

**ASPEN DISTRIBUTION IN NORTH-CENTRAL BRITISH
COLUMBIA: ABUNDANCE, TRENDS, AND IMPLICATIONS
FOR SHALLOW WATER WETLANDS
FINAL REPORT**



PREPARED FOR: SOCIETY FOR ECOSYSTEM RESTORATION IN NORTHERN BRITISH
COLUMBIA

PREPARED BY: ERICA BONDERUD M.SC., DEAN EVANS B.SC., AND SEAN RAPAI M.SC.

STUDY PERIOD: JANUARY 4 – MARCH 31, 2018.

This page is intentionally blank.

ACKNOWLEDGEMENTS

This review was made possible by the Society for Ecosystem Restoration in Northern British Columbia. Special thanks to John Degagne and Marc Steynen for initiating this project, and to the numerous individuals you who were so generous as to provide their time and knowledge in kind to support this project. This includes Alex Bevington, Alex Woods, Bruce Rogers, David Rusch, Dr. Ché Elkin, Dr. Phil Burton, Dr. Sybille Haeussler, Dr. Ted Hogg, Erica Lilles, Hardy Griesbauer, Richard Kabzems, Torsten Kaffanke, Will Mackenzie, Nick Hamilton, and James Steidle.

EXECUTIVE SUMMARY

Aspen (*Populus tremuloides*) is the most widely distributed broadleaf tree species in North America and is associated with a variety of ecosystem services, including nutrient cycling and habitat for numerous bird and mammal species. Despite its ability to occupy a large niche, aspen is experiencing declines across many parts of its North American range, including throughout the western United States and western Canada. Given the ecological importance of aspen, much research has focused on identifying the causes of these declines and threats to aspen persistence on the landscape. In this review, we focus on aspen distribution in north-central BC, discussing trends in aspen distribution, threats to aspen on the landscape, and the ecological implications of aspen loss.

Severe aspen declines were first documented in the western United States in the early 1990s. These declines prompted extensive research into aspen populations and factors contributing to stand persistence. Some of the identified factors, such as climate change, have negative impacts on aspen in some areas whilst creating opportunities for expansion elsewhere. In western Canada, the threats of climate change are echoed with research documenting extensive dieback of aspen along the aspen parkland of the prairie provinces and along the southern edge of the boreal forest in response to drought. Future projections under the threats of climate change show that much of the existing aspen parkland will retreat northward into the boreal forest. In BC, research on aspen abundance and distribution is quite limited. Nonetheless, there are several range-wide threats pertinent to aspen stands in north-central BC. These include: changing fire regimes; ungulate grazing; pathogens and diseases; forest management practices; and climate change and drought.

Aspen is very prone to disease but infection typically only causes large-scale mortality when it occurs in combination with other stressors, such as drought. Throughout western North America, severe aspen dieback has been documented and linked to the synergistic impacts of drought followed by insect defoliation. Climate models predict the future climate of BC to be warmer with increased precipitation, but reduced runoff during the summer and fall. Consequently, aspen stands in north-central BC may experience both heat and moisture stress during the growing season, and become increasingly susceptible to climate-related declines. However, the cumulative effects of climate change on aspen abundance and distribution in the region are unclear. Perhaps the greatest driver of aspen abundance in north-central BC is forest management practices that actively remove aspen from the landscape. In north-central BC, the hardwood has little economic value, and consequently, cutblocks are commonly brushed or treated with herbicide to hinder aspen growth. The degree to which aspen removal is necessary for crop conifer survival in the Omineca and Skeen Regions is uncertain. However, under current free-growing guidelines for these Regions, managed stands may achieve free-growing requirements sooner than stands left to progress naturally, providing incentive for forest licensees to remove aspen from the landscape.

Loss of aspen on the landscape may have far-reaching impacts. In the boreal forest, shallow water wetlands are created and maintained by beaver dams, and beavers selectively harvest aspen for both forage and dam construction material. Thus, this raises the question of whether changes in aspen abundance will have negative effects on beaver populations and associated wetlands. To date little research has actually explored this relationship and there only appears to be one anecdotal reference to beaver population decline in response to aspen decline. In BC, there is also very limited research on the North American beaver,

however, the existing research and expert opinion suggests that it is unlikely that aspen abundance alone is an important driver of beaver-created wetlands in the northern boreal and sub-boreal forests. This is further supported by the fact that aspen is much less tolerant to flooding in this area compared to other preferred species such as willows. Nonetheless, existing forest management practices are potentially threatening to the beaver, such as riparian buffers that appear to be inadequate to support current and future beaver populations, and practices that support conifer over broadleaf regeneration.

Ultimately, there is a general dearth of information regarding aspen distribution, threats to survival, and ecological impacts in north-central BC. This lack of knowledge could be threatening to aspen, beaver-created wetlands and the ecosystem services they provide. Based on the results of this literature review, we provide 3 recommendations for future research and modifications to current management practices.

1. Quantify historical and current trends in aspen distribution in the region, both in upland forest and adjacent to shallow water wetlands, in order to determine whether or not changes in aspen cover are within historical norms.
2. Assess the competitive impacts of aspen on crop conifers in the region, and use these findings to reevaluate and inform free growing guidelines, forest management practices and Forests for Tomorrow Program strategies that actively limit the regeneration of deciduous trees.
3. Evaluate the effectiveness of current forest management practices on maintaining riparian habitat, and the effects of riparian hardwood (i.e., aspen, cottonwood and willow) abundance on beaver populations and, subsequently, shallow water wetland persistence and distribution.

TABLE OF CONTENTS

| | |
|---|------------|
| ACKNOWLEDGEMENTS..... | III |
| EXECUTIVE SUMMARY | IV |
| TABLE OF CONTENTS..... | VI |
| 1.0 INTRODUCTION..... | 1 |
| 2.0 ASPEN CONDITION, ABUNDANCE AND DISTRIBUTION..... | 2 |
| 2.1 NORTH AMERICA..... | 2 |
| 2.2 WESTERN UNITED STATES..... | 2 |
| 2.3 WESTERN CANADA..... | 3 |
| 2.4 BRITISH COLUMBIA | 4 |
| 3.0 THREATS TO ASPEN IN NORTH-CENTRAL BRITISH COLUMBIA..... | 5 |
| 3.1 PATHOGENS AND DISEASE..... | 5 |
| 3.2 CHANGING FIRE REGIMES..... | 6 |
| 3.3 UNGULATE GRAZING | 7 |
| 3.4 FOREST MANAGEMENT PRACTICES | 8 |
| 3.5 DROUGHT AND CLIMATE CHANGE | 9 |
| 4.0 ASPEN AND SHALLOW WATER WETLANDS: A CASE STUDY OF THE BEAVER | 12 |
| 5.0 CONCLUSIONS AND RECOMMENDATIONS..... | 14 |
| 6.0 LITERATURE CITED..... | 18 |

1.0 INTRODUCTION

Aspen (*Populus tremuloides*) is the most widely distributed tree species in North America (Perala 1990), and is associated with a variety of ecosystem services (Peterson and Peterson 1995). Aspen ecosystems promote biodiversity by providing nutrient benefits to forested environments (Simard et al., 2001; Preston et al., 2009), moderating air temperature (Powell and Bork 2007) and increasing the frost free period in the understory (Powell and Bork 2007). Aspen also provide habitat for as many as 55 species of mammals (DeByle and Winokur, 1985; Oaten and Larsen, 2008) and 135 species of birds (Harestad and Keisker 1988; Peterson and Peterson 1995; Martin et al. 2004). Cavity nesting species of birds and mammals also show a distinct preference for excavation in aspen over conifers (Martin et al. 2004), and aspen stands have twice the density and diversity of insects as pure conifer stands (Peterson and Peterson 1995). These insects provide prey for insectivorous birds and bats, while the leaves, buds and bark of aspen provide forage for porcupine, snowshoe hare and ungulates (DeByle and Winokur 1985; Johnston and Robert 1990; Peterson and Peterson 1995; Parsons et al. 2003; Hood and Bayley 2009; Seager et al. 2013). Beaver, in particular, have shown a strong preference for aspen for both forage and dam construction material (Hall 1960; Jenkins and Busher 1979; Naiman et al. 1988; Peterson and Peterson 1992).

Declines in aspen cover have occurred across North America, with the western United States (e.g. Di Orio et al. 2005; Rehfeldt et al. 2009; Clair et al. 2010; Rogers et al. 2014) and western Canada (e.g. Hogg et al. 2002, 2008) hit particularly hard. The Society for Ecosystem Restoration in Northern British Columbia (SERNbc) is concerned that aspen may be declining in north-central British Columbia. SERNbc acknowledges the cumulative negative impacts that climate change, drought, pathogens, and diseases are likely to have on aspen. In addition to this, an increase in natural disturbance intervals may also be impacting aspen distribution in BC. SERNbc theorizes that where the interval between natural disturbances (fire) has been long, aspen and other deciduous species in the upland area adjacent to wetlands may become depleted and the vegetation communities become dominated by coniferous species. SERNbc is not concerned about this pattern at a local or stand level, as the issue would occur naturally at this scale, but is concerned that broader patterns of aspen exclusion throughout north-central British Columbia may be having a negative impact on aspen, and therefore biodiversity and shallow water wetlands.

We are conducting this review to determine if the literature supports SERNbc's assumptions that:

- Aspen are in decline in central BC; and
- This decline could have implications for shallow water wetlands.

In this literature review we discuss the current state of knowledge on aspen in north-central British Columbia (BC), along with broad scale variables and practices that may be influencing aspen abundance and distribution on the landscape. The goal of this review is tripartite:

- Discuss trends in aspen distribution at the continental and regional scales;
- Identify threats to aspen persistence in the forests of north-central BC; and
- Evaluate the impacts of aspen declines in riparian and shallow water wetland ecosystems, using the beaver as a case study.

