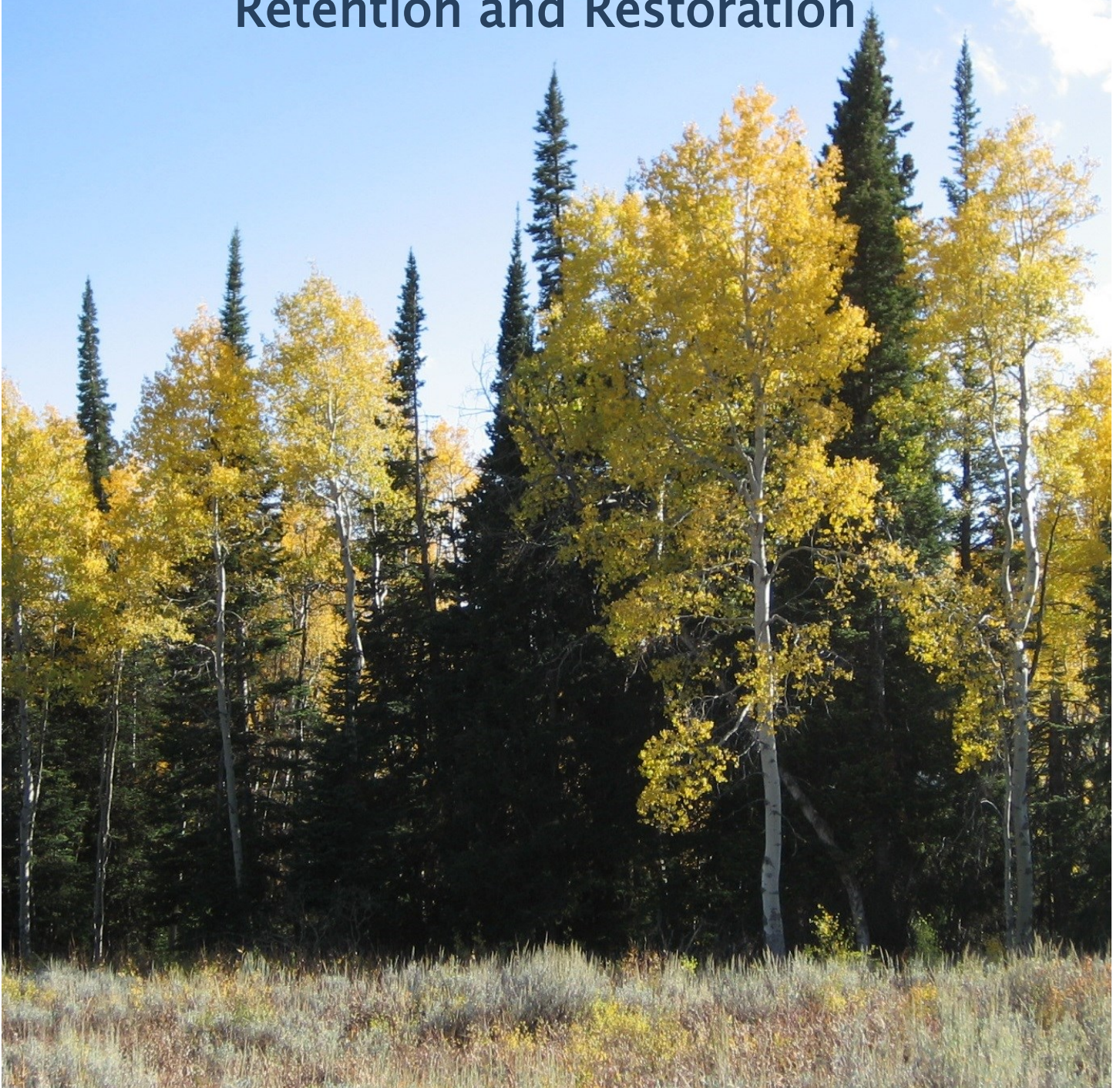


Quaking Aspen in the Northern Rockies Retention and Restoration



University
of Idaho



Quaking Aspen in the Northern Rockies: Retention and Restoration

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On the cover —

Quaking aspen (*Populus tremuloides*) growing with subalpine fir (*Abies lasiocarpa*) in the Teton National Forest. Photo courtesy of Diane Abendroth, National Park Service.

Introduction

Quaking aspen (*Populus tremuloides*) is the most widely distributed native North American tree species and is particularly abundant in the landscapes of the Intermountain West (Fowells 1965; Little 1971; Perala 1990). Quaking aspen, hereafter called aspen, is found across a range of elevations and in a variety of habitats, from sagebrush-steppe to mixed-conifer forests and subalpine meadow ecosystems (Perala 1991). Visually striking and therefore important to people, aspen is ecologically important as one of the only deciduous trees in the Intermountain West (Figure 1). Aspen communities support a large number and diversity of understory and overstory plant species (Anderegg et al. 2012a) and provide habitat for many birds and small mammals (Loose and Anderson 1995; Kalcounis and Brigham 1998; Campbell and Bartos 2001). In some national parks, aspen is one of the 14 “vital signs” monitored for ecosystem health (Strand et al. 2015). Aspen dieback and mortality over the past 150 years is a concern across the western US. However, data are mixed as to the nature and cause of this decline, which vary spatially (Kulakowski et al. 2013b). Studies at fine spatial scales have indicated nearly 100% decline in localized areas (e.g. Worrall et al. 2008), whereas analyses at coarse spatial scales across large areas have shown stable populations (Zier and Baker 2006) or only small declines (~10%) in the Northern Rockies (Brown et al. 2006). Reflecting concerns about aspen decline, many recent studies have been undertaken across the range of the species to restore the abundance or stabilize existing aspen populations. This review provides background necessary to understand site-specific aspen decline causes and to inform restoration planning.

