

Article

The Effect of Smoke-Water on Seed Germination of 18 Grassland Plant Species

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Abstract

There is an urgent and constant need for land reclamation and to restore self-sustaining, stable, and resilient ecosystems. It is necessary 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*); four species showed no change (*Rosa woodsii*, *Crataegus douglasii*, *Lewisia rediviva*, and *Prunus virginiana*); and nine species showed some level of decrease (*Fritillaria affinis*, *Fritillaria pudica*, *Berberis aquifolium*, *Claytonia lanceolata*, *Gaillardia aristata*, *Balsamorhiza sagittata*, *Allium cernuum*, *Amelanchier alnifolia*, and *Lomatium macrocarpum*). Smoke-water also affected germination rate by plant form (herbs > shrubs), plant phenology (spring ephemeral and protracted > summer quiescent and summer mature) and plant dispersal mechanism (wind > animal). 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.

Keywords: wildfire; smoke-water; seed germination; native grassland plants; ecological restoration



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1. Introduction

Seeds from plants in fire-prone areas have evolved to exhibit specific characteristics. Previous studies have shown a positive germination response to smoke-water [1–6], regardless of whether the plants occur in fire-prone ecosystems [7,8]. Smoke due to fire in fire-prone regions can stimulate the seed germination process [9,10]. Moreover, plant-extracted smoke-infused water can be used to enhance the success and rate of seed germination [11,12]. Although the study of smoke and the identification of active smoke compounds on seed germination rate is increasing [8,13–19], screening of the responses of

local native plant species to smoke-infused water is necessary because of potential specific local genetic adaptations [20,21].

The interior grasslands of southern British Columbia, Canada have been shaped by fire over the past several centuries [21,22]. Fires are caused by natural processes, mostly lightning strike, but also through controlled management practices of the Indigenous peoples [22]. 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.

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 this study. Species phenology determines what time of year a species matures, flowers, and disperses seeds [23]. 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 [24]. Each species has difference mechanisms which help in dispersal. For example, hooked structures on larger seeds allow them to attach to the fur of animals, dispersing them further. Similarly, wings on seeds aid in wind dispersal. Understanding how these traits relate to seed germination success is important.

The over-arching 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 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.

Our study objective was to test germination success of 18 native grassland plants of British Columbia to different concentrations of smoke-water, and whether plant form, phenology, and seed dispersal mechanisms influence germination success.

2. Materials and Methods

2.1. Study Area

This 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 [25].

2.2. Seed Collection

Species were not only categorized according to plant form (Table 1), but also to phenology [26], seed dispersal, and plant strategy type.

Table 1. Eighteen forb and shrub species selected for seed collection in the southern interior of BC, and their ecological strategies: phenology and seed dispersal mechanisms. Nomenclature follows the E-Flora BC database.

Scientific Name	Common Name	Plant Form	Phenology	Seed Dispersal
<i>Allium cernuum</i> Roth	Nodding Onion	Forb	Summer Quiescent	Wind
<i>Amelanchier alnifolia</i> (Nutt.) Nutt. ex M. Roem.	Saskatoon	Shrub	Summer Mature	Animal
<i>Arnica latifolia</i> Bong.	Mountain Arnica	Forb	Summer Mature	Wind
<i>Balsamorhiza sagittata</i> (Pursh) Nutt.	Arrow Leaved Balsamroot	Forb	Spring Ephemeral	Animal
<i>Berberis aquifolium</i> Pursh	Oregon Grape	Shrub	Protracted Growth	Animal
<i>Calochortus macrocarpus</i> Douglas	Mariposa Lily	Forb	Summer Quiescent	Wind
<i>Claytonia lanceolata</i> Pall. ex Pursh	Western Spring Beauty	Forb	Spring Ephemeral	Wind
<i>Crataegus douglasii</i> Lindl.	Hawthorne	Shrub	Summer Mature	Animal
<i>Erythronium grandiflorum</i> Pursh	Glacier Lily	Forb	Spring Ephemeral	Wind
<i>Fritillaria affinis</i> (Schult. & Schult. f.) Sealy	Chocolate Lily	Forb	Spring Ephemeral	Wind
<i>Fritillaria pudica</i> (Pursh) Spreng.	Yellow Bell	Forb	Spring Ephemeral	Wind
<i>Gaillardia aristata</i> Pursh	Brown Eyed Susan	Forb	Summer Quiescent	Animal
<i>Lewisia rediviva</i> Pursh	Bitterroot	Forb	Summer Mature	Wind
<i>Lomatium macrocarpum</i> Coult. & Rose	Large Fruited Desert Parsley	Forb	Summer Mature	Wind
<i>Lomatium nudicaule</i> (Pursh) J.M. Coult. & Rose	Barestem Desert Parsley	Forb	Spring Ephemeral	Wind
<i>Prunus virginiana</i> L.	Choke Cherry	Shrub	Summer Mature	Animal
<i>Rosa woodsii</i> Lindl.	Prairie Rose	Shrub	Summer Quiescent	Animal
<i>Shepherdia canadensis</i> Nutt.	Soopolallie	Shrub	Summer Mature	Animal

