Priming Seeds in Aqueous Smoke Solutions Improves Germination of *Agropyron dasystachyum, Dactylis glomerata, Elymus angustus, Elymus junceus*, and *Festuca hallii*

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By
Yusuf Abu

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ABSTRACT

Seeds of many grasses and legumes from the Canadian Prairies have dormancy which prevents the germination of viable seeds in otherwise favorable conditions. Plant-derived smoke can improve germination in dormant seeds. Seeds of eight grasses, two legumes, and *Lactuca sativa* were investigated for the effects of seed priming in aqueous smoke solutions on germination, seedling emergence, seedling growth, and standing crop. Aqueous smoke solutions were produced by bubbling smoke generated from the incomplete combustion of wheat straw (*Triticum aestivum* cv. Unity) or prairie hay (*Festuca hallii*) through distilled water. Seeds were primed for 24 h in darkness using serial dilutions (1/1000v/v, 1/100v/v, 1/10v/v and 1/1v/v) of the aqueous smoke solutions. After priming, seeds were dried at 20°C in darkness for 7d and placed in petri dishes containing filter paper, after which 5 mL of distilled water were applied. Seeds were incubated at 10/0°C or 25/15°C in 12h light/12h darkness or 24 h darkness for 49 d. Seeds were also primed using 1/100v/v aqueous smoke solutions of wheat straw or prairie hay and seeded in the field. Non-primed seeds and those primed in distilled water (0/1v/v) were used as controls. Within species, germination varied significantly ($P \leq 0.05$) among concentrations of aqueous solutions of smoke, smoke type, light, temperature, and their interactions. Total germination of *Astragalus cicer*, *Trifolium ambiguum*, *Hesperostipa comata*, *Stipa viridula*, and *Pascopyrum smithii* was not changed by priming seeds. Depending on light or temperature treatments, priming seeds of *Agropyron dasystachyum*, *Elymus junceus*, *Dactylis glomerata*, *Elymus angustus*, and *Festuca hallii* in aqueous smoke solutions improved germination by 16%, 20%, 32%, 49%, and 50%, respectively. Priming seeds in aqueous smoke solutions reduced the number of days to 50% germination for *Trifolium ambiguum*, *Lactuca sativa*, *Festuca hallii*, and *Stipa viridula* (2 d), *Elymus junceus* (3 d), *Dactylis glomerata* (4 d), *Hesperostipa comata* (10 d),

and *Pascopyrum smithii* (15 d). Priming seeds in aqueous smoke solutions increased seedling lengths (combined hypocotyl and radicle lengths) for *Elymus angustus* and *Hesperostipa comata* by 28% and 100%, respectively, but it reduced seedling lengths of *Lactuca sativa*, *Festuca hallii,* and *Trifolium ambiguum*. Seedlings from seeds primed in aqueous smoke solutions generated from wheat straw were longer for *Lactuca sativa* (83%), *Elymus angustus* (52%), and *Hesperostipa comata* (36%) as compared with prairie hay, respectively. Priming seeds interacted with smoke type to increase seedling lengths for *Pascopyrum smithii* (92%), *Elymus junceus* (100%), and *Agropyron dasystachyum* (100%), but it reduced seedling lengths for *Astralagus cicer* (26%), *Trifolium ambiguum* (55%), and *Dactylis glomerata* (90%). Exposing seeds to aqueous smoke solutions partially substituted a light requirement for germination in *Pascopyrum smithii, Festuca hallii, Hesperostipa comata*, *Dactylis glomerata*, *Agropyron dasystachyum*, *Stipa viridula,* and *Elymus junceus*. Priming seeds in aqueous smoke solutions increased standing crop of *Dactylis glomerata* by 57%, but total seedling emergence and rate of emergence of seedlings in the field were not different ($P>0.05$) among priming treatments. Priming seeds in aqueous smoke solutions generated from wheat straw or prairie hay can stimulate germination in *Agropyron dasystachyum, Dactylis glomerata*, *Elymus junceus*, *Elymus angustus*, and, *Festuca hallii*.

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1.0 INTRODUCTION

Seed germination begins with the absorption of water by a seed and ends when the radicle elongates and penetrates structures surrounding the embryo (Bewley, 1997). Events that follow involve the re-activation of important seed reserves used for early seedling growth (Bewley, 1997). Seed germination is controlled by temperature, water, and oxygen (Vleeshouwers *et al*., 1995, Vleeshouwers and Kproff, 2000). However, even when conditions are favourable for germination, dormant seeds do not germinate (Vleeshouwers *et al.*, 2005). There is no simple way to define dormancy, largely because dormancy may assume different forms according to species (Lange, 1996; Vleeshouwers *et al*., 1995), however, dormancy is commonly understood as the failure of a viable seed to germinate under conditions that are favourable for germination.