Specific objectives of this review are to address the current status and future outlook of aspen across a range of ecosystems in the US Northern Rockies. Specifically, we aim to answer the following questions:

- 1) Is aspen declining in the Northern Rockies, and if so what are the underlying causes?
- 2) Where should aspen regeneration be prioritized?
- 3) What factors influence successful restoration?

To address these questions, we reviewed the scientific literature focusing on aspen in the US Northern Rockies region and studies published after the reviews by Morelli and Carr 2011, Kulakowski et al. 2013b, Rogers et al. 2014, and Forest Ecology and Management Special Issue (2013, Vol. 299).

Aspen functional types and regeneration

Though variations exist, two dominant functional aspen community types are commonly identified: stable and seral (Rogers et al. 2014; see Figure 2). Stable aspen functional forest types remain as aspen communities through time. These include aspen parklands, terrain-isolated aspen stands, and aspect- or elevation-limited aspen communities. A seral aspen community begins as an aspen community, but over time is replaced by conifer species. The seral aspen type is often seen in montane and boreal forests. For effective restoration, identifying the functional type and associated species is important because seral and stable aspen stands occupy different landscapes, have different disturbance histories, and often respond differently to changing conditions and disturbance events (Rogers et al. 2014). Subdivisions or “community aspen types” within these two dominant functional types, which depend on location and associated species, are described in Table 1.



Figure 1. Aspen intermixed with sagebrush/grassland in a foothills location. Aspen is growing where there is sufficient moisture from springs and winter snowdrifts. Photo courtesy of Diane Abendroth, National Parks Service (NPS).

Aspen regenerates by both seed and root sprouting, but clonal root sprouting is the more common mode of regeneration (Turner et al. 2003; Mock et al. 2008). Individual aspen stems are short-lived, normally living 100-150 years, but aspen clones are long-lived (Shepperd et al. 2001). Ideal climatic conditions for widespread germination are rare but have occurred sporadically since the last glaciation (Mock et al. 2008). Many clones across the US date back to the last glaciation (Turner et al. 2003), which highlights the pre-