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 [27]. Seeds were collected from multiple zones (Bunchgrass, Interior Douglas-Fir, and Ponderosa Pine) using the British Columbia Biogeoclimatic Ecosystem Classification [28]. Many collection sites were on or near Indian Reserves of the Nlaka’pamux Nation and have rich historical gathering significance, such as Botanie Valley, which is known for its abundant root crops in early spring and late summer [27]. 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 [29]. 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 combined with no more than 20% of material arising from a single day. Seed collections spanned two growing seasons of the years 2015–2016. All seeds were placed in cold storage (−20 °C) for at least three months prior to commencement of the germination trials.

2.3. Smoke Solution Procedure

Smoke-water was created using the system described by Coons et al. [30]. The plant material used for combustion was the parent plant material of seeds collected and other grasses and trees on the same landscape. The smoke system was operated in a fume hood in the Thompson Rivers University Chemistry Lab. First, 100 g ± 10 g of plant material was weighed and cut into small sections roughly 2–5 mm in length. A single layer of material was placed at the bottom of the stainless-steel bee smoker with attached billows and lit with a lighter (Figure 1). The material burned for 10–30 s, 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 maintain sufficient combustion. Smoke travelled through a rubber heat resistant hose that was fitted tightly at the top of the smoker, with the other end below the surface of the water in a 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.

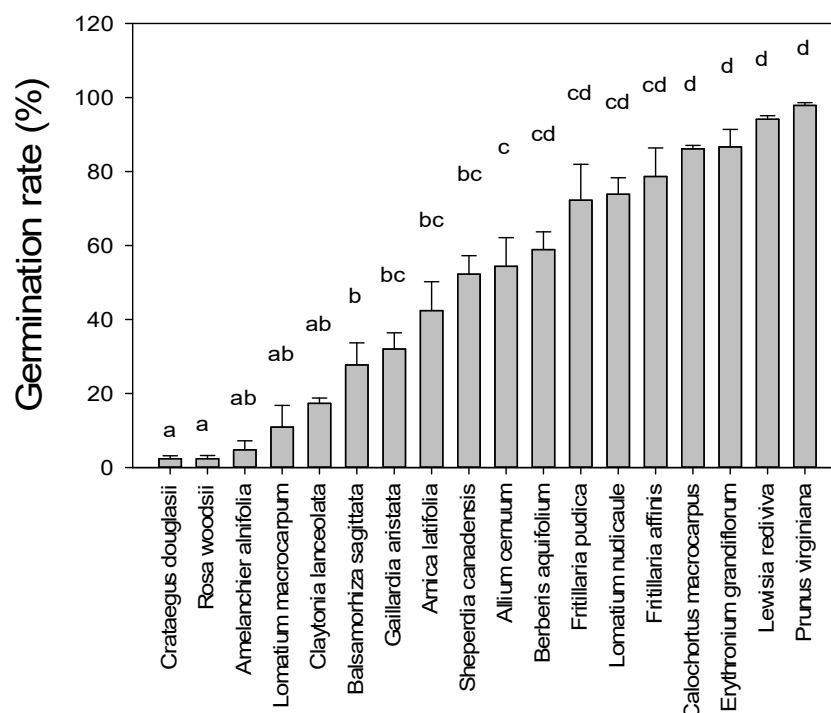


Figure 1. Germination rate of 18 native grassland species. Error bars represent standard errors. Bars sharing the same letter are not significantly different, based on Tukey's HSD.

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 2).

