THE EFFECT OF SMOKE-WATER ON SEED GERMINATION OF 18 NATIVE FORB SPECIES FROM THE INTERIOR GRASSLANDS OF SOUTHERN BRITISH COLUMBIA

By

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ABSTRACT

As government and industries continue to impact and disturb natural areas, there is an urgent and constant need for land reclamation to mitigate the negative impacts of such disturbances and restore self-sustaining, stable, and resilient ecosystems. In order to accomplish this, it is imperative to enhance the frequency, consistency, and success rates of applying native plant seed for ecological restoration. Smoke-water can affect seed germination of plants, regardless of whether they occur in fire-prone ecosystems. Germination trials of 18 native species of Indigenous value in the southern interior grasslands of British Columbia, Canada were conducted using a smoke aqueous solution. Locally sourced parent plant material was burned to produce smoke-water. Seeds were collected from multiple populations of the species across a wide geographic range within the B.C. southern interior to increase the genetic diversity of the seed stock. Seeds were soaked in smoke aqueous solution in various concentrates, including 0% (control), 1% (1:100), 10% (1:10), 20% (1:5), and 100%. The results indicate that germination rates in the presence of smoke-water are species specific. Five species showed an increase in germination with smoke-water: *Erythronium grandiflorum*, *Calochortus macrocarpus*, *Arnica latifolia*, *Lomatium nudicaule* and *Shepherdia canadensis*, 4 species showed no change: *Rosa woodsii, Crataegus douglasii*, *Lewisia rediviva*, and *Prunus virginiana*, and 9 species showed some level of decrease: *Fritillaria affinis*, *Fritillaria pudica*, *Berberis aquifolium*, *Claytonia lanceolata*, *Gaillardia aristate*, *Balsamorhiza sagittata*, *Allium cernuum*, *Amelanchier alnifolia*, and *Lomatium macrocarpum*. The treatments applied to encourage the germination of seeds from interior grassland forbs and shrubs have demonstrated that smoke-water can effectively break dormancy and enhance the germination rate from certain native plant species.

Key words: seed germination, smoke-water, seed diversity, native species, germination trials, grasslands, First Nation land management

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CHAPTER 1: INTRODUCTION

LAND DISTURBANCE

Disturbance—defined as an event or series of events that changes the relationships of organisms and their habitats from their natural state both spatially and temporally (Wali 1999)—is often an integral part of many ecosystems. However, while many disturbances have, and will continue to, occur without human involvement, many other disturbance regimes have been created or modified by humans. Certainly, land use and alteration have been central to the development of human civilizations (Pausas and Leverkus 2023). Anthropogenic land disturbance, particularly through intentional fire use, has significantly shaped human history, influencing societies, cultures, and environments. From traditional land management practices to the ritualistic significance of fire in cultural traditions, intentional fires have left a distinct mark on landscapes. In contemporary times, the controlled use of fire for land management and conservation is a critical aspect, balancing the ecological role of fire with the need to mitigate risks and preserve ecosystems. Yet, the suppression of natural fire regimes in recent history has had detrimental effects, leading to increased fuel loads, more intense wildfires, and ecological imbalances. Recognizing the importance of fire in maintaining healthy ecosystems while addressing the consequences of fire suppression remains a crucial challenge in modern land management practices (Pyne 2021).

In the Interior grasslands of British Columbia, many ecosystems have been dominated by fire disturbance. Fires in the interior, exhibit diverse impacts. Depending on factors such as intensity and frequency, fires create a mosaic of different vegetation types and successional stages, stimulating habitat diversity. Fires can release nutrients stored in vegetation back into the soil, promoting nutrient cycling, in turn this influences the composition and productivity of plant communities. Fire-induced alterations can impact wildlife habitat. The complex interplay of these factors underscores the intricate ecological role of fire in interior grassland ecosystems. However, while fire occurs without human involvement, it is also well-understood that Indigenous manipulation of fire has also been important in maintaining plant abundance and ecosystem processes (Nikolakis et al. 2020). In British Columbia, as in many landscapes, the relationship between land disturbance and human history is complex and diverse. Amongst the relationship between fire and grasslands we take a deeper look into the influence of smoke having the potential to influence seed germination in certain plant species, known as smoke-stimulated germination.

Following European settlement in BC, anthropogenic disturbances have also resulted from practices within agriculture, settlement, mining, natural resource extraction, deforestation, urbanization, transportation, industrialization, and other multifaceted land uses (Hagos et al. 2023, Cagliero et al. 2023). Anthropogenic alteration of disturbance regimes has been occurring both directly through land uses practices and indirectly though human impact on pre-existing disturbance regimes such as that of fire.

In British Columbia (BC), the alteration to our natural fire regimes along with climate change and altered forest management has led to an increase in area burned. British Columbia's four largest fire seasons based on total hectares burnt have occurred in the last seven years: 2017, 2018, 2021 and 2023. The 2017 wildfire season burned over 1.2 million hectares and cost the province over $649 million dollars in suppression fees, the 2018 wildfire season had 2117 wildfires burn over 1.4 million hectares and cost over $615 million dollars, and the 2021 wildfire season had 1610 wildfires burn 868,203 hectares and cost over $565 million dollars. In 2023 between April-Aug 2023, 1,754 wildfires burned about 1.58 million hectares of land (Government of BC - Wildfire Status Update 2023) with nearly 200 homes burned in the Okanagan (CBC News 2023). On top of the land area burned, these intense wildfires are severely affecting communities in BC (Government of BC - Wildfire History and Statistics 2023).

In addition to wildfires, BC's land disturbance co-occurs with extraction of its rich natural resources. Natural resource extraction is a primary economic driver for Canada and BC (Government of BC - Annual Service Plan Report 2015) with forestry, mining, and petroleum-based resources being a significant portion of Canada and BC's economy (Government of BC - Economic Plan 2022). Oil and gas is an important industry in Canada and is projected to continue to be a growth industry, in addition strengthening B.C.'s mining sector through the B.C. Mining Jobs Task Force to ensure environmental and regulatory excellence in mining, and the sustainable exploration for minerals needed in the new economy (Government of BC - Economic Plan 2022). The energy sector currently accounts for approximately three-quarters of today's greenhouse gas emissions, making it a pivotal factor in mitigating the most severe consequences of climate change, an unprecedented challenge in human history (International Energy Agency 2021). There is a list of environmental laws and regulations that govern the oil and gas industry, including environmental assessment, management, and reclamation (Government of BC - Environmental Management Act 2003) but there are still challenges with restoring the land area disturbed.

Much of the land disturbance that is associated with resource exploration and extraction occurs on lands that fall within the traditional territories of multiple First Nations. For example, the Trans Mountain Pipeline (formerly owned by Kinder Morgan) is 1150 km long running from Edmonton, Alberta to Burnaby, British Columbia. The company is currently adding another pipeline that runs parallel to the existing line. The Trans Mountain pipeline expansion includes sensitive grassland habitat including Lac Du Bois Grasslands Protected Area and crosses several First Nations traditional territories and reserve lands. This emphasizes the importance of quality Impact Benefit Agreements (IBA) for First Nations to help support projects like this pipeline. Knowing that resource extraction is economically beneficial and a primary source for employment for Indigenous people (Mining Association of Canada 2013) in Canada it is likely that extraction and exploration will continue well into the future. This will continue to create land disturbance that will require more scientific knowledge to improve restoration practices if we want these areas returned to natural landscapes.

IMPORTANCE OF GRASSLANDS

Natural resource extraction and exploration will continue well into the future causing significant land disturbance to grassland ecosystems. Worldwide, grasslands are a significant contributor to ecosystem services, such as food production, erosion control, pollination, nutrient cycling, wildlife habitat, and water filtration, carbon storage, climate mitigation, and cultural ecosystem services (Bengtsson et al. 2019, Costanza et al. 1997, Xue et al. 2023). Grasslands store ~34% of the terrestrial carbon stock, with ~90% of their carbon stored belowground as root biomass and soil organic carbon (SOC), thus playing a vital role in soil carbon sequestration (Bai and Cotrufo 2022). Grasslands are also considered one of the most species rich habitats and this biodiversity increases resistance and resilience of grasslands to climate change (Petermann and Buzhdygan 2021). Therefore, grasslands are an ecologically important renewable resource and should be conserved or restored whenever possible.

British Columbia's grasslands occupy less than 1% of the province's total surface area and yet are home to over 30 percent of the province's species at risk (GCC of BC 2017). However, the grasslands are declining rapidly due to human pressures such as agriculture, urban development, livestock grazing, mining, and pipelines (GCC of BC 2017). Overgrazing by wild and domestic ungulates, weed invasion, forest ingrowth/encroachment as a result of fire suppression, and habitat fragmentation all pose present threats to the integrity of BC's Interior grassland ecosystems (Gayton 2004).

British Columbia's grasslands have a rich history with First Nations. First Nations have been managing land for millennia with fires being a primary tool in land management practices (Blackstock and McAllister 2004, Miller et al. 2010). First Nations' close relationships with nature are foundational to how they interact with their environments, a kinship that bears responsibility in its management and protection. Indigenous peoples, long-time residents of particular places, acknowledge that their physical, spiritual, mental, and social health depends on the ability to practice their traditional customs by living harmoniously with nature (Zahn et al. 2018). In B.C.'s economic plan we can see the importance of inclusive and sustainable growth. A pillar of the plan is to work towards advancing the government's commitments to reconciliation with Indigenous peoples by partnering with First Nations and Indigenous communities to support new economic initiatives acknowledging, respecting, and upholding Indigenous rights, First Nations title and Indigenous control of their land and resources (Government of BC - Economic Plan 2022).

RECLAMATION OR RESTORATION?

When natural areas are disturbed anthropogenically, there is a need to mitigate the effects impacts of such disturbances in order to reinstate beneficial ecosystem services (Dong et al. 2015). Millions of acres of land have been disturbed by human activities or severe climate events that significant portions of their native plant communities have been lost and their ecosystems have been seriously compromised. As noted, one example of significant disturbance in BC grasslands is the Trans Mountain Pipeline Expansion which goes through Lac du Bois Grasslands Protected Area. However, there is a profound difference between restoring and reclaiming disturbed natural areas.

Reclamation typically refers to the process of restoring or rehabilitating land that has been disturbed or degraded by human activities such as mining, agriculture, or industrial development (Lima et al. 2016). It aims to make the land productive or suitable for certain uses again. The primary goal of reclamation is often utilitarian. Reclamation focuses on bringing the land back into a functional state for human activities, such as agriculture, or development (Beckett and Keeling 2019) and reclamation projects often prioritize economic benefits and may not always aim for ecological restoration (Gerwing et al. 2022).

Restoration, on the other hand, refers to the process of returning a degraded or altered ecosystem to its original, natural condition as closely as possible. It aims to reestablish the ecological functions and biodiversity of the ecosystem (Curran et al. 2023, Cusser and Goodell). Restoration is primarily driven by ecological and conservation goals and the focus is on repairing ecosystems, enhancing biodiversity, and improving ecosystem services (Cairns and Heckman 1996). Restoration efforts often involve planting native species, managing invasive species, restoring natural hydrology, and minimizing human disturbance. The goal is to mimic natural processes and promote ecosystem health (Gobster 2005).

One way to steer the world and the environment in a better direction, is by adopting a "restorative culture." This means combining ideas from restoration ecology and public health medicine and to understand that biodiversity is crucial for our well-being (Cross et al. 2019). The Society for Ecological Restoration (SER) is an international non-profit organization with members in 70 countries. SER advances the science, practice and policy of ecological restoration to sustain biodiversity, improve resilience in a changing climate, and re-establish an ecologically healthy relationship between nature and culture (Gann et al. 2019).