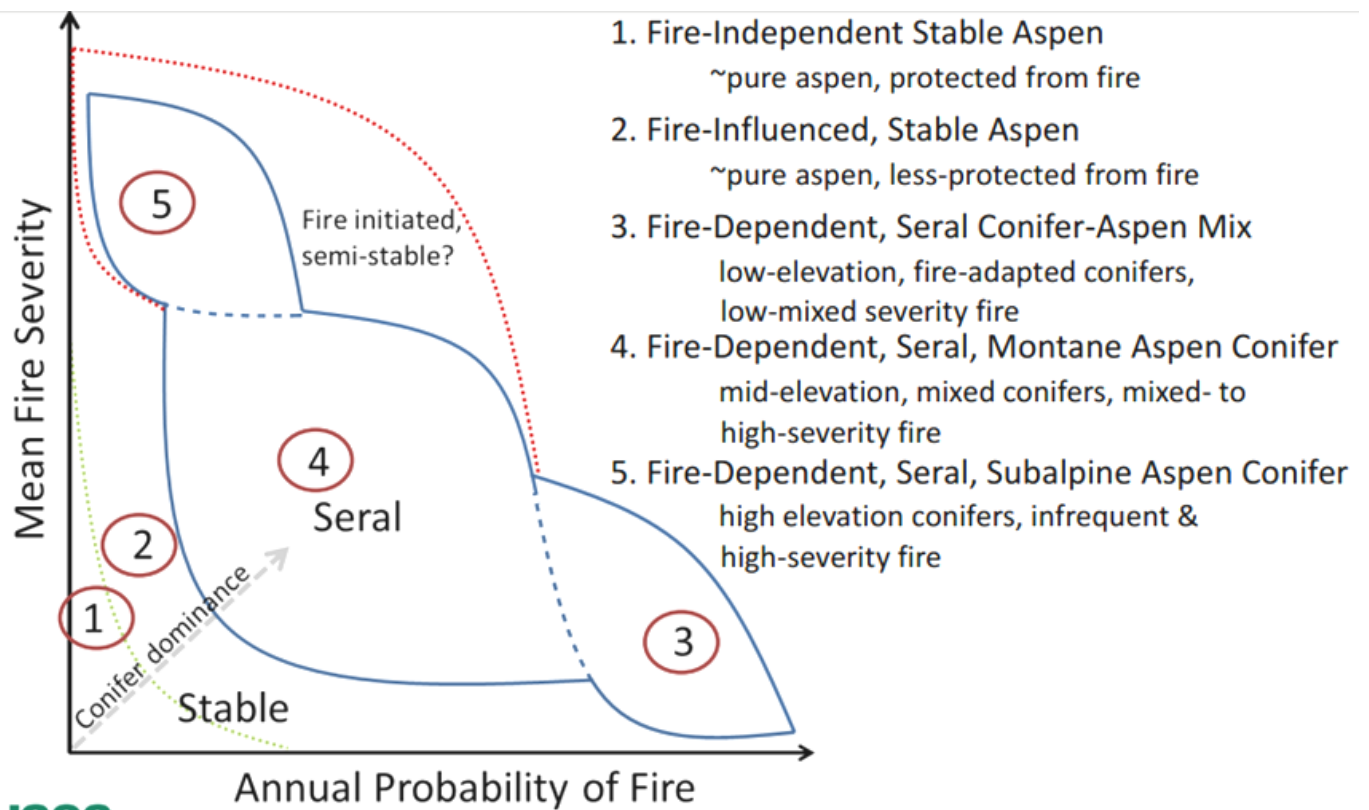


Figure 2. Fire relationships for aspen functional types with *probability of a fire* in each functional type on the x axis and the *mean fire severity* (also referred to as burn severity) on the y-axis. Stable aspen communities are much less likely to burn and generally burn at lower severity when a fire occurs. Seral communities burn under a wide range of frequencies and severities, which are largely determined by location and species associations (From Shinneman et al. 2013).

Table 1. Northern Rockies aspen community or stand types by location, associated species, fire relationships, and functional type. Adapted from Rogers et al. (2014); Shepperd et al. (2006); Shinneman et al. (2013).

Community or Stand Type	Environmental Preference	Common Associated Species in the US Northern Rockies	Fire Relationship	Functional Type
Riparian	Permanent or seasonal waterway	Mixed-conifer forests, deciduous/riparian woodlands (<i>Abies magnifica</i> , <i>Picea engelmannii</i> , <i>P. pungens</i> , <i>Populus angustifolia</i>)	Fire dependent & Fire independent	Seral/stable
Meadow fringe	Dry meadows	Low-elevation, open forests (<i>Pinus ponderosa</i> , <i>Pseudotsuga menziesii</i> , <i>Juniperus occidentalis</i>)	Fire dependent	Seral
Upland aspen/conifer (montane)	Away from streams	Mixed-conifer forests (<i>Abies lasiocarpa</i> , <i>A. magnifica</i> , <i>Juniperus occidentalis</i> , <i>Picea engelmannii</i> , <i>Pinus contorta</i> , <i>P. ponderosa</i> , <i>Pseudotsuga menziesii</i>)	Fire dependent	Seral
Upland pure aspen	Variable site conditions	Aspen stands with little to no conifer encroachment	Influenced/Independent	Stable
Snow pockets	Areas of snow accumulation	Grasslands/shrublands with isolated aspen pockets (<i>Artemisia tridentata</i>)	Influenced/Independent	Stable

dominance of clonal regeneration in the Rocky Mountains. However, when the right moisture and soil conditions coincide with low levels of competition, rare establishment from seed has been documented (Turner et al. 2003, Mock et al. 2008). This is discussed in the Yellowstone National Park Case Study in this review.

Fire regimes

Given the variety of occupied sites, diversity of associated plant communities, and large geographic range of aspen, it is difficult to identify a single dominant fire regime or even a few most prevalent fire regimes (Shinneman et al. 2013). However, several statements apply to all aspen woodlands, regardless of their functional type. First, if a fire occurs within, or spreads into aspen stands, overstory aspen tree mortality is likely to occur regardless of fire intensity or flame height. Second, aspen stands are generally not highly flammable, so fires typically burn with low rates of spread and low intensities or fail to burn even when surrounding forests or shrublands burn. Third, where aspen does burn, the thin bark and low heat tolerance of aspen stems often results in nearly 100% aboveground aspen mortality. As a result, few trees survive with fire scars. Finally, aspen often sprouts prolifically following fires, though this may not be evident where rates of herbivory are high.



Figure 3. Prolific aspen sprouting a few years after an unplanned wildfire in mixed aspen and conifer forest (lodgepole pine, subalpine fir). Photo courtesy of Jill Randall, Wyoming Game and Fish Department.

In the past decade, multiple researchers have attempted to discern the effect of fire on the various functional aspen community types. Although there are glaringly few fire studies focused on pure aspen communities, researchers now recognize that fire potential and burn severity and effects vary between aspen community types. Some func-

tional types are fire independent, where fire is unnecessary for regeneration needed for stand replacement, while other functional types need periodic fire to retain aspen within the community assemblages. Stable aspen communities are much less likely to burn and generally burn at low severity if a fire occurs, whereas seral communities burn under a wide range of frequencies and severities, and fire potential and effects are dependent on associated species and location. The various functional aspen types and their relationship to fire are illustrated in Figure 2 from Shinneman et al. (2013).

