THESIS

ASPEN FORESTS ON THE UNCOMPAHGRE PLATEAU: CURRENT AND FUTURE EXPECTATIONS

Submitted by

Attia A Mussa Alsanousi

Department of Forest and Rangeland Stewardship

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Fall 2012

Master's Committee:

Advisor: Daniel Binkley

Frederick W. Smith
Jason S. Sibold

Copyright by Attia Alsanousi 2012

All Rights Reserved

ABSTRACT

ASPEN FORESTS ON THE UNCOMPAHGRE PLATEAU: CURRENT AND FUTURE EXPECTATION

Dynamic changes in aspen cover on the Uncompahgre Plateau have raised concerns among researchers and communities about the stability and long-term survivorship of aspen forests. In the summer of 2010, aspen increment cores were measured for current age distribution from sixty-three random locations across the Plateau including pure aspen and mixed conifer-aspen stands, to provide insights about aspen forests in the near future.

Most of aspen trees on the Plateau in 2010 were 100 to 130 years old, having established after the last major landscape-scale fire in 1879. Trees older than 140 years accounted for about 2% of all stems, with the oldest tree in our random sample being 272 years at breast height. Aspen cover will likely decline over the next five decades, as young cohorts (<80 years) have fewer stems than older cohorts (100- 130 years). Several ecological processes or events could accelerate aspen decline, including conifer replacement of aspens in mixed stands and severe drought. The three survivorship scenarios showed that the reduction in aspen cover by 2060 will likely vary from about 40% of current aspen cover in the most optimistic scenario to an 84% reduction in a higher mortality scenario. The Plateau currently has abundant numbers of aspen suckers, but few of these escape browsing pressure to become trees. The aspen decline predicted in the scenarios may continue beyond 2060 if recruitment remains low, or could be turned around if widespread disturbance regenerates forests, or if browsing pressure drops substantially.

ACKNOWLEDGEMENTS

Many people contributed to this work. Thanks to Forest Service and the Uncompahgre National Forest in Montrose, especially Tim Garvey, Delta; and Norwood Ranger District for providing housing and logistical support during field season. Thanks to my great field assistants Ben Lowrance and Drew Derderian for their help in collecting aspen cores from all samples locations. Taylor Elm and the Montrose High School interns with their teacher Rusty George for helping in some of these locations. Bill Romme contributed to the overall design of the project, and thanks to Peter Brown for advice on dating cores and Randy Walsh for help with mounting and dating cores. I also thank my committee members Frederick (Skip) Smith and Jason Sibold for editorial comments and suggestions. Finally, this work would have not been possible without the guidance and knowledge of my advisor Dan Binkley.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Quaking aspen (*Populus tremuloides* Michx*)* is one of the most abundant and valuable species in the Rocky Mountain area (Daubenmire 1943, Packard 1947, Little 1971, White et al. 1998, Knight 2001). It is the most widely distributed tree in North America, and around 75% of aspen trees in the western United States occur in Colorado and Utah (Bartos, 2001). Aspen communities can be found in pure stands or mixed stands with conifer trees across a great range of elevation. These aspen communities have high biodiversity and provide valuable wildlife habitat (White et al. 2003). Compared to surrounding conifer forests, aspen stands have more suitable habitat for variety and richness of plants and bird species (Winternitz 1980, Turchi et al. 1995, Dieni and Anderson 1997). Colorado has nearly 8.5 million hectares of forested lands, and aspen is the dominant species in 17% of these forests, second in area to only spruce-fir (*Picea engelmannii*) and (*Abies lasiocarpa*) (Benson and Green 1987). Aspen reproduction from seed is uncommon in the Rocky Mountains due to the highly specific environmental conditions needed (McDonough 1985, Kay 1993, Mitton and Grant 1996, Romme et al. 1997). Most aspen trees originate from sexual reproduction of suckers or shoots sprouting from roots, which may occur at distances of up to -10 m from the parent stem (DeByle and Winokur 1985, Sheppard 1990).

Aspen Growth

Recent studies have indicated gradual, steady, loss of aspen trees across the Uncompahgre National Forest (Johnson 2001, Smith and Smith 2005, Strand et al. 2009). Several ecological and environmental processes may have contributed to this noticeable reduction in aspen recruitment.

Sudden aspen decline (SAD) became obvious in 2004 as landscape of leafless white trees developed (and remained standing on the site for several years, Ciesla 2008). SAD is distinguishable from insect defoliation and other types of forest damage by the complete defoliation of trees branches dieback (Worrall et al. 2007).A drought was probably responsible for this aspen decline (Hogg et al. 2008, Worrall et al. 2008, Worrall et al. 2010, Anderegg et al. 2011). Other factors that may have contributed to this mortality event are low elevation, south and southwest aspect, site and stand factors, and the biotic agents (Worrall et al. 2010).

Replacement of aspen by conifers is another challenge facing aspen stands on the Plateau. This replacement process is most noticeable at higher elevations (Kulakowski et al. 2004). Aspen trees may dominate a site that has been severely disturbed (Sheppered et al. 2001, Kulakowski et al. 2004), with rapid early growth outpacing conifers. Conifers may grow taller than aspen and outlive aspen, though increasing conifer dominance does not typically remove all aspen trees from stands. Pure aspen stands comprise about 16% of the Plateau's forests, with mixed aspen-conifer stands covering about 62% (Smith 2004, Smith and Smith 2005). Despite the fact that aspen dominance tends to decline in older mixed conifer-aspen stands, many stands continue to show aspen codominance with conifers including ponderosa pine (*Pinus ponderosa*), Engelmann spruce (*Picea engelmanii*), blue spruce (*Picea pungens*), and Douglas-fir (*Pseudotsuga menziesii*).

Heavy browsing on young aspen shoots may prevent some young aspen shoots from reaching the canopy and becoming large trees. Aspen stands are also important for providing food and habitat for elk and deer in summer seasons (Hess and Alexander 1986, Johnston 2001). Browsing by elk has been identified as one of most important factors in decline of the aspen forests in the Rocky Mountain area (Ripple et al, 2001). Livestock browsing may also hinder aspen regeneration. The large number of cattle and other herbivores in the area may greatly reduce the recruitment of young shoots and affecting the long term existence of aspen trees in this forest.

Forest Structure in the Uncompahgre National Forest

The Uncompahgre Plateau covers 344,000 hectares on the western slope of the Colorado Rocky Mountains with elevation ranging from 1700 m to 3000 m (Smith 2004, Smith and Smith 2005). The most common species that cover large portions of the plateau are: aspen, ponderosa pine, Engelmann spruce, blue spruce, and Douglas-fir. Pure aspen stands are classified based on 80% or more of stand basal area are aspen trees. Aspen often comprises less than half the stand basal area in mixed aspen-conifer stands. Aspen trees tend to maintain dominance in pure aspen stands on the Plateau, but lose out to conifers in mixed stands (Smith and Smith, 2005).

In this study, we examined the age structure of aspen trees on the Uncompahgre Plateau to gauge whether recent regeneration might be sufficient for sustaining aspen at historical levels on the Plateau. We sampled aspen trees from 63 random locations across the Plateau to evaluate the overall current age distribution of aspens and gain insights about the likely age distribution and shape of aspen forests in the future. Our analysis of the field data from the summer of 2010 addressed the following questions:

1- How old are aspen trees on the Uncompahgre Plateau?

2- How much variation occurred among decadal cohorts over the past two centuries?

3- How might the aspen forests appear in 50 years?

4- Is there a high risk of a substantial reduction of aspen cover on the Plateau?