Dormancy is a natural seed property that determines the environmental requirements in which the seed can germinate (William and Gerhard, 2006). Similar cellular and metabolic events are known to occur in non-dormant and dormant seeds. However, non-dormant seeds germinate, but for some reasons, dormant seeds do not germinate even after completing the metabolic steps required for germination (Bewley, 1997). Dormancy can be released by treatments such as priming, alternating temperatures, stratification, scarification, light, and the use of plant hormones (Fenner, 1991; Gutterman, 2000). Alternating temperatures with amplitude of 10^{o}C enhanced germination in *Dactylis glomerata* L. (orchardgrass) and *Pascopyrum smithii* Rydb. (western wheatgrass) (Qiu *et al*., 2008). Exposing seeds to fluctuating temperatures may be a critical requirement to complete dormancy breaking in some species (Benech-Arnold *et al*., 2000).

Fire is a major selective force that influences seed dormancy release and the structure and composition of the plant communities that follows (Robert and James, 1998). Some species have evolved seeds that respond to fire-related germination cues such as smoke which has the potential to break dormancy and stimulate germination in fire prone and non-fire prone species (van Staden *et al.,* 2000). Smoke plays important roles in the re-establishment of plant communities including the chaparral in southern California (Keeley and Pizzorno, 1986), fynbos in South Africa (De Lange and Boucher, 1990), Kwongan in Australia (Dixon *et al.*, 1995), and the Mediterranean Basin (Crosti *et al.,* 2006). Heat from fire and the chemical components that can be derived from charred wood and smoke can potentially break seed dormancy and influence seedling establishment and density (Gerhard *et al*., 2006). Treating seeds with smoke promotes germination in several western Australian species when applied under field or controlled environmental conditions (Dixon *et al.,* 1995). Smoke can also stimulate flowering, root initiation (Taylor and van Staden, 1996), and seedling vigour (Baxter and van Staden, 1994; Sparg *et al.*, 2005). High concentrations of smoke may inhibit seedling growth (Light *et al.*, 2002) as observed in seedlings of *Acacia robusta* Burch. (ankle thorn) (Kulkarni *et al.*, 2007).

Findings on the mechanisms involved in smoke action are not conclusive, but smoke enhances the passage of solutes through the seed membranes of some species (Keeley and Fotheringham, 1997). Smoke can also act on the seed coat in a way similar to scarification, thereby increasing seed coat permeability to water and oxygen (Egerton-Warburton, 1998). This mechanism may be dependent on species (Baxter *et al.,* 1995; Keeley and Fotheringham, 1997), but dormancy breaking effects of smoke are not dependent on plant life-form (Dixon and Roche, 1995) and differences in species responses to smoke may be due to varied sensitivities to active compounds.

Seeds may not respond to smoke treatments at high concentrations (Brown and van Staden, 1994; Jager *et al.*, 1996); however, butenolide 3-methyl-2*H*-furo [2,3-*c*]-pyran-2-one isolated from plant derived smoke (Daws *et al.*, 2008) and burned cellulose (Flematti *et.al.*, 2004) may promote the germination of several species at high concentrations (Baldwin *et al.*, 1994). Three-methyl-2H furo [2, 3-c] pyran-2-one is active at 10^{-9} M concentrations, but it is not inhibitory at higher concentrations (van Staden *et al.*, 2004). Slow combustion of dry or green plant materials produce compounds that are volatile, water soluble, and can potentially break seed dormancy and stimulate germination (Jager *et al.*, 1996). The active chemical compounds in smoke are produced at temperatures in the range of 160-200^{o}C, becoming volatile at higher temperatures (Jager *et al.*, 1996; Brown and van Staden, 1997). It is possible that multiple compounds in smoke may stimulate germination (Flematti *et al.*, 2009). Twelve compounds were identified in smoke extracts of *Themeda triandra* Forssk. (red oat grass); seven of these compounds were also present in extracts of smoke from *Passerina vulgaris* Meisn. (gonnabos) (Jager *et al.*,1996). At least three compounds in smoke promote germination of *Nicotiana attenuata* Steyd. (coyote tobacco) (Baldwin *et al.*, 1994).