Table 2. 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	4740
p-Cresol	0.156	0.500	9260

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

2.4. 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 the desired concentration with distilled water. Each treatment was replicated three times, with 15–25 seeds for each replicate, depending on seed size [31], 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 in November 2016. Seeds were soaked for 24 h [32], rinsed with distilled water, and wrapped in disposable brown hand towel paper moistened with distilled water [33]. The seeds were then refrigerated at 4 °C for 90 days for cold moist stratification [34,35].

In February 2017, the stratified seeds were placed in 90 mm glass Petri dishes on three layers of filter paper, moistened with distilled water [36], and exposed to 20 °C and

indirect light with a 12 h light/12 h dark photoperiod, resembling a day and night cycle [37]. The seeds were monitored daily for the appearance of radicles and seed germination [38]. Germination is usually marked by the rupture of the covering layers and radicle protrusion, which is regarded as the completion of the germination process [39].

2.5. Data Analysis

Germination data were analyzed using two-way Analysis of Variance (ANOVA) with smoke treatment and species as the two factors, and eighteen one-way ANOVAs for each species, with smoke treatment as the factor. Tukey's HSD was used to separate treatment means [31]. Similarly, two-way ANOVAs were used to analyze smoke treatment and (1) plant form (forb vs. shrub), (2) phenology, and (3) seed dispersal. Normal distribution was confirmed using the Shapiro–Wilk test. Two species, *Calochortus macrocarpus* and *Lewisia rediviva*, were log-transformed to meet assumptions of normal distribution. To account for increased risk for type II error running 18 one-way ANOVAs, Bonferroni correction was applied with ($p < 0.0028$).

3. 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 (Figure 1; 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 (Figure 2).