Fire activity in aspen has been influenced by fire suppression, land use, and, more recently, climate change. As few studies focus specifically on aspen, most of this information is inferred from studies primarily focused on nearby conifer forests. Further, fire effects vary across the broad mix of associated species, elevations, sites occupied, and cover types within and surrounding aspen. Aspen at lower elevations and in more dry community types has likely seen an increase in burn severity from historical to current fire regimes, while aspen at wetter and higher elevation sites has likely not experienced a dramatic change from the historical fire regimes (Fule et al. 2003; Westerling et al. 2006; Littell et al. 2009).

Causes of aspen mortality

Aspen mortality and dieback on the landscape is often influenced by a combination of factors. Aspen is adapted to disturbances, but it often succumbs to mortality when disturbances are severe or there are multiple interacting disturbances. Ungulate browsing, lack of fire, drought, and climate change are considered the primary drivers of aspen decline and die off.

Excessive browsing on immature stems by ungulates is a common cause of aspen decline. Intensive, repeated browsing by cattle, sheep, elk, and deer stunts aspen growth and often kills aspen sprouts and prevents recruitment of new stems into the overstory (Foster et al. 2007; Kulakowski et al. 2013b; Seager et al. 2013; Beschta et al. 2014). Repeated browsing can lead to a loss of stable aspen community types by inhibiting growth of new aspen stems, which results in aging stands (Seager et al. 2013; Rogers and Mittanck 2014) and can mean sharp declines in overstory aspen density (Kimble et al. 2011). Because aspen has fairly short-lived stems, the loss of young stems can have a large impact on the community assemblage in a short time period (Seager et al. 2013). Similarly, herbivory can lead to ear-



Figure 4. Browsed aspen in Grand Teton National Park 10 years after prescribed fire in an area with year-round elk use. Photo courtesy of Diane Abendroth, NPS.

lier onset of conifer encroachment in seral aspen communities (Seager et al. 2013). The ungulate-aspen relationship is so strong that some have linked large elk populations to lower aspen recruitment (Rogers et al. 2015).

‘Sudden aspen decline’ (SAD) is a term commonly used to describe rapid and synchronous branch dieback, crown thinning, and mortality of aspen stems over multiple years on a landscape scale in the absence of stem resprouting or regeneration (Worrall et al. 2010; Anderegg and Anderegg 2013). Sometimes entire clones or the complete underground network of roots connecting above-ground stems can be lost to SAD. Causes of SAD are wide ranging and include climate changes, multi-year droughts, seasonal droughts, and/or insect or pathogen outbreaks (Steed and Kearns 2010). By 2008, SAD impacted 220,000 ha or 17% of the aspen cover type in Colorado (Worrall et al. 2010), while aspen stands in Utah, Nevada, and western Wyoming experienced as much as 31% dieback (Morelli and Carr 2011). Additional large and recent SAD events have been observed in Arizona (Fairweather et al. 2008; Zegler et al. 2012) and across the southwestern US (Morelli and Carr 2011). Though some localized SAD events were reported in the Northern Rockies and southern Canada (Bartos and Campbell 1998; Frey et al. 2004; Hogg et al. 2008), these events have been larger and more recent in the southern aspen range (Morelli and Carr 2011).

Both SAD and more gradual decline are often attributed to

fire and climate change, but because fire histories and patterns of regeneration differ between the seral and stable functional aspen types, these contributors to decline vary by functional type. Stable aspen communities, which are largely fire resistant, experience tree self-replacement without disturbance and historically burned only under extreme fire weather conditions (Kurzel et al. 2007; Shinneman et al. 2013). Historically, regeneration in seral type communities was largely driven by large disturbances. Today, fire suppression and conifer competition are major causes of change in aspen populations in seral functional aspen stands (e.g. DeByle et al. 1987; Kay 2001; Kulakowski et al. 2006; Strand et al. 2009).

Fire suppression across the western US has resulted in the conversion of many seral aspen stands to conifer-dominated forests through gradual infilling (Rogers and Mittanck 2014). However, it is important to note that while fire suppression and land use have changed the fire frequency in many dry forests, there have been fewer effects of fire suppression on the fire frequency in cold, high-elevation forests where the intervals between fires were historically much longer (Schoennagel et al. 2004). In seral aspen stands, competition between aspen and conifers negatively impacts aspen growth and increases overstory stem mortality more in older than in younger stands (Kaye et al. 2005; Calder and St. Clair 2012). Seral aspen stands can be replaced by conifers in the absence of disturbances as aspen stems age, but disturbances help stands resist conifer dominance by increasing the abundance of young stems in the absence of heavy herbivory.



Figure 5. Conifer encroachment in an aspen stand as a result of a long fire-return interval on the BTNF. Photo courtesy of Diane Abendroth, NPS.

Climate change, through changes in water availability and drought, is influencing aspen decline and stem mortality (Anderegg and Anderegg 2013; Rogers and Mittanck 2014), and geographic shifts to remain within optimal climate envelopes are likely altering aspen growth patterns (Rehfeldt et al. 2009; Worrall et al. 2013). Climate envelopes describe the climatic environment where a species can survive and grow, and can include seasonal or annual measures of precipitation, temperature, and drought (e.g., Worrall et al. 2013). Given the large geographical and elevational range of aspen, the climate envelope is variable across the species range (Greer et al. 2016); however, individual clones are subject to mortality as changing climate alters site-specific climatic conditions. Dieback has been observed for drought-stressed aspen on many sites across the western US (Rogers et al. 2010; Ganey and Vojta 2011; Hanna and Kulakowski 2012; Huang and Anderegg 2012). Though it is postulated that aspen and other tree species are most at risk in transitional zones or at the edge of their geographic ranges (Ganey and Vojta 2011; Worrall et al. 2013), aspen die-back has been observed across the range of the species, not only in climatically marginal areas (Allen et al. 2010; Hanna and Kulakowski 2012). Climate change is expected to continue to impact aspen and result in continued mortality (Rehfeldt et al. 2006, 2009; Bell et al. 2014).