The chemical compounds present in smoke may interact with other environmental factors such as heat, incubation temperature, and light to stimulate germination (Brown *et al.*, 1994). Seed germination may be largely dependent on smoke concentrations; *Syncarpha vestita* L. (cape everlasting) had 85% germination in 1:5 v/v aqueous smoke concentrations and 66% germination in 1:500v/v aqueous smoke concentrations (Brown *et al.*, 1993; Jager *et al.*, 1996). Five to 10% concentrations of aqueous smoke solutions were optimal for stimulating germination of monocots while 10 to 20% concentrations of aqueous smoke stimulated germination in dicots (Adkins and Peters, 2001). Similarly, aqueous smoke solutions promoted germination of *Avena*

fatua L. (wild oat) over a range of 2 to 20% concentrations; germination was reduced at concentrations between 50% and 100% (Adkins and Peters, 2001).

Even though the stimulating effects of smoke on germination have been investigated in many species (Adkins and Peters, 2001), there is a need for further research on the ecological significance of this response **(**Reyes and Trabaud, 2009). Apparently no studies in Canada have evaluated the effects of pre-treating seeds of legumes and grasses in the prairies with aqueous smoke solutions produced by burning wheat (*Triticum aestivum* L.) straw or prairie hay (*Festuca hallii* Vasey.) on seed germination, seedling growth, and standing crop. The main objective of this research was to determine the efficacy of aqueous extracts of smoke, derived from wheat straw and hay collected from native, Fescue Prairie (*Festuca hallii* Vasey.), in germination, seedling emergence, and standing crop of eight grasses and two legumes that are difficult to establish from seed. It was hypothesized that: 1) various dilutions of aqueous smoke solutions affect seed germination differently; 2) aqueous smoke solutions either act alone or interact with alternating temperatures and light to affect germination; 3) aqueous smoke solutions prepared from wheat straw or prairie hay do not have the same effects on seed germination, and; 4) treating seeds with aqueous smoke solutions influence seedling emergence and standing crop in the field**.**

2.0 LITERATURE REVIEW

2.1 Seed germination and effects of priming on seed germination

Water, suitable temperature, and oxygen are conditions required for germination (Mayer and Poljakoff-Maber, 1982). Water uptake is an important step in seed germination. The process of water uptake in a mature seed is triphasic (Bewley, 1997) marked by a rapid initial water uptake (Phase I or imbibition), followed by a plateau phase (Phase II or activation) involving the re-activation and use of food reserves such as carbohydrates, fats and proteins and a third phase (Phase III or growth phase) which involves a further increase in water uptake after germination is completed. Water uptake is rapid during Phase I with dormant and non-dormant seeds having similar responses (Bewley and Black, 1994). However, it has been reported that during the initial imbibition phase, non-dormant seeds of *Avena fatua* absorbed water faster than dormant seeds (Hou *et al.,* 1997). It may take months or years to complete Phase II in dormant seeds due to low metabolic activities (Bradford, 1995). Dormant seeds may not enter Phase III because they do not complete germination (Qiu *et al.,* 2008). Following water uptake, metabolic activities resume in quiescent and dry seeds, and the structures and enzymes responsible for this are thought to be present within the dry seed and re-introducing water through imbibition is adequate for metabolic activities to resume (Bewley, 1997).

Seed priming involves partial hydration of seeds followed by drying, such that germination processes begin, but the radicle does not emerge (Guttridge and Bright, 1978; Tavili *et al.,* 2010). Seed priming improves seed germination in some species, particularly under unfavorable conditions (Tavili *et al.,* 2010). Seeds may be primed in water or osmotic solutions (Khan, 1992). Seed priming is often employed to reduce the time to seedling emergence (Parera and Cantliffe, 1994). Interactions among factors such as plant species, duration of priming, temperature, seed

vigour, storage conditions of the primed seeds, and the water potential of the priming agents usually determine the success of seed priming (Parera and Cantliffe, 1994).

Previous studies using aqueous smoke solutions for seed priming indicate benefits to seed germination and seedling vigour. Priming treatments significantly promoted total germination and seedling vigour of *Bromus inermis* Leyss. (smooth brome) by 12% and 6%, respectively (Tavili *et al.*, 2010). Treating seeds with aqueous smoke solutions increased total germination of *Themeda triandra* from 43% to 67%, and *Tristachya leucothrix* Nees. (trident grass) from 35% to 63%. Seeds of *Themeda triandra* primed in aqueous smoke solutions also had longer shoots and roots. However, the degree of response varied among species and temperatures. With increasing temperatures (>30°C), *Aristida junciformis* Trin. & Rupr. (bristle grass), *Hyparrhenia hirta* L. (thatching grass), and *Panicum maximum* Jacq. (guineagrass) responded positively to aqueous smoke solutions, suggesting that plant derived smoke solutions interact with temperature to influence seed germination and seedling growth (Ghebrehiwot *et al.*, 2009). Priming seeds in aqueous smoke solutions also increased the mass of *Acacia hebeclada* DC. (candle thorn) seedlings.