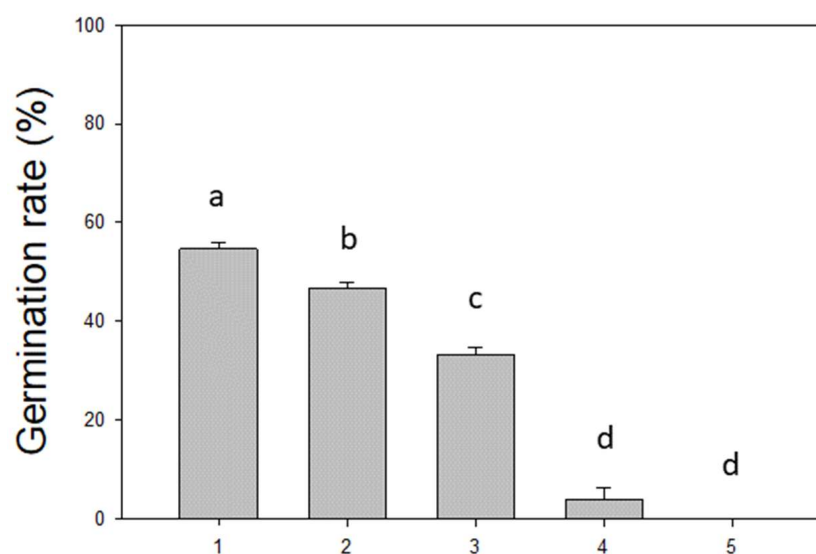


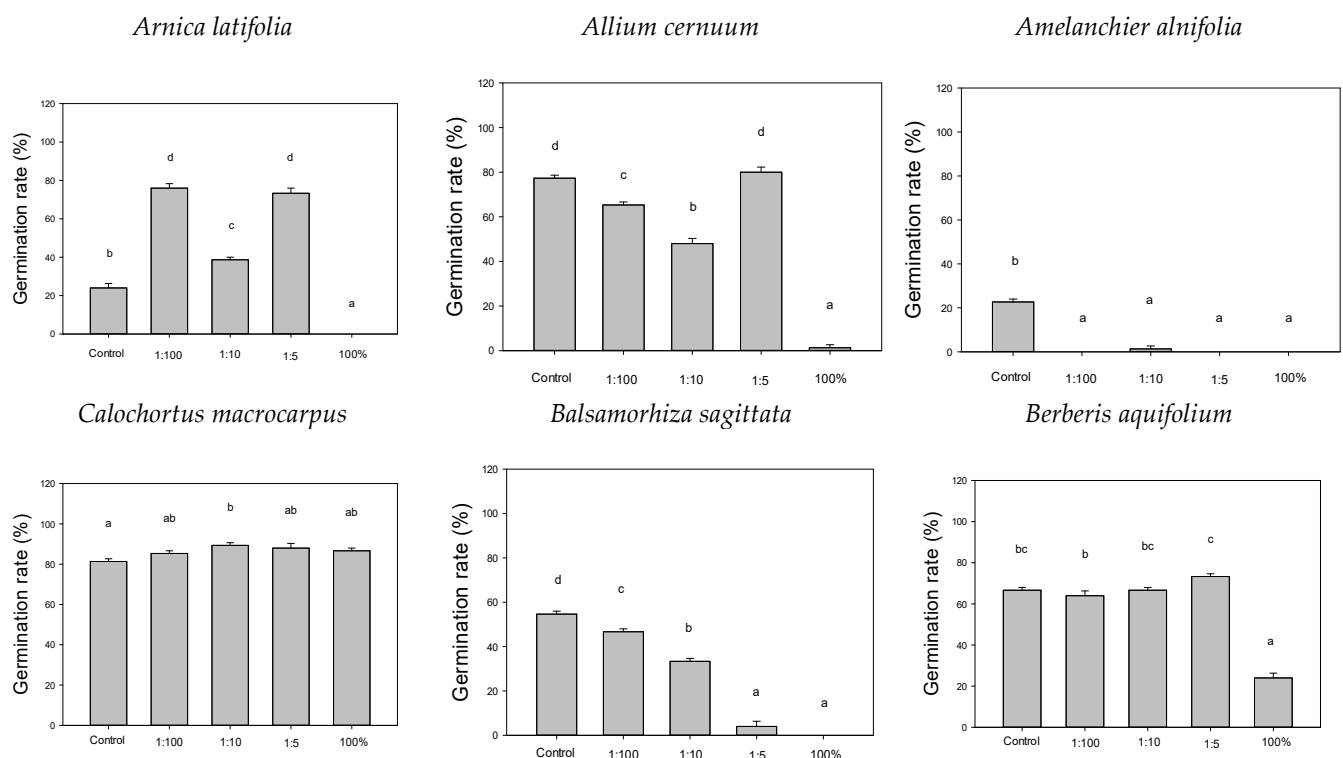
Figure 2. Germination rates of all 18 native grassland species combined and as affected by smoke-water concentration. 1 = control (0%), 2 = 1:100 (1%), 3 = 1:10 (10%), 4 = 1:5 (20%), and 5 = 100% smoke-water concentration. Error bars represent standard errors. Bars sharing the same letter are not significantly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

Although the control trials were found to have the highest germination rate (Figure 2, 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 3 and Figure 3). Overall, five species showed an increase in germination with smoke-water, four species showed no change, and nine species showed some level of decrease.

Table 3. Eighteen one-way ANOVA results for smoke-water concentration with respect to species.

Species	Mean Squares	F-Ratio	p-Value
<i>Allium cernuum</i>	3118.4	324.83	<0.001
<i>Amelanchier alnifolia</i>	300.3	140.75	<0.001
<i>Arnica latifolia</i>	3177.1	270.77	<0.001
<i>Balsamorhiza sagittata</i>	1835.7	286.83	<0.001
<i>Berberis aquifolium</i>	1179.7	122.89	<0.001
<i>Calochortus macrocarpus</i>	28.3	3.79	0.04
<i>Claytonia lanceolata</i>	101.3	31.67	<0.001
<i>Crataegus douglasii</i>	14.4	2.25	0.136
<i>Erythronium grandiflorum</i>	1144.0	134.06	<0.001
<i>Fritillaria affinis</i>	3093.3	322.22	<0.001
<i>Fritillaria pudica</i>	4907.7	511.22	<0.001
<i>Gaillardia aristata</i>	994.7	116.56	<0.001
<i>Lewisia rediviva</i>	12.3	0.89	0.507
<i>Lomatium macrocarpum</i>	1793.1	1681.00	<0.001
<i>Lomatium nudicaule</i>	1540.3	144.40	<0.001
<i>Prunus virginiana</i>	4.3	0.40	0.804
<i>Rosa woodsii</i>	9.1	0.77	0.567
<i>Sheperdia canadensis</i>	1299.7	135.39	<0.001

Germination response was impacted by functional group, with forbs (or herbs) having higher germination rates than shrubs (Figure 4; 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 3.** Cont.