METHODS

Study area

The Uncompahgre National Forest is on the western slope of the Colorado Rocky Mountains and cover an area of about 344,000 hectares (Figure 1). The upper elevations of the Plateau are relatively flat, although the total elevation range spans from 1700 m to 3000 m (Hughes 1995). Running northwest to southeast, the major forest structure types on the plateau are dominated by: quaking aspen (*Populus tremuloides*), ponderosa pine/mixed conifer (*Pinus ponderosa* and *Pseudotsuga menziesii*), spruce/fir forests (*Picea engelmannii* and *Abies lasiocarpa*) (USDA Forest Service, 1983), and gambel oak (*Quercus gambelii*). Some lower elevation forests occur outside the range of aspen dominated by juniper (*Juniperus osteosperma*) and pinyon pine (*Pinus edulis*) (Smith 2004, Smith and Smith 2005).

Data collection

Field data for this study were collected during the summer of 2010 between June and September as a part of The Uncompahgre Plateau Collaborative Restoration Project. The project was a collaboration with the Uncompahgre Partnership, USDA Forest Service, and Colorado State University. The Plateau was gridded at 2 x 2 km, and a random subset of 50 plots was chosen. After these were sampled, a second set of 50 random plots was chosen, and time allowed 13 of these additional locations to be sampled for a total sample size of 63 locations. Forest community types and basal area were determined for all tree species in the study area. Fifty-one of the 63 random locations had at least one aspen tree encountered with our sampling design.

At each location, 9 points were sampled in a triangular design (Figure 3) at 50-m intervals (150 m for each side of the triangle). At each sampling point, a prism (1.15 m^2/ha for most plots, or 2.30 m^2/ha for high density locations) was used to determine aspen sample trees. From 0 to 30 cores were included in each prism plot. The 567 prism plots (across 63 locations) tallied from 0 to 30 trees/plot. Six of all trees included in prism plots were too small to core (< 3cm), 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^3/ha prism.

Aspen cores were placed into paper straws for several days for air drying. After drying, cores were mounted into wooden blocks and then sanded with finer grit sandpaper for a better definition of the annual rings. Growth rings for these cores 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). Aspen regeneration and new shoots were presented in all of these sampling sites.

Data analysis

I 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 Binkley (2008). First, I calculated the number of trees/ha represented by each tree included by the prism (using the prism basal area factor and the basal area of each tree). Next, the age of the sampled tree was assumed to be the age of the calculated number of trees. Finally, this information was extrapolated across the Plateau by summing the estimated tree number for all 9 prism points and dividing by 9, then summing across the entire Plateau and dividing by 63 (the number of random locations sampled). I used Microsoft Excel to plot and graph data for age and diameter at breast height distribution for aspen trees on the Plateau.

Many of aspen trees in the study area had rotten cores and the age patterns for the Plateau were evaluated based on trees of known age. I investigated whether inclusion of undated trees might change the overall patterns across the landscape. The age of each undatable tree was estimated based on the relationship between tree diameter and age from all the datable trees (r^2= 0.3315, p-value: < 0.001) using R statistical software (v.2.15.0; R Development Core Team, 2012) (Figure 5-c). Data for aspen age were grouped into 10 years age classes and data for forest vegetation type at each plot were analyzed to estimate basal area for all tree species located in sampling plots.

The likely future age structure of aspen on the Plateau was explored with three scenarios with different survivorship rates per decade: 70%, 80%, and 90%. The two lower rates bracket patterns observed in other aspen studies in the region (Clendenen 1972, Binkley et al. 2006, Binkley 2008), and the 90% survivorship is may represent the most optimistic scenario that could develop. Age-dbh relationship was also used to estimate the potential increase in aspen diameter at breast height for all aspen trees in the next five decades. I added the expected diameter increase in the next five decades to the actual 2010 dbh records for each of the surviving aspen trees, and used them to estimate change in aspen basal area in each of the three survivorship scenarios.

RESULTS

Aspen trees occurred in one or more of the 9 prism plots in 51 of the 63 random triangle locations (Table 2) (Figure 1). Aspen shoots (suckers) were present in all of the triangles with aspen trees, and were also encountered in the other 12 locations without aspen trees in the prism plots. Aspens comprised 45% of the total basal area of forest in these 51 sampling locations with mean BA of 10.2 m^2/ha. Conifers accounted for 49% of total basal area: 4.8 m^2/ha for ponderosa pine, 0.9 m^2/ha for Douglas fir, 1.8 m^2/ha for spruce (blue and Engelmann combined), and 3.7 m^2/ha for subalpine fir. Gamble oak was present in forest understory in some locations comprising an overall average of 6% of the total basal area (1.4 m^2/ha). The majority of aspen trees on the Uncompahgre Plateau occurred in mixed stands with conifers (92% of the Plateau) (Figure 2). The majority of aspen basal area occurred in age classes between 70-140 years with almost 83% of the total aspen basal area, and around 3% of total aspen basal area for age classes ≤ 50 years, and 14% for aspens older than 140 years.

Size and Age structure of the Sample Cores

A total of 1892 aspen trees were included in the prism plots, and 1371 trees were datable (72%) and 521 trees were undatable (28%). We also encountered 630 standing dead trees (Figure 4). The youngest tree was 9 years old (year of reaching breast height was 2001, with a diameter in 2010 of 3.1 cm), and the oldest tree was 272 years old (reaching breast height in 1738, with a diameter in 2010 of 33.8 cm).

The distribution of diameters at breast height followed right- skewed distribution with more small-sized aspen stems in understory and younger cohorts than big aspens per hectare (Figure 5). The smallest dbh recorded was 2.8 cm, and the largest was 67 cm. Most of aspen trees with large dbh occurred in mixed conifer- aspen stands. The 15 cm diameter class had the greatest number of trees per ha (both datable and rotten), comprising almost 20% of all aspen. The number of trees per hectare declined in larger size classes to fewer than 10 stem/ha in all size classes greater than 40 cm (≤ 1.1% of total aspen data). The analysis also shows a decrease in the number of datable aspen cores from sampling plots with increasing diameter, and the chance for large-size aspen trees of being rotten is greater compared to small-sized aspens (Figure 5-b). The proportion of datable trees declined with increasing tree diameter, from 100% for the smallest trees to less than 40 % for the largest trees.

Size and Age Structure of the Plateau Population

Current age distribution of aspen trees on the Uncompahgre Plateau (Figure 6) showed a constant increase in the number of young aspen trees per hectare for trees ≤ 50 years in age (35% of all aspen stems).

Fewer aspen trees became established 50 to70 years ago, and these two decadal cohorts represent less than 7% of all aspen trees with an average of 5.5 tree/ha.

For trees in age between 70-140 years, the number of aspen trees/ha continue to rise and comprise the majority of aspen trees on the Plateau with an average of 13 tree/ha for 70 to 140 age classes. The peak of all age classes and the maximum value where the majority of aspen trees occur was 17 trees/ha for trees in age between 120-130 years. Aspen trees between 70- 140 years old accounted for 56% of all aspen on the plateau. The cohort with the greatest number of aspen trees dated to 1880- 1910, consistent with results from previous studies of aspen trees on the plateau (Smith 2004, Smith and Smith 2005), and with the expectation of extensive aspen recruitment after a major fire in 1879 (Brown and Shepperd 2003). Almost half the aspen trees on the Plateau were between 100 and 130 years of age.

The number of aspen trees/ha start to decline rapidly beyond 140 years with an average of 1 tree/ha or even less, comprising 2% of all aspen trees on the Plateau.