2.2 Seed dormancy

Seed dormancy is an intrinsic block to seed germination. Seed dormancy may occur under otherwise adequate hydric, thermal, and gaseous conditions. Once the block is removed, seeds may germinate under a wide range of environmental conditions (Roach and Wulff, 1987). Dormancy is a genetic trait established during seed maturation (Roach and Wulff, 1987), and modified by environmental factors influencing the parent plant and the seed before and after dispersal (Kegode and Pearce 1998; Taylor-son 1982). Dormancy is an adaptive trait of seeds (Vleeshouwers *et al.*, 1995), and should be defined in a way that differentiates the internal and external factors that affect seed germination. Total germination is usually used to indicate

dormancy change because germination is a measure of seed response to environmental conditions and germination requirements. Baskin and Baskin (2004) used germination percentage from a fixed duration germination test (4 weeks) under various environmental conditions to classify seeds into dormant (seeds fail to germinate in favourable conditions), non-dormant (seeds germinate to ≥80% in 4 weeks or less) and conditionally dormant (germinate to high percentages under some conditions, but not others).

Seed dormancy promotes the persistence of seeds in the seed bank by prolonging their germination and emergence (Benech-Arnold *et al.*, 2000). The time at which a seed germinates is critical for seedling growth and subsequent survival (Bradford, 2002), because it may not be beneficial for a seed to germinate, even in favourable conditions. For instance, germination of annuals in the spring allows time for vegetative growth and the subsequent production of seeds, but germination under similar conditions in the fall may lead to adverse effects during the winter (Bewley, 1997). Seed dormancy may be desirable in some instances such as during seed development because it prevents premature seed germination, but it is generally undesirable where rapid germination and growth are desired. Seeds of many grasses and legumes have dormancy, making it important to study this topic.

2.3 Types of Seed dormancy

Dormancy can be classified as primary (innate) or secondary (induced). Primary dormancy is established during seed development and maturation (Bewley and Black, 1994) while secondary dormancy is induced in mature seeds, which subsequently lose their ability to germinate (Mayer and Poljakoff-Mayber, 1982). Nikolaeva (1977) divided dormancy types into those that are endogenous (embryo based) or exogenous (based on endosperm or other tissues) of the seed or fruit. Baskin & Baskin (1998, 2004) further classified seed dormancy into

physiological dormancy (PD), morphological dormancy (MD), morpho-physiological dormancy (MPD), physical (PY) and combinational dormancy (PY+PD). Physiological dormancy is the major form of dormancy in many species including *Lactuca sativa* L., *Avena fatua*, and several cereals. Physiological dormancy can be divided into deep, intermediate, and non-deep (Baskin & Baskin, 2004). Embryos obtained from seeds with deep PD either do not grow or they produce abnormal seedlings. Several months of cold or warm stratification are needed to stimulate germination in physiologically dormant seeds, and gibberellic acid (GA) treatment does not break this dormancy (Baskin & Baskin, 2004). The majority of seeds have non-deep PD (Baskin & Baskin, 2004). Embryos from these seeds produce normal seedlings; GA treatments can break dormancy and, depending on species, dormancy can also be broken by scarification, after-ripening, and cold or warm stratification.

Morphological dormancy (MD) occurs in seeds with underdeveloped embryos (in terms of size), but have differentiated (e.g. into cotyledons and hypocotyl-radicle). These embryos are not physiologically dormant, but simply need time to mature. Morpho-physiological dormancy (MPD) is a characteristic of seeds with underdeveloped embryos, but also having a physiological component to their dormancy (Baskin & Baskin, 2004). Seeds with morpho-physiological dormancy require a dormancy-breaking treatment, such as a combination of warm and/or cold stratification which may be replaced by GA application. Physical dormancy (PY) is caused by water-impermeable layers of palisade cells in the seed or fruit coat that control water movement. Mechanical or chemical scarification can break PY dormancy. Combinational dormancy (PY +PD) is found in seeds with water-impermeable coats (as in PY) combined with physiological embryo dormancy (Baskin & Baskin, 2004).

