ECOLOGY OF ASPEN

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1. INTRODUCTION

Aspen (*Populus tremuloides*) are the most widespread broadleaf tree in North America and are frequently the only broadleaf species in otherwise conifer-dominated boreal landscapes (Kitchen et al. 2019). Often referred to as a keystone species (Wilson 1992), aspen serve a disproportionately important role in the biodiversity and functioning of the ecosystems in which they appear (Kay 1997). They also provide a number of critical ecosystem services including nutrient cycling, carbon sequestration, and both food and shelter for many species of plants, insects, microbes, and animals (Kouki and Martikaenen, 2004). Aspen exist across diverse ecological settings and as a result, exhibit a variety of ecological roles, making generalizations challenging and context specific studies of aspen necessary for well-informed management (Romme et al. 2001). This paper explores the complex ecology of aspen focusing on (1) the abiotic habitat factors that aspen tend to inhabit, (2) landscape mosaic/patch dynamics, biodiversity, and ecosystem services (biogeochemical cycling), (3) competition, and (4) the role of disturbance in determining aspen habitat. Finally, this paper describes the setting for this particular study.

2. ABIOTIC FACTORS

As the most widely distributed tree species in North America, aspen thrive across a diverse range of habitats from boreal forests to montane areas (Mitton & Grant, 1996). The range of aspen-dominated landscapes are largely shaped by abiotic factors including temperature, precipitation, snowpack and timing of snowmelt, soil composition, elevation and other topographic factors.

2.1 Climate and precipitation

Climatic conditions are highly variable over aspen's range, especially annual precipitation and temperature extremes. Precipitation within aspen's native range across North America can be as low as 16 cm annually in the semiarid west and may exceed 750 cm in Canada (DeByle and Winkour, 1985). In addition, aspen can tolerate a wide range of temperature extremes, and have been documented in areas that experience winter minimum temperatures as low as -57° C and summer high temperatures up to 41°

C (Perala et al. 1990). Given these relatively broad conditions, the range of aspen is still limited by growing season temperatures, availability of sunlight, and its requirement for a surplus water supply when the overall water balance exceeds evapotranspiration (Perala et al. 1990).

Declining winter snowpack (Mote et. al. 2005 and 2018) and both faster and earlier spring snowmelt may impact aspen populations (Brodie et. al. 2012). The reason for this is two-fold: (1) aspen have a relatively shallow root system and are unable to tap into deep groundwater supplies as done by conifers. As a result, aspen rely largely on snowmelt and rainfall during the growing season to satisfy water needs. (2) A deep snowpack may help young aspen suckers avoid being browsed by elk and deer simply by being covered during the winter months. In contrast, a shallow snowpack (a) leaves aspen suckers vulnerable to browsing during these months, (b) melts more quickly in the spring and early summer, and (c) provides limited water during the growing season. Stress from drought conditions damages aspen's xylem and this damage accumulates over time, which allows the impact of drought to persist sometimes for years after a prolonged period of drought (Anderegg et al. 2013).

2.2 Soils and topography

Aspen grow on a variety of soils ranging from shallow and rocky to deep loamy sands and heavy clays (USDA, 1975). Soils that are well drained, loamy, and high in organic matter, calcium, magnesium, potassium, and nitrogen tend to support aspen well (Boyle et al. 1973). While soils tend to be only a minor limiting factor for aspen, another study suggests soil structure may be linked to the age and successional type of aspen stands with stable aspen habitats frequently associated with a thick mollic horizon and Pachic Cryoborolls soil type (Cryer & Murray, 1992). Stands tend to expand into soils with thinner mollic horizons, but tend to thicken the rich mollic horizon as the trees mature and drop leaves and build organic matter in the soil (Buol et al. 1989). Seral stands that interface with conifers that encroach are often on less rich soils. Aspen functional types are influenced by the structure and composition of the soil that they grow in while also influencing the soil composition and structure (Cryer & Murray, 1992).