GRASSLAND RESTORATION CHALLENGES

Grasslands are recognized globally for their high biodiversity and their social and cultural values, but once disturbed, restoring these ecosystems is challenging and complex. Grasslands are difficult to restore because they are found in semi-arid environments with low annual precipitation and typically low site productivity (Zhang et al. 2023). Low site productivity limits vegetative growth, making it difficult to restore grassland ecosystem properties, such as soil development and plant community composition (Skousen and Venable 2008). Grassland restoration also often requires improving soil health, which may have been degraded due to natural or human caused land disturbances. Soil erosion, compaction, and nutrient imbalances can impede the growth of native grasses and forbs (Bai and Cotrufo 2022). Invasive species add to the challenge of restoration. In many cases, invasive plants and animals have taken over native grassland habitats, outcompeting native species. Removing these invasive species and preventing their return can be a long and ongoing process (Assis et al. 2020, Byun 2023).

Grasslands are often fragmented by roads, urban development, and other human activities. Restoring connectivity between fragmented patches can be difficult, as wildlife may struggle to move between areas, leading to genetic isolation and reduced biodiversity (Valkó et al. 2023). Restoring grasslands often requires substantial financial resources for land acquisition, habitat restoration, and ongoing management. Securing funding for these activities can be a significant challenge (Lakner et al. 2020, Lampinen and Anttila 2021).

Alteration of fire regimes has also impacted grasslands as they are adapted to regular natural fires. Indigenous people used fire to maintain browse for ungulates, suppress sagebrush, and encourage herb growth and to manage tree encroachment but the colonial worldview was that fires were destructive to timber supply and dangerous to communities (Blackstock and McAllister 2004). Fire suppression policies have disrupted these natural fire regimes, leading to the encroachment of woody vegetation and non-native species (Blair et al. 2014). Restoration should include reintroducing controlled burns and managing fire risk, but this can be challenging and require careful planning (Case and Staver 2017).

Climate change can exacerbate the challenges of grassland restoration. Shifts in temperature and precipitation patterns can affect the suitability of native species (Lyons et al. 2023). Successful restoration requires long-term monitoring and adaptive management to assess progress, address unexpected challenges, and make necessary adjustments to the restoration plan. Engaging the public and raising awareness about the importance of grassland ecosystems is crucial for their long-term conservation and restoration, however educating communities and stakeholders can be a significant challenge (Klaus 2023).

First Nations have relied on BC's Grasslands since time immemorial. BC Government continues to commit to work with Indigenous Peoples to address barriers to their full participation and leadership in all aspects of B.C.'s economy; supporting First Nations control over their own land and resources; acknowledging, respecting, and upholding Indigenous rights and First Nations title; and building enduring and productive forums for Indigenous Peoples to lead and contribute to economic development initiatives (Government of BC - Economic Plan 2022). In 2019 BC's provincial government passed The Declaration on the Rights of Indigenous Peoples Act (Government of BC - Declaration Act 2019). Through this act stronger decision-making authority will be shared between Indigenous governments and the province. The Declaration Act aims to create a path forward that respects the human rights of Indigenous Peoples while introducing better transparency and predictability in the work British Columbians do together. With more supportive laws and participation First Nations will have a stronger influence on the use, reclamation, and restoration of BC's Grasslands.

NATIVE SEED USE IN RESTORATION AND RECLAMATION

British Columbia has a history of seeding with agronomic species for forage in disturbed areas. These reclamation efforts often select species for their high productivity and resilience which causes them to out compete native species preventing natural succession (Burton and

Burton 2002). Native species are necessary to ensure a healthy ecosystem, maintaining soil structure, hydrology, and nutrient cycling. Over the years, non-native species have been used to reclaim disturbed areas, and this has caused concern surrounding natural biodiversity and ecological processes (Huff 2010). Use of native species builds a diverse and resilient plant community which benefits the surrounding ecosystem.

Historically, productive forage grass and forb species were seeded in disturbed areas, faster growing species like grasses were preferred for erosion mitigation (Cerda and Robichaud 2009). Native species have been encouraged more in recent years for reclamation of disturbed areas in the United States but, due to cost and availability their use is limited (Smith et al. 2007; Beyers 2004).

In BC, there are no laws restricting the use of non-native plant species in reclamation. Often, non-native grasses and legumes are used in revegetation projects because they have been cultivated and commercialized, they are easy to grow, they are low in cost, and they are readily available in large quantities compared to native species (Burton and Burton 2002; Skousen and Venable 2008; Oliveira et al. 2013, McCormick et al. 2021, Pedrini et al. 2022). Native species are often expensive and difficult to obtain in large quantities, yet attention is shifting towards the use of native species in revegetation projects worldwide (Burton and Burton 2002; Skousen et al. 2008; Kiehl et al. 2010). Further, restoration with native species is often a desirable land-use objective for First Nations groups, who are often primary stakeholders of lands disturbed by industry and government.

The foundation of a successful revegetation or restoration program is quality native seed. This requires careful collection, processing, and storage (Lippitt et al.1994, McCormick et al. 2021, De Vitis et al. 2020). Having a goal to restore disturbed sites to their natural, pre-disturbed condition, there is a great need for a more abundant, consistent, and higher quality supply of native seed (Burton and Burton 2002). Restoring impaired ecosystems requires a supply of diverse native plant seeds that are well suited to the climates, soils, and other living species of the system (Pedrini et al. 2020). Native seeds are also in demand for applications in urban land management, roadside maintenance, conservation agriculture, and other restorative activities that take into account the connection between native plant communities and the increasingly urgent need for resilient landscapes (National Academies of Sciences, Engineering and Medicine 2020). Due to the current and growing need of native seed there is a lack of supply. In addition, there is a lack of research on seed storage methods, seed viability, and germination success of native plants. Native species are often expensive and difficult to obtain in large quantities (Burton and Burton 2002, Pedrini et al. 2022).

ROLE OF SMOKE IN GERMINATION

Forest fires are a fundamental and recurring component of natural ecosystems, shaping landscapes and influencing the evolution of flora and fauna. Over millennia, numerous plant species have evolved specific adaptations to not only endure the effects of wildfires but to harness them as cues for germination and growth (Landis 2000). These adaptations have led to an ecological relationship between wildfires and plant communities. In particular, many seeds have developed intricate mechanisms that enable them to respond positively to the presence of smoke (Dixon et al.1995), a key characteristic of wildfire-affected environments. From common vegetables to native seeds in diverse ecosystems, the influence of smoke on seed germination and dormancy is increasingly recognized as a crucial ecological phenomenon (Franzese and Ghermandi 2011, Gonzalez and Ghermandi 2012, Landis 2000, Read and Bellairs 1999).

The semi-arid grassland ecosystems of British Columbia, like many others worldwide, have evolved in the context of periodic wildfires. These ecosystems are characterised by a unique blend of native plant species that have evolved and adapted their life cycles to the disturbances caused by fire events (Cao et al. 2021). While wildfires can devastate existing vegetation, their impact also creates opportunities for post-fire regeneration and renewal. Chemical release, present in smoke, is just one of several factors driving this process (Beveridge et al. 2020).

Smoke's influence on seed germination holds both ecological and practical significance. As wildfires become more frequent and severe due to climate change, it is essential to comprehend how smoke can trigger seed germination, impacting the resilience of natural ecosystems. Furthermore, land management practices such as controlled burns and ecological restoration often necessitate strategies to enhance seed germination and the recovery of native plant communities (Sanchez et al. 2022). Recognizing the pivotal role of smoke in this process may lead to innovative and sustainable approaches to ecosystem restoration and conservation. Native plants evolved in a landscape where fire was common and have developed natural defenses to maximize survival potential post fire or disturbance. Root strategies are found commonly among native plants. These strategies include a deep taproot to endure fire, rhizomatous root structures, which can produce new roots and plant material, and stolons which can effectively establish clones to increase survival (Guo et al. 2021). Strategies evolved in tandem with root systems, such as seed germination triggered by detecting smoke concentration in water, serve to promote the germination of native species. Supporting the efficacy of smoke-water as a germination tool, research conducted in the Brazilian Savannahs demonstrates a significant increase in germination rates and stimulated root growth in certain grass species (Ramos et al. 2019). Diverse studies have consistently demonstrated a positive germination response to smoke-water application, spanning various plant species and ecosystems (Brown & van Staden 1997, Franzese & Ghermandi 2011, Kępczyński 2018, Zirondi et al. 2019, Alahakoon et al. 2020). Additionally, employing plant-extracted smoke-water has emerged as an effective method to augment the success and pace of seed germination (Chumpookam et al. 2012, Read 2000, Cox et al. 2017).

OBJECTIVES FOR THESIS STUDY

The primary aim of this thesis is to investigate smoke infused water as an effective seed germination approach for the restoration of disrupted semi-arid grasslands within the interior of British Columbia. Specifically, it focuses on the utilization of native species with an emphasis on traditional food and medicine species of the local First Nations with a goal to further seeding techniques to rejuvenate these disturbed ecosystems. One of the main objectives of this study is to assess how native seeds respond to the application of smoke-water. Smoke-water, also known as smoke extract or smoke solution, is a liquid solution derived from the condensation of smoke generated from burning plant material, or other organic matter. It mimics the natural cues provided by wildfires and can enhance the germination of seeds from certain species. Smoke-water application may help to simulate wildfire response in grassland ecosystem species. This study aims to identify plants adapted to or benefiting from wildfire-related cues, responding positively to chemicals released during wildfires, thus promoting their germination and growth.

Chapter 2 will focus on the germination response of 18 native grassland plants of British Columbia to different concentrations of smoke-water. The chapter also addresses whether plant form, phenology, seed dispersal mechanisms, and fire strategies influence germination success. Chapter 3 will outline research conclusions, management implication, and the direction for future research. The insights obtained from this study will contribute to advancing the field of semi-arid grassland restoration in British Columbia.

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CHAPTER 2 – THE EFFECT OF SMOKE-WATER ON SEED GERMINATION OF 18 NATIVE FORB SPECIES FROM THE INTERIOR GRASSLANDS OF SOUTHERN BRITISH COLUMBIA, CANADA

INTRODUCTION

Seeds from plants in fire-prone areas have evolved to exhibit specific characteristics. Some species' seeds experience increased germination success by the heat of fire (e.g., the serotinous cones of woody plants) (Lamont et al. 1991) while other species' seeds demonstrate increased germination rates following exposure to fire smoke (Brown and van Staden 1997, Cox et al. 2017). Previous studies have shown a positive germination response to smoke-water (Brown and van Staden 1997, Franzese and Ghermandi 2011, Kępczyński 2018, Zirondi et al. 2019, Alahakoon et al. 2020) regardless of whether the plants occur in fire-prone ecosystems (Light 2018, Van Staden et al. 2004). Smoke due to fire in fire-prone regions can stimulate the seed germination process (De Lange 1990, Keeley 1998). Moreover, plant-extracted smoke-infused water can be used to enhance success and rate of seed germination (Read 2000, Cox et al. 2017). Although the study of smoke, and the identification of active smoke compounds, on seed germination rate is increasing (Van Staden et al. 2004, Kulkarni et al. 2006, Merritt et al. 2007, Dixon et al. 2009, Jefferson et al. 2014, Govindaraj et al. 2016, Aslam et al. 2017, Mackenzie and Naeth 2019, Khatoon et al. 2020) screening of the responses of local native plant species to smoke-infused water is necessary because of potential specific local genetic adaptations (Osuna-Mascaró et al. 2023, Ryan et al. 2013).