2.4 Breaking seed dormancy

Dormancy in seeds can be broken in many ways (Bewley and Black, 1994), and breaking seed dormancy is an important step in improving seed germination (Bell *et al*., 1993). Some seeds lose their dormancy in the dry state (after-ripening) when their rate of metabolism is low. However, imbibed, dormant seeds are metabolically active and can receive an external signal such as light, chilling, alternating temperatures, chemical, and/or hormonal treatment that can stimulate germination. Dormancy release involves the reception of germination stimulus by the embryo and the immediate signal transduction chain that leads other metabolic and hormonal changes (Bewley, 1997). Depending on the type of dormancy, stratification, light, scarification, growth regulators, alternating temperatures and/or exposure to chemicals, may break dormancy and promote germination (Bradbeer, 1988; Bewley and Black, 1994). Smoke and its chemical components can also break dormancy (van Staden *et al.,* 2000). Smoke can stimulate germination in numerous species such as *Lactuca sativa,* but most studies have focused on species native to fire-prone ecosystems (Drewes *et al*., 1995). The use of smoke, temperature, and light in dormancy breaking is discussed further in the following sections.

2.5 Effects of smoke treatment on dormancy breaking and (or) germination

Smoke released from burning vegetation contains chemicals that affect seed germination in some species. Smoke can be applied to seeds immediately before sowing, or seeds may be pre-treated and stored until sowing (van Staden *et al.,* 2000). Active compounds in smoke are volatile, heat stable, water soluble, and long lasting in aqueous solutions; smoke treatment is effective on many seeds requiring light for germination (van Staden *et al.,* 2000). Effects at various concentrations of aqueous smoke solutions, resembling that of hormonal responses, have been reported (van Staden *et al.,* 2000), and stimulation of germination by aqueous smoke

solutions more closely matched that of gibberellic acids than potassium nitrate (Adkins and Peters, 2001).

2.6 Active ingredients in smoke

The products in smoke that trigger germination can be applied to seeds as vapour or liquid from smoke or soil particles (Keeley and Pizzorno, 1986). Nitrate ion, nitrous oxide, carbon dioxide, ethylene, and methane have been dismissed as likely germination cues in smoke (Keeley and Fotheringham, 1997, 1998a). Carbon monoxide, sulphuric acid, and hydrogen peroxide, may be involved in the stimulating effects of smoke, however, nitrogen oxides may have the strongest and most consistent effect (Keeley and Fotheringham, 1997). It has been proposed that germination in *Nicotiana attenuata* is not correlated with nitrogenous compounds because germination is stimulated by pyrolysis products of α-cellulose (Baldwin *et al*., 1994) even though cellulose and hemi-cellulose are not known to contain NO_2 or NO nitrogenous compounds. Pyrolysis products of α-cellulose and hemi-cellulose are also short of nitrogenous compounds generated on the soil surface layer by heat from fires (Fig. 2.1).

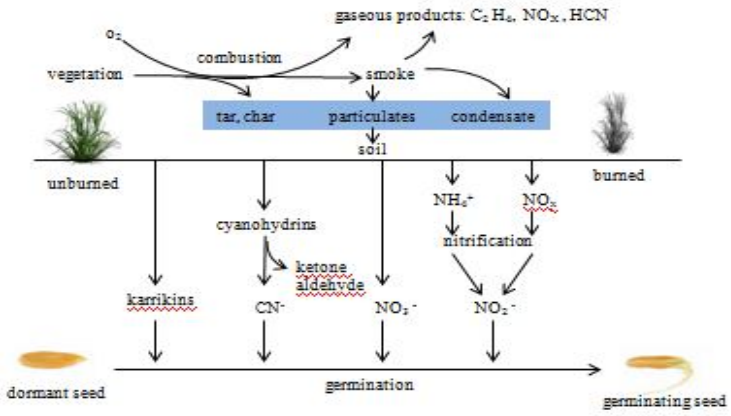

Figure 2.1 Germination stimulants produced from burning of plant material. Karrikins, CN^-, NO_3^- and NO_2^- are known to stimulate seed germination. NO_x may be NO or NO_2 derivable through combustion, or microbial activity in the soil. The oxidation of NH_4^+ or NO_x to NO_2^- (nitrite) or NO_3^- (nitrate) may be a result of microbial nitrification. Rain would normally elute chemicals into the soil (Redrawn from Nelson *et al.,* 2012).