Climate variability can also have compounding effects on aspen growth. Low snowpack may alter ungulate behavior such that winter browsing on aspen increases (Brodie et al. 2012). This is a concern in the Northern Rockies, given predictions of earlier onset of spring weather conditions (Westerling et al. 2006) and projected changes in snow/rain dynamics in the coming decades (McCabe et al. 2007). Klos et al. (2014) project that by mid-21st century, the US Northern Rocky Mountain region will see greater than 50% reduction in land area dominated by snow in the winter and fewer snow-dominated winter months. This could impact aspen occupying dry, low-elevation habitats as well as ‘snow pocket’ aspen (Table 1), which rely on slowly released water from snow packs during dry, early summer months.

Several other factors impact aspen mortality but are considered secondary agents that often work in concert with drought, such as wood boring insects and fungi (Kashian et al., 2007; Fairweather et al., 2008; Marchetti et al., 2011).

Regional status

The US Northern Rockies are uniquely situated in the mid-

dle of the aspen range, and aspen communities in the Northern Rockies are some of the most genetically and structurally diverse (Callahan et al. 2013). This region supports both stable and seral aspen types that regenerate from root sprouts and seeds (Callahan et al. 2013). Perhaps because of the functional diversity of aspen in the Northern Rockies, SAD was not prevalent in the forested regions of Montana and northern Idaho in the 2010 Forest Health Protection report (Stead and Kerns 2010). However, slower, more gradual aspen decline was still observed in the absence of fire and conifer encroachment in the Northern Rockies (Stead and Kearns 2010).

Successful restoration

Successful aspen restoration depends on several key factors, many of which are interrelated. First, identification of the aspen community and functional type helps to identify strategies for restoration (Rogers et al. 2014; Table 1). For example, reintroduction of fire into seral functional types may promote aspen growth, but this may not be necessary for stable aspen communities. Additionally, given the extensive impact of ungulates on aspen regeneration, the successful reintroduction of fire to promote regeneration is more likely in areas with low ungulate densities. In the Northern Rockies, recommendations for encouraging aspen growth and dominance include increasing disturbances in seral community types that are currently dominated by lodgepole pine (*Pinus contorta*) and other conifers. Retaining or promoting early seral communities of aspen through the reintroduction of fire may be most successful on wetter, north-facing and/or high-elevation sites, where water availability is favorable for successful aspen establishment, regeneration, and growth (Bollenbacher et al. 2014).

Excluding browsing (through fencing or deferred livestock grazing) until aspen stems reach 6.5 feet (2 m) tall has improved aspen restoration success, especially in areas with high elk densities (Rogers and Mittanck 2014). However, building tall fences is costly and time intensive, so these efforts should be focused on optimal growing sites. If enclosures are not possible, consider larger treatment areas. On active grazing allotments, consider a rest season immediately following treatments.

Discussions between federal and state resource specialists and stakeholders during planning and implementation phases of aspen restoration promotes investment in restoration projects and increases the likelihood of restoration

success. A commitment to monitoring pre- and post-management is also critical to restoration success. Long-term monitoring and revisiting permanent plots is necessary to accurately track the state of individual aspen communities and types. Furthermore, this will continue to improve the understanding of the effectiveness of various restoration efforts, as well as both vegetation and fire management (Strand et al. 2015).

Case study 1: Yellowstone National Park - Establishment after Ungulates, Carnivores, and Wildfire

In the Greater Yellowstone Ecosystem (GYE), aspen loss or death was about 10%, which is substantial considering aspen's great ecological importance and relative scarcity (1-2% of the GYE) (Brown et al. 2006). In addition to its aspen diversity, the fire and management history of the GYE makes Yellowstone an interesting case study for aspen recovery. The past wolf extirpation and then successful wolf reintroduction allowed for a direct study of the multi-level interactions between elk, wolves, and aspen (Romme et al. 2001). Before the reintroduction of wolves, the elk influence on aspen populations was documented in the area through long-term use of elk exclosures (Halofsky and Ripple 2008; Beschta et al. 2014). Halofsky and Ripple (2008) demonstrated continued aspen regeneration within the exclosures, but no aspen regeneration outside the exclosures after wolf extirpation in 1920. Successful aspen regeneration began outside of the elk exclosures following wolf reintroduction in the 1990s. Successful aspen regeneration in recent decades in Yellowstone has been linked to the reintroduction of wolves and the resulting changes in populations and behavior of elk (Ripple and Larsen 2001; Kauffman et al. 2010, 2011; Eisenberg et al. 2013). It has long been a recommendation that one vital way to restore aspen communities is to reintroduce and restore carnivore populations (White et al. 1998).