Plant life history characteristics are evolutionary adaptations to habitat type, climate, and biological interactions. Noble and Slatyer (1980) posed distinctive plant life history categories according to disturbance. Rowe (1983) presented a modification of Noble and Slatyer's (1980) vital attributes to disturbance in the context of fire by grouping species types into five categories representing a means of survival for plants: endurers, resisters, evaders, invaders, and avoiders. Endurers are resprouting species, with shallow or deep-buried perennating buds. Resisters can survive low severity fire as adults, but juveniles are usually vulnerable. Evaders are species with relatively long-lived seeds that are typically heat-germinated. Invaders are species that establish early and rapidly by wind-dispersed seed. Avoiders are shade tolerant species that slowly re-occupy burned sites, cannot tolerate fire, but tend to occupy protected unburned microsites such as depressions (Allen 2008, Archibald et al. 2019, Botha et al. 2020). There has been no research to test how seeds of these vital attribute fire strategy types respond to smoke-infused water with respect to germination.

The interior grasslands of southern British Columbia, Canada were shaped by fire over the past several centuries (Gayton 2013, Ryan et al. 2013). Fires are caused by natural processes, mostly lightning strike, but also through controlled management practices of the Indigenous peoples (Gayton 2013). A history of fire causes evolutionary selection in plant species and plant species' traits. Learning the evolutionary response of grassland plants to wildfire is essential to better understand the restoration of these ecosystems that have experienced disturbance, whether by fire or other natural or human-caused factors.

The study and practice of ecological restoration and ecosystem reclamation is critical as a response to human-caused and natural disturbance across the landscape. The goals of ecosystem reclamation following disturbances caused by natural resource extraction have evolved from the simple revegetation of the site with agronomic monocultures to the reclamation of diverse, native plant communities and ecosystems. Therefore, there is a growing need for native seed, but a lack of supply (Smreciu et al. 2003). In addition, there is a lack of research on seed storage methods, seed viability, germination success of native plants, all aspects of site preparation, and seed delivery (Shaw et al. 2020). Native species' seeds are often expensive and difficult to obtain in large quantities (Burton and Burton 2002) and re-establishing native plant communities can also be very difficult (Native Plant Working Group 2001). Non-native agronomic grasses and legumes are used in revegetation projects because they have been cultivated and commercialized, they are easy to grow, they are low in cost, and they are readily available in large quantities compared to native species (Oliveira et al. 2013). However, attention is shifting towards the use of native species in revegetation projects worldwide (Whalley et al. 2013, Corlett 2016, Gao et al. 2018, Nsikani et al. 2020). Further, restoration with native species is often a desirable land-use objective for Indigenous groups, who are often primary stakeholders of lands disturbed by industry and government (Wittenberg and Cock 2001).

In studying native seed germination success factors such as plant form, phenology, and seed dispersal mechanisms should be considered. Understanding plant forms, such as forbs (herbs), grasses, and shrubs, is essential for assessing how different species respond to smoke-water germination trials. There tends to be more seed germination information on grasses. Yet for many of the forb and shrub species that are vital to grassland ecosystems in British Columbia such information is lacking, so these broadleaved groups will be a focus of my study. Species phenology determines what time of year a species matures, flowers, and disperses seeds (Fenner 1998). Mature seeds are dispersed using wind and animal transportation, or a combination of both. Seeds which are dispersed by wind are typically smaller and lighter than species which use animals as a dispersal mechanism (Traveset et al. 2014). Each species has difference mechanisms which help in dispersal, hooked structures on larger seeds to attach to fur of animals allow the seed to disperse further much like wings on seeds which aid in wind dispersal. Understanding how these traits relate to seed germination success is important.

The main objective of the current research is to provide critical information on seed germination success of native grassland species of British Columbia. Such information will promote increased use of native species in reclamation and restoration projects. Grasses, such as Indian ricegrass (*Achnatherum hymenoides*), stiff needlegrass (*Achnatherum occidentale*), spreading needlegrass (*Achnatherum richardsonii*), pinegrass (*Calamagrostis rubescens*), rough fescue (*Festuca campestris*), Sandberg bluegrass (*Poa secunda*), and bluebunch wheatgrass (*Pseudoroegneria spicata*) are the most dominant species in the study grassland areas. However, forbs and shrubs found in grasslands are a large and important part of the food and medicine crop harvested by Indigenous peoples, and there is a lack of information on the seed germination of forbs compared to grasses. Therefore, the focus of this study was on seeds collected from forbs and shrubs growing in B.C.'s interior grasslands.

I tested germination success of 18 native grassland plants of British Columbia to different concentrations of smoke-water, and whether plant form, phenology, seed dispersal mechanisms, and fire strategies influence germination success.

MATERIALS AND METHODS

Study Area

The study focused on grassland species of the Interior Plateau in the central region of south and central British Columbia, Canada. Grasslands of this area are generally associated with valley bottoms, steep canyon walls, river terraces, and adjacent plateau surfaces along the river systems (Wikeem and Wikeem 2004).

Seed Collection

Species were not only categorized according to plant form (Table 1), but also to phenology, seed dispersal and to plant strategy type (Table 2). Species were grouped into 4 phenological categories outlined for grassland species by Pitt and Wikeem (1990) that are based on adaptation to spatial and temporal distribution of soil moisture. Spring ephemerals are plants that start to grow very early in spring, flower and terminate growth before summer drought, and rarely resprout in fall. Summer mature plants start growth early, flower rapidly, and mature before or soon after summer drought begins. Summer quiescent plants start growth early in spring, develop fairly rapidly, but flower later than summer mature species and become only semidormant during summer drought. They also exhibit significant regrowth in response to fall moisture. Protracted growth plants have delayed spring growth, followed by fall flowering. These tend to be deeply rooted shrubs that continue to grow and develop slowly throughout the frost-free period. Plants may have different fire strategies depending on the fire intensity and may exhibit primary response, such as survival through root strategies, and secondary responses like seed production. For this study fire strategy was based on the predominant plant response to a low intensity fire as outlined by Mah (2000).

Table 1. Eighteen forb and shrub species selected for seed collection in the southern interior of BC. Nomenclature follows E-Flora BC database.

Scientific name	**Abb.**	**Family**	**Common Name**	**Plant Form**
Allium cernuum Roth	*Al.Ce.*	*Liliaceae*	Nodding Onion	Forb
Amelanchier alnifolia (Nutt.) Nutt. ex M. Roem.	*Am.Al.*	*Rosaceae*	Saskatoon	Shrub
Arnica latifolia Bong.	*Ar.La.*	*Asteraceae*	Mountain Arnica	Forb
Balsamorhiza sagittata (Pursh) Nutt.	*Ba.Sa.*	*Asteraceae*	Arrow Leaved Balsamroot	Forb
Berberis aquifolium Pursh	*Be.Aq.*	*Berberidaceae*	Oregon Grape	Shrub
Calochortus macrocarpus Douglas	*Ca.Ma.*	*Liliaceae*	Mariposa Lily	Forb
Claytonia lanceolata Pall. ex Pursh	*Cl.La.*	*Portulacaceae*	Western Spring Beauty	Forb
Crataegus douglasii Lindl.	*Cr.Do.*	*Rosaceae*	Hawthorne	Shrub
Erythronium grandiflorum Pursh	*Er.Gr.*	*Liliaceae*	Glacier Lily	Forb
Fritillaria affinis (Schult. & Schult. f.) Sealy	*Fr.Af.*	*Liliaceae*	Chocolate Lily	Forb
Fritillaria pudica (Pursh) Spreng.	*Fr.Pu.*	*Liliaceae*	Yellow Bell	Forb
Gaillardia aristata Pursh	*Ga.Ar.*	*Asteraceae*	Brown Eyed Susan	Forb
Lewisia rediviva Pursh	*Le.Re.*	*Montiaceae*	Bitterroot	Forb
Lomatium macrocarpum Coult. & Rose	*La.Ma.*	*Apiaceae*	Large Fruited Desert Parsley	Forb
Lomatium nudicaule (Pursh) J.M. Coult. & Rose	*Lo.Nu.*	*Apiaceae*	Barestem Desert Parsley	Forb
Prunus virginiana L.	*Pr.Vi.*	*Rosaceae*	Choke Cherry	Shrub
Rosa woodsii Lindl.	*Ro.Wo.*	*Rosaceae*	Prairie Rose	Shrub
Shepherdia canadensis Nutt.	*Sh.Ca.*	*Elaeagnaceae*	Soopolallie	Shrub

Table 2. The ecological strategies of species: phenology, seed dispersal mechanisms and fire strategy (Mah 2000).

Scientific Name	Phenology	Seed Dispersal	Fire Strategies
Allium cernuum Roth	Summer Quiescent	Wind	Endurer
Amelanchier alnifolia (Nutt.) Nutt. ex M. Roem.	Summer Mature	Animal	Endurer
Arnica latifolia Bong.	Summer Mature	Wind	Endurer
Balsamorhiza sagittata (Pursh) Nutt.	Spring Ephemeral	Animal	Endurer
Berberis aquifolium Pursh	Protracted Growth	Animal	Endurer/Invader
Calochortus macrocarpus Douglas	Summer Quiescent	Wind	Endurer
Claytonia lanceolata Pall. ex Pursh	Spring Ephemeral	Wind	Endurer
Crataegus douglasii Lindl.	Summer Mature	Animal	Endurer
Erythronium grandiflorum Pursh	Spring Ephemeral	Wind	Endurer
Fritillaria affinis (Schult. & Schult. f.) Sealy	Spring Ephemeral	Wind	Endurer
Fritillaria pudica (Pursh) Spreng.	Spring Ephemeral	Wind	Endurer
Gaillardia aristata Pursh	Summer Quiescent	Animal	Endurer/Invader
Lewisia rediviva Pursh	Summer Mature	Wind	Endurer
Lomatium macrocarpum Coult. & Rose	Summer Mature	Wind	Endurer
Lomatium nudicaule (Pursh) J.M. Coult. & Rose	Spring Ephemeral	Wind	Endurer
Prunus virginiana L.	Summer Mature	Animal	Endurer
Rosa woodsii Lindl.	Summer Quiescent	Animal	Endurer
Shepherdia canadensis Nutt.	Summer Mature	Animal	Endurer

Species were also selected based on their significance as food and medicinal plants used by local Indigenous people, relayed in discussions with Lower Nicola Indian Band Elders and Wisdom-holders along with other members of the Nlaka'pamux First Nation, and from Turner et al. (1990). Seeds were collected from multiple zones (Bunchgrass, Interior Douglas-Fir, and Ponderosa Pine) using the British Columbia Biogeoclimatic Ecosystem Classification (Pojar et al. 1987). Many collection sites were on or near Indian Reserves of the Nlaka'pamux Nation; and have rich historical gathering significance, such as Botanie Valley that is known for its abundant root crops in early spring and late summer (Turner et al.

1990). Seeds were collected from multiple populations of the species across a wide geographic range to increase the genetic diversity of the seed stock. Seed collection protocols followed the Seeds of Success program initiated by the Bureau of Land Management (Bureau of Land Management 2012). All seeds were derived from wild populations and seed collection was sourced from at least 50 individuals. Material was collected on multiple dates from the same population and was combined with no more than 20% of material arising from a single day. Seed collections spanned two growing seasons of the years 2015-2016.

Smoke Solution Procedure

Smoke-water was created using the system described by Coons et al. (2014). The plant material used for combustion was the parent plant material of seeds collected, and other grasses and trees on the same landscape (Table 3). The smoke system was operated in a fume hood in the Thompson Rivers University Chemistry Lab. 100g +/- 10g of plant material was weighed and cut into small sections roughly 2-5 mm in length. A single layer of material was placed to the bottom of the stainless-steel bee smoker with attached billows and lit with a lighter (Fig. 1). Material burned for 10-30 seconds, and then more plant material was added to put out the flame and increase the quantity of smoke. The bellow on the bee smoker was compressed periodically to keep sufficient combustion. Smoke travelled through a rubber heat resistant hose that was fitted tightly at the tip of the smoker with the other end below the surface of the water in the 1000 mL volumetric flask. A rubber cork was used for an airtight seal for the hose and the mouth of the flask. A water aspirator was attached to the sidearm flask creating a consistent vacuum draw of smoke. After all the material was combusted the smoke solution was filtered by vacuum filtration and transferred to a plastic bottle, capped, and stored at 4°C.