2.0 ASPEN CONDITION, ABUNDANCE AND DISTRIBUTION

2.1 NORTH AMERICA

Ranging from the east coast of Newfoundland and Labrador, Canada, to the west coast of Alaska, USA, to as far south as Mexico, aspen is the most widely distributed tree species in North America (Perala 1990). With its large transcontinental distribution, aspen occupy many diverse landscapes that vary across temperature, moisture, and soil gradients (Perala 1990; Clair et al. 2010). The largest span of aspen can be found at its northern reach in the boreal forest of Canada and Alaska where it is the most predominant broadleaf species (Michaelian et al. 2011; Rogers et al. 2014). In eastern Canada and the United States, aspen is distributed fairly continuously as compared to the west where it is more confined to suitable montane and high plateau habitat (Jones 1985). Despite its ability to occupy a large niche, aspen are experiencing declines across many parts of its range, specifically in western Canada (e.g. Hogg et al. 2002, 2008) and across much of the western United States (e.g. Di Orio et al. 2005; Rehfeldt et al. 2009; Clair et al. 2010; Rogers et al. 2014). Interestingly, this pattern of decline is not consistent across its range and in some areas aspen are experiencing growth and expansion as a result of disturbance (Smith et al. 2011; Kulakowski et al. 2013b,a; Gill et al. 2017) and climate change (Landhäusser et al. 2010). It is evident that the presence of aspen on the landscape has been fluctuating for centuries (Gill et al. 2017) and because of this it is debated that recent declines in some areas are possibly within the historical norm (Kulakowski et al. 2006, 2013b).

2.2 WESTERN UNITED STATES

In the western United States, aspen has a spotty distribution across all of the western contiguous states and Alaska (Jones 1985; Kulakowski et al. 2013a). Extensive pure stands of aspen can be found in the Colorado Plateau ecoregion, which expands to parts of New Mexico, Arizona, Utah, and Colorado (Kulakowski et al. 2013a; Rogers et al. 2014). Here, the highest concentration of aspen can be found in Utah and Colorado which contains approximately 75% of western aspen (Shepperd et al. 2001). Elsewhere, in smaller patches, aspen is distributed throughout montane areas, such as the Rocky Mountains, where they can be located in seral, stable, and riparian communities (Rogers et al. 2014; Rogers 2017). Because of the large distribution and variety of ecological roles played by aspen, trends in aspen growth and declines in the western United States vary both geographically and temporally (Kulakowski et al. 2004, 2006, 2013a; Sankey 2008; Rogers et al. 2014). At the end of the 20th century there was great concern over the declining condition and abundance of aspen that was observed during the span of the last century (e.g. Kay, 1997; Shepperd et al., 2001) and considerable research into aspen persistence and decline has been conducted since.

There is extensive evidence documenting aspen population decline in the western United States during the latter part of the 20th century (e.g. Bartos and Campbell, 1998; Di Orio et al., 2005; Kay and Bartos, 2000; Rogers, 2002) as well as the beginning of the 21st century (e.g. Hanna and Kulakowski, 2012; Huang and Anderegg, 2012; Worrall et al., 2008). However, it remains unknown if the cumulative effects of aspen mortality and regeneration are resulting in growth or decline (Kulakowski et al. 2013a). A review of local-scale aspen studies in the western United States by Sankey (2008) showed that there is a great deal of regional spatial variability in aspen dynamics with different studies showing areas of decline, persistence, and even increases. Kulakowski et al. (2013a) suggests that that changes in aspen dominance through time is

likely dependent on the factors influencing both regeneration and mortality within specific geographic and ecological areas. For example, research in Colorado suggests that fire suppression during the 20th century is more important for lower elevation stands as compared to high elevation stands that experience more infrequent fires (Kulakowski et al. 2004, 2006, 2013a). The effect of climate change is also an important factor to consider in changing aspen distribution. Predictions of future aspen dynamics in response to a changing climate show potentially drastic declines in parts of its range in the coming decades (Rehfeldt et al. 2009). In other areas, climate change could also favor aspen dominance as a result of increased bark beetle outbreaks, shifts in precipitation and temperature regimes, increased wildfires, and compounded disturbances (Kulakowski et al. 2013a). Ultimately, it is important to recognize that there is no single solution to understanding the changes in aspen distribution and abundance that have been observed over the past century and that spatial and temporal considerations must be made to understand the future of aspen in the west.

2.3 WESTERN CANADA

The transcontinental distribution of aspen spans the entirety of Canada, including every province and territory (Perala 1990). In the western Canadian provinces of Manitoba, Saskatchewan, Alberta, and BC, knowledge of the importance of aspen as a commercial resource increased drastically during the latter half of the 1980s (Peterson and Peterson 1992). Aspen is a dominant and important deciduous tree of the mixedwood boreal forest which expands across the northern portions of Canada's western provinces (Peterson and Peterson 1992; Brandt et al. 2003; Hogg et al. 2005). Farther south, starting in the Peace River country of BC and Alberta and extending across the prairie provinces of Alberta, Saskatchewan, and Manitoba, aspen is found in the aspen parkland region, the transitional zone between the boreal forest and the prairies, where it is the predominate tree species in forest patches interspersed with cropland and grassland (Hogg and Hurdle 1995; Hogg et al. 2005; Rogers et al. 2014). To the west, aspen is an important component of Rocky Mountain ecosystems where it covers a small portion (<5%) of lower elevation montane areas in either large stands on debris cones or smaller stands scattered throughout lodgepole pine and Douglas-fir forests (White et al. 1998). In BC, aspen can be found in all biogeoclimatic zones east of the Coast Mountains (Peterson and Peterson 1995).

Much like the United States, western Canadian aspen populations have also been experiencing declines in parts of its range (Hogg et al. 2002, 2008; Michaelian et al. 2011; Chen et al. 2018). Within the mixedwood boreal forest, aspen dominance and distribution is primarily driven by disturbance (Rogers et al. 2014). Over the duration of the 20th century the lengthening fire cycle indicates that fire no longer plays a historical role in aspen regeneration (Peterson and Peterson 1992). However, harvesting appears to be an alternative disturbance in the mixedwood boreal forest resulting in a shift from conifer-dominated areas to hardwood-dominated stands (Peterson and Peterson 1992; Rogers et al. 2014). Within the aspen parkland areas of the prairie provinces, aspen coverage has expanded southward as a result of the extirpation of bison (*Bison bison*) and fire suppression following European settlement (Campbell et al. 1994; Rogers et al. 2014). At the beginning of the 1990s, a regional assessment of aspen forest in western Canada concluded that aspen forests were generally healthy (Brandt et al. 2003). However, since then, reports of aspen mortality and

dieback have been on the rise, resulting in public and industry concern (Hogg et al. 2002, 2005, 2008; Frey et al. 2004).

In response to these concerns, the Canadian Forest Service established Climate Impacts on Productivity and Health of Aspen (CIPHA) in 2000 to track long-term changes in aspen forests. The CIPHA monitoring system consists of 180 research plots across the aspen parkland and mixedwood boreal of Manitoba, Saskatchewan, Alberta, and northeastern BC (Hogg et al. 2005, 2008). Major findings of this initiative suggest that climatic factors, especially drought, play an important factor in the growth and decline of aspen across drought sensitive areas of the mixedwood boreal forest and aspen parkland (Hogg et al. 2005, 2008; Hogg and Michaelian 2015). This is concerning considering projections of a more arid climate as a result of climate change (Seager et al. 2007; Hogg et al. 2008). Under future climate change it is believed that much of the aspen will be lost from the current aspen parkland area and retreat northward into the boreal forest (Hogg and Hurdle 1995; Worrall et al. 2013; Rogers et al. 2014). Many knowledge gaps still exist in understanding Canadian aspen abundance and dieback which merits the need for continued stand monitoring and research (Frey et al. 2004; Hogg et al. 2005).

2.4 BRITISH COLUMBIA

In BC, aspen is the most widely distributed and abundant deciduous tree species (Meidinger and Pojar 1991). It can be found throughout much of the province except for west of the Coast Mountains where it can be found uncommonly in several valleys and in sporadic clones on Vancouver Island (Peterson and Peterson 1995). Aspen stands are a common component of forested areas of the Interior Plateau and boreal forest regions, and found in nine of BC's biogeoclimatic zones: Interior Cedar–Hemlock (ICH), Interior Douglas-fir (IDF), Montane Spruce (MS), Ponderosa Pine (PP), Sub-Boreal Pine–Spruce (SBPS), Sub-Boreal Spruce (SBS), Bunchgrass (BG), Engelmann Spruce–Subalpine Fir (ESSF), and Boreal White and Black Spruce (BWBS) (Meidinger and Pojar 1991; Peterson and Peterson 1995). The greatest abundance of aspen can be found in the BWBS and SBS zones of northeastern and north-central BC where it comprises 15,184,632 ha and 10,079,417 ha, respectively (Hamann et al. 2005).

Aspen's ability to occupy and thrive in such a wide range of ecosystems across BC can be attributed to the species' ecology. The clonal nature of aspen allows it to quickly pioneer disturbed sites through root suckering where it often out competes slower establishing species such as conifers (Peterson and Peterson 1995; Frey et al. 2003; Harper 2015). The clonal root system can be several hundreds of years old and as large as several hectares in size (on average less than 1 ha) with vertical roots extending as deep as 2.5 meters and most lateral roots within 30 centimetres of the soil surface (McCulloch and Kabzems 2009). Aspen growth is limited primarily by water in warmer areas of southern BC and by temperature in the northern parts of the province and at higher elevations (Chen et al. 2002). Furthermore, it is most successful on soils with medium-rich nutrients and slightly dry to fresh/moist moisture regimes (Klinka et al. 1999; McCulloch and Kabzems 2009). Although a fierce competitor and dominant early seral species in BC's forests, there are numerous threats to aspen regeneration and persistence in the province.

3.0 THREATS TO ASPEN IN NORTH-CENTRAL BRITISH COLUMBIA

Across the North American range, aspen experiences threats to growth, regeneration and, ultimately, survival. Patterns of aspen mortality can be classified in to three categories based on the geographic scale, type of cover loss, and the endogenous or exogenous processes at play (Worrall et al. 2013):

1. *Cohort dynamics*: Defined as stem mortality as a normal part of stand development and succession. Stem mortality is greatest in immature suckers and slows as stems mature. Eventually the mature stems die and the cohort deteriorates, but regeneration maintains aspen cover. This type of aspen mortality occurs at the stand scale and is due primarily to endogenous processes;
2. *Long-term successional loss*: Defined as a gradual decrease in aspen cover on the regional scale due to exogenous variables. For example, decreased habitat disturbance (i.e., fire suppression) may lead to reduced aspen regeneration and greater conifer establishment, while the introduction of disturbances like herbivory may result in increased sucker death. This type of aspen mortality can be viewed as ‘enhanced succession’, and results in a change in forest cover type from aspen-dominated to conifer-dominated;
3. *Large-scale, episodic decline*: Defined as multi-year episodes of unusually high overstory crown thinning, dieback, and mortality due to multiple exogenous variables. This type of aspen mortality usually has a well-defined onset and occurs at the landscape scale. Unlike the first two categories of aspen mortality, forest cover is lost following large-scale, episodic declines (i.e., aspen mortality outside natural forest succession).