The elevational distribution of aspen in North America ranges from sea level on the Atlantic and Pacific coasts to approximately 3500 meters in northern Colorado (DeByle & Winokur, 1985). Near the northern limit of the range, aspen are not found above 910 meters and near the southern limit, aspen do not occur below about 2440 meters. Individual aspen trees tend to be poorly developed at either end of the elevation limits with most trees in Colorado and Utah found between 1280 and 3350 meters (Perala et al. 1990). In the Intermountain West, aspen can be found on all aspects and grow well wherever there is sufficient soil moisture. However, north-facing slopes tend to provide more favorable soil moisture conditions (Mueggler, 1988).

2.3 The aspen niche in the Greater Yellowstone Ecosystem

While there have not been extensive studies characterizing aspen's niche in eastern Idaho specifically, a study by Brown et al. 2006 focused on characterizing aspen's niche within the Greater Yellowstone Ecosystem (GYE). Given that the GYE is at largely higher elevations than most of eastern Idaho, the findings from this study are not entirely transferable, though it does provide a thorough characterization for a neighboring geographic region. Brown's study reports aspen are typically found between 1559 to 2921 meters in elevation. It also reported that aspen grow best in warmer and more mesic conditions with low conifer cover and clay-rich soils (> 40% clay), though outliers were found in soil types that contained as little as 17% clay, which is within the range of described aspen soils in Buol et al. 1989 and Cryer & Murrey 1992. Aspen's niche in the GYE is characterized by warm temperatures (average annual temperature of 2.1° C with average annual temperature ranging from –2.1° to 6.1° C), more mesic areas with high availability of sunlight (shortwave radiation values > 68.9 W m^2) and annual precipitation from snowpack and rainfall ranging between 33.8 to 153.4 cm per year. At the landscape scale, patches of aspen stands are often found interspersed between patches of sagebrush steppe, grasslands, and lower-elevation conifer forests (Rogers et al. 2020).

3. BEACONS OF BIODIVERSITY

3.1 Diversity of flora and fauna

Highly productive and structurally diverse, non-riparian aspen forests support greater biodiversity than any other upland forest type in the western United States (Chong et al. 2001; Mueggler 1985), providing critical ecosystem services including the indirect sunlight needed to support a biologically diverse understory (Mueggler 1985). When aspen dominated landscapes transition to other types, notable biodiversity is lost in vascular plants, nonvascular plants, vertebrates, and invertebrate organisms (Bartos and Amacher 1998; Bartos and Campbell 1998a, b; Kuhn 2011). Furthermore, many species of plants, animals, insects, and microbes rely on the services provided by aspen (Kouki and Martikainen 2004) including hare, black bear, deer, elk, grouse, and numerous songbirds (Scott and Crouch 1987; Patton and Jones 1977). Old and decaying aspen are important for wildlife (DeByle and Winkour, 1985), suggesting the ecological importance of aspen across all life stages. Aspen corridors also enhance the connectivity of a variety of species including pollinators, small mammals, and birds that would otherwise be subject to the negative impacts of habitat fragmentation (DeByle and Winkour, 1985). Connected networks of aspen maintain ecological processes and species interactions, but as aspen-dominated ecosystems decline, so do these benefits and many species suffer as a result.

3.2 Trophic interactions

The recruitment of aspen suckers following disturbance can be negatively impacted by browsing and grazing ungulates like deer and elk (Walker et al. 2014). While cattle typically do not browse aspen, they can still negatively impact sucker recruitment by trampling young stems (Bork et al 2013). Case studies in the GYE suggest long term large herbivore exclusion in areas where aspen are starting to regenerate could result in higher aspen recruitment rates (Beschta et al. 2016). The re-establishment of a more balanced predator-prey relationship through the reintroduction of wolves in the GYE has been shown to reduce ungulate populations and establish a landscape of fear (Laundre & Ripple, 2010) which influences the behavior and spatial range of prey animals. This population reduction may in turn help decrease winter browsing pressure from deer and elk and promote a more beneficial use of aspen groves by beaver resulting in an improved local hydrology. Ultimately, these changes may allow aspen to better establish after a disturbance (Beschta et al. 2016).