Table 3. Quantities of parent plant material combusted for 25 Litres of smoke aqueous solution.

Material #1	**Amount Used**	**Material #2**	**Amount Used**	**Solution Yield**
Lomatium nudicaule	299.43g			1500 mL
Pinus ponderosa bark	929.92g			4500 mL
Pinus ponderosa wood	206.17g			1000 mL
Wheat grass	817.76g			4000 mL
Wheat grass	102.83g	Glacier lily	6.51g	500 mL
Wheat grass	20.88g	*Claytonia lanceolata*	81.89g	500 mL
Wheat grass	46.60g	*Calichortus Macrocapus*	55.97	500 mL
Pinus ponderosa wood	25.84g	Chocolate lily	74.45g	500 mL
Rosa woodsii	58.19g	Wheat grass	42.81g	500 mL
Wheat grass	71.44g	*Rosa woodsii*	28.71g	500 mL
Wheat grass	72.73g	*Rosa woodsii*	28.83g	500 mL
Wheat grass	61.20g	*Pinus ponderosa*	38.00g	500 mL
Wheat grass	68.36g	*Rosa woodsii*	31.51g	500 mL
Wheat grass	83.03g	*Rosa woodsii*	18.46g	500 mL
Artemisia tridentata	201.54g			1000 mL
Lomatium Macrocarpum	100.48g			500 mL
Amelanchier alnifolia	200.36g			1000 mL
Balsamorhiza sagittata	98.42g			500 mL
Berberis aquifolium	101.21g			500 mL
Erthyroniyum grandifolim	99.78g			500 mL
Fritillaria pudica	100.09g			500 mL
Prunus virginiana	202.16g			1000 mL
Shepherdia canadensis	201.11g			1000 mL
Crategeous douglasii	200.65g			1000 mL
Pseudotsuga menziesii	305.79g			1500 mL
			Total	25 L

Figure 1. Smoke apparatus with stainless steel bee smoker (photo: Peterson, 2016)

The smoke-water was analyzed for active phenols by Supra Research and Development, Inc., Kelowna, British Columbia, Canada, using a simultaneous headspace-gas chromatography-tandem mass spectrometry (HS-GC/MS) method (Table 4).

Table 4. Analysis of four phenols in smoke-water.

Analyte	MDL (ng/mL)	MRL (ng/mL)	Free VPs (ng/mL)
4-Methylguaiacol	0.142	0.500	15,300
Guaiacol	0.095	0.500	26,000
o-Cresol	0.116	1.00	4,740
p-Cresol	0.156	0.500	9,260

VP = volatile phenol, MDL = method detection limit, MRL = method reporting limit.

Seed Germination Trial

Five smoke-water concentrations were tested on 18 species: 1:100 (1%), 1:10 (10%), 1:5 (20%), and 100%, and a control (0%) of distilled water. The aqueous smoke solution was diluted to desired concentration with distilled water. Each treatment was replicated three times, with 15-25 seeds for each replicate, depending on seed size (Zhou et al. 2012), for a total of 54 germination tests per smoke-water treatment and a total of 270 germination tests overall.

The germination tests were placed in separate sandwich size Ziploc bags and filled with 200 mL of aqueous solution of the treatment being tested. Seeds were soaked for 24 hours (Elsadek and Yousef 2019), rinsed with distilled water and wrapped in distilled water moistened disposable brown hand towel paper (Sabongari and Aliero 2004). Seeds were then refrigerated at 4ºC for a 90 day cold moist stratification (Landis and Dumroese 2000, Bonner and Karrfalt 2008).

Stratified seeds were placed in 90 mm glass Petri-dishes on three layers of filter paper, moistened with distilled water (Yusoff et al. 2019) and were exposed to 20ºC, and indirect light with a 12-hour light and 12-hour dark photoperiod, resembling a day and night cycle (Tobe et al. 2005). Seeds were monitored daily for the appearance of radical and seed germination was considered successful with the appearance of the radicle (Wolny et al. 2018) Germination is generally defined as the commencement of water uptake by imbibition of the dry seed, followed by embryo expansion. This usually results in the rupture of the covering layers and radicle protrusion, which is regarded as the completion of the germination process (Kucera et al. 2005).

Data Analysis

Germination and seedling growth data were analyzed using two-way Analysis of Variance (ANOVA) with smoke treatment and species as the two-factor variables, and eighteen one-way ANOVAs for each species, with smoke treatment as the factor variable. Tukey's HSD was used to separate treatment means (Zhou et al. 2012). Similarly, two-way ANOVAs were used to analyze smoke treatment and (1) plant form (forb vs. shrub), (2) phenology, (3) seed dispersal, and (4) fire strategy type. Normal distribution was confirmed using Shapiro-Wilk test. Two species *Calochortus macrocarpus* and *Lewisia redivia* were log transformed to meet assumptions of normal distribution. To account for increased risk for type II error running 18 one-way ANOVAs, a Bonferroni correction was applied with ($p < 0.0028$).

RESULTS

The two species with the highest rates of germination (>90%) of the eighteen species, without considering smoke-water treatment effects, were *Prunus virginiana* and *Lewisia* *rediviva*, while the two species with the lowest rates (<5%) were *Crataegus douglasii* and *Rosa woodsii* species (Fig. 2; F-ratio = 42.198, df = 17, $p < 0.001$). The highest germination rate, when all species were pooled, was found for the control treatment, with reduced percent germination as smoke-water increased in concentration (Fig. 3).

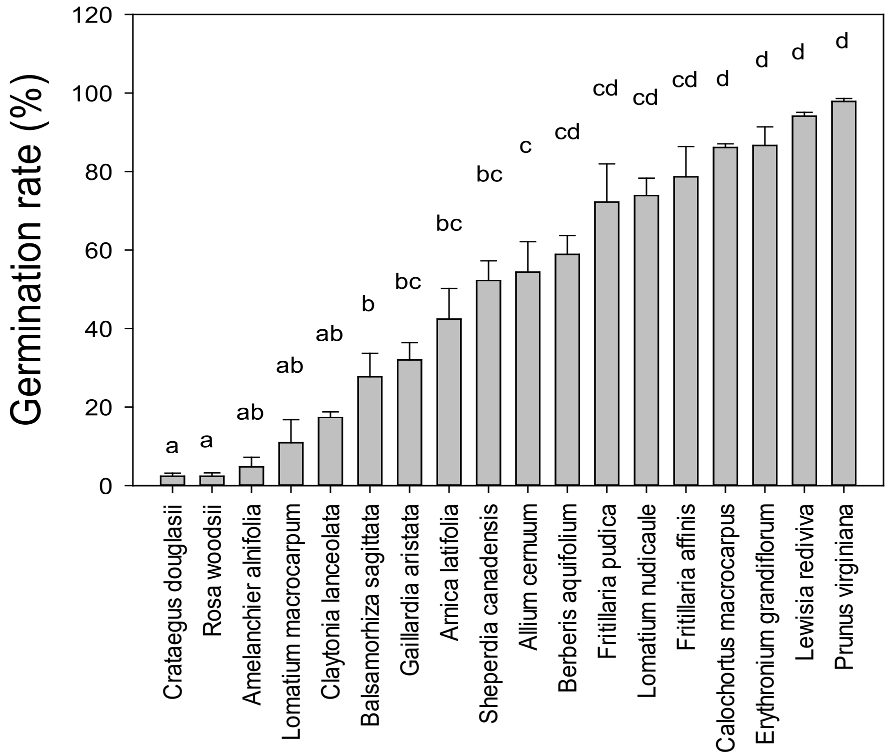


Figure 2. Germination rate of 18 native grassland species. Error bars represent Standard Error. Bars sharing the same letter are not significantly different using Tukey's HSD.

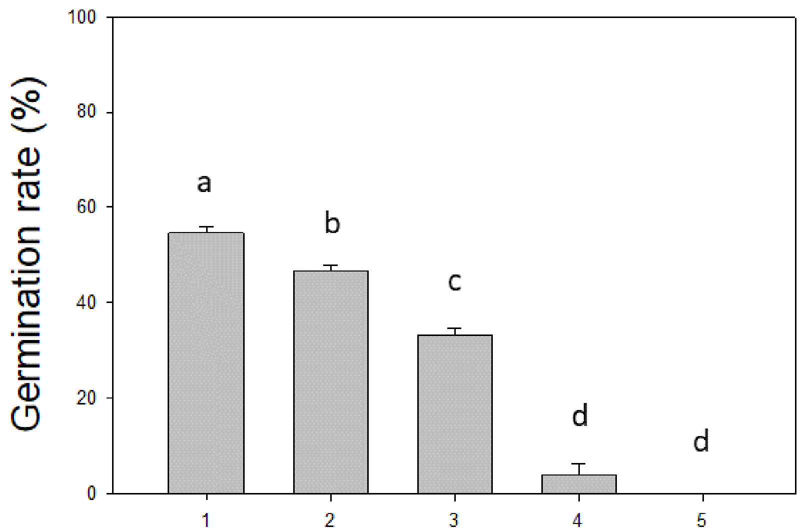


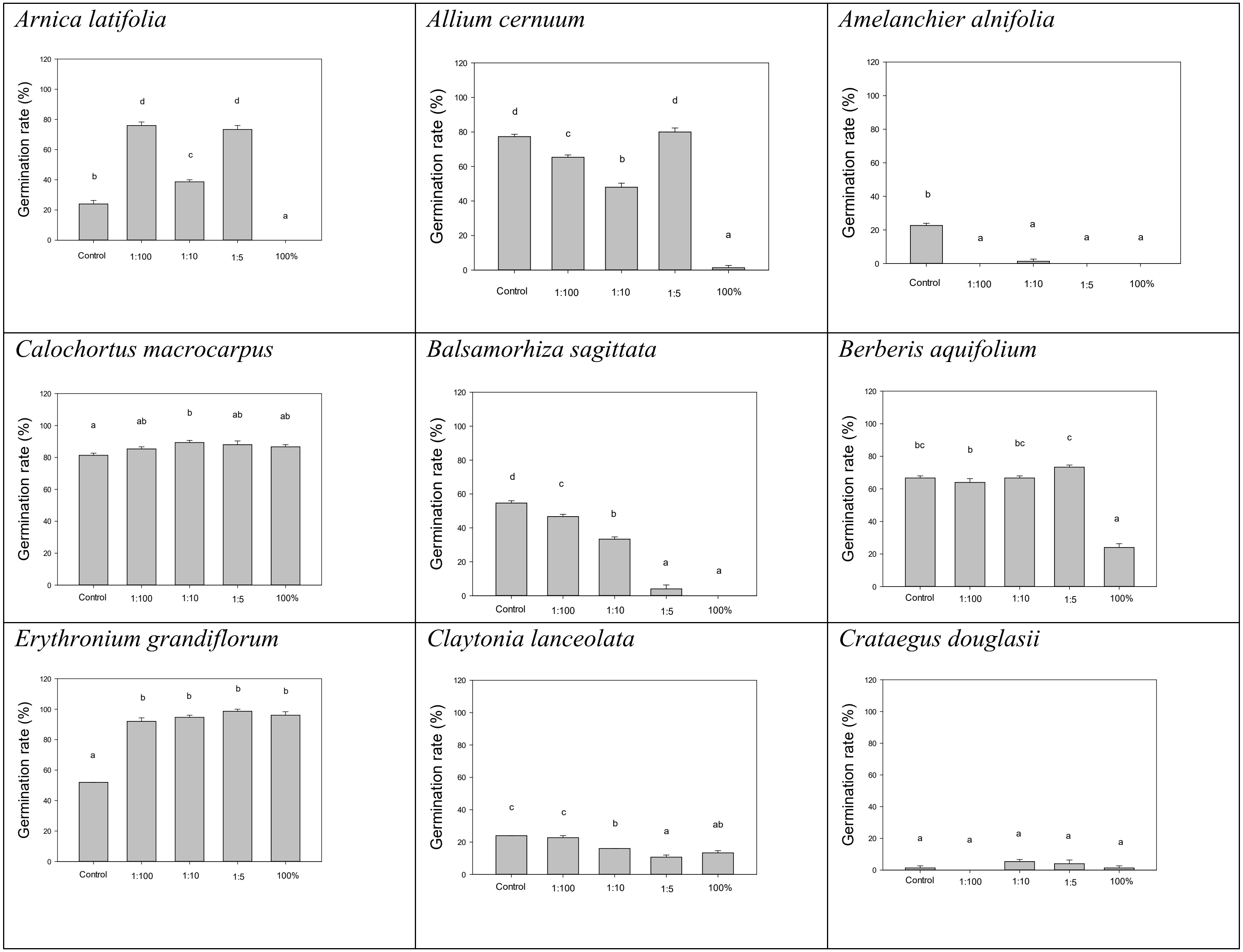
Figure 3. Germination rate of all 18 native grassland species combined and as affected by smoke-water concentration. 1=control (0%), 2=1:100 (1%), 3=1:10 (10%), 4=1:5 (20%), and 5=100% smoke-water concentration. Error bars represent Standard Error. Bars sharing the same letter are not significantly different using Tukey's HSD.