In the following sections we discuss threats to aspen in north-central BC. There are several range-wide threats pertinent to aspen stands in this region, including: (1) pathogens and diseases; (2) changing fire regimes; (3) ungulate grazing; (4) forest management practices; and (5) climate change and drought. Where possible, we draw from region-specific literature; however, literature from surrounding regions in western Canada and the United States is also synthesized and discussed in context to north-central BC.

3.1 PATHOGENS AND DISEASE

Aspen is very prone to disease; infection and the resulting decay and eventual mortality are part of normal cohort dynamics and successional processes (Peterson and Peterson 1995). In fact, disease and decay are necessary for many of aspen’s ecological functions, including the creation of habitat features (e.g., nesting cavities and feeding sites) and nutrient cycling (Peterson and Peterson 1995; Callan 1998). Although disease is common in aspen, infection alone rarely causes mortality at a scale larger than the individual tree or clone (Callan 1998; Sturrock et al. 2011). However, when infection occurs as a secondary stressor in combination with primary stressors, such as drought, landscape-scale dieback and mortality can occur (Hogg et al. 2008; Sturrock et al. 2011; Worrall et al. 2013, 2015).

Within north-central BC, aspen stands are commonly infected with fungi and defoliating insects, including: stem cankers (e.g., *Cytospora* spp., *Ceratocystis* spp.), heart and butt rots (e.g., *Phellinus tremulae*), Venturia blight (*Venturia* spp.), aspen leaf miner (*Phyllocnistis populiella*), forest tent caterpillar (*Malacosoma disstria*), and satin

moth (*Leucoma salicis*) (Callan 1998; Westfall and Ebata 2016). Although rot-inducing fungi do not typically cause wide-spread damage, defoliating insects have the potential to do so during outbreak years. Aspen leaf miner in particular has caused significant defoliation in the Omineca Region, with 386,366 ha of defoliated aspen mapped in 2016 (Westfall and Ebata 2016). In addition, forest tent caterpillar damaged 135,768 ha of aspen in the region in 2016 (Westfall and Ebata 2016). Although these massive defoliation events have not yet caused large-scale aspen dieback and decline in north-central BC, there is the potential for this to occur if stands become impacted by other stressors, like the climatic variability associated with climate change (Hogg et al. 2013).

The impacts of climate change on forest disease are unpredictable, however, in general: “climate change will alter the life cycles and biological synchronicity of many forest trees and pathogens, resulting in changes in the distribution of [outbreak] events (Sturrock et al. 2011).” In particular, climate change is predicted to impose greater overall primary stressors (e.g., drought, warmer temperatures) on forest trees, likely increasing tree susceptibility to secondary infection and mortality (Sturrock et al. 2011; Hogg et al. 2013). As we discuss in section 3.5, significant aspen dieback and declines have been documented in western North America and attributed to the combined impacts of climate-change-related droughts and subsequent infection by defoliating insects (Hogg et al. 2008, 2013, Worrall et al. 2013, 2015).

3.2 CHANGING FIRE REGIMES

Aspen is known to regenerate prolifically following disturbance, however, the importance of disturbance to stand initiation and persistence is dependent on whether the stand is seral or persistent (Kurzel et al. 2007; Krasnow and Stephens 2015). In western Colorado, the development of seral aspen stands is dependent on severe fire disturbance, whereas aspen regeneration occurs in persistent stands in the absence of severe disturbance (Kurzel et al. 2007). Within north-central BC, aspen is associated primarily with the Sub-Boreal Spruce (SBS) and Boreal White and Black Spruce (BWBS) biogeoclimatic zones (Peterson and Peterson 1995). The SBS and BWBS zones experience stand-replacing fires approximately every 125-200 years (Wong et al. 2003). However, in the SBS zone, these intervals increase along a moisture gradient: fire cycles range from 125 years in the dry subzone, to 244 years in the moist subzone, to 500 years in the wet subzone (Wong et al. 2003). This variation in timing of stand replacement creates a mosaic of early successional deciduous-dominated and late successional conifer-dominated forests (Meidinger and Pojar 1991; BC Ministry of Forests 1998). As such, aspen in north-central BC can be considered seral and dependent on high-severity, stand-replacing disturbances for initiation and persistence.

There is significant evidence linking disturbance by high-severity fire to aspen regeneration and initial dominance in seral stands (Kurzel et al. 2007; Shinneman et al. 2013; Krasnow and Stephens 2015). Because of the general dependence of aspen on high-severity fire, fire suppression has been proposed as a factor contributing to conifer encroachment and subsequent aspen decline in North America (reviewed in Kulakowski et al. 2013). Changes in the fire regime in northeastern (Wallenius et al. 2011) and north-central BC (Wong et al. 2003) have dramatically reduced the percentage of land impacted by fire annually. Within the SBS zone, fire historically (1850-1970) disturbed an estimated 2% of the landscape, while more recently (1970-1990), only 0.15% of land has been impacted annually (Wong et al. 2003). This recent decline corresponds with the onset of fire suppression in north-central BC (Corbould 2002). Meyn et al. (2013)

found the decrease in annual area burned in BC over the last century corresponds to increased summer precipitation, suggesting both natural (i.e., climate) and anthropogenic (i.e., fire suppression) factors may be altering fire regimes. However, it is possible the fire cycles in north-central BC may not occur on temporal scales short enough for the last 50-100 years of fire suppression to impact forest succession and structure in this region (but see: Corbould 2002). If so, aspen loss in north-central BC due to conifer encroachment may be natural succession in a post-fire forest (i.e., aspen-dominated) returning to pre-fire state (i.e., conifer dominated).

In western Canada, climate change models predict fire regimes changing towards more frequent and severe fire events, and a doubling or tripling of area burned by the latter half of this century (Johnston et al. 2009). For disturbance-dependent species, like aspen, this change in fire regime may be beneficial. For aspen stands in the Sierra Nevada, greater fire severity yields increased aspen sprout density and growth rates post-fire (Krasnow and Stephens 2015). Thus, although warmer temperatures and droughts associated with climate change may impose stress on aspen (see section 3.5), more frequent, high-severity fires may provide an opportunity for aspen to regenerate and persist on the landscape (Krasnow and Stephens 2015). In 2005, however, the BC government implemented the Forests for Tomorrow Program, which works to restore fire-impacted stands to a productive state by replanting conifers and limiting regeneration of deciduous trees (BC Ministry of Forests, Lands and Natural Resource Operations 2013). Consequently, aspen regeneration expected following large-scale, high-intensity fires may be inhibited by this program.

3.3 UNGULATE GRAZING

Early seral aspen forests provide important forage for many ungulates, as aspen has higher nutrient and protein content than other deciduous species (McCulloch and Kabzems 2009; Seager et al. 2013). Prolonged or high-intensity grazing, however, can impede aspen regeneration and stand persistence (Suzuki et al. 1999; Kay and Bartos 2000; Smith et al. 2011; Seager et al. 2013; Kaufmann et al. 2014). In north-central BC, aspen is an important forage species for moose (*Alces alces*), particularly in stands regenerating following fire or harvest (Blood 2000; Rea and Booth 2011). In a simulated browsing experiment, Carson et al. (2009) demonstrated mechanical damage inflicted on aspen stems by moose browsing stimulates biomass production. However, the realized benefit of browsing on aspen regeneration is dependent on both aspen density and grazing intensity. Field data from three northern BC study areas (Grouse Mountain prescribed burn, Inga Lake site preparation trial, Babine River watershed) indicate that browsing by moose and other ungulates can prevent successful aspen regeneration when aspen sucker densities are relatively low (Personal Communication: Sybille Haeussler, March 6, 2018). Further, field studies have shown heavily browsed aspen stems grow at a slower rate than lightly browsed stems (Conway and Johnstone 2017), with browsing beginning to negatively impact growth following >40% sucker biomass removal growth (Jones et al. 2009; Bartos et al. 2014)

There is concern that clearcut harvesting in BC may concentrate ungulates in these high-quality foraging habitats, resulting in high-intensity browsing and aspen overgrazing. Although this theory has yet been investigated, field evidence from the Cariboo Region suggests wild ungulate browsing inhibits aspen sucker growth regeneration in clearcut sites. However, this relationship was dependent on habitat type: in drier, less productive habitat, ungulate browsing impeded aspen sucker growth and allowed for greater conifer

establishment within cutblocks, whereas browsing had negligible effects in moister, more productive habitat (Personal Communication: Nick Hamilton, March 12, 2018).

Within BC, a large proportion of available livestock forage is under aspen and mixed wood stands, thus, overgrazing may be of concern to aspen stand management (Peterson and Peterson 1995). However, in a study near Dawson Creek, BC, Krzic et al. (2003, 2005) found 4-10 years of cattle grazing had no significant impact on aspen regeneration and cover. Likewise, neither aspen recruitment nor basal area are impacted by cattle grazing in the Cariboo Region (Personal Communication: Nick Hamilton, March 12, 2018). Further, cattle grazing is not common in north-central BC; thus, any potential impacts of cattle in this region are likely negligible.

3.4 FOREST MANAGEMENT PRACTICES

British Columbia has a unique history with aspen; a history of suppression, herbicide treatment, and removal (Peterson and Peterson 1995; Vyse and Simard 2007; Dhar et al. 2015). Perhaps the greatest driver of aspen abundance in north-central BC is forest management practices that actively remove aspen from the landscape (Personal Communication: Dr. Ché Elkin March 6, 2018). Although the ecological value of aspen in the forests of BC is recognized (Pojar 1995; Manning et al. 2001), management of the hardwood is region-specific and retention is dependent primarily on commercial value (McCulloch and Kabzems 2009). In north-central BC (Cariboo, Omineca, Skeena Regions), the hardwood has little economic value, and consequently is generally viewed and managed as a competitor with highly-valued conifer species (Haeussler and Coates 1986; BC Ministry of Forests 2000; Vyse and Simard 2007; Harper 2015, 2017). Whereas in northeastern BC (Northeast Region), the commercial use of aspen has significant commercial value, and thus, aspen is commonly promoted on the landscape (Chen et al. 1998; McCulloch and Kabzems 2009). Although the general trends are aspen suppression in north-central BC, and aspen encouragement in northeastern BC, there is variation between the forest regions with respect to the extent of aspen removal.