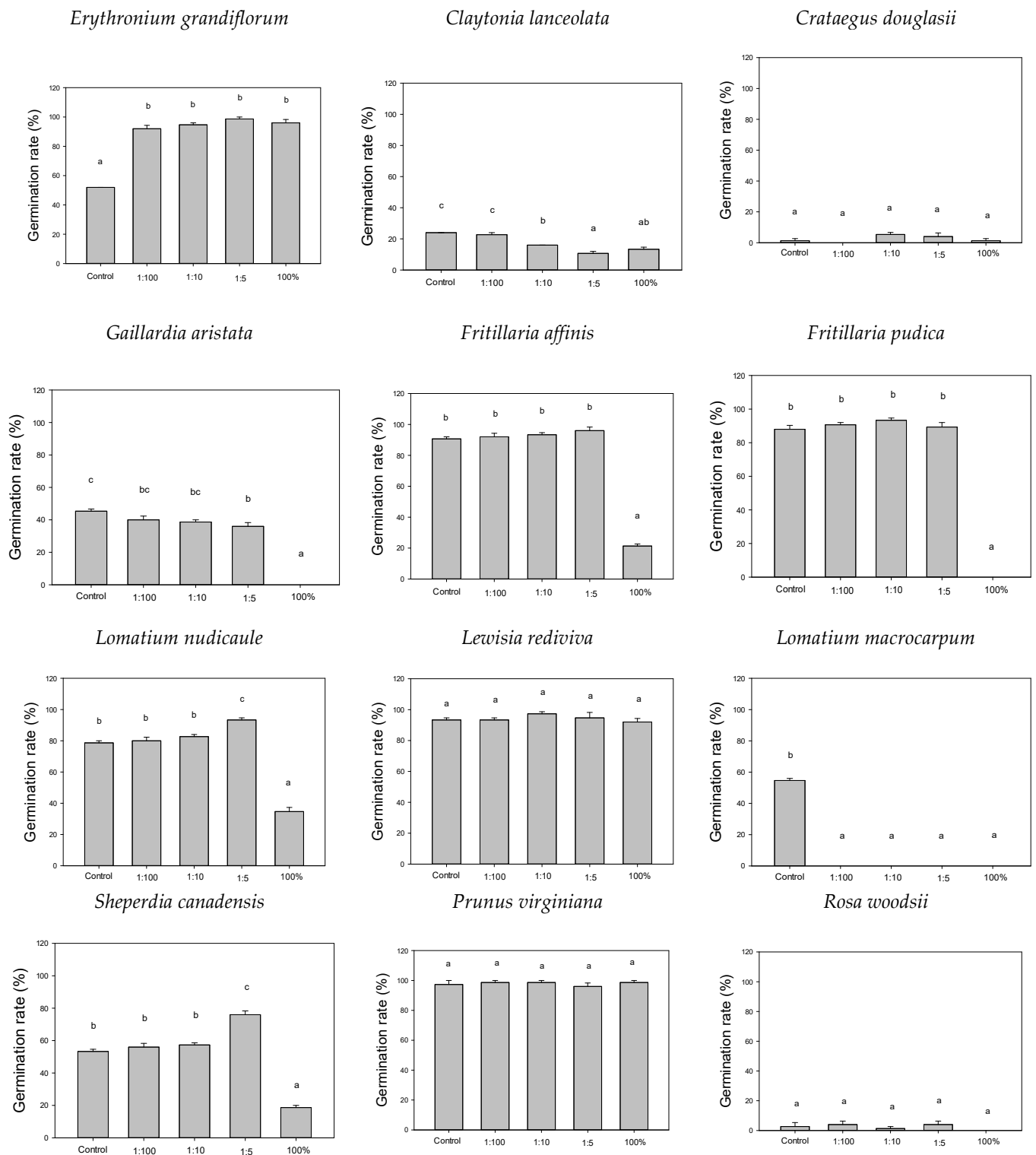


Figure 3. Germination rate of each of the 18 native grassland species as affected by smoke-water concentration. The horizontal axis is the smoke concentration in the water. Error bars represent standard errors. Bars sharing the same letter are not significantly different, based on Tukey's HSD.