Although the control trials were found to have the highest germination rate (Fig. 3, F-ratio = 6.637, df = 4, $p < 0.001$), some species displayed equivalent or higher germination rates in the smoke-water treatments as compared to the control treatment for that species (Table 5; Fig. 4). Overall, five species showed an increase in germination with smoke-water, 4 species showed no change, and 9 species showed some level of decrease.

Table 5. Eighteen one-way ANOVA results for smoke-water concentration with respect to species.

Species	Mean Squares	F-ratio	P-value
Allium cernuum	3118.4	324.83	<0.001
Amelanchier alnifolia	300.3	140.75	<0.001
Arnica latifolia	3177.1	270.77	<0.001
Balsamorhiza sagittata	1835.7	286.83	<0.001
Berberis aquifolium	1179.7	122.89	<0.001
Calochortus macrocarpus	28.3	3.79	0.04
Claytonia lanceolata	101.3	31.67	<0.001
Crataegus douglasii	14.4	2.25	0.136
Erythronium grandiflorum	1144.0	134.06	<0.001
Fritillaria affinis	3093.3	322.22	<0.001

Fritillaria pudica	4907.7	511.22	<0.001
Gaillardia aristata	994.7	116.56	<0.001
Lewisia rediviva	12.3	0.89	0.507
Lomatium macrocarpum	1793.1	1681.00	<0.001
Lomatium nudicaule	1540.3	144.40	<0.001
Prunus virginiana	4.3	0.40	0.804
Rosa woodsii	9.1	0.77	0.567
Sheperdia canadensis	1299.7	135.39	<0.001


Arnica latifolia
Allium cernuum
Amelanchier alnifolia
Calochortus macrocarpus
Balsamorhiza sagittata
Berberis aquifolium
Erythronium grandiflorum
Claytonia lanceolata
Crataegus douglasii
Germination rate (%)
Control
1:100
1:10
1:5
100%

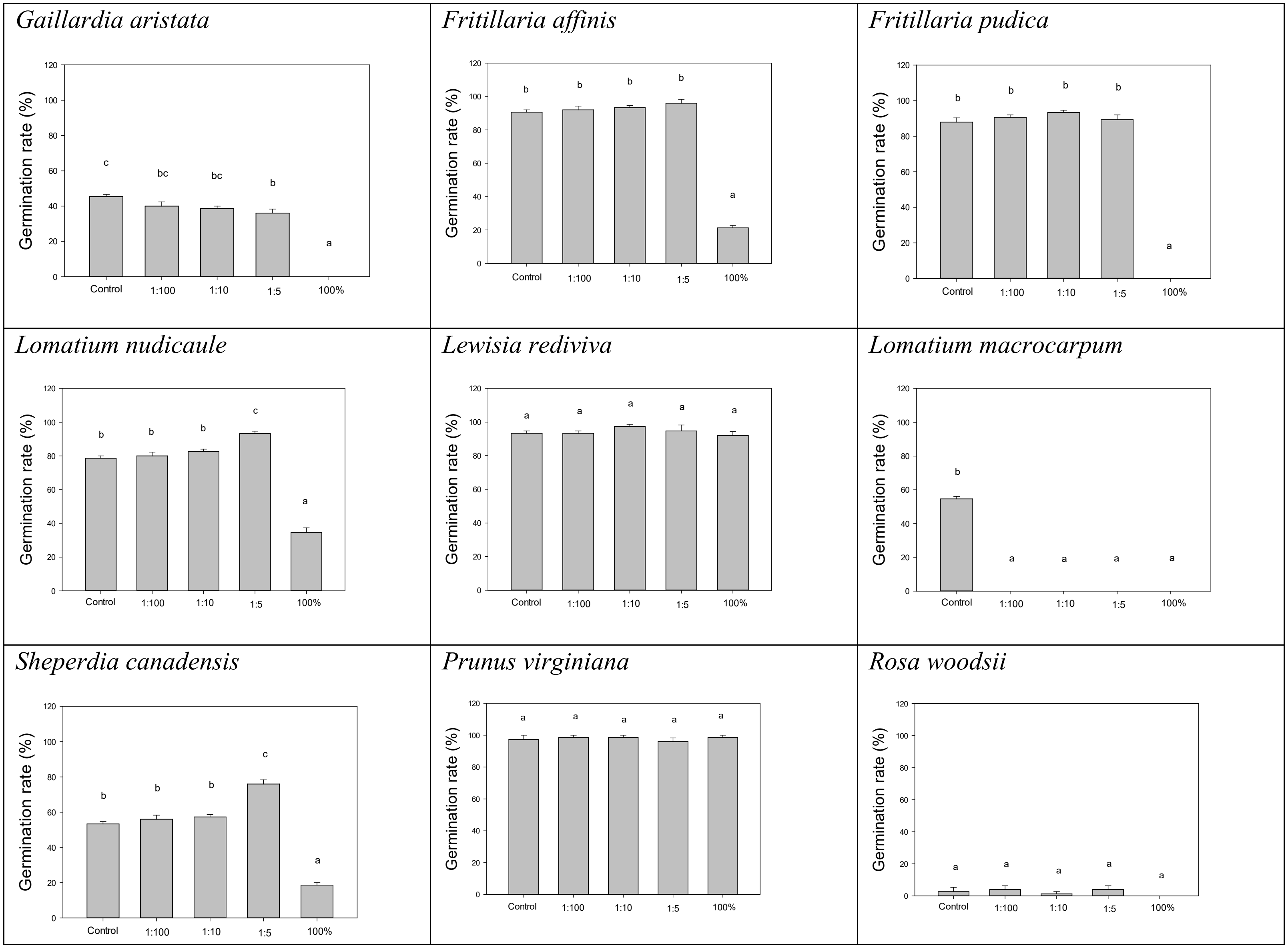


Figure 4. Germination rate of each of the 18 native grassland species as affected by smoke-water concentration. The horizontal axis is smoke concentration in water. Error bars represent Standard Error. Bars sharing the same letter are not significantly different using Tukey's HSD.

Germination response was impacted by functional group with forbs (or herbs) having higher germination rates than shrubs (Fig. 5; F-ratio = 19.30, df = 1, $p < 0.001$). There was no interaction between smoke water treatment and functional group type (F-ratio = 0.747, df = 4, $p = 0.561$).

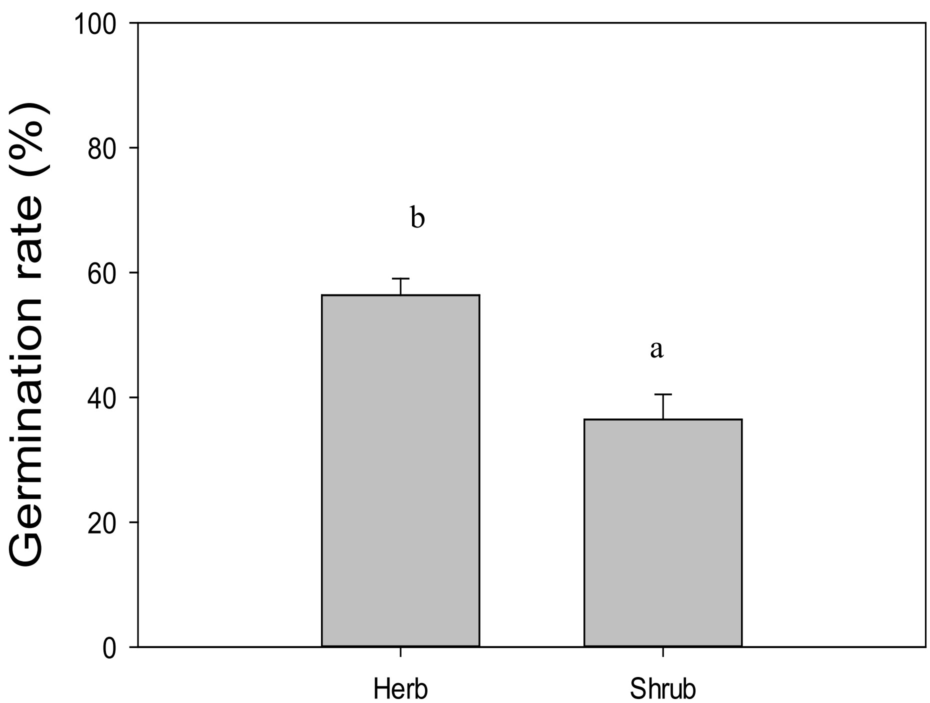


Figure 5. Germination rate of species by plant form (herbs or forbs and shrubs). Error bars represent Standard Error. Bars sharing the same letter are not significantly different.

Phenology also had a significant impact on germination success (Fig. 6; F-ratio = 4.06, df = 3, p = 0.008). There was no interaction between smoke water treatment and phenology (F-ratio = 0.383, df = 12, p = 0.969). The spring ephemerals and protracted growth categories displayed a higher germination rate than those species in the summer quiescent and summer mature categories.