There are two general strategies for managing aspen at the stand level: (1) aspen or mixedwood objective, under which aspen growth is allowed, and (2) conifer objective, under which aspen growth is hindered to allow for pure conifer stands (McCulloch and Kabzems 2009; Fort St. John Pilot Project 2010). In north-central BC where aspen is not a crop species, forest management practices take a conifer objective. Following clearcut harvest, cutblocks are replanted with conifers and aspen regeneration is typically controlled by herbicides, brushing or girdling (McCulloch and Kabzems 2009). To put the extent of this removal into context, during the early 1990s, more than one million dollars was spent annually in the Prince George Forest Region on aspen control (DeLong and Tanner 1993). In northeastern BC, both the commercial and ecological benefits of aspen have been recognized and management practices in the region have evolved from serious removal to the balance between broadleaf retention and maximization of conifer growth (Greene et al. 2002; Comeau et al. 2005; Heineman et al. 2010). Here, forest management practices take a mixedwood objective (Fort St. John Pilot Project 2010). Although this approach allows for both conifer and deciduous cover on the landscape, intimate mixtures that simulate natural forest structure are rarely the goal. Rather, the designation of mixedwood cover is managed at the landscape level through the relative proportions of coniferous and deciduous volume contained within discrete, single species sites (McCulloch and Kabzems 2009; Fort St. John Pilot Project 2010). Under this “un-mix the mix” strategy,

aspen growth is inhibited in areas designated as coniferous cover through herbicide, brushing or girdling treatments.

Aspen is typically removed from conifer blocks in order for forest licensees to meet the free-growing requirements of the Provincial Forest and Range Practices Act (BC Ministry of Forests 2000; BC MFLNRO 2018), as aspen can compete with establishing conifers and potentially inhibit stand growth (Newsome et al. 2008, 2010; Heineman et al. 2009). In the SBS and BWBS zones of the Prince George Forest Region, the crop conifer must be 150% the height of competing vegetation within a 1 m radius to be considered free-growing (BC Ministry of Forests 2000). Field studies from the Cariboo Region, however, suggest this value should be reassessed, as aspen competition is not as serious of a problem in conifer blocks as previously thought. Here, 24 years of field data indicates aspen does not inhibit conifer growth unless >125% conifer height (Newsome and Heineman 2016). In addition, aspen density decreases naturally as stands age, with significant declines in aspen stem density by year 18 (Newsome and Heineman 2016). Crop conifer survival is similar in brushed and un-brushed stands (Heineman et al. 2009), indicating aspen-conifer competition does not inhibit conifer stand development in certain site series. Still, forest licensees commonly conduct manual brushing or herbicide treatments in conifer blocks (Newsome and Heineman 2016), as aspen removal nearly doubles the density of conifer stems classified as free-growing (Heineman et al. 2009). Thus, managed stands may achieve free-growing requirements sooner than stands left to progress naturally, providing incentive for forest licensees to remove aspen from the landscape even when removal is not necessary for crop conifer survival in select site series within the Cariboo Region.

3.5 DROUGHT AND CLIMATE CHANGE

Understanding the links between climate variability and tree mortality has been a focus of much current ecological research. Incidents of dramatic landscape-scale aspen dieback have been documented throughout the western United States and linked to climatic stressors. Sudden aspen decline was first observed in Colorado in 2004, and by 2008, 17% of the total aspen cover in the state (220,000 ha) had experienced significant dieback and mortality (Worrall et al. 2010). The disease subsequently spread in to new regions, and damaged a total of 535,000 ha of aspen throughout the western United States (Worrall et al. 2015). Severe drought prior to the onset of dieback was common to all affected regions, indicating moisture stress induced the declines (Worrall et al. 2010, 2015). In addition, severely impacted stands had poor regeneration (Worrall et al. 2013). Bell et al. (2014) found younger, less developed stands are less impacted by moisture stress, suggesting stand structure may mediate the effects of drought on aspen mortality. Thus, increasing aridity associated with climate change may lead to mortality of aging aspen stands and loss of mature aspen cover.

Within western Canada, similar aspen dieback has been noted in the parklands and boreal forests of Alberta and Saskatchewan since the early 1990s. Tree-ring analysis showed forests in these regions have experienced historical declines in aspen growth following periods of drought and infestation of defoliating insects (e.g., tent caterpillars) (Hogg et al. 2002, 2005, 2008, Chen et al. 2017, 2018). Most recently, a severe and widespread drought in 2001-2002 triggered extensive aspen dieback in the parklands and boreal forests of Alberta and Saskatchewan (Hogg et al. 2005; Michaelian et al. 2011). During the drought years, aspen in

these regions experienced a two-fold increase in mortality (Hogg et al. 2008), resulting in an estimated 28 Mt of dead biomass (Michaelian et al. 2011).

Incidents of drought-related aspen declines, like those described above, have been documented in other areas of western Canada and BC (Personal Communication: Ted Hogg, March 19, 2018). “While normal aspen mortality in a stand is approximately 2%/year, or 8%/over 4 years, mean stem mortality of 64%, 35%, 27% and 18% between 2012 – 2016 has been identified at monitoring sites in Dunvegan (BC Northeast Region), Poplar River (Northwest Territories), Notikewin (northern Alberta) and Fort Nelson (BC Northeast Region), respectfully (Personal Communication: Ted Hogg, March 19, 2018)” Further, provincial aerial overview surveys in 2016 documented 5,386 ha of aspen dieback province-wide, with the majority (5,234 ha) occurring in the Cariboo Region (Westfall and Ebata 2016). Smaller occurrences of aspen decline were documented in the Thompson/Okanagan Region (152 ha) and Skeena Region (single spot disturbance).

The stress of reduced soil moisture availability impacts aspen growth immediately and directly, but also indirectly through physiological lags, such as carbohydrate exhaustion, and ecological lags, such as insect infection, that intensify and prolong the negative impacts of drought (Hogg et al. 2013). The incidences of aspen decline described above have been linked to the synergistic effects of drought and insect/fungal infections (Hogg et al. 2008, 2013, Worrall et al. 2013, 2015). Climate change is predicted to alter disease-host interaction, directly through climate-related stressors (e.g., increased drought), but also indirectly by altering disease pathogenicity and host susceptibility to infection (Sturrock et al. 2011). While the effects of climate change on pathogens and their hosts are ultimately context-specific, climate change is generally predicted to alter the phenological synchrony of pathogens and their hosts, resulting in changes in disease incidence and severity (Sturrock et al. 2011).

Projections for future aspen distribution in BC show that climatically suitable habitat for aspen will decrease in area and shift to higher latitudes and elevations (Hamann and Wang 2006; Gray and Hamann 2013). By mid-century, aspen is predicted to decline in the SBS and BWSB zones by 0.3% and 1.8%, respectively (Hamann and Wang 2006). The impacts of climate change on aspen distribution are primarily related to forecasted changes in temperature and moisture regimes. For example, in the BWBS zone of northeastern BC, it is predicted that climate change will have negative effects on aspen currently located moisture limiting areas and positive effects on aspen in areas that are not moisture limited (Leonelli et al. 2008). In northern BC, moisture regimes are generally nival, with inputs dominated by snow runoff (Schnorbus et al. 2014). In the Peace River Region, 54% of annual precipitation falls as snow, and 64% of streamflow occurs during freshet months of May-July (Schnorbus et al. 2014). Although annual precipitation has increased (+12% per century) province-wide from 1900-2013, average temperatures have warmed (+1.4°C per century) province-wide, snow packs have declined (-5% per century) in the Central Interior, and the bulk of runoff and river flow is occurring earlier in the year (British Columbia Ministry of Environment 2016). Climate models predict these trends to continue into the latter decade of this century, and the future climate of BC is expected to be warmer with increased precipitation, but reduced runoff during the summer and fall (Schnorbus et al. 2014; British Columbia Ministry of Environment 2016). Consequently, aspen stands in

north-central BC may experience both heat and moisture stress during the growing season, and become increasingly susceptible to climate-related declines.

4.0 ASPEN AND SHALLOW WATER WETLANDS: A CASE STUDY OF THE BEAVER

Approximately 13% of Canada's terrestrial area is comprised of wetlands, representing almost 25% of the remaining wetlands in the world (Environment and Climate Change Canada 2016). Most of Canada's wetlands (25%) can be found within the boreal landscape (Environment and Climate Change Canada 2016) where they are essential to ecosystem function and the support of wildlife (Foote and Krogman 2006; Martell et al. 2006). One mammal of particular interest for its relationship to aspen is the North American beaver (*Castor canadensis*). The beaver is often considered a keystone species (Naiman et al., 1986; Pollock et al., 2015), or perhaps more accurately, as a keystone modifier (Mills et al., 1993) or ecosystem engineer (Rosell et al., 2005), because of its ability to structure its surrounding ecological community through its feeding and dam building behaviours (Martell 2004; Martell et al. 2006; Pollock et al., 2015). Beavers eat the leaves, twigs and bark of woody plants and herbaceous plants that grow near water (Chabreck, 1958; Jenkins and Busher, 1979), and show a strong preference for aspen, followed by willow (*Salix* spp.), for both forage and dam construction material (Hall 1960; Jenkins and Busher 1979; Naiman et al. 1988; Peterson and Peterson 1992). Thus, it is of little coincidence that the range of aspen and the beaver across North America resemble each other (Hall 1960; Müller-Schwarze and Sun 2003). In the United States, the restoration of aspen forests has been said to be important for promoting habitat for the beaver, and, therefore, the presence of beaver-created wetlands (Beck et al. 2010). This raises the question of whether changes in aspen abundance and distribution can influence the presence of the North American beaver and ultimately the occurrence of shallow water wetlands on the landscape in north-central BC.

Little research has been conducted on the impact of aspen decline on the North American beaver. To our knowledge, only one instance of beaver decline has been attributed to the loss of aspen (Yellowstone National Park, United States; see Smith and Tyers 2012). More commonly, aspen declines are attributed to beaver herbivory; beaver harvest aspen with such preference that they can clear an area of aspen and colony abandonment may result (Province of British Columbia 1988; Clements 1991; Rosell et al. 2005; Bergeron et al. 2014). Beaver harvesting activities result in opening of the canopy, which can release understory conifers and accelerate successional process (Johnston and Naiman 1990; Martell 2004; Bergeron et al. 2014). Selective aspen harvest can lead to a reduction of suitable habitat for beaver (Fryxell 2008), thus managers may have to intervene in beaver-harvested areas to ensure aspen regeneration (Peterson and Peterson 1992) and beaver colony reestablishment can occur (Beck et al. 2010).