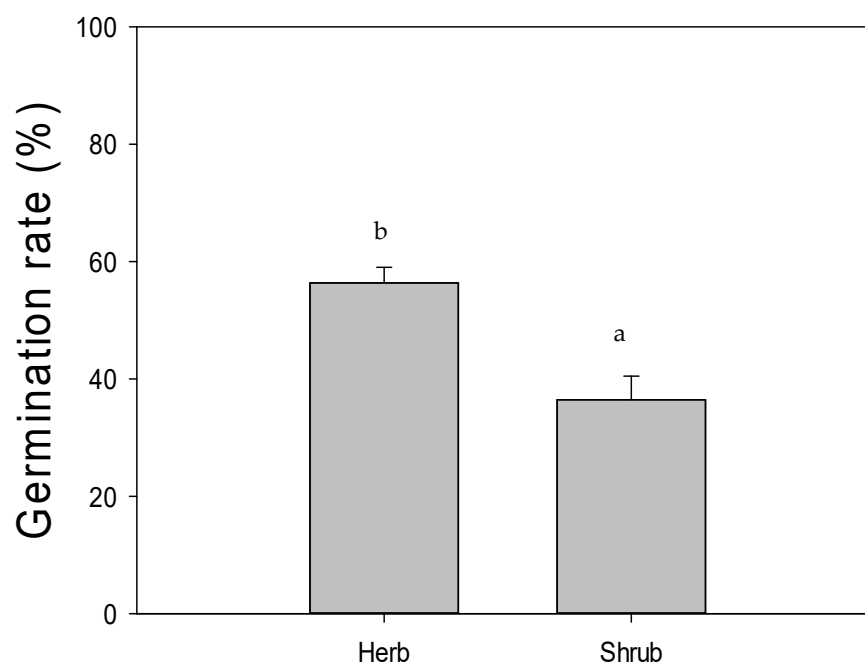


Figure 4. Germination rates of species by plant form (herbs or forbs and shrubs). Error bars represent standard errors. Bars sharing the same letter are not significantly different.

Phenology also had a significant impact on germination success (Figure 5; 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.

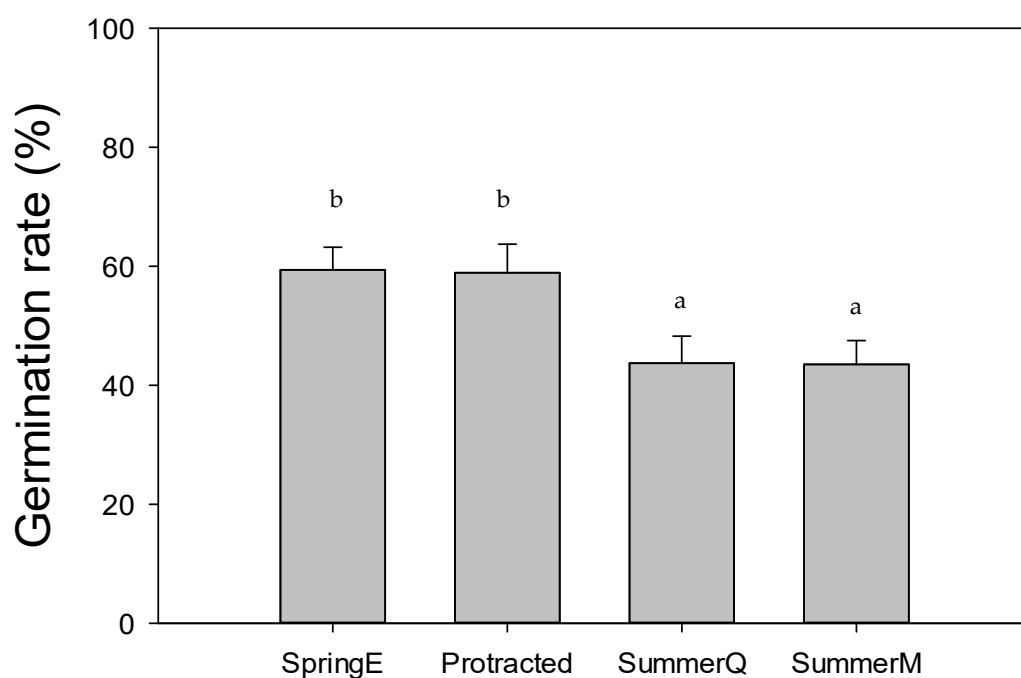


Figure 5. Germination rates of species by phenology as affected by smoke-water concentration. Error bars represent standard errors. Bars sharing the same letter are not significantly different, based on Tukey's HSD.