Large wildfires in Yellowstone in 1988 provided an opportunity for landscape-scale analysis of post-fire aspen recovery. Aspen establishment from seed instead of clonal regeneration was observed and confirmed in Yellowstone following the 1988 wildfires (Turner et al. 2003). Genetic studies in Yellowstone confirmed that the widespread, yet patchy expansion of aspen was due to seedling establishment and not clonal sprouting (Tuskan et al. 1996; Romme et al. 2011). These events were largely linked to ideal cli-

mate and site conditions following the large fires (Turner et al. 2003). Following the 1988 fires, the highest density of aspen seedlings occurred in forested areas on low-elevation, south-facing slopes with shallow soils that burned with high severity (Turner et al. 2003). Proximity to adult aspen clones was also important, with higher seedling densities downwind of and closer to aspen trees that survived the fires.

Case study 2: Bridger Teton National Forest and Grand Teton National Park - Prescribed Fire and Restoration

In western Wyoming, managers have used prescribed fire for decades to set back succession in aspen stands for the benefit of wildlife and for vegetation diversity. Many prescribed fires, including some that have resulted in crown fires have been conducted in the Bridger-Teton National Forest (BTNF) and Grand Teton National Park (GTNP). A fire effects monitoring program has tracked the effects of these burns for over 15 years.

Aspen stem regeneration was variable following prescribed fire and/or cutting treatments, but generally density increased with burn severity and was greatest on sites with high pre-treatment aspen density. Treatment success was



Figure 6. Patchy aspen regeneration two years following a prescribed fire conducted in high fuel loads on the BTNF. Fire effects were severe but aspen sprouting still occurred. Photo courtesy of Diane Abendroth, NPS.

defined by dominance of young aspen trees and a reduction in conifer tree density in the decades after the treat-

ments. Aspen regeneration had to exceed the height of ungulate browsing (10 ft (3.05 m)) in order to meet restoration objectives. Monitoring objectives also included an adequate regenerating aspen stem density of 1000 stems/acre above this height for successful restoration. Adequate aspen stem heights and densities were not often seen until 15 or more years after treatment. Other general findings and recommendations from BTNF and GTNP restoration treatments of seral aspen communities include:

- Pre-burn cutting of conifers and overstory aspen created a temporary fuel bed, which could increase burn severity for up to 3 years. Moist or cold weather burning facilitates less complex prescribed fire operations.
- Cutting conifers alone can promote aspen stem recruitment but typically results in sprout densities lower than that of burned stands.
- Spring burning of aspen stands can achieve moderate burn severity if understory shrubs are dormant and sufficiently dense.
- High-severity burns appeared to produce new stems that were more palatable and otherwise attractive to ungulates, especially in the first year. These young sprouts were very vulnerable to browsing.
- Low-severity burns did produce regenerating stem densities of more than 3000/acre, but post-fire stem densities were often variable.
- Browsing up to 30% of aspen stems each year during the dormant season did not appear to jeopardize aspen stand recruitment.
- If regenerating aspen stems reached 3 feet (1 m) or more in height within 5 years of fire they were likely to reach tree height even in the presence of ungulates.
- Roughly 3000 stems per acre (or more) are necessary by the 2nd post-fire year to reach long-term objectives of 1000 aspen stems per acre 15 years after treatment.

Conclusions

These case studies highlight two modes of restoration: passive and active. While much more research is needed to fully understand aspen dieback and successful restoration methods, these offer some possibilities. However, these case studies represent only one part of the Northern Rockies and successful restoration may differ with varying site conditions across the region.

The widespread fires of recent decades (Morgan et al. 2008, 2014) and forecast for larger and more frequent fu-

ture fires (Littell et al. 2009) may benefit seral aspen stands where post-fire herbivory is not too heavy. Repeated or interacting forest disturbances (wildfires, bark beetle outbreaks, wind, and logging) may also benefit seral aspen stands through mortality of conifers. Disturbances in quick succession can reduce conifer seed sources, thus limiting competition for aspen sprouts, assuming below-ground aspen roots survive these disturbances (Kulakowski et al. 2013a). However, whether aspen increases or decreases over time depends, in part, on the aspen functional type and how it responds to changing climates, disturbances and restoration treatments.

Aspen is diverse in its fire regimes, functional types, and associated species. Because of this variability, we are only beginning to understand its complex ecology. However, we have several tools to effectively manage for the future viability and restoration of aspen. Climate change, land use changes, increasing browsing pressure, and changing fire regimes have left many aspen stands vulnerable to habitat loss. In the US Northern Rockies, aspen populations have not suffered from SAD or other extensive die-back as severely as other western states have, and within the Northern Rockies, several case studies of aspen recovery exist. However, it is still a species of high concern given its ecological importance and potential for decline in the coming decades. Several researchers and managers have begun to establish guidelines and recommendations for restoration best practices such as those outlined above for the BTNF and GTNP. There is no one-size-fits all model for aspen retention and/or restoration, and many factors such as functional type, browsing pressure, and stakeholder priorities need to be acknowledged and considered for successful retention and restoration.