The classification of ecosystem engineer, or keystone species, is often applied to the beaver because their dam building and foraging behaviors have cascading ecological impacts on the surrounding landscape (Rosell et al., 2005). Through dam construction, beaver are responsible for creating and maintaining many of the wetlands in boreal regions of Canada (Naiman et al. 1986; Pastor and Naiman 1992; Martell 2004; Martell et al. 2006). Specifically, beaver dams work to create stream systems with slow, deep water pools and wetlands (Pollock et al., 2015). These wetlands provide a variety of ecological benefits that include: reducing freshet volumes, promoting waterfowl habitat, increased groundwater recharge, increased late season water flows downstream, decreased peak flows, expanded habitat area and complexity, increased wetland area, sediment retention, moderation of water temperatures, nutrient cycling, and containment of contaminants (Naiman et al. 1986; Naiman et al. 1988; reviewed in Pollock et al. 2003; Burchsted and Daniels 2014).

Research specific to aspen and the beaver's role in the creation and maintenance of wetlands is sparse in BC. One study of beaver colony density near Prince George, BC showed that the length of aspen along the shorelines of lakes (but not streams) was important in predicting colony density (Slough and Sadleir 1977). In the boreal and sub-boreal regions of BC aspen is more associated with upland areas than riparian areas (Personal Communication: Richard Kabzems, Will Mackenzie, March 6, 2018), which can likely be attributed in part to the region's moisture regime of fresh-moist soils and an intolerance to flooding (McCulloch and Kabzems 2009). Still, it is unknown how the presence of beaver-formed wetlands is impacted by aspen abundance in this region. Other woody deciduous species, such as willow and alder (*Alnus* spp.), are also considered key plants in a beaver's habitat because they can withstand beaver flooding (Slough and Sadleir 1977). These species are common along water in north-central BC (Slough 1978). Outside of the province, research suggests beaver can thrive in the absence of aspen by relying on other woody plants (Hall 1960; Jenkins 1975; Barnes and Dibble 1988). A local example of this is documented by a 2013 study in the sub-boreal forests east of Prince George, BC, in which the forage selection of beavers across eight riparian areas show preference for willow species when aspen is sparse (Gerwing et al. 2013). Furthermore, a recent study in northeastern BC found that deciduous vegetation class richness (a measure of habitat quality) near open water is positively associated with the occurrence of beaver on the landscape (Mumma et al. 2018), suggesting the presence of multiple deciduous vegetation types is important to support beaver in northern BC. Although there is little literature pertaining to aspen and beaver in BC, the existing literature, as well as input from regional experts, suggests that for the successful management of beaver and associated wetlands one should consider aspects that influence the availability and quality of all deciduous vegetation in proximity to water rather than aspen alone.

The lack of research in BC on the importance of the beaver and their creation of wetlands makes them vulnerable to forestry practices that can impact their habitat (Green and Westbrook 2009). To maintain beaver habitat on the landscape, aspen, cottonwood (*Populus balsamifera* subsp. *trichocarpa*) and willow are typically retained within 30 m of streams or lake shores, with an ideal mix of young stems for food and older stems for dam building (Peterson and Peterson, 1995). However, Martell (2004) argues that riparian buffer requirements of 30 m for forest harvesting is inadequate for the beaver in the mixedwood boreal forests of Alberta. Under the Forest and Range Practices Act of British Columbia, only riparian areas classified as S1B, S2, and S3 (fish bearing streams of widths 20-100 m, 5-19 m, and 1.5-4 m respectively) have riparian reserve zones (buffers) that prevent the cutting and removal of trees within 50 m, 30 m, and 20 m (respectively) of the water edge (BC MFLNRO, 2018). Beavers typically require 50-60 m of forgeable land adjacent to the water in the mixedwood boreal, in addition to the 15-20 m consumed by a beaver-created wetland (Martell 2004). After flooding, this would leave only 0-25 m of harvestable land, depending on the size of the stream, which is less than 50% of the required land needed to sustain a beaver population. Furthermore, the maximum buffer required to be left adjacent to an existing wetland in the province of BC is only 10 m (BC MFLNRO, 2018), which based on the literature, is inadequate to support a beaver population.

5.0 CONCLUSIONS AND RECOMMENDATIONS

Compared to much of North America, little is known about the trends in aspen abundance in BC. With the future projections of climate threatening aspen abundance and distribution, it is necessary to establish continued research and monitoring of aspen in the province. Although there have been aspen declines documented in BC, there is little historical distribution data to compare these trends with. Without this baseline data, it is impossible to assess whether current and future trends are outside historical norms. In seral forests, such as those in north-central BC, declines in aspen cover is inherent to normal successional processes. Thus, in order to evaluate changes in aspen cover, it is necessary to consider the pre-disturbance state of the stand. In a study conducted in Colorado, USA, Kulakowski et al. (2006) found most post-fire aspen stands that were being replaced by conifers were conifer-dominated prior to the last severe fire, indicating the loss in aspen cover was part of normal stand succession. Although this point may be valid in fire-impacted stands, the dynamics of aspen loss in managed stands differ.

Through this review, we have identified forest management practices as the greatest threat to aspen in north-central BC, and it is perhaps because of these practices that there is little to no research on trends of aspen abundance in the region. The degree to which aspen removal is necessary for crop conifer survival in the Omineca and Skeena Regions is uncertain. However, under current free-growing guidelines for these Regions, managed stands may achieve free-growing requirements sooner than stands left to progress naturally, providing incentive for forest licensees to remove aspen from the landscape. To rectify this, we recommend free growing guidelines for the Skeena and Omineca Regions be reevaluated to more accurately reflect the impacts of aspen competition on crop conifer survival and growth, as has been done in the Cariboo Region (Newsome and Heineman 2016).

With such a strong relationship between beaver and aspen it is surprising that little research has explored the impacts of aspen decline on the species. Future research into the effects of aspen distribution and abundance on the beaver should be explored, especially in areas of serious documented aspen declines (e.g. Hogg et al., 2008; Worrall et al., 2008). In the sub-boreal and boreal regions of BC, future research into factors that can impact aspen and other important riparian deciduous vegetation should be investigated, especially given that existing forest management practices appear to be inadequate for supporting the beaver. As previously discussed, aspen and other broadleaf species are managed as a competitor to crop conifer species in much of northern BC (Newsome et al. 2008; Heineman et al. 2010), resulting in the suppression of aspen and other broadleaves to ensure conifer success (Roach 2013; Harper 2015, 2017). Because conifers are often selected against by the beaver (Jenkins 1975; Slough 1978) the suppression of broadleaves outside of the 10m riparian buffer areas could be detrimental to beaver.

The need for more research is also crucial when considering climate change, as it is expected to alter the abundance and distribution of aspen and other broadleaf species in BC (Hamann and Wang 2006; Gray and Hamann 2013). Furthermore, the presence of beaver has the potential to offset the effects of climate change induced loss of wetlands (Dittbrenner et al. 2018) which necessitates the promotion and protection habitat that can support beaver populations in the province. For management plans intended to increase or support beaver created wetlands in northern BC it is unlikely that managing aspen alone will be successful. Other species, especially willow, appear to be just as important for beaver within British Columbia and outside as

well. Furthermore, there are many other factors to consider when planning to promote beaver activity that must be considered (e.g. abiotic factors such as stream width), however, these are outside the scope of this review (see Pollock et al. 2015).

In conclusion, there is a general dearth of information regarding aspen in north-central BC. Specifically, knowledge gaps exist with respect to reference information for the historic norms for aspen distribution, and the importance of aspen to beaver habitat and shallow water wetlands. To fill these knowledge gaps, we recommend future research in the following areas:

1. Quantify historical and current trends in aspen distribution in the region, both in upland forest and adjacent to shallow water wetlands, in order to determine whether or not changes in aspen cover are within historical norms.

There are documented instances of aspen decline in parts of BC, but there is little reference information on the historical distribution of aspen. It is debated that recent decline in aspen are within historical norms (Kulakowski et al. 2006, 2013b). Without baseline data on aspen distribution there will continue to be uncertainty on whether the current and future trends in aspen distribution and abundance are outside of historical norms.

There appears to be 3 key case studies on which the investigation of this research question can draw methodological examples from:

- i) Kulakowski et al. (2006) employed a 1 : 253,000 scale geo referenced map of vegetation and fire occurrence from 1898 and modern USFS map (1998) to examine trends in aspen dominance in a 348,586 ha area in north-western Colorado. Thirty aspen-dominated stands (10 aspen burned, 10 burned spruce-fir, and 10 unburned aspen) were then sampled in the field to identify the age of the aspen stands and influence of pre-disturbance vegetation on aspen (Kilakowski et al., 2006).
- ii) In a study completed by Halabisky et al. (2017), Landsat archived images were used to map wetlands across the Columbia Plateau Ecoregion to reconstruct the hydrologic dynamics over a 30 year time period. The 30-meter Landsat pixels provide a snapshot every 16 days dating back to 1972. This study successfully reconstructed wetland hydrology across an ecoregion. However, there is uncertainty regarding the accuracy of the technique for mapping hydrology in areas with canopy interference.
- iii) Conversation with Alex Bevington, of the Ministry of Forests, Lands and Natural Resource Operations and Rural Development, are planned for the near future to explore the use of aerial and satellite imagery to answer this question. Potential issues when using aerial photos do include, differentiating aspen percent composition from other broadleaf species.

It is clear that the next step in this study will need to be led by data, in order to provide an objective understanding of historical aspen abundance and distribution in north-central BC. The most defensible approach for a future study is one based around a chronosequene of photos or satellite imagery that allows for change in wetland size or canopy composition to be interpreted. Ground truthing and surveys using a

randomized sampling method can then be employed to quantify aspen and deciduous stems and percentage canopy composition in the identified upland forest or riparian areas.

Discussions with regional experts further identified the BC Vegetation Resources Inventory as a valuable resource, along with Predicted Ecosystem Mapping. The literature and discussions with regional experts also indicate that aspen is a foundational species that is important to biodiversity and ecosystem processes. Thus, any data gathering exercise should work to identify canopy composition to species level, ensuring that the aspen component relative to other broadleaf species is quantified, as this could have implications on biodiversity.

2. Assess the competitive impacts of aspen on crop conifers in the region, and use these findings to reevaluate and inform free growing guidelines, forest management practices and the Forests for Tomorrow Program strategies that actively limit the regeneration of deciduous trees.

Consistent feedback from northern experts is that the biggest threat to aspen in north-central BC, excluding the Northeast, is likely forest management practices that remove/reduce broadleaf presence in young plantations. This was identified as a policy issue, which seeks to reduce broadleaf competitors within managed stands. There was consistent opinion that aspen is unlikely to be threatened in any significant way in the near future, and that it may in fact do better in northern British Columbia under future climate change scenarios. However, synergistic impacts of drought, insects, and disease could create a negative scenario for the aspen that is difficult to predict.