Scenarios for the Future of Aspen

The low number of aspen younger than 100 years raises concern about the future of aspen trees on the Uncompahgre Plateau. These concerns about the population age structure have been exacerbated by rapid increases in aspen mortality. The long-term age structure has resulted from influences of major fires, gradual changes in competition with conifers, and browsing of aspen shoots by cattle and wildlife.

If overall mortality rates follow historical trends, aspen cover on the plateau in the next 50 years (at year 2060) will probably experience a major reduction in the total number of mature trees, regardless of the assumed rate of mortality (Figures 7, 8). The current stocking of younger trees is too low to replace the current number of older trees.

These scenarios do not include in-growth of young stems because the factors influencing recruitment are very uncertain. Very large disturbances (such as extensive fire) might lead to a large new cohort of stems. Indeed, the current density of suckers was quite high across the plateau in 2010, with over 900 suckers/ha. Most of these were browsed too heavily to become tree-size stems, so future cohorts of young aspen will also depend on whether recent levels of browsing continue. Without major changes, we suspect aspen regeneration will remain too low to sustain the historical number of aspen in older cohorts.

I focused on scenarios for the future of aspen cohorts currently on the Plateau. In the optimistic scenario of 90% survivorship per decade, about 60% of current aspen trees on the plateau will still be present (and 50 years older) in 2060. Older age class aspen trees would actually be more common than in 2010. The 170-180- year cohort would have the greatest density, with about 10 trees/ha across the Plateau. The 130-140- year cohort would have 9 trees/ha, and 50-80-year cohorts would each have between 3 and 8 trees/ha.

A survivorship of 80% may be more likely, based on the cohort structure of aspen on the Kaibab Plateau (Binkley et al. 2006). After 50 years, only one-third of current trees would be alive. As in the 90% survival rate scenario, the highest survival rate is in age class 170- 180 with less number of trees/ ha in this survival scenario: only 5 trees/ ha for this age class. For other age classes, the expected number of trees/ ha for each would be around half the number of trees / ha for the same age class in the 90% survival scenario.

A 70% survivorship would match the cohort pattern reported for Rocky Mountain National Park (Binkley 2008), and fewer than 20% of current aspens would survive for 50 years. The total number of aspen on the Plateau would be lower in all age classes, and again the 170-180- year cohort would dominate the age classes.

DISCUSSION

Almost half the Plateau's aspen trees established soon after widespread fires in the late 1800s. Time of establishment for aspen on the Plateau is similar to that reported in Rocky Mountain National Park and in the surrounding Roosevelt National Forest (Suzuki et al. 1999). Similar patterns and time of establishment were reported in Yellowstone National Park that suggest almost 85% of pure aspen stands were established between 1871 and 1920 and only small percent of pure aspen were established after that range (Larsen and Ripple 2001). Healthy aspen forest in age classes between 70- 140 years present around 56% of total aspens on the Plateau, and only few trees that exceed 140 years exist on the Plateau in both pure and mixed stands and present only 2% of the total aspen cover.

The low number of trees older than 140 years on the Plateau underscores the likely consequences of limited survivorship, especially if coupled with low recruitment into younger age classes. The ability of older aspen trees to survive for longer time and survive ecological challenges is unpredictable, and the risk of being replaced by other aspens or shifting dominance to conifers is high. Recent studies of aspens on the Uncompahgre Plateau suggest that the change of aspen cover on the plateau might be the start of shifting dominance between aspen and conifers (Romme et al. 2001, Manier and Laven 2002, Smith and Smith 2005). The cause of this reduction of older aspen trees might be as a result of not so many aspen trees survived the major fire in 1879 which burned most of the Uncompahgre lands including aspen areas.

The three scenarios I developed in this study were based on the survival rate that aspen trees show during the next five decades, and all of these scenarios suggest an appreciable reduction in aspen cover on the Plateau given the current growth conditions. The likely reduction in the number of aspen trees per hectare will vary from 40% in the most optimistic scenario (90% survival/decade) to about 80% in the third scenario (70% survival/decade) which is the less fortune case scenario in this study but might not be the worst expected scenario for aspen forests on the Plateau (Mueggler 1994, Binkley 2008). The reduction in aspen basal area on the Plateau may not be as significant as in the number of aspen trees per hectare since many young aspen trees, 80 years old or less, are expected to add more biomass to the total aspen basal area in the next five decades. The variation from 90% to 70% survival rate each decade depends on how old aspen forests will tolerate change in their cover and survive site and environmental factors that might affect their distribution across the Plateau. In the absence of disturbances that alter aspen forests and encourage their growth, current ecological elements such as sudden aspen decline, replacement of conifers to current aspen forests, heavy browsing of young aspen suckers by cattle and wildlife, and disease outbreaks will be crucial factors in reducing aspen cover on the Plateau.

Recruitment of suckers into trees over the next 50 years was not included in the three survivorship scenarios, and their chance to become a part of future aspen forests will depend on how they will tolerate competition with neighbor trees and survive browsing by wildlife and cattle during early growth stages. Future studies to evaluate aspen regeneration on the Plateau and monitoring change in aspen forests through time are highly recommended, and management actions are required to help maintain healthy aspen forests especially in mixed conifer- aspen stands.

Table 1: Forest dominant species and basal area in 51 random locations with aspen trees encountered in one or more of the 9 prism plots in each location.

Forest dominant species	**Number of stands**	**Mean BA m^2/ ha**	**Percent of stand %**
Aspen	51	10.2	45
Ponderosa pine	26	4.8	21
Douglas fir	10	0.9	4
Spruce	19	1.8	8
Subalpine fir	28	3.7	16
Gamble oak	21	1.4	6

Note: Spruce forest species include Engelmann spruce- *Picea engelmannii*, and blue spruce- *Picea pungens*.

Table 2: The distribution of sampled aspen locations on the Uncompahgre Plateau based on UTM coordinate system. The table Shows the number of sampled aspen trees in each location, oldest and youngest tree encountered, and the total aspen basal area

UTM Coordinates range for the UP	Number of sampled aspen locations	Number of sampled aspen trees	Age of oldest aspen tree (years)	Age of youngest aspen tree (years)	Aspen basal area (m^2/ha)
N^0 38.72458- 38.66536 E^0 -108.7651- -108.6441	9	171	141	12	4.8
N^0 38.66535- 38.60543 E^0 -108.673- -108.5246	3	136	169	21	11.6
N^0 38.60542- 38.54620 E^0 -108.7210- -108.6817	1	2	40	35	0.5
N^0 38.60542- 38.48697 E^0 -108.6808- -108.4095	9	329	221	9	14.3
N^0 38.48696- 38.42774 E^0 -108.5108- -108.2917	8	257	219	35	11.2
N^0 38.36851- 38.42775 E^0 -108.2954- -108.2497	1	67	183	30	17.1
N^0 38.3685- 38.30928 E^0 -108.3456- -1081277	8	334	230	26	13.1
N^0 38.309279- 38.25006 E^0-108.1429- -107. 9587	7	279	228	35	10.2
$N^0$38.250059- 38.190839 E^0 -108.031- -108. 0143	3	165	190	40	17
$N^0$38.196838- 38.131618 E^0 -108.0729- -108.0321	1	16	272	81	2