3.3 Carbon sequestration and biogeochemical cycles

With shallow root systems and abundant deciduous leaves, aspen are effective at sequestering large amounts of carbon and provide enough indirect sunlight for a biologically diverse understory (Boča and Van Miegroet, 2017). Their rapid growth and high nutrient demand also play a role in enriching soils (Ste-Marie and Pare, 1999) and cycling nutrients including water, carbon, nitrogen, and phosphorus (Kurth et al. 2014).

4. COMPETITION IS KEY

4.1 Conifers

Across much of its range, aspen compete with conifers (Bartos, 2001). At lower elevations (below 2000 m) and under more xeric conditions --where soil moisture is limiting-- juniper (*Juniperus spp.*) can quickly encroach in areas previously dominated by aspen (Wall et al. 2001). Extended drought conditions and long periods between disturbance by fire can limit aspen’s ability to regenerate clonally, leaving stands vulnerable to replacement by more drought tolerant species like juniper. Juniper encroachment often coincides with drier, warmer climate conditions that are well-suited for juniper seed production and establishment. Unlike aspen which cycles nutrients quickly and enriches soils to promote a biodiverse understory, juniper acidifies the soil and cycles nutrients much more slowly, making it difficult for aspen to re-establish (Bates et al. 2006).

At the upper end of aspen’s elevational range, competition with conifers such as Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) is more common. Aspen grow quickly after disturbance by fire, but after enough time post-disturbance taller conifers tend to shade out aspen causing individual aspen stands to decline. However, the cycle of competition restarts after another major disturbance. Under current climate conditions, lowland aspen stands and aspen in wet microsites near streams transition to conifer cover more slowly while upland mixed aspen/conifer stands experience more rapid conifer establishment. A 2009 study quantifying successional rates in western aspen woodlands determined an average fire return interval of 50-70 years is desirable for the maintenance of aspen in upland areas where conifers are present. Under longer fire return intervals, many aspen in mixed aspen/conifer forests could be lost within 80-200 years (Strand et al. 2009). However, with increasing fire frequency (Weber & Yadav, 2020) this trend may be reversed in favor of aspen. Conversely, increasing drought severity (Anderegg et al. 2013) causes stress to aspen and could negate potential gains from increasing fire disturbance.

4.2 Other damaging agents

In addition to browsing pressure and competition with other vegetation types for critical resources like water, nutrients, and sunlight, aspen is also susceptible to numerous damaging agents including diseases and pests. Some of the more common infections in the western US include various shoot blights, leaf spots, leaf rust fungi, powdery mildew, viruses, trunk rot fungi, bacteria, and an array of cankers (Perala, 1990). As a host to a wide variety of insects (DeByle & Winkour, 1985), only a few types have been known to potentially cause severe damage to aspen. These groups of concern are 1) defoliators like the western tent caterpillar (*Malacasoma califonicum*) and leaf miners like the aspen leaf miners (*Phyllocnistis populiella*), aspen blotch miners (*Phyllonorycter tremuloidiella* and *Lithocolletic salicifoliella),* 2) borers like the poplar borer (*Superda calcaruta*) which opens up channels that make aspen more susceptible to fungal infections, and 3) sucking insects including the vagabond aphid (Mordvilkoja vagabunda) which causes a twisted gall of leaves at twig tips and aphids of the genus *Pemphigus* as well as leafhoppers in the genera *Idiocerus* in the western US which cause leaf browning and can rupture twig bark (Perala, 1990).