Questions were raised by northern experts during discussions on whether forest management practices that remove/reduce broadleaf presence in young plantations may be, in part, unnecessary in terms of crop tree survival. The practice of broadleaf removal is currently incentivized, as managed stands can achieve free-growing requirements sooner than a stand left to progress naturally. Currently, the extent to which broadleaf species compete with crop conifers in the Skeena and Omineca Regions may not be entirely clear. Future studies that investigate this question could include the methodology employed by Newsome et al. (2008; 2010) and Newsome and Heineman (2016) in the Cariboo Region. This being said, the absence of baseline information (reference conditions) on the abundance and distribution of aspen on the landscape and how this compares with historical norms is uncertain. If the goal is to restore aspen on the landscape so that it is comparable with the historical abundance and distribution (reference condition), then the historical distribution of aspen in the region must first be quantified.

3. Evaluate the effectiveness of current forest management practices on maintaining riparian habitat, and the effects of riparian hardwood (i.e., aspen, cottonwood and willow) abundance on beaver populations and, subsequently, shallow water wetland persistence and distribution.

A concern raised by SERNbc and Torsten Kaffanke is that practices that prevent the periodic renewal/replacement/re-invigoration of aspen along stream and shallow water wetlands could negatively impact the long-term hydrologic properties of catchments as a whole. In addition to this, the literature indicates that forest management processes that reduce deciduous forage within 50 – 60 m adjacent to water in the mixedwood boreal may be inadequate to support beaver populations. Given the cascading ecological benefits associated water impoundment by beaver, further investigation of this subject is warranted.

It is understood that both beaver activity and aspen availability is a cyclical process. Periods of active beaver colonization and then subsequent abandonment appears to be driven, in part, by the abundance of aspen, but also willow, and perhaps alder and cottonwood. The extent to which beaver colony abandonment is tied to aspen specifically remains unclear. Future research could employ the mapping, aerial photo, or satellite imagery based approaches described by Kulakowski et al. (2006) and Halabisky et al. (2017) to help in quantifying this relationship between aspen and deciduous canopy cover on beaver activity, and shallow water wetland persistence and distribution. It is our recommendation that the first step in answering this question is to quantify historical and current trends in aspen distribution in the region. This will determine whether or not changes in aspen distribution and abundance in north-central BC is within historical norms.

6.0 LITERATURE CITED

- B.C. Ministry of Forests, Lands and Natural Resource Operations (BC MFLNRO). 2018. Forest and Range Practices Act.
- Barnes, W. J., and E. Dibble. 1988. The effects of beaver in riverbank forest succession. *Can. J. Bot.* 66:40–44.
- Bartos, D. L., and R. B. Campbell. 1998. Decline of quaking aspen in the Interior West - examples from Utah. *Rangel.* 20 1 17-24 17–24.
- Bartos, D. L., K. Tshireletso, and J. C. Malechek. 2014. Response of Aspen Suckers to Simulated Browsing. *For. Sci.* 60:402–408.
- BC Ministry of Forests. 1998. The ecology of the sub-boreal spruce zone. British Columbia Ministry of Forests, Victoria, BC.
- BC Ministry of Forests. 2000. Establishment to free growing guidebook. Prince George Forest Region. Rev. ed., Version 2.2. *For. Prac. Br., B.C. Min. For., Victoria, B.C. Forest Practices Code of British Columbia Guidebook.*
- Beck, J. L., D. C. Dauwalter, K. G. Gerow, and G. D. Hayward. 2010. Design to monitor trend in abundance and presence of American beaver (*Castor canadensis*) at the national forest scale. *Environ. Monit. Assess.* 164:463–479.
- 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.
- Bergeron, Y., H. Y. H. Chen, N. C. Kenkel, A. L. Leduc, and S. E. Macdonald. 2014. Boreal mixedwood stand dynamics: ecological processes underlying multiple pathways. *For. Chron.* 90:202–213.
- Blood, D.A. 2000. Moose in British Columbia: ecology, conservation and management. British Columbia Ministry of Environment, Lands and Parks, Victoria, BC.
- Brandt, J. P., H. F. Cerezke, K. I. Mallett, W. J. A. Volney, and J. D. Weber. 2003. Factors affecting trembling aspen (*Populus tremuloides* Michx.) health in the boreal forest of Alberta, Saskatchewan, and Manitoba, Canada. *For. Ecol. Manag.* 178:287–300.
- British Columbia Ministry of Environment. 2016. Indicators of climate change for British Columbia, 2016 update. British Columbia Ministry of Environment, Victoria.
- Burchsted, D., and M. D. Daniels. 2014. Classification of the alterations of beaver dams to headwater streams in northeastern Connecticut, U.S.A. *Geomorphology* 205:36–50.
- Callan, B.E. 1998. Diseases of *Populus* in British Columbia: A Diagnostic Manual. Natural Res. Canada, Canadian For. Service, Victoria, B.C. 157 pp.
- Campbell, C., I. D. Campbell, C. B. Blyth, and J. H. McAndrews. 1994. Bison extirpation may have caused aspen expansion in western Canada. *Ecography* 17:360–362.
- Carson, A. W., R. V. Rea, and A. L. Fredeen. 2009. Compensatory Shoot Growth in Trembling Aspen (*Populus tremuloides* Michx.) in Response to Simulated Browsing. *Alces* 45:101–108.
- Chabreck, R.H. 1958. Beaver-forest relationships in St. Tammany Parish, Louisiana. *Journal of Wildlife Management.* 22, 179-183.
- Chen, H. Y. H., K. Klinka, and R. D. Kabzems. 1998. Height growth and site index models for trembling aspen (*Populus tremuloides* Michx.) in northern British Columbia. *For. Ecol. Manag.* 102:157–165.

- Chen, H. Y., P. V. Krestov, and K. Klinka. 2002. Trembling aspen site index in relation to environmental measures of site quality at two spatial scales. *Can. J. For. Res.* 32:112–119.
- Chen, L., J.-G. Huang, A. Dawson, L. Zhai, K. J. Stadt, P. G. Comeau, and C. Whitehouse. 2018. Contributions of insects and droughts to growth decline of trembling aspen mixed boreal forest of western Canada. *Glob. Change Biol.* 24:655–667.
- Chen, L., J.-G. Huang, S. A. Alam, L. Zhai, A. Dawson, K. J. Stadt, and P. G. Comeau. 2017. Drought causes reduced growth of trembling aspen in western Canada. *Glob. Change Biol.* 23:2887–2902.
- Clair, S. B. S., J. Guyon, and J. Donaldson. 2010. Quaking Aspen's Current and Future Status in Western North America: The Role of Succession, Climate, Biotic Agents and Its Clonal Nature. Pp. 371–400 in *Progress in Botany 71*. Springer, Berlin, Heidelberg.
- Clements, C. 1991. Beavers and riparian ecosystems. *Rangel. USA*.
- Comeau, P. G., R. Kabzems, J. McClarnon, and J. L. Heineman. 2005. Implications of selected approaches for regenerating and managing western boreal mixedwoods. *For. Chron.* 81:559–574.
- Conway, A. J., and J. F. Johnstone. 2017. Moose alter the rate but not the trajectory of forest canopy succession after low and high severity fire in Alaska. *For. Ecol. Manag.* 391:154–163.
- Corbould, F.B. 2002. Ingenika River prescribed burn, 2001. Peace/Williston Fish and Wildlife Compensation Program, Report No. 249. 8pp plus appendices.
- DeByle, N., C. D. Bevins, and W. C. Fischer. 1987. Wildfire occurrence in aspen in the interior western United States. *West. J. Appl. For.* 2:73–76.
- DeByle, N.V., Winokur, R.P. 1985. Aspen: Ecology and management in the western United States. USDA.
- DeLong, C., and D. Tanner. 1993. Effect of Aspen Competition on Survival and Growth of Lodgepole Pine and White Spruce. P. in P. G. Comeau, G. J. Harper, M. E. Blache, J. O. Boateng, and K. D. Thomas, eds. *Ecology and Management of B.C. Hardwoods: Workshop Proceedings*. B.C. Ministry of Forests.
- Dhar, A., J. Wang, and C. Hawkins. 2015. Interaction of Trembling Aspen and Lodgepole Pine in a Young Sub-Boreal Mixedwood Stand in Central British Columbia. *Open J. For.* 129–138.
- Di Orio, A. P., R. Callas, and R. J. Schaefer. 2005. Forty-eight year decline and fragmentation of aspen (*Populus tremuloides*) in the South Warner Mountains of California. *For. Ecol. Manag.* 206:307–313.
- Dittbrenner, B. J., M. M. Pollock, J. W. Schilling, J. D. Olden, J. J. Lawler, and C. E. Torgersen. 2018. Modeling intrinsic potential for beaver (*Castor canadensis*) habitat to inform restoration and climate change adaptation. *PLOS ONE* 13:e0192538.
- Environment and Climate Change Canada. 2016. Canadian Environmental Sustainability Indicators: Extent of Canada's Wetlands. Environment and Climate Change Canada.
- Foote, L., and N. Krogman. 2006. Wetlands in Canada's western boreal forest: Agents of Change. *For. Chron.* 82:825–833.
- Fort St. John Pilot Project. 2010. Mixedwood management guidelines. Available from: http://www.fsjpilotproject.com/documents/Appendix_10_Mixedwood_Mgt_Guidelines_2010_05_07.pdf
- Frey, B. R., V. J. Lieffers, E. Hogg, and S. M. Landhäusser. 2004. Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. *Can. J. For. Res.* 34:1379–1390.