Seed dispersal tactics were also evaluated, and the results indicate that wind-dispersed seeds had higher germination rates than animal-dispersed seeds (Figure 6; 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, $df = 4$, $p = 0.651$).

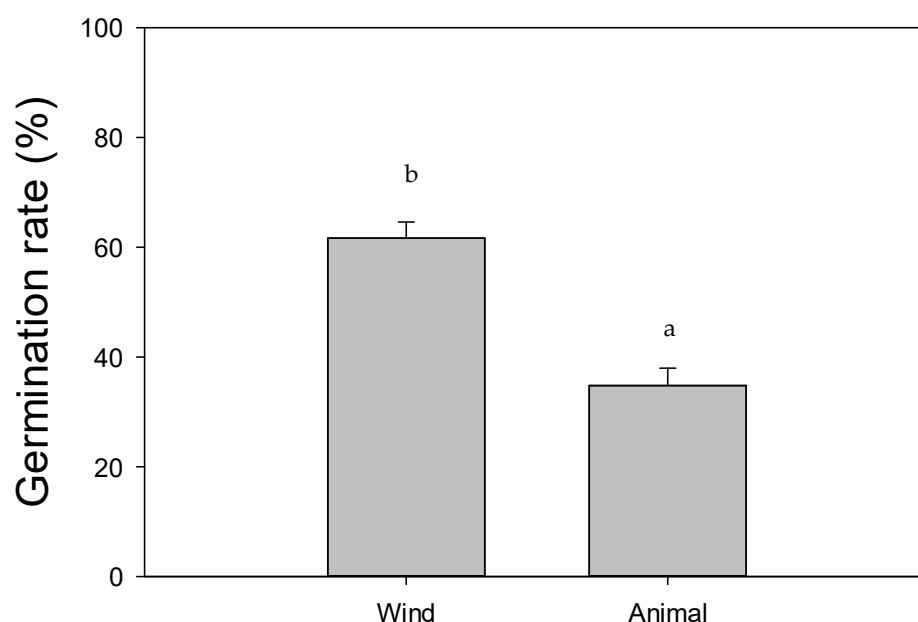


Figure 6. Germination rates of species by seed dispersal as affected by smoke-water concentration. Error bars represent standard errors. Bars sharing the same letter are not significantly different.

4. Discussion

4.1. 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 [40,41]. Smoke-water was able to provide moisture, resulting in 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. However, 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 [42,43]. 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 [44]. 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 [45].

Mountain arnica had the highest germination rate, with 1% and 20% smoke-water resulting in rates almost triple 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 [46]. Mountain arnica usually survives cool to moderately severe fires but is susceptible to fire-kill at higher intensities [47], making establishment from seeds more important in those situations. This species has dried pappus achene seeds, which can absorb water quickly [48]. 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. The location and size of the pappus on the flower head can also contribute to germination success [49]. Moreover, the rhizome root structures of mountain arnica contribute to its resilience against fire, allowing for effective fire endurance strategies [50].

Both barestem desert parsley and soopolallie showed an increase in germination with the 20% treatment concentration, but a decrease compared to all treatments at the 100% concentration. Barestem desert parsley seeds germinate well following cold, moist exposure conditions [51], and so the increased warm stratification of smoke-water was less effective than in species such as the glacier lily. Soopolallie, a species that 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 [52], and its 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 [53].

4.2. 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 aristata*), 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 rates that remained similar across 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 has shown only 20% germination rates in other control trials [54]. There is limited literature specific to seed germination of chocolate lily. However, there is more literature supporting the use of bulbs or rice grains as the main sources for propagation [55]. Oregon grape shows the importance of bear digestion in aiding and increasing the germination rates of 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 struc-

tures which allow for prompt recovery after a fire [56]. Both yellow bell and chocolate lily have the same Liliaceae bulb characteristics that aid in subsurface survival.

Brown-eyed Susan showed a slight decrease in germination at higher levels of smoke-water, with no germination response at the 100% treatment concentration. Brown-eyed Susan species have achenes, which presumably need some biomechanical treatments, instead of smoke-water, to break their seed dormancy for growth. Mensah and Ekeke [57] revealed that water uptake treatment has a smaller 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 how root strategies, such as large tuber structures, serve as the primary means of survival through mild to moderate fires. These tubers have long held significance among First Nations communities for their food value.