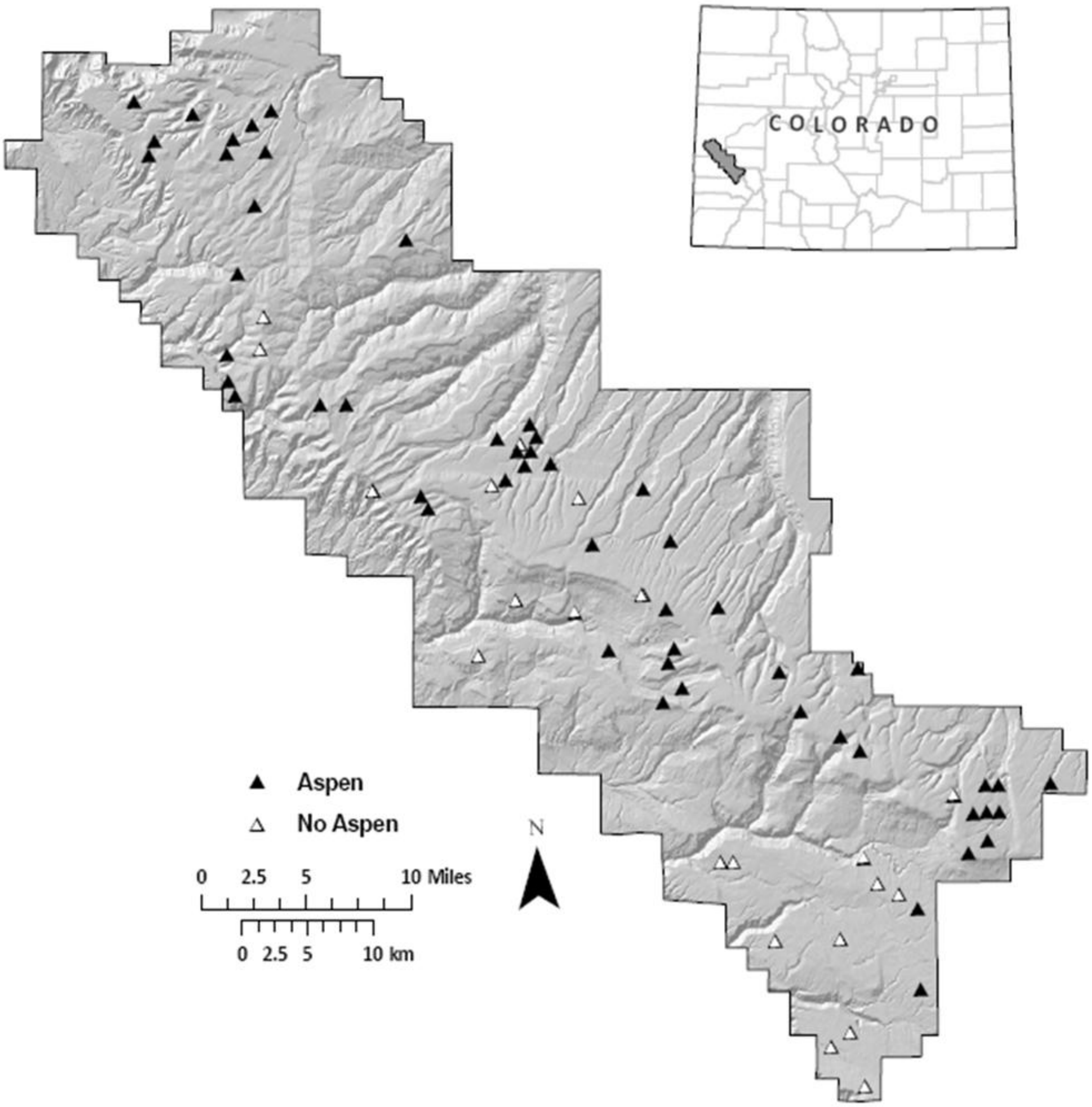

Figure 1: Map shows the study area: Uncompahgre National Forest land with aspen sampling triangles shown across the plateau. Aspen trees occur in 51 sites (solid triangles), and 12 sites (white triangles) do not have mature aspen trees in their range, and occur mostly in southern parts of the Plateau at lower elevations (Binkley 2011).

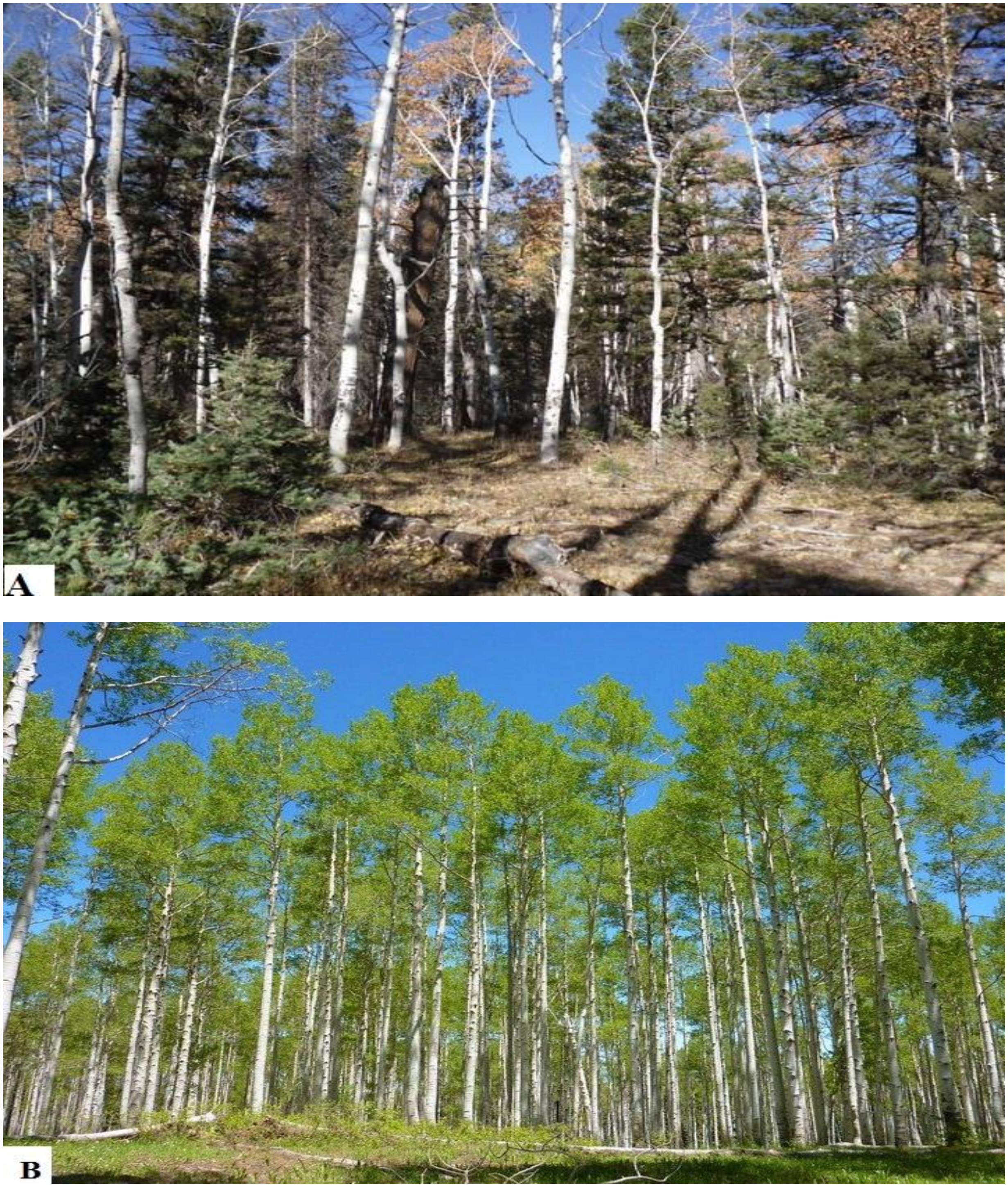

Figure 2: **A**) Mixed conifer-aspen stands present 92% of aspen forests on the Plateau, and **B**) pure aspen stands present 8% of total aspen forests. Photos were taken during summer 2010 at the Uncompahgre Plateau.