- Frey, B. R., V. J. Lieffers, S. M. Landhäusser, P. G. Comeau, and K. J. Greenway. 2003. An analysis of sucker regeneration of trembling aspen. *Can. J. For. Res.* 33:1169–1179.
- Fryxell, J. M. 2008. Habitat suitability and source–sink dynamics of beavers. *J. Anim. Ecol.* 70:310–316.
- Gerwing, T. G., C. J. Johnson, and C. Alström-Rapaport. 2013. Factors influencing forage selection by the North American beaver (*Castor canadensis*). *Mamm. Biol. - Z. Für Säugetierkd.* 78:79–86.
- Gill, N. S., F. Sangermano, B. Buma, and D. Kulakowski. 2017. *Populus tremuloides* seedling establishment: An underexplored vector for forest type conversion after multiple disturbances. *For. Ecol. Manag.* 404:156–164.
- Gray, L. K., and A. Hamann. 2013. Tracking suitable habitat for tree populations under climate change in western North America. *Clim. Change* 117:289–303.
- Green, K. C., and C. J. Westbrook. 2009. Changes in riparian area structure, channel hydraulics, and sediment yield following loss of beaver dams. *J. Ecosyst. Manag.* 10.
- Greene, D. F., D. D. Kneeshaw, C. Messier, V. Lieffers, D. Cormier, R. Doucet, K. D. Coates, A. Groot, G. Grover, and C. Calogeropoulos. 2002. Modelling silvicultural alternatives for conifer regeneration in boreal mixedwood stands (aspen/white spruce/balsam fir). *For. Chron.* 78:281–295.
- Haeussler, S. and A. de Groot. 2008. Effects of Prescribed Burning on Aspen Mortality and Vigour. Unpublished report prepared for the Bulkley Valley Research Centre, Smithers, BC.
- Haeussler, S., and K. D. Coates. 1986. Autecological characteristics of selected species that compete with conifers in British Columbia: a literature review. British Columbia Ministry of Forests, Victoria, B.C.
- Halabisky, M., SY Lee, S. D. Hall, and M. Rule. 2017. Can We Conserve Wetlands Under A Changing Climate? Mapping wetland hydrology across an ecoregion and developing climate adaptation recommendations. Technical Report.
- Hall, J. G. 1960. Willow and Aspen in the Ecology of Beaver on Sagehen Creek, California. *Ecology* 41:484–494.
- Hamann, A., and T. Wang. 2006. Potential Effects of Climate Change on Ecosystem and Tree Species Distribution in British Columbia. *Ecology* 87:2773–2786.
- Hamann, A., P. Smets, A. D. Yanchuk, and S. N. Aitken. 2005. An ecogeographic framework for in situ conservation of forest trees in British Columbia. *Can. J. For. Res.* 35:2553–2561.
- Hanna, P., and D. Kulakowski. 2012. The influences of climate on aspen dieback. *For. Ecol. Manag.* 274:91–98.
- Harestad, A. S., Keisker, D. G. 1989. Nest tree use by primary cavity-nesting birds in south central British Columbia. *Canadian Journal of Zoology*, 67: 1067-1073.
- Harper, G. 2017. Lodgepole pine and trembling aspen competition: Neighbourhood studies within 22 to 39 year-old pine plantations of northern British Columbia. *For. Chron.* 93:226–240.
- Harper, G. 2015. Lodgepole pine and trembling aspen mixedwoods: Growth and yield within 22 to 39 year old pine plantations of northern interior British Columbia. *For. Chron.* 91:502–518.
- Heineman, J. L., D. L. Sachs, S. W. Simard, and W. Jean Mather. 2010. Climate and site characteristics affect juvenile trembling aspen development in conifer plantations across southern British Columbia. *For. Ecol. Manag.* 260:1975–1984.

- Heineman, J. L., S. W. Simard, D. L. Sachs, and W. J. Mather. 2009. Trembling Aspen Removal Effects on Lodgepole Pine in Southern Interior British Columbia: Ten-Year Results. *West. J. Appl. For.* 24:17–23.
- Hogg, E. H., J. P. Brandt, and B. Kochtubajda. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951–2000. *Can. J. For. Res.* 35:610–622.
- Hogg, E. H., J. P. Brandt, and M. Michaelian. 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Can. J. For. Res.* 38:1373–1384.
- Hogg, E. H., A. G. Barr, and T. A. Black. 2013. A simple soil moisture index for representing multi-year drought impacts on aspen productivity in the western Canadian interior. *Agric. For. Meteorol.* 178–179:173–182.
- Hogg, E. H., and M. Michaelian. 2015. Factors affecting fall down rates of dead aspen (*Populus tremuloides*) biomass following severe drought in west-central Canada. *Glob. Change Biol.* 21:1968–1979.
- Hogg, E. H., J. P. Brandt, and B. Kochtubajda. 2002. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Can. J. For. Res.* 32:823–832.
- Hogg, E., and P. Hurdle. 1995. The aspen parkland in western Canada: A dry-climate analogue for the future boreal forest? *Water, Air, Soil Pollut.* 82:391–400.
- Hood, G. A., and S. E. Bayley. 2009. A comparison of riparian plant community response to herbivory by beavers (*Castor canadensis*) and ungulates in Canada's boreal mixed-wood forest. *Forest Ecology and Management* 258:1979–1989.
- Huang, C.-Y., and W. R. L. Anderegg. 2012. Large drought-induced aboveground live biomass losses in southern Rocky Mountain aspen forests. *Glob. Change Biol.* 18:1016–1027.
- Jenkins, S. H. 1975. Food selection by beavers: A multidimensional contingency table analysis. *Oecologia* 21:157–173.
- Jenkins, S. H., and P. E. Busher. 1979. *Castor canadensis*. *Mamm. Species* 1–8.
- Jenkins, S.H. Food selection by beavers. 1975. *Oecologia*. 21, 157-173.
- Johnston, C. A., and R. J. Naiman. 1990. Browse selection by beaver: effects on riparian forest composition. *Can. J. For. Res.* 20:1036–1043.
- Johnston, M. H., M. Campagna, and Canadian Council of Forest Ministers. 2009. Vulnerability of Canada's tree species to climate change and management options for adaptation: an overview for policy makers and practitioners. Canadian Council of Forest Ministers, Ottawa, Ont.
- Jones, B. E., D. F. Lile, and K. W. Tate. 2009. Effect of Simulated Browsing on Aspen Regeneration: Implications for Restoration. *Rangel. Ecol. Manag.* 62:557–563.
- Jones, J. R. 1985. Distribution. Pp. 9–10 in N. V. DeByle and R. P. Winokur, eds. *Aspen: Ecology and Management in the Western United States*. USDA Forest Service.
- Kaufmann, J., E. W. Bork, M. J. Alexander, and P. V. Blenis. 2014. Effects of open-range cattle grazing on deciduous tree regeneration, damage, and mortality following patch logging. *Can. J. For. Res.* 44:777–783.
- Kay, C. E. 1997. Is aspen doomed? *J. For.* 95:4–11.
- Kay, C., and D. Bartos. 2000. Ungulate herbivory on Utah aspen: assessment of long-term exclosures. *J. Range Manag.* 53:145–153.

- Klinka, K., J. Worrall, L. Skoda, and P. Varga. 1999. The distribution and synopsis of ecological and silvical characteristics of tree species of British Columbia's forests. Canadian Cartographics Ltd., Coquitlam, B.C.
- Krasnow, K. D., and S. L. Stephens. 2015. Evolving paradigms of aspen ecology and management: impacts of stand condition and fire severity on vegetation dynamics. *Ecosphere* 6:1–16.
- Krzic, M., H. Page, R. Newman, and K. Broersma. 2005. Aspen regeneration, forage production, and soil compaction on harvested and grazed boreal aspen stands. *J. Ecosyst. Manag.* 5.
- Krzic, M., R. F. Newman, and K. Broersma. 2003. Plant species diversity and soil quality in harvested and grazed boreal aspen stands of northeastern British Columbia. *For. Ecol. Manag.* 182:315–325.
- Kulakowski, D., C. Matthews, D. Jarvis, and T. T. Veblen. 2013b. Compounded disturbances in sub-alpine forests in western Colorado favour future dominance by quaking aspen (*Populus tremuloides*). *J. Veg. Sci.* 24:168–176.
- Kulakowski, D., M. W. Kaye, and D. M. Kashian. 2013. Long-term aspen cover change in the western US. *For. Ecol. Manag.* 299:52–59.
- Kulakowski, D., T. T. Veblen, and B. P. Kurznel. 2006. Influences of infrequent fire, elevation and pre-fire vegetation on the persistence of quaking aspen (*Populus tremuloides* Michx.) in the Flat Tops area, Colorado, USA. *J. Biogeogr.* 33:1397–1413.
- Kulakowski, D., T. T. Veblen, and S. Drinkwater. 2004. The Persistence of Quaking Aspen (*Populus tremuloides*) in the Grand Mesa Area, Colorado. *Ecol. Appl.* 14:1603–1614.
- Kurznel, B. P., T. T. Veblen, and D. Kulakowski. 2007. A typology of stand structure and dynamics of Quaking aspen in northwestern Colorado. *For. Ecol. Manag.* 252:176–190.
- Landhäusser, S. M., D. Deshaies, and V. J. Lieffers. 2010. Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. *J. Biogeogr.* 37:68–76.
- Leonelli, G., B. Dennerler, and Y. Bergeron. 2008. Climate sensitivity of trembling aspen radial growth along a productivity gradient in northeastern British Columbia, Canada. *Can. J. For. Res.* 38:1211–1222.
- Manning, E. T., L. M. Darling, P. Chytyk, British Columbia, and Wildlife Branch. 2001. Woody debris and wildlife trees in aspen and mixed-wood forests of northeastern British Columbia. British Columbia Wildlife Branch, Victoria.
- Martell, K. A. 2004. Patterns of riparian disturbance in Alberta's boreal mixedwood forest; beavers, roads and buffers. University of Alberta, Edmonton, Alberta.
- Martell, K. A., A. L. Foote, and S. G. Cumming. 2006. Riparian disturbance due to beavers (*Castor canadensis*) in Alberta's boreal mixedwood forests: Implications for forest management. *Ecoscience* 13:164–171.
- Martin, K., Aitken, K. E., Wiebe, K. L. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. *The Condor.* 106: 5-19.
- McCulloch, L., and R. Kabzems. 2009. British Columbia's Northeastern Forests: Aspen Complex Stand Establishment Decision Aid. *J. Ecosyst. Manag.* 10.
- Meidinger, D. V., and J. Pojar (eds). 1991. *Ecosystems of British Columbia*. B.C. Ministry of Forests, Victoria, B.C.