Arrowleaf balsamroot, with a deep tap root, can tolerate fire, grazing, trampling, and drought [58]; however, it does not germinate or transplant readily [59]. Bowen [60] 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, with the smallest reactions to environmental drivers [61]. Following fires, arrowleaf balsamroot will often regenerate from the persisting caudex [62].

Nodding onion has a bloom period of mid- to late summer, anytime from June to October [47]. Seeds become mature in this period, which occurs simultaneously with wildfire season in British Columbia. In 1% and 10% smoke-water concentration trials, nodding onion showed decreased germination, and in the 20% trial, its germination rate increased to 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 its survival.

Saskatoon and large-fruited desert parsley responded negatively to smoke-water compared to the control, with little to no germination with the application of smoke-water. This indicates 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 indicated that alternating stratification strategies play a larger role in germination rates [63]. Saskatoon is considered a fleshy fruit, and passage through an animal can increase germination in these species. For example, some fleshy fruit seeds have shown higher germination success with bear digestion [64]. Large-fruited desert parsley had 60% germination in the control but no germination with any smoke-water application. Admittedly, this was not expected, considering it is 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 [63] showed that large-fruited desert parsley had 80% germination in their control, with only 23% for barestem desert parsley showing that they indeed behave differently on the same treatments. However, these species can resist fire, and even if they lose aboveground anatomy, their roots and rhizomes near topsoil can sprout again [65,66].

4.3. No Change in Germination

Four species showed no change in germination rate from the control to the 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. The 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 [67]. Both rose and hawthorn fruits are significant food source for bears and other animals. Animal digestion increases germination and distribution of many species [64,68,69]. 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 [70].

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 in bitterroot [71]. Chokecherry's fleshy fruits provide a food source for birds and a mechanism for seed dispersal, with high germination rates achieved through defecation or regurgitation [72]. The high rate of germination success possibly leads to the depredation of young saplings [73]. The ecological strategy of bitterroot is to go dormant in early summer, so its deep, branched taproot escapes most wildfires [65]. The combination of root and seed strategies maximizes the potential for survival and fitness.

4.4. Other Factors

Herbs/forbs showed greater seed germination success compared to shrubs. Herbs typically produce smaller seeds compared to shrubs, which allows for quicker water absorption and penetration, facilitating the germination process [74]. Herbs often utilize a broader range of seed dispersal mechanisms. 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 [75,76]. Quick germination and establishment allow them to complete their life cycle rapidly, taking advantage of favorable conditions for growth and reproduction [77].

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 four phenological groups (summer mature, summer quiescent, protracted growth, and spring ephemerals), which are hypothesized to reflect adaptation to the spatial and temporal distribution of soil moisture [26]. These groups reflect the seasonal changes of the year and give us species' adaptive responses to not only sunlight, temperatures, and moisture but also to potential seasonal land disturbances, like wildfire, and caloric timing value for animals [78]. They also provide flushes in botanical composition, forage production, and nutrient availability, which should be reflected within grassland management [26]. 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 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 species to take advantage of post-fire environments, where competition from other plants is reduced, allowing for successful establishment and growth [79]. 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 [42]. 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 [80–82].

The ongoing exploration of smoke and the identification of active smoke compounds that influence seed germination rates are rapidly advancing [8,13–19,46]. 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 [83]. 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.

5. Implications

Native plant species in British Columbia are often confronted with the need to compete with agronomic species that 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 purposes 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. Since there was no published information on dormancy of the species used in this study, we treated all seeds equally, and smoke-water was the primary and only treatment. Future studies should provide further testing on dormancy. The results from our study indicate that germination rates were highest in the control and decreased with increasing concentrations of smoke-water. However, the results also indicate plant-specific responses, with five species showing an increase in germination with smoke-water, four species showing no change, and nine species showing some level of decrease.

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 in various ways, supporting the development of multiple strategies to increase the availability of native species to seed in reclamation projects. This approach promotes the successful establishment and long-term establishment of these species.

The use of smoke-water, enriched with native plant materials, is a low-cost approach that is useful for promoting germination of some native species found in the natural grassland ecosystems in the southern interior of British Columbia. 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 also stimulate germination responses in these seeds. For example, altering the order of smoke-water application after cold stratification could potentially yield different results. Responses 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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