Additional aspen information sources include -

[Western Aspen Alliance](#)

[Fire Effects Information System - Aspen Studies](#)

[2012 Society for Range Management Aspen Symposium](#)

[Northern Rockies Fire Science Network](#)

- [Research & Publications Database](#)
- [Webinar & Video Archive](#)

Literature cited

- Allen, C. D., A. K. Macalady, H. Chenchouni [and others]. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*. 259(4): 660–684.
- Anderegg, W.R.L., L.D.L. Anderegg, C. Sherman [and others]. 2012a. Effects of widespread drought-induced aspen mortality on understory plants. *Conservation Biology*. 26: 1082–1090.
- Anderegg, W.R.L., J.A. Berry, D.D. Smith [and others]. 2012b. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences*. 109: 233–237.
- Beschta, R.L.C. Eisenberg, J.W. Laundré [and others]. 2014. Predation risk, elk, and aspen: comment. *Ecology*. 95: 2669–2671.
- Bell, D.M., J.B. Bradford, and W.K. Lauenroth. 2014. Forest stand structure, productivity, and age mediate climatic effects on aspen decline. *Ecology*. 95: 2040–2046.
- Bollenbacher, B.L., R.T. Graham, and K.M. Reynolds. 2014. Regional forest landscape restoration priorities: Integrating historical conditions and an uncertain future in the northern Rocky Mountains. *Journal of Forestry*. 112(5): 474–483.
- Brodie, J., E. Post, F. Watson [and others]. 2012. Climate change intensification of herbivore impacts on tree recruitment. *Proceedings of the Royal Society B – Biological Sciences*. 279: 1366–1370.
- Brown, K., A.J. Hansen, R.E. Keane [and others]. 2006. Complex interactions shaping aspen dynamics in the greater Yellowstone ecosystem. *Landscape Ecology*. 21(6): 933–951.
- Calder, J. and S.B. St Clair. 2012. Facilitation drives mortality patterns on succession gradients of aspen-conifer forests. *Ecosphere*. 3(6): 1–11.
- Eisenberg, C., S.T. Seager, and D.E. Hibbs. 2013. Wolf, elk, and aspen food web relationships: context and complexity. *Forest Ecology and Management*. 255: 70–80.
- Fulé, P.Z., J.E. Crouse, T.A. Heinlein [and others]. 2003. Mixed-severity fire regime in a high-elevation forest of Grand Canyon, Arizona, USA. *Landscape Ecology*. 18: 465–486.
- Ganey, J.L. and S.C. Vojta. 2011. Tree mortality in drought-stressed mixed-conifer and ponderosa pine forests, Arizona, USA. *Forest Ecology and Management*. 261(1): 162–168.
- Hanna, P. and D. Kulakowski. 2012. The influences of climate on aspen dieback. *Forest Ecology and Management*. 274: 91–98.
- Huang, C.Y. and W.R.L. Anderegg. 2012. Large drought-induced aboveground live biomass losses in southern Rocky Mountain aspen forests. *Global Change Biology*. 18: 1016–1027.
- Kauffman, M.J., J.F. Brodie, and E.A. Jules. 2010. Are wolves saving Yellowstone’s aspen? A landscape-level test of behaviorally mediated trophic cascades. *Ecology*. 91(9): 274–2755.
- Kay, C.E. 2001. Evaluation of burned aspen communities in Jackson Hole, Wyoming. Pages 215–223 *in*: Sustaining aspen in western landscapes. USDA Forest Service Rocky Mountain Forest and Range Experimental Station, Fort Collins, CO.
- Kaye, M.W. 2011. Mesoscale synchrony in quaking aspen establishment across the interior western US. *Forest Ecology and Management*. 262(3): 389–397.
- Kaye, M.W., D. Binkley, and T.J. Stohlgren. 2005. Effects of conifers and elk browsing on quaking aspen forests in the central Rocky Mountains, USA. *Ecological Applications*. 15 (4): 1284–1295.
- Klos, K.Z., T.E. Link, and J.T. Abatzoglou, 2014. Extent of the rain-snow transition zone in the western US under historic and projected climate. *Geophysical Research Letters*. 41 (13): 4560–4568.
- Kulakowski, D., C. Matthews, D. Jarvis [and others]. 2013. Compounded disturbances in subalpine forests in western Colorado favor future dominance by quaking aspen (*Populus tremuloides*). *Journal of Vegetation Science*. 24: 168–176.
- Kulakowski, D., M.W. Kaye, and D.M. Kashian. 2013. Long-term aspen cover change in the western US. *Forest Ecology and Management*. 255: 53–59.
- Kurzel, B.P., T.T. Veblen, and D. Kulakowski. 2007. A typology of stand structure and dynamics of quaking aspen in northwestern Colorado. *Forest Ecology and Management*. 252(1–3): 176–190.
- Littell, J.S., D. McKenzie, D.L. Peterson [and others]. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. *Ecological Applications*. 19: 1003–1021.
- McCabe, G.J., L.E. Hay, and M.P. Clark. 2007. Rain-on-snow events in the western United States. *Bulletin American Meteorological Society*. 88: 319–328.
- Mock, K.E., C.A. Rowe, M.B. Hooten [and others]. 2008. Clonal dynamics in 848 western North American aspen