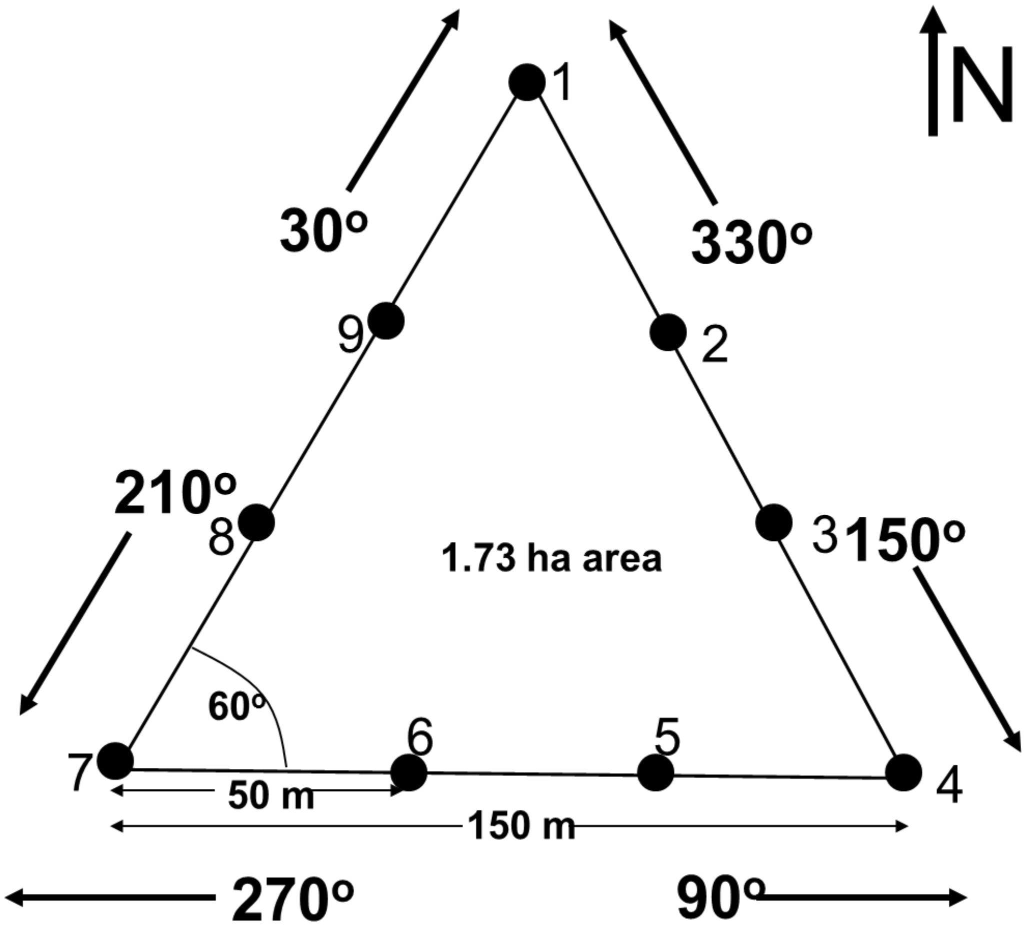

Figure 3: Aspen triangles design which are used in all of the 63 sampling locations. 9 plots of sampling at each triangle with 50 m distance between each two plots (Binkley 2011).

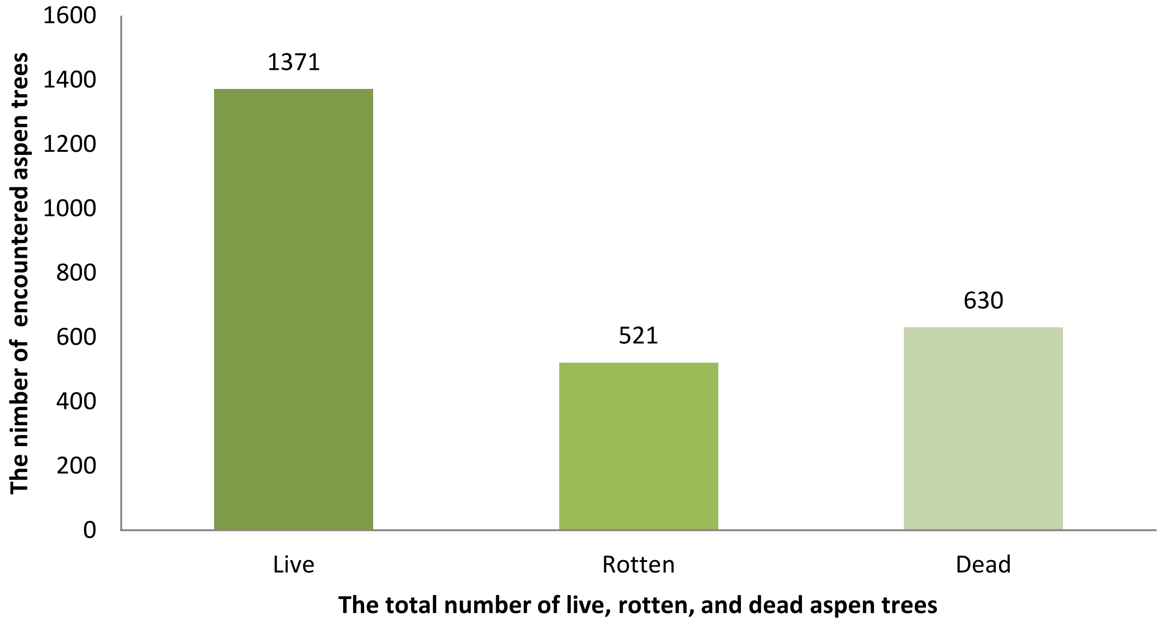

Figure 4: The number of live, rotten, and dead aspen trees on the plateau to the total number of aspen trees included in this study. Live trees present 54% of the total aspen trees, and 25% for dead trees, and 21% for rotten trees.