- Meyn, A., S. Schmidtlein, S. W. Taylor, M. P. Girardin, K. Thonicke, and W. Cramer. 2013. Precipitation-driven decrease in wildfires in British Columbia. *Reg. Environ. Change* 13:165–177.
- Michaelian, M., E. H. Hogg, R. J. Hall, and E. Arseneault. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Glob. Change Biol.* 17:2084–2094.
- Mills, L.S., Soule, M.E., Doak, D.F. 1993. The keystone-species concept in ecology and conservation. *BioScience*. 43, 219-224.
- Müller-Schwarze, D., and L. Sun. 2003. *The Beaver: Natural History of a Wetlands Engineer*. Cornell University Press.
- Mumma, M. A., M. P. Gillingham, C. J. Johnson, and K. L. Parker. 2018. Where beavers (*Castor canadensis*) build: testing the influence of habitat quality, predation risk, and anthropogenic disturbance on colony occurrence. *Can. J. Zool.*, doi: 10.1139/cjz-2017-0327.
- Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American Streams by Beaver. *BioScience* 38:753–762.
- Naiman, R. J., J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem Alteration of Boreal Forest Streams by Beaver (*Castor canadensis*). *Ecology* 67:1254–1269.
- Naiman, R.J., Johnston, C.A., Kelley, J.C. 1988. How animals shape their ecosystems. 38, 753-762.
- Naiman, R.J., Melillo, J.M., Hobbie, J.E. 1986. Alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*. 67, 1254-1269.
- Natural Resources Canada. 2017. Climate impacts on health and productivity of aspen. Available from: <http://www.nrcan.gc.ca/forests/climate-change/impacts/13119>
- Newsome, T. A., J. L. Heineman, and A. F. L. Nemeč. 2008. Competitive interactions between juvenile trembling aspen and lodgepole pine: A comparison of two interior British Columbia ecosystems. *For. Ecol. Manag.* 255:2950–2962.
- Newsome, T. A., J. L. Heineman, and A. F. L. Nemeč. 2010. A comparison of lodgepole pine responses to varying levels of trembling aspen removal in two dry south-central British Columbia ecosystems. *For. Ecol. Manag.* 259:1170–1180.
- Newsome, T.A. and J.L. Heineman. 2016. Adjusting free-growing guidance regarding aspen retention in the Cariboo-Chilcotin: research to operational implementation. *Prov. B.C., Victoria, B.C. Tech. Rep.* 102. Available from: www.for.gov.bc.ca/hfd/pubs/Docs/Tr/Tr102.htm
- Nitschke, C. R., M. Amoroso, K. D. Coates, and R. Astrup. 2012. The influence of climate change, site type, and disturbance on stand dynamics in northwest British Columbia, Canada. *Ecosphere* 3:1–21.
- Oaten, D. K., Larsen, K. W. 2008. Aspen stands as small mammal “hotspots” within dry forest ecosystems of British Columbia. *Northwest Science*, 82: 276-285.
- Parsons, S., K. J. Lewis, and J. M. Psyllakis. 2003. Relationships between roosting habitat of bats and decay of aspen in the sub-boreal forests of British Columbia. *Forest Ecology and Management* 177:559–570.
- Pastor, J., and R. J. Naiman. 1992. Selective Foraging and Ecosystem Processes in Boreal Forests. *Am. Nat.* 139:690–705.
- Perala, A. D. 1990. *Populus tremuloides* Michx. Quaking aspen. Pp. 555–569 in R. M. Burns and B. H. Honkala, eds. *Silvics of North America, Vol. 2. Hardwoods*. Agriculture Handbook, No. 654. United States Department of Agriculture (USDA), Forest Service.

- Peterson, E. B., and N. M. Peterson. 1992. Ecology, management and use of aspen and balsam poplar in the prairie provinces, Canada. Special Report 1.
- Peterson, E. B., and N. M. Peterson. 1995. Aspen managers' handbook for British Columbia. Natural Resources Canada, Canadian Forest Service.
- Pojar, R. A. 1995. Breeding bird communities in aspen forests of the sub-boreal spruce (dk subzone) in the Prince George Forest Region. Province of British Columbia, Ministry of Forests Research Program, Victoria, B.C.
- Pollock, M. M., M. Heim, and D. Werner. 2003. Hydrologic and geomorphic effects of beaver dams and their influence on fishes. Pages 213-233 in S. V. Gregory, K. Boyer, and A. Gurnell, editors. The ecology and management of wood in world rivers. American Fisheries Society, Bethesda, Maryland.
- Pollock, M.M., Lewallen, G., Woodruff, K., Jordan, C.E., Castro, J.M. 2015. The beaver restoration guidebook: working with beaver to restore streams, wetlands, and floodplains. Version 1.02. United States Fish and Wildlife Service, Portland, Oregon. 189 pp.
- Powell, G.W., Bork, E.W. 2007. Effects of aspen canopy removal and root trenching on understory microenvironment and soil moisture. *Agroforest Syst.* 70, 113-124.
- Preston, C.M., Nault, J.R., Trofymow, J.A., Smyth, C., CIDET Working Group. 2009. Chemical changes during 6 years of decomposition of 11 litters in some Canadian forest sites: Part 1. Elemental composition, tannins, phenolics, and proximate fractions. *Ecosystems.* 12, 1053-1077.
- Province of British Columbia. 1988. Beaver Management Guidelines in British Columbia. Province of British Columbia, Wildlife Branch.
- Rea, R.V., Booth, A.L. 2011. Use of trembling aspen bark by moose in a browse-abundant habitat during winter. *Wildlife Afield.* 8:104-107.
- Rehfeldt, G. E., D. E. Ferguson, and N. L. Crookston. 2009. Aspen, climate, and sudden decline in western USA. *For. Ecol. Manag.* 258:2353–2364.
- Roach, J. 2013. Potential impacts of including broadleaf trees in managed boreal and sub-boreal forest stands in British Columbia: A literature review.
- Rogers, P. 2002. Using Forest Health Monitoring to assess aspen forest cover change in the southern Rockies ecoregion. *For. Ecol. Manag.* 155:223–236.
- Rogers, P. C. 2017. Guide to Quaking Aspen Ecology and Management with Emphasis on Bureau of Land Management Lands in the Western United States. Logan, Utah.
- Rogers, P. C., S. M. Landhäusser, B. D. Pinno, and R. J. Ryel. 2014. A Functional Framework for Improved Management of Western North American Aspen (*Populus tremuloides* Michx.). *For. Sci.* 60:345–359.
- Rosell, F., Bozser, O., Collen, P., Parker, H. Ecological impacts of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review.* 35, 248 – 276,
- Sankey, T. T. 2008. Learning from spatial variability: Aspen persistence in the Centennial Valley, Montana. *For. Ecol. Manag.* 255:1219–1225.
- Schnorbus, M., A. Werner, and K. Bennett. 2014. Impacts of climate change in three hydrologic regimes in British Columbia, Canada. *Hydrol. Process.* 28:1170–1189.
- Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H.-P. Huang, N. Harnik, A. Leetmaa, N.-C. Lau, C. Li, J. Velez, and N. Naik. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316:1181–1184.

- Seager, S. T., C. Eisenberg, and S. B. St. Clair. 2013. Patterns and consequences of ungulate herbivory on aspen in western North America. *For. Ecol. Manag.* 299:81–90.
- Shepperd, W. D., D. Binkley, D. L. Bartos, T. J. Stohlgren, and L. G. Eskew. 2001. Sustaining aspen in western landscapes: Symposium proceedings. P. in Proceedings RMRS-P-18. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 460 p.
- Shinneman, D. J., W. L. Baker, P. C. Rogers, and D. Kulakowski. 2013. Fire regimes of quaking aspen in the Mountain West. *For. Ecol. Manag.* 299:22–34.
- Simard, S. W., Heineman, J.L., Mather, W.J., Sachs, D.L., Vyse, A. 2001. Effects of operational brushing on conifers and plant communities in the southern interior of British Columbia. Results from PROBE 1991-2000 Protocol for Operational Brushing Evaluations. 398 pp.
- Slough, B. G. 1978. Beaver Food Cache Structure and Utilization. *J. Wildl. Manag.* 42:644–646.
- Slough, B. G., and R. M. F. S. Sadleir. 1977. A land capability classification system for beaver (*Castor canadensis* Kuhl). *Can. J. Zool.* 55:1324–1335.
- Smith, D. W., and D. B. Tyers. 2012. The History and Current Status and Distribution of Beavers in Yellowstone National Park. *Northwest Sci.* 86:276–288.
- Smith, E. A., D. O’Loughlin, J. R. Buck, and S. B. St. Clair. 2011. The influences of conifer succession, physiographic conditions and herbivory on quaking aspen regeneration after fire. *For. Ecol. Manag.* 262:325–330.
- Smith, E. A., D. O’Loughlin, J. R. Buck, and S. B. St. Clair. 2011. The influences of conifer succession, physiographic conditions and herbivory on quaking aspen regeneration after fire. *For. Ecol. Manag.* 262:325–330.
- Sturrock, R. N., S. J. Frankel, A. V. Brown, P. E. Hennon, J. T. Kliejunas, K. J. Lewis, J. J. Worrall, and A. J. Woods. 2011. Climate change and forest diseases. *Plant Pathol.* 60:133–149.
- Suzuki, K., H. Suzuki, D. Binkley, and T. J. Stohlgren. 1999. Aspen regeneration in the Colorado Front Range: differences at local and landscape scales. *Landsc. Ecol.* 14:231–237.
- Vyse, A., and S. Simard. 2007. Broadleaved species status report for the British Columbia Interior. Forest Genetics Council of British Columbia.
- Wallenius, T. H., J. Pennanen, and P. J. Burton. 2011. Long-term decreasing trend in forest fires in northwestern Canada. *Ecosphere* 2:1–16.
- Westfall, J. and Ebata, T. 2016. Summary of the forest health conditions in British Columbia. British Columbia Ministry of Forests, Lands and Natural Resource Operations. Pest Management Report Number 15. 86 pp.
- White, C. A., C. E. Olmsted, and C. E. Kay. 1998. Aspen, Elk, and Fire in the Rocky Mountain National Parks of North America. *Wildl. Soc. Bull.* 1973-2006 26:449–462.
- Wong, C., B. Dorner, and H. Sandmann. 2003. Estimating historical variability of natural disturbances in British Columbia. British Columbia, Forest Science Program, Victoria, BC.
- Worrall, J. J., A. G. Keck, and S. B. Marchetti. 2015. *Populus tremuloides* stands continue to deteriorate after drought-incited sudden aspen decline. *Can. J. For. Res.* 45:1768–1774.
- Worrall, J. J., G. E. Rehfeldt, A. Hamann, E. H. Hogg, S. B. Marchetti, M. Michaelian, and L. K. Gray. 2013. Recent declines of *Populus tremuloides* in North America linked to climate. *For. Ecol. Manag.* 299:35–51.

- Worrall, J. J., L. Egeland, T. Eager, R. A. Mask, E. W. Johnson, P. A. Kemp, and W. D. Shepperd. 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. *For. Ecol. Manag.* 255:686–696.
- Worrall, J. J., S. B. Marchetti, L. Egeland, R. A. Mask, T. Eager, and B. Howell. 2010. Effects and etiology of sudden aspen decline in southwestern Colorado, USA. *For. Ecol. Manag.* 260:638–648.