- (*Populus tremuloides*). *Molecular Ecology*. 17: 4827-4844.
- Morelli, T.L. and S.C. Carr. 2011. Review of the potential effects of climate change on quaking aspen (*Populus tremuloides*) in the western United States and a new tool for surveying aspen decline. General Technical Report PSW-GTR-235.
- Morgan, P., E.K. Heyerdahl, C. Miller [and others]. 2014. northern Rockies pyrogeography: An example of fire atlas utility. *Fire Ecology*. 10(1): 14-30.
- Morgan, P., E.K. Heyerdahl, and C.E. Gibson. 2008. Multi-season climate synchronized widespread forest fires throughout the 20th-century, Northern Rocky Mountains. *USA Ecology*. 89(3): 717-728.
- Perala, D.A. 1991. *Populus tremuloides* Michx. Pages 555-569 in: Burns, R.M. and B.H. Honkala, editors. *Silvics of North America*, Vol. 2. United States Department of Agriculture Handbook 654.
- Rehfeldt, G.E., N.L. Crookston, M.V. Warwell [and others]. 2006. Empirical analyses of plant-climate relationships for the western United States. *International Journal of Plant Sciences*. 167 (6): 1123-1150.
- Rehfeldt, G.E., D.E. Ferguson, and N.L. Crookston. 2009. Aspen, climate, and sudden decline in western USA. *Forest Ecology and Management*. 258: 2353-2363.
- Ripple, W.J. and E.J. Larsen. 2001. The role of postfire coarse woody debris in aspen regeneration. *Western Journal of Applied Forestry*. 16: 61-64.
- Rogers, P.C., A.J. Leffler, and R.J. Ryel. 2010. Landscape assessment of a stable aspen community in southern Utah, USA. *Forest Ecology and Management*. 259(3): 487-495.
- Rogers, P.C., S.M. Landhausser, B.D. Plnno, and R.J. Ryel. 2014. A functional framework for improved management of western North American aspen (*Populus tremuloides* Michx.). *Forest Science*. 60: 345-359.
- Rogers, P.C. and C.D. Mittanck. 2014. Herbivory strains resilience in drought-prone aspen landscapes of the western United States. *Journal of Vegetation Science*. 25: 457-469.
- Romme, W.H., L. Floyd-Hanna, D.D. Hanna [and others]. 2000. Aspen's ecological role in the west. RMRS-P-18. U.S. Department of Agriculture, Forest Service, Fort Collins, CO.
- Schoennagel, T., T.T. Veblen, and W.H. Romme. 2004. The interaction of fire, fuels and climate across Rocky Mountain forests. *BioScience*. 54(7): 661-676.
- Seager, S.T., C. Eisenberg, and S.B. St. Clair. 2013. Patterns and consequences of ungulate herbivory on aspen in western North America. *Forest Ecology and Management*. 255: 81-90.
- Shepperd, W.D., D.L. Bartos, and S.A. Mata. 2001. Above-and below-ground effects of aspen clonal regeneration and succession to conifers. *Canadian Journal of Forest Research*. 31: 739-745.
- Shinneman, D. J., W.L. Baker, P.C. Rogers, and D. Kulakowski. 2013. Fire regimes of quaking aspen in the Mountain West. *Forest Ecology and Management*. 299: 22-34.
- Steed, B.E. and H.S.J. Kearns. 2010. Damage agents and condition of mature aspen stands in Montana and northern Idaho. USDA Forest Service, Forest Health Protection, Northern Region. Numbered Report 10-03. Coeur d'Alene, ID.
- Strand, E.K., L.A. Vierling, S.C. Bunting [and others]. 2009. Quantifying successional rates in western aspen woodlands: current conditions, future predictions. *Forest Ecology and Management*. 257(8): 1705-1715.
- Strand, E.K., S.C. Bunting, L.A. Starcevich [and others]. 2015. Long-term monitoring of western aspen-lessons learned. *Environmental Monitoring and Assessment*. 187: 528.
- Turner, M.G., W.H. Romme, R.A. Reed [and others]. 2003. Post-fire aspen seedling recruitment across the Yellowstone (USA) landscapes. *Landscape Ecology*. 18(2): 127-140.
- Westerling, A.L., H.G. Hidalgo, D.R. Cayan [and others]. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science*. 313: 940-943.
- 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* 26(3): 449-462.
- Worrall, J.J., L. Egeland, T. Eager [and others]. 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 [and others]. 2010. Effects and etiology of sudden aspen decline in southwestern Colorado, USA. *Forest Ecology and Management*. 260: 638-648.
- Worrall, J.J., G.E. Rehfeldt, A. Hamann [and others]. 2013. Recent declines of *Populus tremuloides* in North America linked to climate. *Forest Ecology and Management*. 255: 35-51.
- Zegler, T.J., M.M. Moore, M.J. Fairweather [and others]. 2012. *Populus tremuloides* mortality near the southwestern edge of its range. *Forest Ecology and Management*. 282: 196-207.
- Zier, J.L. and W.L. Baker. 2006. A century of vegetation change in the San Juan Mountains, Colorado: an analysis using repeat photography. *Forest Ecology and Management*. 228(1-3): 251-262.



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