All of these factors including competition, disturbance, insects, and diseases are critical components of a functioning aspen ecosystem and under ideal conditions, would not be cause for concern. However, changing climate patterns like increasingly prolonged and severe drought conditions leave aspen stressed, resulting in increased vulnerability to infection by secondary agents like insects and disease (Sucoff, 1982).

5. DISTURBANCE DYNAMICS AND CONSERVATION MEASURES

Aspen woodlands can range from highly fire-dependent seral communities succeeded by conifers to relatively stable, self-replacing, non-seral communities that may not require fire to stimulate regeneration (Shinneman et al. 2013). While aspen do reproduce sexually, their ability to produce asexually to form an aggregation of genetically identical stems following a disturbance like fire or clearcutting gives them a competitive advantage to act as an early successional species in comparison to slower-growing, non-clonal conifers (Burton, 1966). Aspen's vegetative growth mechanisms are often enhanced by disturbance, allowing for quick succession into suitable areas post-disturbance (Long & Mock, 2012). Fire return intervals vary greatly, but in a well-functioning ecosystem, fire is frequent enough (50-70 years) to stimulate sufficient post-disturbance suckering to satiate browsing requirements (Endress et al. 2012).

Understanding disturbance dynamics can help natural resource managers to make ecologically informed management decisions in aspen-dominated systems. Research in the field of environmental conservation shows that small prescribed fires may encourage some aspen regeneration, but may not facilitate long-term aspen gain due to continued pressure from over-browsing, rapid establishment of grasses and shrubs, and limited reduction of competing conifer populations (Wilde 2014). Wilde 2014 also suggests higher severity, controlled fires may be a useful management tool to improve aspen regeneration and recruitment by reducing conifer competition while increasing suckering and growth rate and encouraging higher concentrations of defensive compounds including phenolic glycosides and condensed tannins (Lindroth & Clair, 2013) which may increase aspen's resilience to herbivory (Wan et al. 2014).

6. LANDSCAPE LEGACIES

In addition to being shaped by a variety of abiotic factors, aspen distribution is also influenced by humans, who simplify landscape patterns (Krummel et al. 1987) through activities such as fire suppression, expansion of the wildland urban interface (WUI), clearcutting, and emitting large quantities of greenhouse gases that contribute to warming climate trends (Romme et al. 2001). Historic fire suppression over the 20th century dramatically altered fire return interval and forest structure in fire-adapted ecosystems leaving a wide range of long-lasting impacts on landscapes across the western US. This resulted in dense, overstocked forests, a large accumulation of flammable forest material, compromised forest health and resilience, and as a result increasingly large and destructive wildfires.

Between shifting narratives surrounding wildfire, changing leadership, and prescribed fires gone wrong, the pendulum of management frameworks has fluctuated over the course of the 20th century and into the 21st. Presently, land management agencies like the Bureau of Land Management (BLM) are seeking more holistic, proactive approaches to caring for historically fire-adapted landscapes like those that aspen inhabit, but historic fire suppression will continue to have impacts on ecosystems throughout the western US for many years to come. It is important to note that managing to restore landscapes to a previous "natural state" can be problematic, as what we perceive as the natural state of a landscape today is likely the result of centuries worth of human interactions and alterations (Turner & Gardner, 2015).

7. THIS STUDY

While aspen has been declining across the western United States (Singer et al. 2019) there have been numerous studies investigating losses of aspen in Colorado, but few studies with focus on aspen in eastern Idaho. This study aims to quantify trends in aspen population size and distribution on a landscape scale across four Bureau of Land Management field districts in eastern Idaho (Figure 1). The study uses remotely sensed data from Landsat 5 Thematic Mapper (TM), Landsat 8 Operational Land Imager (OLI), and Landsat 9 Operational Land Imager Plus (OLI+) in addition to aerial imagery, climate data, and *in situ* observations. These data will be used to build a model that can detect/predict aspen in order to investigate trends, changes, and relationships in aspen populations at a landscape scale. Project partners at the Bureau of Land Management plan to use findings from this study to inform future targeted management decisions with the goal of promoting aspen health and overall ecosystem function in aspen-dominated landscapes within their jurisdictional boundaries.