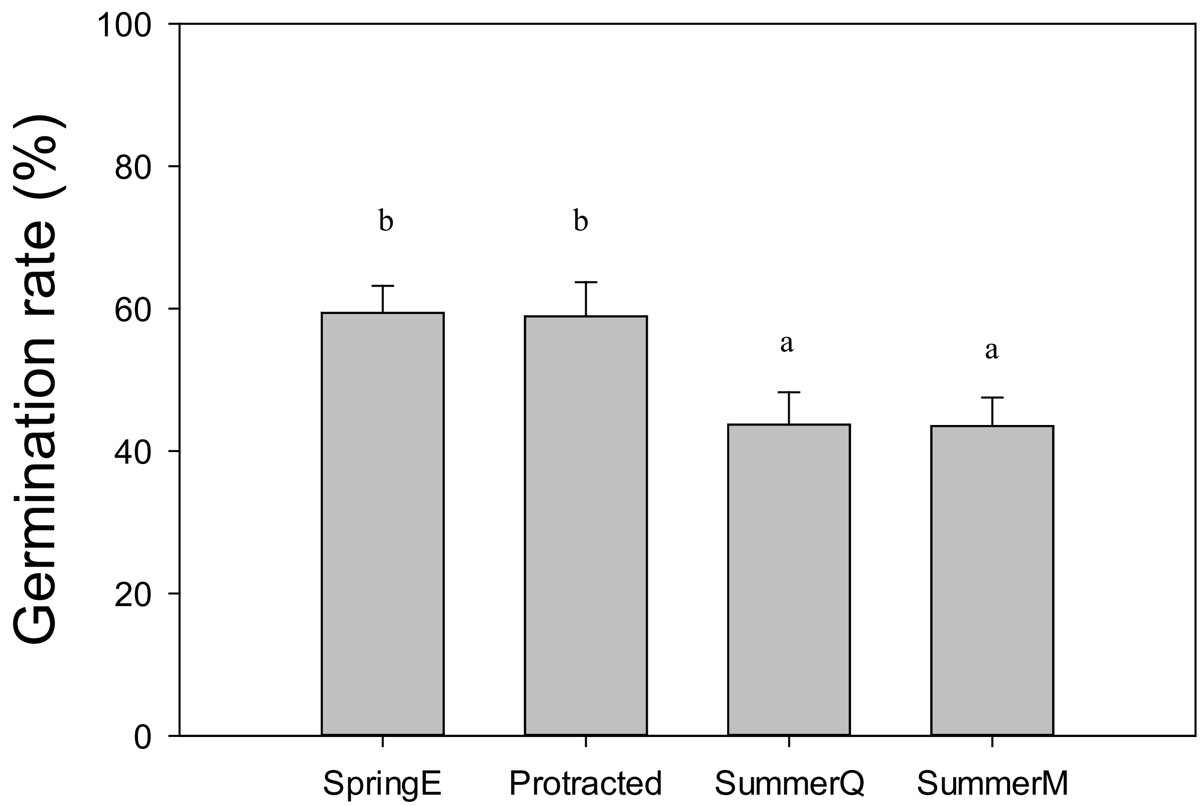


Figure 6. Germination rate of species by phenology as affected by smoke-water concentration. Error bars represent Standard Error. Bars sharing the same letter are not significantly different using Tukey's HSD.

Seed dispersal tactics were also evaluated and indicated that wind-dispersed seeds had higher germination rates than animal-dispersed seeds (Fig. 7; F-ratio = 42.07, df = 1, p < 0.001). There was no significant interaction between smoke water treatment and dispersal type (F-ratio = 0.617, df = 4, p=0.651).

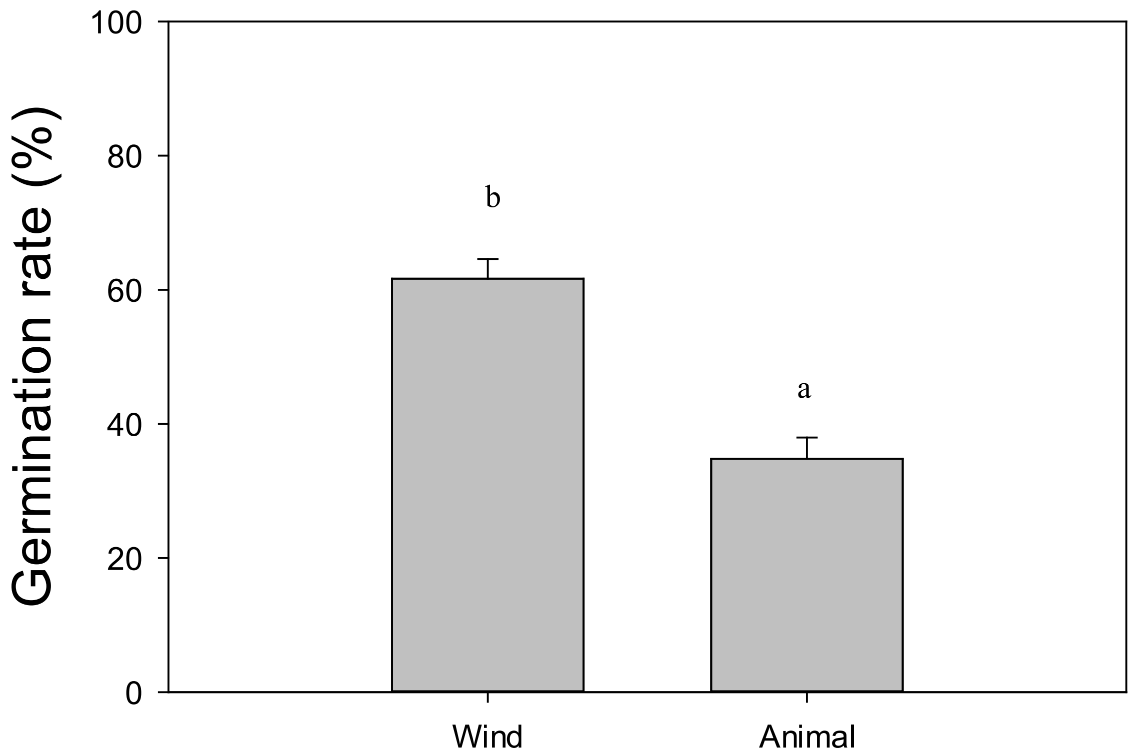


Figure 7. Germination rate of species by seed dispersal as affected by smoke-water concentration. Error bars represent Standard Error. Bars sharing the same letter are not significantly different.

Plant fire tactics are an important part of how a plant evolved. All of the plants in this study were classified as endurers or endures/invaders meaning their primary response to a low intensity fire is to regrowth from below ground material (Table 2). There was no significant difference by fire strategy type (F-ratio = 0.460, df = 1, p = 0.498) and no treatment by fire strategy interaction (F-ratio = 0.198, df = 4, p = 0.939).

DISCUSSION

Increased Germination

Five species showed an increase with germination over the control at some level of smoke-water concentration. Glacier lily (*Erythronium grandiflorum*), Mariposa lily (*Calochortus macrocarpus*), mountain arnica (*Arnica latifolia*), barestem desert parsley (*Lomatium nudicaule*) and soopolallie (*Shepherdia canadensis*) all had some level of increased germination in response to the addition of smoke-water although the response did vary by species.

Glacier lily germination increased significantly with the addition of smoke-water and maintained high germination rates across all concentrations with germination rates approaching 100% with smoke-water and being closer to 50% without. This may be explained by the fact that the embryo of glacier lily's seeds requires moisture and warm stratification to break seed dormancy (Baskin and Baskin 1985, Park 2019). Smoke-water was able to provide the moisture resulting in the increased germination rates. The increased concentration of particles in smoke-water seemed to provide some other stimulant or enhancement which warrants further investigation.

Mariposa lily had just above 80% germination in the control but there was a slight increase with all concentrations of smoke-water but only the 10% smoke water concentration resulted in a significant increase bringing the germination closer to 90%. While both species are classified under the Liliaceae family and share fundamental botanical characteristics, notable distinctions set them apart. The glacier lily, flourishing in moister, sub-alpine environments, contrasts with the mariposa lily's preference for drier sagebrush slopes (Loewen et al. 2001, Miller et al. 2004). Morphologically, the glacier lily's flowers display a drooping or nodding structure, while the mariposa lily exhibits an erect, cupping form with a broader spectrum of color variations and intricate patterns.

Adapting to wildfire-prone habitats, both species employ well-developed underground storage structures. The glacier lily employs bulb structures that not only facilitate propagation but also exhibit resilience to disturbances, with individual cloves or scales capable of detaching during events such as land disruption caused by activities like bear foraging (Tardiff and Stanford 1998). In contrast, the mariposa lily relies on corms characterized by a robust, fleshy, swollen stem structure, contributing to its ability to endure top-growth disturbances and ensure subsurface survival. Despite their botanical differences, both species follow a similar phenological pattern, emerging early in the spring, with flowering commencing in the early spring and persisting until the early summer (Lambert et al. 2010).

Mountain arnica had the highest germination rate with 1% and 20% smoked water with the germination rate almost tripling over that of the control. However, there was no germination at the highest concentration of smoke water. Others have also found an increase in germination with smoke water but when it is used in low concentrations (Gupta et al. 2019). Mountain arnica usually survives cool to moderately severe fires but is susceptible to fire-kill at higher intensities (Fischer 1987) making establishment from seed more important in those situations. This species has dried-pappus achene seeds which can absorb water quickly (Meng et al. 2014). The seeds of mountain arnica exhibit pappus achene structures, enabling wind dispersal mechanisms that may facilitate post-fire invasion strategies. This capability takes advantage of the cleared vegetation after fires, creating opportunities for increased access to light and resources. Location and size of the pappus on the flower head can also contribute to the germination success (Sugier et al. 2022). Moreover, the rhizome root structures of mountain arnica contribute to its resilience against fire, allowing for effective fire endurance strategies (Pausas et al. 2018).

Both barestem desert parsley and soopolallie showed an increase in germination with the 20% treatment concentration and but a decrease compared to all treatments at the 100% concentration. Barestem desert parsley seeds germinate well following cold, moist exposure conditions (Scholten 2011) and so the increased warm stratification of smoke-water was less effective than in species such as the glacier lily. Soopolallie, a species which thrives under open canopy, may respond to higher smoke concentrations as a cue to maximize germination during a fire-disturbance event that will likely remove the canopy. Soopolallie is also a historically important plant for Indigenous communities in interior British Columbia (Turner 2014) and berries, which ripen in summer, can be used for food throughout winter. This species has a strong negative correlation between canopy cover and fruit production (Hamer 1996).

Decreased Germination

Nine species responded with decreased germination when smoke-water was used. Chocolate lily (*Fritillaria affinis*), yellow bell (*Fritillaria pudica*), Oregon grape (*Berberis aquifolium*), western spring beauty (*Claytonia lanceolata*), brown eyed Susan (*Gaillardia aristate*), arrowleaf balsamroot (*Balsamorhiza sagittata*), nodding onion (*Allium cernuum*), saskatoon (*Amelanchier alnifolia*), and large fruited desert parsley (*Lomatium macrocarpum)* all showed some level of decrease although response varied by species.

Chocolate lily, yellow bell and Oregon grape all had high germination that remained the similar between the control and smoke-water treatments at levels of 1,10 and 20% but germination response decreased substantially when 100% smoke-water was used. The response to 100% smoke-water across most species tested had similar results, potentially indicating excessive toxicity at this concentration, leading to seed mortality or sterilization. Yellow bell was shown only 20% germination rate in other control trials (Love and Akins 2019). Chocolate lily has limited literature specific to seed germination. However, there is more literature supporting bulbs or rice grains being the main source for propagation (Macfarlane 2000). Oregon grape shows the importance of bear digestion aiding in and increase in higher germination rates with fleshy berry fruits. However, all these species possess the ability to endure wildfires with root strategies. For example, Oregon grape has a rhizome and taproot structures which allowing for prompt recover after a fire (Barkley, 2002). Both yellow bell and chocolate lily have the same Liliaceae bulb characteristics aiding in subsurface survival.

Brown eyed Susan showed a slight decrease in germination at higher levels of smoke water, having no germination response at the 100% treatment concentration. Brown eyed Susan species have achenes which presumably need some biomechanical treatments, instead of the smoke-water, to break their seed dormancy for growing. Mensah and Ekeke (2016) have revealed that water uptake treatment has less effect on the germination rate of an achene seed species.

Western spring beauty also demonstrated decreased germination with the application of smoke-water. This may demonstrate a prime example of the primary survival being root strategies with large tuber structures allowing survival through mild to moderate fires. These tubers have long held significance among First Nations communities for their food value.