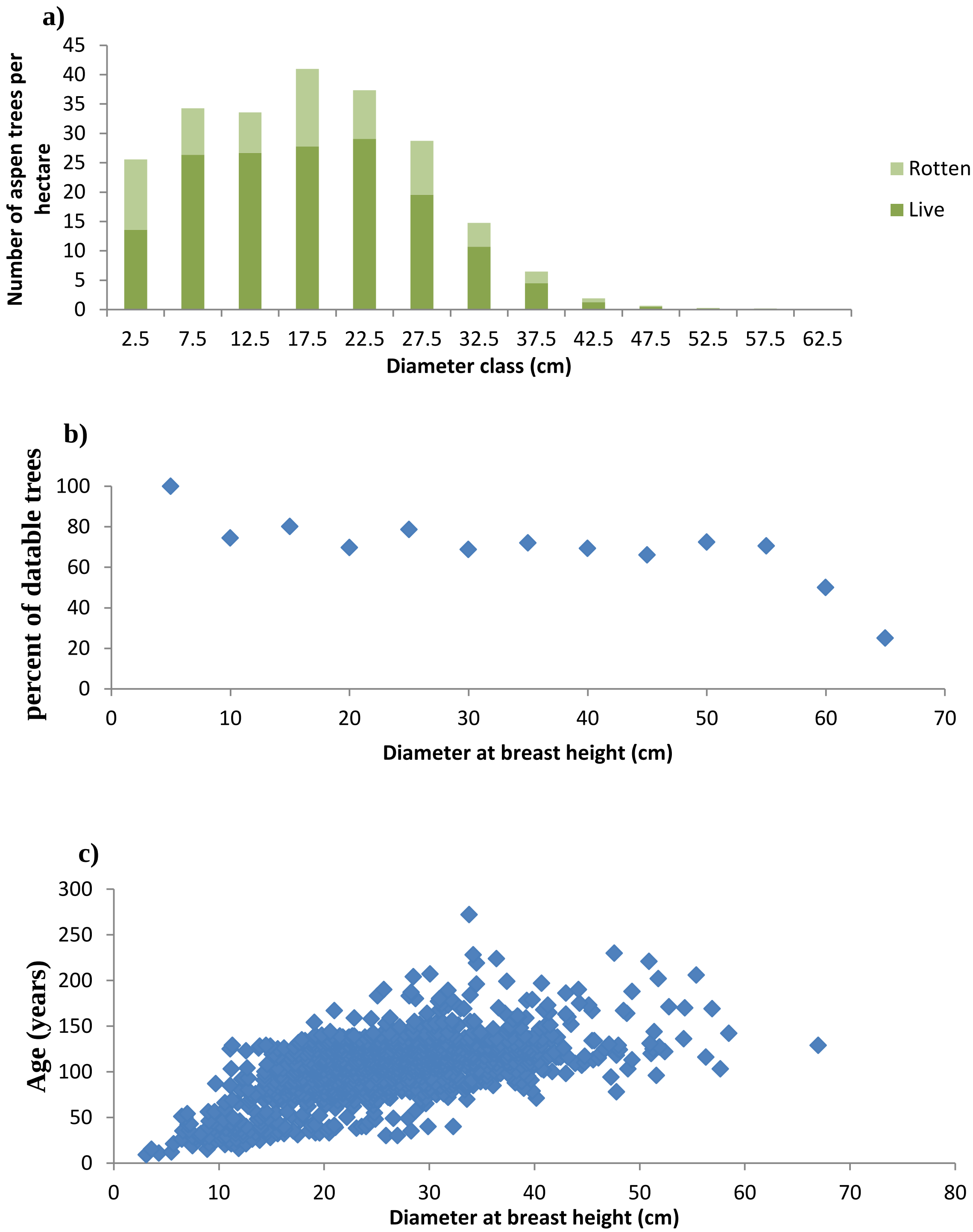

Figure 5: **a)** Diameter at breast height distribution for all aspen trees. More small aspen trees exist and very few aspens larger than 40 cm exist on the Plateau. **b)** The percent of datable aspen trees declined with increasing age to less than 50% for trees larger than 55 cm. **c)** Age-dbh relationship to estimate age for undatable aspen cores (r^2=0.3315, p-value < 0.001).

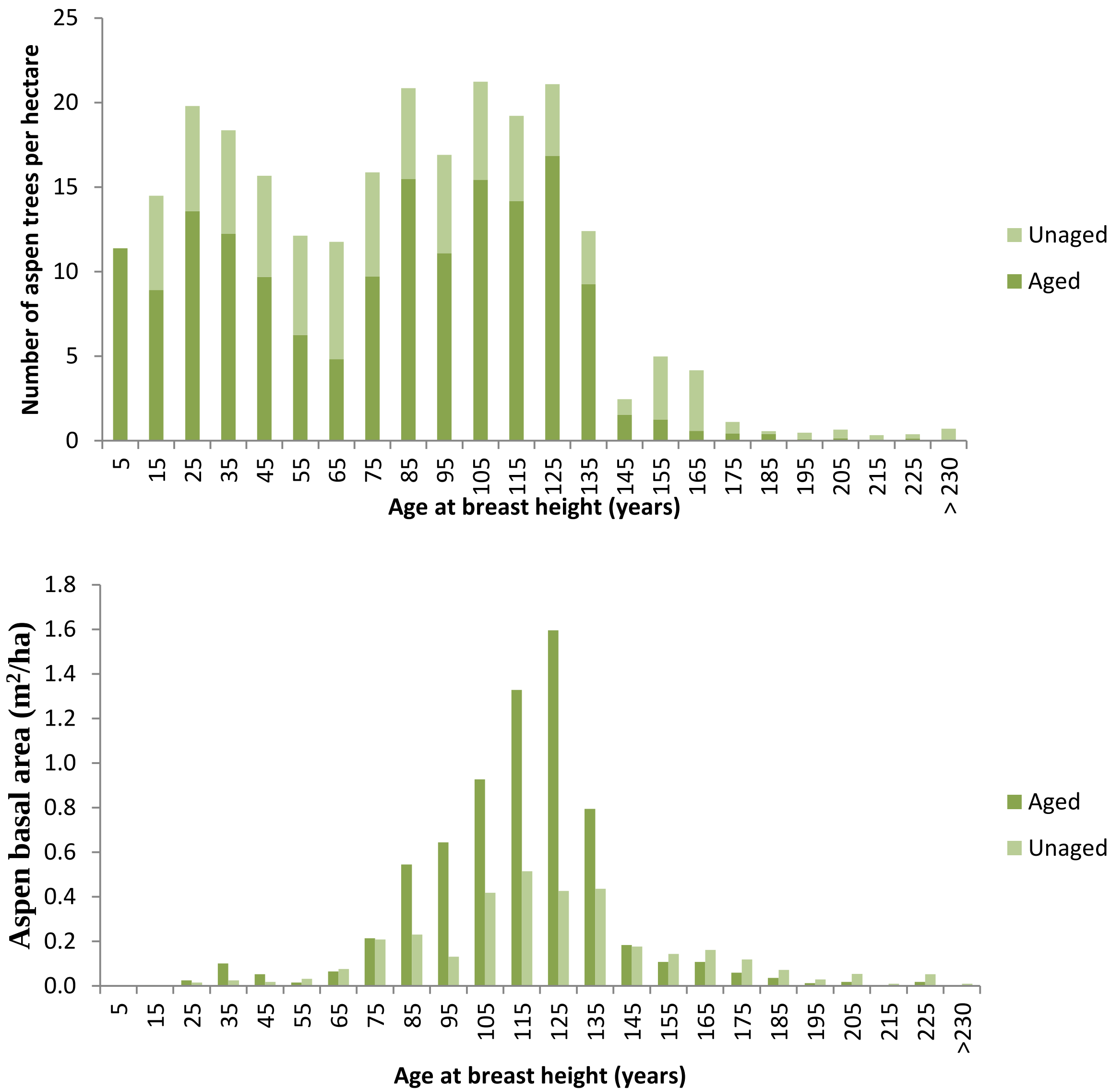

Figure 6: Age distribution for aspen trees on the Uncompahgre Plateau. Aged trees (dark green) show that the majority of aspen trees on the Plateau occur in age between 100-140 years. Unaged trees (light green) were estimated based on age-dbh relationship and show gradual increase in their number with increasing age, and age pattern is similar for both dated and undated (estimated) aspen trees.