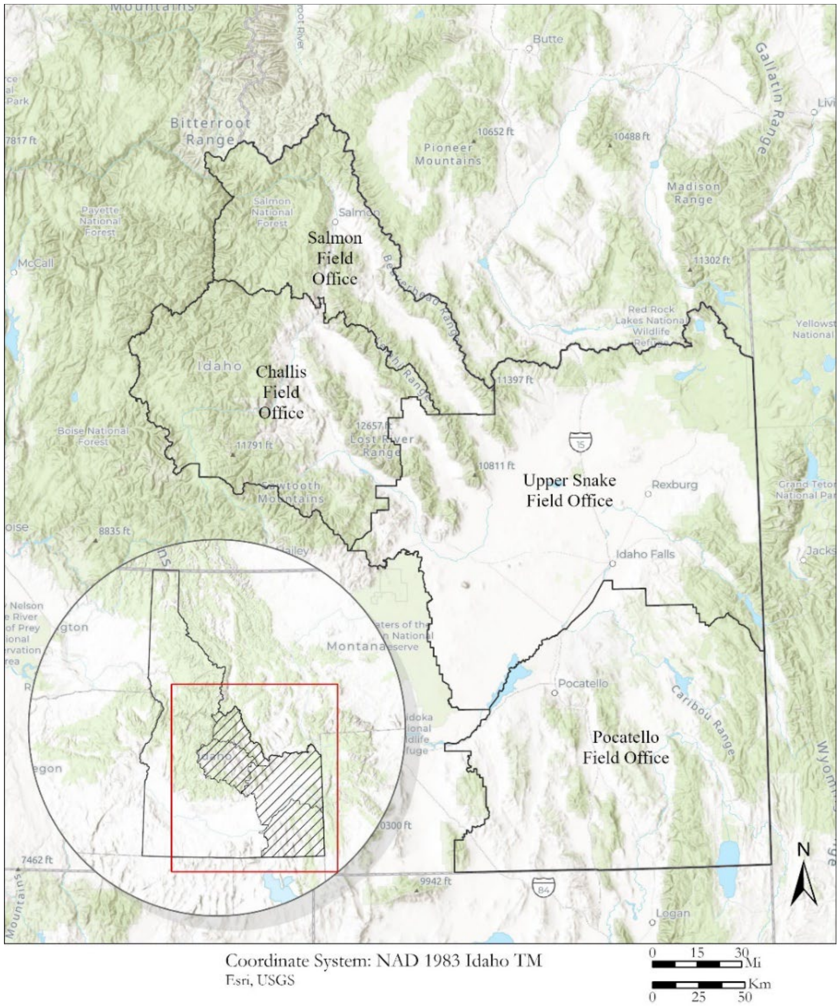

Figure 1. *The study area comprised of four Bureau of Land Management field offices in eastern Idaho; Pocatello, Salmon, Challis, and Upper Snake Field Offices.*

8. NOTES FROM THE FIELD SEASON

Over the course of the 2024 summer field season, we were able to observe aspen on the landscape across eastern Idaho. In the southern portion of our study area (lower elevations of 1600-1750 m, many aspen stands were patches near water surrounded by sagebrush steppe. These stands seemed to be minimally disturbed by browsing, though there was an abundance of cattle that appeared to be trampling some of the young aspen recruits. Towards the center of our study area (at elevations of 1750-1900 m), aspen were found in larger swaths of mixed-age stands, interspersed with sagebrush steppe and Douglas fir forests. Towards the northeast section of the study area (at higher elevations 1900-2200 m), we found much smaller stands interspersed among dense lodgepole pine forest, with more evidence of disturbance by ungulate browsing. The understory of aspen patches varied widely in composition across the surveyed areas, but was often lush.