Arrowleaf balsamroot, having a deep tap root, can tolerate fire, grazing, trampling, and drought (Stevens and Monsen 2004); however, it does not germinate or transplant readily (Turner 1999). Bowen (2006) showed increased germination with ethylene treatment of this species. Seeds sown in media soaked in an ethylene solution of 10 ml to 14.4 L water averaged 28% germination. Increasing the concentration of smoke in the water generally decreased the germination rates of seeds which may be due to the fact that oilseeds have low enzymatic activities, having the least reactions to environmental drivers (Egli et al. 2002). Following fires, the arrowleaf balsamroot will often regenerate from the persisting caudex (John 2012).

The nodding onion has a bloom period of mid to late summer, anytime from June to October (Fischer 1987). Seeds become mature in this period which occurs simultaneously with wildfire seasons in British Columbia. In 1% and 10% smoke-water concentration trials nodding onion decreased germination and in the 20% trial germination rate increased to that of rates comparable to the control treatment. This increase appears to be a defense mechanism, as increase in smoke-water signifies a large fire or a fire close to the plant, the dramatic response to smoke-water allows the plant to germinate at a higher rate to further the plants survival.

Saskatoon and large fruited desert parsley responded negatively to smoke-water compared to control, with little to no germination with the application of smoke-water indicating that smoke-water application for these species may possibly be toxic and cause sterilization. Saskatoon had only 20% germination in the control and other studies indicate that alternating stratification strategies play a larger role in germination rate (Love and Akins 2018). Saskatoon is considered a fleshy fruit and passing through an animal can increase germination in these species. For example, some fleshy fruit seeds have shown higher germination success with bear digestion (Garcia-Rodriguez et al. 2021). Large fruited desert parsley had 60% germination in the control but no germination with any smoke water application. Admittedly this was not expected, considering being so similar to barestem desert parsley (*Lomatium nudicaule*) which showed an increase in germination with the application of smoke-water. Germination trials from Love and Akins (2019) showed large fruited desert parsley had 80% germination in their control with only 23% for barestem desert parsley showing that they indeed behave differently on same treatments. However, these species can resist fire, and even if they lose aboveground anatomy, their roots and rhizomes near topsoil can sprout again (Mah 2000; Fuchs 2001).

No Change in Germination

Four species showed no change in germination rate from control through smoke-water treatments. Prairie rose (*Rosa woodsii),* hawthorne (*Crataegus douglasii*), bitterroot (*Lewisia rediviva*), and choke cherry (*Prunus virginiana*) all did not change in response to the addition of smoke-water but showed differing levels of germination overall.

Prairie rose and hawthorne had no significant change with the application of smoke-water. Germination success of these two species was poor regardless of treatment including control. In seed ecology, the fleshy seed and oily endosperm are a potential form of stress resistance and can be used to compensate for a lack of resource availability in the environment (Dermott et al. 1979). Both rose and hawthorns fruits are significant food source for bears and other animals. Animal digestion increases germination and distribution of many species. (Cosyns et al. 2005, Garcia-Rodriguez et al. 2021, Schuppe 1993). Many Rosa species exhibit different types of seed dormancy, such as physical dormancy caused by hard seed coats and physiological dormancy due to internal mechanisms. Overcoming seed dormancy often requires specific treatments, including cold stratification, scarification, or chemical treatments, to promote germination (Stoian-Dod et al. 2023).

Bitterroot and chokecherry both showed no change to treatment and had high germination rates close to 100% across all treatments. Plant propagation protocols showed the importance of stratification with only 5% germination with no stratification and 100% germination with 90-day stratification with bitterroot (Plant Propagation Protocol 2015). Chokecherry's fleshy fruits provide a food source for birds and provide a mechanism for seed dispersal with high germination across defecation or regurgitation (Meyer and Witmer 1998). Possibly the high rate of germination success leads to the depredation of young saplings (Parciak 2002). The ecological strategy of bitterroot is to go dormant in early summer, so its deep, branched taproot escapes most wildfires (Mah 2000). The combination of root and seed strategies maximizes the potential for survival and fitness.

Other Factors

Herbs/forbs showed greater seed germination success compared to shrubs (Fig. 5). Herbs typically produce smaller seeds compared to shrubs and this allows for quicker water absorption and penetration, facilitating the germination process (Bond et al. 1999). Herbs often utilize a broader range of seed dispersal mechanisms and this diversity in dispersal methods can increase the chances of seeds reaching suitable germination sites. Herbs may also have simpler germination requirements compared to shrubs but often have shorter life cycles. Some herbs may exhibit a more generalized response to environmental cues, making them adaptable to a wider range of conditions for successful germination (Aragon et al. 2009, Lan et al. 2016). Quick germination and establishment allow them to complete their life cycle rapidly, taking advantage of favorable conditions for growth and reproduction (Lovett-Doust 2002).

Phenology is the timing and seasonal events in the life cycle of plants and includes the timing of leaf emergence, flowering, fruiting, and senescence (aging and deterioration). Phenological events are crucial for understanding how plants respond to their environment and how their life cycles are synchronized with changing seasons particularly with pressures from climate change. Plant species were classified within 4 phenological groups (summer mature, summer quiescent, protracted growth, and spring ephemerals) that are hypothesized to reflect adaptation to spatial and temporal distribution of soil moisture (Pitt et al. 1990) (Fig. 6). Theses groups reflect the seasonal changes of the year and give us species adaptive response to not only sunlight, temperatures, and moisture but response to potential seasonal land disturbance like wildfire, and caloric timing value for animals (Liu et al. 2022). They also provide flushes in botanical composition, forage production, and nutrient availability that should be reflected within grassland management (Pitt and Wikeem 1990). Oregon grape

(*Berberis aquifolium*), the only species tested belonging to the protracted growth taxa, exhibits unique growth patterns characterized by delayed spring growth and fall flowering. This species might demonstrate a higher germination rate after smoke-water treatment due to its potential adaptation of evolving to thrive in fire-affected areas, where smoke-water treatment could mimic natural fire-related cues, stimulating the germination of its seeds. This adaptation might enable the species to take advantage of post-fire environments, where competition from other plants is reduced, allowing for successful establishment and growth (Noste and Bushey 1987). Seeds of spring ephemerals mature and fall to the ground before the typical fire season begins. This timing is advantageous for these plants because the seeds are already dispersed and lying dormant in the soil when fires occur (Loewen et al. 2001). The fire, acting as a natural disturbance, can play a crucial role in triggering successful seed germination for these plants for several possible reasons such as scarification and seed coat cracking, chemical cues for breaking dormancy, nutrient release, and reduced competition (Gonzalez et al. 2022, López-Mársico et al. 2019, Ma et al. 2018).

Plants have adapted to fire in several ways, including resprouting, regrowing, or re-establishing from residual seed after a fire (Vernon et al. 2020). These strategies have been classified into resister, endurer, avoider, evader, and invader categories. All the species in my study were classified as primarily responding as endurers in response to a low intensity fire with two also being classified as invaders (Table 2). Grassland plant species have evolved survival strategies in response to wildfires, adopting an endurer strategy crucial for their persistence. Most of the species exhibit adaptation wherein their underground vegetation serves as a protective shield, allowing the tops to burn while ensuring the survival of the species. These underground structures, like rhizomes, bulbs, and taproots act as a resource reserve, enabling the plants to regenerate post-fire and quickly sprout new growth (Zupo et al. 2021). However, it’s worth noting that over the last 200 years, fire suppression efforts driven by colonial policies may have inadvertently led to evolutionary adaptations in some species, potentially altering their response strategies to fire disturbance. For instance, prolonged periods without fire may have favored traits that prioritize above-ground growth over below-ground storage, affecting the resilience of these species to future fire events.

Such evolutionary shifts could have significant implications for ecosystem dynamics and resilience in fire-prone grassland habitats.

Frequent light fires play a role in stimulating growth and seed germination, facilitating the continuation of these species. However, severe fires can pose a significant threat as they reach underground and cause below-ground death, impacting the plant's ability to regenerate from the root system (Pourreza et al. 2014, Thomsen and Ooi 2022). As a result, seed production becomes a secondary mechanism for survival, enabling these plants to repopulate affected areas by utilizing evasion or invasion strategies through seed dispersal (Mah 2000).

Understanding these mechanisms is crucial not only for the resilience of grassland ecosystems but also for implementing effective land restoration practices. While these plants have adapted to natural wildfires, they haven't evolved to withstand human-made disturbances like excavation from mining or other resource extraction activities. These disruptions have the potential to damage underground structures vital for the survival of these plants, thereby compromising their natural ability to regenerate. Consequently, these plants are forced to rely solely on secondary mechanisms of establishment through seed germination.

Seeds from plants inhabiting fire-prone regions have undergone evolutionary adaptations, acquiring specific characteristics that enable them to respond to the ecological disturbance caused by fire. Some species have developed seeds that exhibit increased germination success triggered by fire-induced heat, as seen in the case of serotinous cones in certain woody plants (Lamont et al. 1991). Conversely, an intriguing phenomenon observed in certain plant species is the increased germination rate stimulated by fire smoke exposure (Brown and Van Staden 1997, Cox et al. 2017). Diverse studies have consistently demonstrated a positive germination response to smoke-water application, spanning various plant species and ecosystems (Brown & Van Staden 1997, Franzese and Ghermandi 2011, Kępczyński 2018, Zirondi et al. 2019, Alahakoon et al. 2020). This positive response remains consistent irrespective of whether the plants naturally occur in fire-prone environments (Light 2018, Van Staden et al. 2004). Smoke generated during fires in these regions plays a pivotal role in stimulating the seed germination process (De Lange 1990, Keeley 1998).

Additionally, employing plant-extracted smoke-water has emerged as an effective method to augment the success and pace of seed germination (Chumpookam et al. 2012, Read 2000, Cox et al. 2017). In some species the application of smoke, when combined with applied heat, resembling the conditions of a wildfire, has shown not only higher germination rates but has also accelerated the pace of germination. Exploring the combined impact of heat and smoke-water in germination processes holds significant implications for future studies (Hodges et al. 2021). Other species of course have shown lethal results with the additional application of heat in conjunction with smoke-water (Dayamba et al. 2010). Understanding how these factors interact and influence germination dynamics can provide invaluable insights into the mechanisms that drive seed response to fire-related cues (Hodges et al. 2021). Using established germination protocols, particularly incorporating cold stratification in conjunction with smoke-water, has yielded higher germination rates. This underscores the point that while the application of smoke-water is beneficial, its combination with cold stratification can significantly enhance germination outcomes (Krock et al. 2016).

The ongoing exploration of smoke and the identification of active smoke compounds that influence seed germination rates are rapidly advancing (Van Staden et al. 2004, Kulkarni et al. 2006, Merritt et al. 2007, Dixon et al. 2009, Jefferson et al. 2014, Govindaraj et al. 2016, Aslam et al. 2017, Mackenzie and Naeth 2019, Gupta et al. 2019, Khatoon et al. 2020). The significance of the parent plant material in the production of smoke-water plays a crucial role in determining the efficacy of the application. The combustion of different plant materials results in the release of unique compounds into the smoke, influencing the composition of smoke-water. These compounds, vary among plant species and contribute to the specificity of the germination response (Ren and Bai 2016). In addition, it remains essential to conduct targeted screenings of local native plant species' responses to smoke-water. This need arises from the genetic specificity of plant species and their unique adaptability to the local ecological context. Understanding how native plant species respond to smoke-water applications is critical, ensuring a more nuanced comprehension of their germination dynamics and potential implications for conservation and restoration efforts within their respective habitats. Native plant species in British Columbia are often confronted with the need to compete with agronomic species which are historically seeded after disturbance due to their fast-growing nature, availability, and economical price. The lack of availability of native species seed for reclamation and restoration purpose poses a gap in reclamation and restoration efforts where native species are vital to the ecosystem. Better understanding how to increase germination in native forb and shrub species can help to increase their use in restoration work. The results from my study indicate that germination rates are highest in the control and decrease with increasing concentrations of smoke-water. However, the results also indicate plant specific response with 5 species showing an increase in germination with smoke-water, 4 species showing no change, and 9 species showing some level of decrease.

