of Forest Management, Oregon State University, Corvallis, Oregon.

Duncan, RP . 1989. An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrycarpus dacrydioides*). N.Z. Nat. Sci. **16**: 31–37.

Egler, F.E. 1977. The nature of vegetation, its management and mismanagement: an introduction to vegetation science. [Published by the author.]

Fulé, P.Z., Crouse, J.E., Heinlein, T.A., Moore, M.M., Covington, W.W., and Verkamp, G. 2003. Mixed-severity fire regime in a high-elevation forest: Grand Canyon, Arizona. Landsc. Ecol. **18**: 465–486. doi:10.1023/A:1026012118011.

Hughes, T., Kingston, R., and Cencich, B. 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, Washington, DC.

Johnston, B. 2001. Multiple factors affect aspen regeneration on the Uncompahgre Plateau, west-central Colorado. *In* Sustaining aspen in western landscapes. *Edited by* W.D. Shepperd, D. Binkley, D. Bartos, T.J. Stohlgren, and L.G. Eskew. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, Gen. Tech. Rep. RMRS-P-18. pp. 395–414.

Kaye, M. 2011. Mesoscale synchrony in quaking aspen establishment across the interior western US. For. Ecol. Manage. **262**: 389–397. doi:10.1016/j.foreco.2011.04.003.

Kaye, M.W., Binkley, D., and Stohlgren, T.J. 2005. Long-term impacts of conifer invasion and elk browsing on quaking aspen forests in the central Rocky Mountains, U.S.A. Ecol. Appl. **15**: 1284–1295. doi:10.1890/03-5395.

Kulakowski, D., Kaye, M.W., and Kashian, D.M. 2013. Long-term aspen cover change in the western US. For. Ecol. Manage. **299**: 52–59.

Mueggler, W.F. 1989. Age distribution and reproduction of intermountain aspen stands. West. J. Appl. For. **4**: 41–45.

Mueggler, W.F. 1994. Sixty years of change in tree numbers and basal area in central Utah aspen stands. USDA Forest Service Research Paper INT-RP-478.

Puettmann, K.J., Messier, C., and Coates, K.D. 2008. A critique of silviculture: managing for complexity. Island Press, Washington, DC.

Rogers, P.C., Eisenberg, C., and St. Clair, S.B. 2013. Resilience in quaking aspen: recent advances and future needs. For. Ecol. Manage. **299**: 1–5. doi:10.1016/j.foreco.2012.11.008.

Sherriff, R.L., and Veblen, T.T. 2007. A spatially explicit reconstruction of historical fire occurrence in the ponderosa pine zone of the Colorado Front Range. Ecosystems, **10**: 311–323. doi:10.1007/s10021-007-9022-2.

Shinneman, D.J., Baker, W.L., Rogers, P.C., and Kulakowski, D. 2013. Fire regimes of quaking aspen in the Mountain West. For. Ecol. Manage. **299**: 22–34. doi:10.1016/j.foreco.2012.11.032.

Sibold, J.S., Veblen, T.T., and Gonzalez, M.E. 2006. Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, U.S.A. J. Biogeogr. **32**: 631–647. doi:10.1111/j.1365-2699.2005.01404.x.

Smith, A.E., and Smith, F.W. 2005. Twenty-year change in aspen dominance in pure aspen and mixed aspen/conifer stands on the Uncompahgre Plateau, Colorado, U.S.A. For. Ecol. Manage. **213**: 338–348. doi:10.1016/j.foreco.2005.03.018.

Stokes, M.A., and Smiley, T.L. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, Illinois.

U.S. Geological Survey. 1975. Geologic map of Colorado. Published by Colorado Geologic Survey, Denver, Colorado.