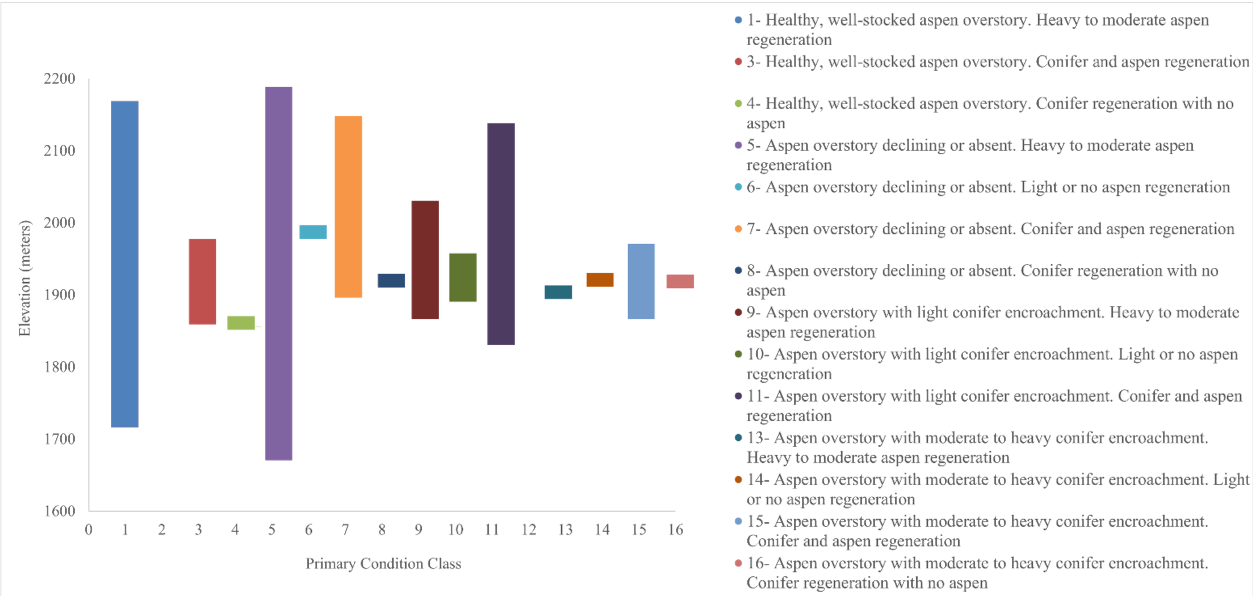

Figure 2. *Primary condition class of aspen stands surveyed during the 2024 summer field season compared to elevation of sample points. Stands with healthy, absent, or declining aspen canopy cover but vigorous aspen regeneration ranged from 1650 to 2200 m in elevation. Stands with varying degrees of conifer encroachment and aspen regeneration were more limited in range from around 1850 m to 2100 m.*

Aspen stands felt cool and damp in comparison to adjacent sagebrush steppe patches and, much brighter and warmer in comparison to dense, well shaded coniferous forest. Touted as beacons of biodiversity on the landscape, the sounds of aspen stands were distinct from those heard in other cover types. While standing in an aspen grove, you could almost always hear songbirds, the low buzz of insects, the distinct rustle of aspen's namesake trembling leaves, and the faint sound of nearby running water.

Observations from the aspen stand health survey suggest the health and successional status of stands within the sampled area varies widely (Figure 2). Some stands appeared to be in good health with abundant mixed age stems, minimal crown damage, low to no evidence of browsing, minimal conifer encroachment, and a diverse understory. Others appeared to be in poor or declining condition with minimal sucker recruitment, browsing damage, and substantial conifer cover. As part of a larger study, these observations will provide additional context when used in conjunction with historical satellite imagery and ancillary datasets to analyze trends in aspen populations and potential climatic drivers of distribution change over eastern Idaho.

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