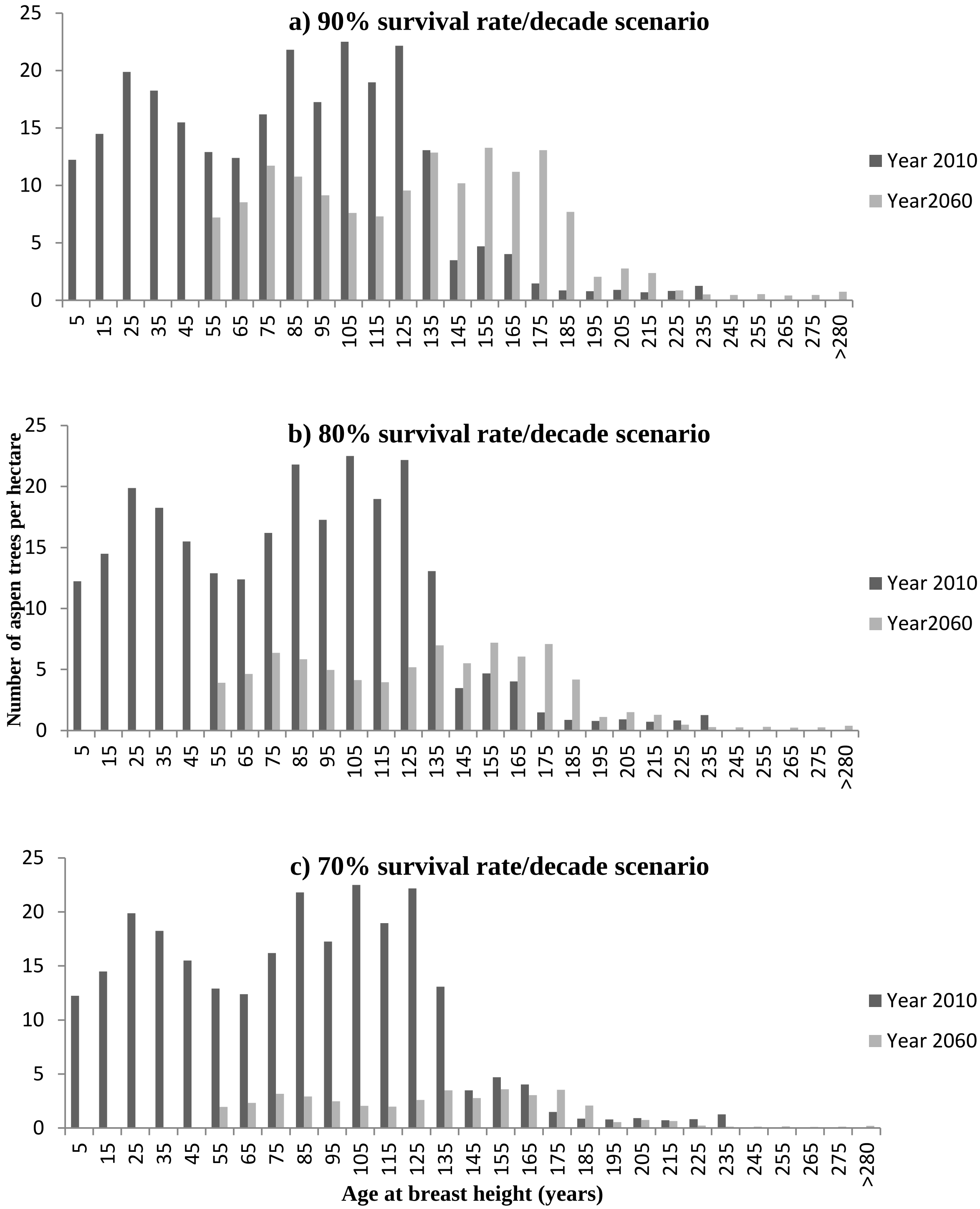

Figure 7: Expected reduction in aspen cover on the Uncompahgre Plateau in the next 50 years. a) 59% survival expected in 90% survival/decade scenario. b) 32% survival expected in 80% survival/ decade scenario. c) 16% survival expected in 70% survival/ decade scenario.

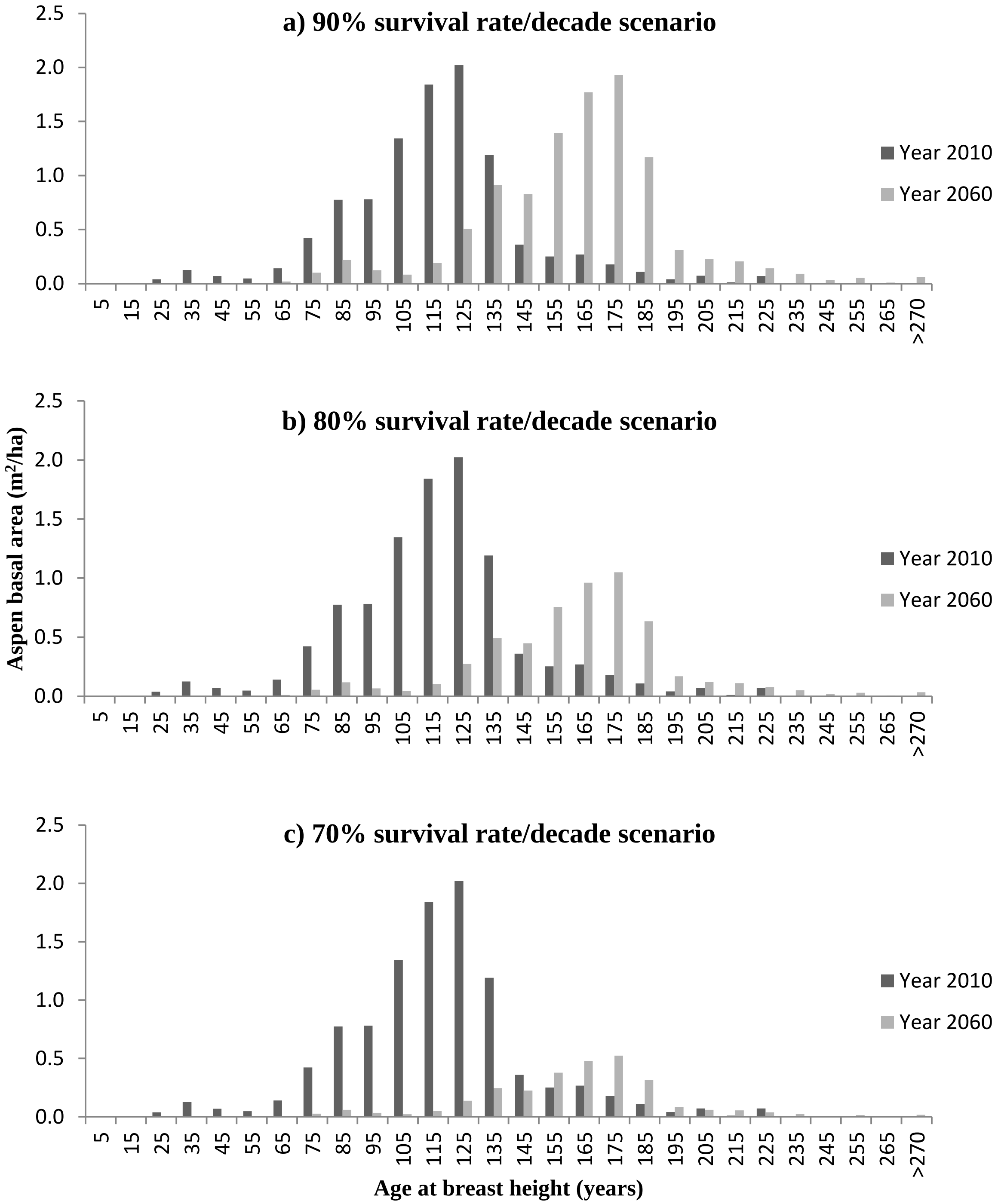

Figure 8: Expected reduction in current aspen basal area on the Uncompahgre Plateau in the next 50 years. a) 59% survival expected in 90% survival/decade scenario. b) 32% survival expected in 80% survival/ decade scenario. c) 16% survival expected in 70% survival/ decade scenario.

REFERENCES

Anderegg, W.R.L., J.A. Berry, D.D. Smith, J.S. Sperry, L.D.L. Anderegg, and C.B. Field. 2011. The roles of hydraulic and carbon stress in widespread climate- induced forests die-off. PNAS (2012). Vol.109. No 1. Pages 233-237.