CONCLUSION

Utilization of smoke-water to promote native seed germination and stimulate growth is an important tool to encourage and foster novel techniques for successful native plant restoration. Smoke water germination of native seeds can be applied to a variety of applications developing multiple strategies to increase availability of native species to be seeded in reclamation projects and promoting their successful establishment as well as long term establishment of species.

The use of smoke-water, enriched with native plant materials, is a low-cost approach and useful for promoting germination of some native species found in the natural grassland ecosystems in the southern interior of British Columbia. A greater knowledge about the growing conditions of seeds and germination response to smoke in areas with frequent fire regimes can accelerate the restoration of forest and grassland ecosystems. The use of smoke-water made from native parent materials, was successful in breaking dormancy and improving germination of 5 of the 18 species tested. However, considering that some of the species with poor responses originate from fire-adapted regions, testing under different conditions may indeed reveal that smoke-water can stimulate germination responses in these seeds as well. For example, altering the order of smoke-water application after cold stratification could potentially yield different results. Response did vary with smoke water concentration, and the 100% treatment resulted in a negative response in many of the species tested.

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CHAPTER 3 – SUSTAINING TRADITIONS, MANAGEMENT CONSIDERATIONS, AND FUTURE RESEARCH

PRESERVING THE LIVING HERITAGE: FIRST NATIONS' ONGOING HARVEST OF TRADITIONAL FOODS

British Columbia's (BC) grassland ecosystems have developed unique and adaptive species diversity, this unique biodiversity extends to include First Nation species of cultural significance, embodying a rich tapestry of plant life vital to Indigenous heritage and traditions. The ancient traditions of British Columbia's First Nations, particularly in the grassland regions, continue to thrive through the practice of harvesting and utilizing traditional foods, including berries, roots, and medicinal plants. Despite the passage of time and the encroachment of modernity, these cultural practices persist as living testimonies to the enduring connection between Indigenous communities and their ancestral lands.

Traditional foods, hold profound cultural significance among First Nations, serving as more than mere sustenance. They are deeply intertwined with stories, ceremonies, and a way of life that has been passed down through generations. From the vibrant red hues of soopolallie to the earthy richness of huckleberries and saskatoon berries, these fruits not only provide nourishment but also play crucial roles in cultural rituals and medicinal remedies. Traditional knowledge surrounding the gathering, preparation, and preservation of these foods continues to be shared within Indigenous communities, symbolizing the preservation of cultural heritage.

Moreover, the grasslands of British Columbia offer a bounty of food. Indigenous practices involve the gathering of various roots, shoots, and plants that sustain both the body and the spirit. *Claytonia lanceolata* (wild potato), for instance, a flowering plant with edible corms, remains a staple food source and holds cultural significance. Other plants like glacier lily, bitterroots, and various tubers contribute to the rich array of Indigenous cuisine, embodying a deep connection to the land. The significance of these traditional foods extends beyond their culinary value; they encompass a holistic approach to health and wellness. Many of these plants possess medicinal properties that have been respected for their healing properties for centuries. The knowledge of using these plants for medicinal purposes—treating ailments, healing wounds, and addressing various health issues—remains integral to Indigenous communities' well-being.

It's imperative to recognize that these practices are not relics of a forgone era but are vibrant, living traditions that continue to be practiced today. First Nations actively engage in the stewardship of their lands, cultivating and preserving these traditional foods while passing down invaluable knowledge to future generations. Preserving these practices is crucial, not only for safeguarding cultural heritage but also for fostering biodiversity and maintaining the delicate balance of ecosystems. First Nations' sustainable harvesting practices are deeply rooted in respect for nature and the understanding that the land provides for their needs but must be cared for and respected in return.

Efforts to conserve and support these traditions involve acknowledging and respecting Indigenous rights to land, resources, and traditional practices. It necessitates collaborative partnerships between Indigenous communities, governmental bodies, conservation organizations, and researchers to ensure the continued vitality of these cultural practices. In essence, the ongoing practices of harvesting traditional foods, underscore the living connection between Indigenous communities and their ancestral lands. These traditions are not static artifacts of history but vibrant and evolving elements that demand recognition, respect, and preservation for the benefit of present and future generations.

CLOSING KNOWLEDGE GAPS: NATIVE PLANT PROPAGATION IN RESTORATION PROJECTS

The reproductive creativity and indisputable miracle of passing one’s genetic profile into a tiny package known to us as a seed, to other’s food, to other’s life, to other’s the future. Seed is the cornerstone of my thesis.

With plants having abundant reproductive diversity it has created many mechanisms for seed characteristics. Several of these distinctive characteristics include dispersal mechanisms, quantity of seed per flower and flower per plant, seasonal timing, gestation maturity, conditional viability, size, and numerous other unique characteristics (Pakeman 2001). Amongst these characteristics is the effect of fire on seed. Fire has always been a natural part of Earth’s history, driving ecological processes over evolutionary time and making necessary contributions to the strength, diversity, and replenishment of its ecosystems (Bond and Keely 2005). The response of seeds to fire creates a whole complex evolutionary pathway; selecting one particular aspect of this evolution, the response of seeds to smoke, helps narrow the knowledge gap on germination success of British Columbia's grasslands species. The application of smoke water had definite success on certain species. Using smoke water as a germination cue has shown high viability on many species worldwide with studies from multiple continents (Brown and Van Staden 1997, Keeley and Fotheringham 1998, Baker et al. 2005, Kulkarni et al. 2011).

Land disturbance has shaped Earth's natural history in diverse ways, with micro and macro impacts. This spectrum ranges from catastrophic extinctions shown in the fossil records to more localized events like a small-scale landslide. In addition to natural land disturbance there is an increase in anthropogenic disturbance with natural resource extraction, urban development, agriculture, and other human development pressures. This increase in anthropogenic disturbance has helped further develop the fields of restoration and reclamation. However, the need for restoration and reclamation is often driven by economic value. With species diversity loss and ecosystem services being diminished many of the modern colonized world is beginning to see value in other motives for restoration and reclamation. These are values that have been held by Indigenous culture's worldwide (Agrawal 1995, Xu et al. 2005, McGregor 2012, Popova 2014). Indigenous motives often looked at a more holistic-connected approach (Sobrevila 2008, Tangihaere and Twiname 2011, Cunsolo et al. 2012, Martin 2012), with sustainability practices to help assure that whatever commodity or resource was used would also be available to the future generations yet to come.

Although this response may seem elementary or common-sense it is not easy in practice (Holt 2005, Rands et al. 2010). Many projects have spent large amounts of resources on planting native seeds but many of these seeds do not germinate or perform so poorly that the land becomes dominated by unwanted invasive species. The use of agronomic species could produce value in land stabilization, as well as forage crops for beef and other ungulates (Pilliod et al. 2017). This path is tempting but does not meet the criteria of restoration, for this native species are required. The knowledge gap on native plant propagation has been slowly closing and this knowledge gap is what fuelled this project.

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

In honour of the very word restoration, it only seems appropriate to really know what was there before. In honour of all our ancestry I hope we can look back and create a place in which we all want to live and most importantly provide a place that seven generations from now our posterity can swim and drink in the waters that our ancestors did, that our posterity can harvest the roots and berries from the same hillsides.

We are living in unprecedented times with wild spaces diminishing every year in the name of human progress. I imagine us walking forward towards a cliff with certain demise; it is past time for us to recognise what progress really measures or what forward thinking might mean. If we turn around 180 degrees and step forward, it truly will be a step forward. Life on this planet is relying on us to turn around and begin to step forward to our Indigenous practices that have been used since time immemorial.

The foundational Indigenous perspective is built upon connection, that we are woven into the great web of life. The colonized perspective based on us being outside the system and having dominion over it has developed a detached approach (Scalercio 2018). This detached approach helps us to justify over harvesting, pollution, or any other unsustainable practices. In every part of the world, we can see the devastating ecosystem losses from unsustainable and polluting practices. Loss of our coral reefs at unprecedented rates, loss of the great cod numbers in the Atlantic, loss of salmon in the Pacific Northwest, loss of forest in the Amazon, pages could be filled with examples of change to our Earth in a mere human lifetime.

When we approach with connection, we recognize that we are emulsified in the great story of life. With the modern recognition of human impacts we have begun to realize the importance of diversity and the value of each individual organism (Walker 1992, Sinclair et al. 1995, Hooper et al. 2005, Brudvig 2011). We recognize all the biotic and abiotic factors that play a role in the current and future life of our planet. With this recognition governments have helped to develop policies and laws that begin our journey in turning to a more connected approach.

The Canadian government has pressured industry and government to consult with First Nations. Through the consultation and engagement of Indigenous relations there is a wonderful opportunity for us to reflect upon what a future or amended project can look like. The consultation process helps to recognize that Indigenous people have occupied the affected land area from a proposed or current project since time immemorial. This allows us to reflect upon the sustainability practices used.

The consultation process with First Nation's should be an opportunity to help gain understanding and insight. Through consultation we can have a bird's eye view of potential impacts, particularly cumulative effects (Runge 1998, Tollefson and Wipond 1998, Solomon et al. 2016). Cumulative effects are so important and can easily fall in line with the parable of the camel whose back was broken from one last straw. When we separate and divide up impacts, they can often look like a small piece of straw. This separation and division also results in a narrow vision making it difficult for us to see the relationships of everything intertwined.

The consultation and engagement process should not be considered simply a negotiation. The advent of Impact Benefit Agreements to provide legal certainty for industry and governments to justify moving forward with projects should not be a means to an end (Craik et al. 2017). Fundamentals of communication are built upon understanding. It is paramount that industry and government understand that consultation and engagement is built upon the deep connection we have with all living and non-living things.

First Nation's relationship to fire can help us to gain a better relationship of one of the practices used for land management. Having unprecedented wildland fires in the past decade (Government of BC 2019) demonstrates that there is a need to reflect upon our strategies for forest management, especially our wild land interface with urban development. Fires in modern history have been looked upon as having a negative and destructive impact upon our lands but much of this is a result of our past land practices.

FUTURE RESEARCH

Response of plants to fire varies greatly by species. For plants that have evolved in areas with fairly frequent fire regimes using smoke-water as a tool may help to increase germination success. This project looked at a small number of BC grassland species and focused only on forbs and shrubs. The application of smoke water needs to be explored on a larger number of species and include grasses. Using smoke water in conjunction with other germination practices such as scarification should also be explored.

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APPENDIX 1 – SEED COLLECTION DATA SHEET

Date of collection: ___________________________

Collector name(s): ______________________________

Genus Species: ____

Common name: ____

Number of individuals collected: ____1-10, _____10-50, ____ 50 or more

Number of species within 5 meters of this sample: ___ 0, ___ 1-10, __10-50, __to 50 or more.

Distance between this sample and nearest other sample from which seeds were collected. ____ 0.5 meter (minimum), ___ 0.5-3 meters, _____3-30 meters___ more than 30 meters.

Soil: ___ Rocky ___ Gravel ___ Sand ___ Loam ___ Clay

Biogeoclimatic zone: ____Bunchgrass ____Interior Douglas-Fir ____Ponderosa Pine.

Topography: ___ Flat ___ Slope (Aspect: ___ N ___ S ___ E ___ W)

Photos have been taken ___________

Seed lot number _______________

Region _____________________________ Province _____________________________________

GPS Coordinates: lat _______._____________ long _______._____________ elevation _______meters

Seeds were separated from parent plant material by hand. Cleaned seed was then put in Ziploc bags; all seeds were then put in an unplugged deep freezer, put in dry-cool-basement, ranging temperatures from 13-19 degrees Celsius. Seeds were monitored monthly for presence of mold/mildew and rodent damage.