Bartos, D.L. 2001. Landscape dynamics of aspen and conifer forest. Rocky Mountain Research Station, USDA Forest Service, Logan, UT., 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.

Binkley, D., M.M. Moore, W.H. Romme, and P.M. Brown. 2006. Was Aldo Leopold right about the Kaibab deer herd? Ecosystems (2006) 9: 227–241.

Binkley, D. 2008. Age distribution of aspen in Rocky Mountain National Park, USA. Forest Ecology and Management 255:797-802.

Binkley, D. 2011. How old are aspens on the Uncompahgre Plateau? Colorado Forest Restoration Institute. Project Report.

Brown, P.M., and Shepperd, W.D., 2003. Preliminary Fire History in Ponderosa Pine Forests of the Uncompahgre Plateau. Project report. Rocky Mountain Experiment Station. Fort Collins, CO, 7pp.

Ciesla, W.M. 2008. Aspen decline and other factors affecting the health of aspen on the Colorado Front Range [Poster]. In: Sudden aspen decline (SAD) meeting. Fort Collins, CO. http://www.aspensite.org/. (15 March 2010).

Clendenen, G.W. 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.

Daubenmire, R.F. 1943. Vegetational zonation in the Rocky Mountains. Botanical Review, Vol.9, No. 6, pp 325-393.

DeByle, N.V. and Winokur, R.P. (eds) (1985) Aspen: ecology and management in the western United States. United States Forest Service General Technical Report RM-119, USDA Forest Service, Fort Collins, CO.

Dieni, J.S. and Anderson, S.H. 1997. Ecology and management of aspen forests in Wyoming; literature review and bibliography. Aspen Bibliography. Paper 1539.

Duncan, R.P. 1989. An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrycarpus dacrydioides*). New Zealand National Science 16: 31-37.

Hess, K., and R. R. Alexander. 1986. Forest vegetation of the Arapaho and Roosevelt National Forests in central Colorado: A habitat type classification. Research Paper RM-266. Fort Collins, CO: Rocky Mountain Forest and Range Experiment Station. Pp 48.

Hogg, E.H.T., Brandt, J.P., Michaelian, M., 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Can. J. Forest Res. 38, 1373-1384.

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.

Johnston, B.C. 2001. Multiple factors affect aspen regeneration on The Uncompahgre Plateau, West and Central Colorado – USDA Forest Service Proceeding RMRS-P-18. 2001.

Kay, C.E. 1993. Aspen seedlings in recently burned areas of Grand Teton a Yellowstone National Parks. Northwest Science, 67, 94–104.

Knight, D.H. 2001. Summary: Aspen decline in the west. USDA Forest Service Rocky Mountain Forest and Range Experiment Station. Symposium Proceeding RMRS- P- 18.

Kulakowski, D.,T.T. Veblen., and S.Drinkwater., 2004. The persistence of quaking aspen (Populus tremuloides) in the Grand Mesa Area, Colorado. The Ecological Society of America, 14(5), 2004, pp. 1603- 1614.

Manier, D.J., and R.D. Laven. 2002. Change 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.

Mueggler, W.F. 1994. Sixty years of change in tree numbers and basal area in Central Utah aspen stands. All U.S. Government Documents (Utah Regional Depository). Paper 356. http://digitalcommons.usu.edu/govdocs/356.

Little, E. L Jr. 1971. Atlas of United States trees: Vol. 1. Conifers and important hardwoods. U.S. Department of Agriculture, Forest Service, Miscellaneous Publication 1146, 9 p. +202 maps. Washington, DC.

McDonough, W.T. 1985. Sexual reproduction, seeds and seedlings. Aspen: ecology and management in the western United States (ed. by N.V. DeByle and R.P. Winokur). pp. 25–28. United States Forest Service General Technical Report RM-119, USDA Forest Service, Fort Collins, CO.

Mitton, J.B., and Grant, M.C. 1996. Genetic variation and the natural history of quaking aspen. Bioscience, 46, 25–31.

Packard, F.M. 1947. A survey of the beaver population of Rocky Mountain National Park, Colorado – Journal of Mammalogy 1947, Vol. 28, No. 3, pages 219 – 227.

R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Ripple, W.J., E.J. Larsen, R.A. Renkin., and D.W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biological Conservation. Volume 102, Issue 3, December 2001, pages 227- 234.

Romme, W.H., M.G. Turner, R.H. Gardner, W.W. Hargrove, G.A. Tuskan, D.G. Despain, and, R.A. Renkin. 1997. A rare episode of sexual reproduction in aspen (Populus tremuloides Michx.). Following the 1988 Yellowstone fires. Natural Areas Journal, 17, 17–25.

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, Proceeding RMRS-P-18. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO: 243-259.

Shepperd, W.D. 1990. A classification of quaking aspen in the central Rocky Mountains based on growth and stand characteristics. Western Journal of Applied Forestry, 5, 69–75.

Shepperd, W.D., D.L. Bartos., and S.A. Mata. 2001. Above- and below- ground effects of aspen clonal regeneration and succession to conifers. Can. J. For. Res. 31: 739-745 (2001).

Smith, A.E. 2004. Aspen and conifer interaction over a twenty- year period on the Uncompahgre Plateau, Colorado. M.Sc. Thesis. Department of Forest, Rangeland, and Watershed Stewardship. Colorado State University. Ft.Collins, CO.

Smith, A.E, and F.W. Smith. 2005. Twenty- year change in aspen dominance in pure aspen and mixed aspen/conifer stands on the Uncompahgre Plateau, Colorado, USA - Forest Ecology and Management vol 213, Issues 1-3, 18 July 2005, pages 338- 348.

Stokes, M. A, and T. L. Smiley. 1968. An Introduction to Tree Ring Dating. University of Chicago Press, Chicago.

Strand, E.K., L.A. Vierling, S.C. Bunting, and P.E. Gessler. 2009. Quantifying successional rates in western aspen woodlands: current conditions, future predictions – Forest Ecology and Management. Vol. 257, issue 8, 31 March 2009, pages 1705- 1715.

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.

Turchi, G.M., P.L. Kennedy, D. Urban, and D. Hein. 1995. Bird species richness in relation to isolation of aspen habitats. The Wilson Bulletin. Vol. 107, No. 3, pp 463-474.

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

White, C.A., C.E. Olmsted, and C.E. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain National Parks of North America – Wildlife Society Bulletin 1998, Vol. 26, No. 3, pp 449 – 462.

White, C.A., M.C. Feller, and S. Bayley. 2003. Predation risk and the functional response of elk-aspen herbivory. Forest Ecology and Management. Volume 181, Issues 1-2, 3 August 2003, pages 77- 97.

Winternitz, B.L. 1980. Birds in aspen. Aspen Bibliography. pp 4492. Source: Intermountain Forest and Range Experiment Station, pp 247- 257.

Worrall, J., L. Egeland, T. Eager, R. Mask, E. Johnson, P. Kemp, and W. Shepperd. 2007. Sudden aspen decline in southwest Colorado: site and stand factors and hypothesis on etiology. Western International Forest Disease Work Conference, 55: 1-4.

Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., Shepperd, W.D., 2008. Rapid mortality of Populus tremuloides in southwestern Colorado, USA. Forest Ecology and Management. 255, 686-696.

Worrall, J.J., S.B. Marchetti, L. Egeland, R.A. Mask, T. Eager, and B. Howell. 2010. Effect and etiology of sudden aspen decline in southwestern Colorado, USA. Forest Ecology and Management. 260 (2010) 638–648.