A family of butenolide (3-methyl-2H furo [2, 3-c] pyran-2-one) (Flematti *et al.,* 2004; van Staden *et al.,* 2004) are thought to be the main active ingredients in smoke (Nelson *et. al,* 2012). However, this conclusion is inconclusive because more than 4,000 compounds have been identified in smoke. Furthermore, different compounds or two or more compounds acting together may be responsible for smoke-stimulated germination (Jager *et al.,* 1996; Flematti *et al.,* 2009). Just as smoke, butenolide can improve seedling vigour in *Lycopersicon esculentum* Mill.(tomato), *Abelmoschus esculentus* Moench. (okra), *Phaseolus vulgaris* L. (bean) and *Zea mays* L. (corn) (van Staden *et al.,* 2006). Therefore, butenolide may have broad applicability to stimulate germination (Flematti *et al.,* 2004; Light and van Staden, 2004).

2.7 Mechanism of smoke-stimulating effects on germination

Dormant seeds of *Emmenanthe penduliflora* Benth. (whispering bells) readily imbibe water. However, while it has a seed coat that is permeable to water and solutes, a semi-permeable subdermal cuticle allows water to pass, but it blocks larger molecular weight solutes (Keeley and Fotheringham, 1997; 1998a; b). Nitrogen dioxide in smoke changes the

characteristics of impermeable membranes, allowing diffusion of solute that otherwise is blocked. However, it is likely that this mechanism varies with species. Seed germination and dormancy are controlled by phytohormones, gibberellins (GAs) and abscisic acid (ABA) in a variety of species (Derkx *et al.*, 1994; Koornneef *et al.*, 2002; Olszewski *et al.*, 2002). Changes in the synthesis/metabolism of endogenous hormones, and/or increased sensitivity to hormones, are possible reasons that smoke stimulates germination (van Staden *et al.*, 2000). Elevated GA_3 content in *Lactuca sativa* seeds has been measured after smoke treatment (Gardner *et al.*, 2001), and studies on *Nicotiana attenuata* seeds (Schwachtje and Baldwin, 2004) demonstrated that smoke alters the patterns of endogenous GA and ABA during germination. Smoke affects how seeds respond to light and GA, and appears to influence endogenous synthesis and ABA content (van Staden *et al*., 2000). Schwachtje and Baldwin (2004) reported a dramatic decrease in extractable GA_{1+3} pools in seeds of *Nicotiana attenuata* within 2 h of smoke exposure, which was followed by an increase between 2 and 4 h. Conversely, extractable ABA pools increased shortly after imbibition and remained stable in seeds imbibed in water but it decreased sharply in seeds treated with smoke.

Similarly, smoke substitutes for red light (640 nm) in the germination of *Lactuca sativa*, promoting germination in darkness or in far-red (730 nm) light (Drewes *et al.*, 1995; van Staden *et al.*, 1995). It is unlikely that the initiation of germination is driven by *de novo* synthesis of GAs; rather a change of sensitivity of the seed to stored GAs is thought to start the process (Karssen and Laçka, 1986; Derkx *et al.*, 1994). However, *de novo* GA synthesis is necessary to complete germination, which is under the control of activated phytochromes (Casal and Sánchez, 1998; Yamaguchi *et al*. 1998).

2.8 Factors affecting the dormancy-breaking effects of smoke

Environmental factors affect dormancy and germination (Benech-Arnold *et al*. 2000) such that, a narrow range of environmental conditions may be needed to break dormancy. Conversely, a wider range of environmental conditions are needed to promote germination of non-dormant seeds (Knapp, 2000). Growth and development of many species can be directly related to the amount of light they receive (Maloof *et al.,* 2000). Seeds of *Calluna vulgaris* L. (ling heather) and *Erica tetralix* L. (cross leaved heath) germinate in response to light (Pons, 1989a). Diurnal fluctuations in soil temperatures can also break innate dormancy of seeds of some species in seed banks (Brits, 1986; Pierce and Moll, 1994). Breaking of dormancy is affected by variation in seasonal and diurnal temperatures, thereby influencing germination. Chilling and daily fluctuations in temperature may be required to break dormancy in some species (Baskin and Baskin, 1998).

Germination of some species is also controlled by the interaction of temperature and light (Hurtt and Hodgson, 1987). The active chemical compounds in smoke interact with temperature and light (Brown *et al.,* 1994). Aqueous smoke solutions at a concentration of 1:1000 v/v promoted germination in darkness and partially reversed the negative effects of far red light (van Staden *et al.,* 1995). Under red light, seeds of *Syncarpha vestita* did not germinate, but seeds germinated in darkness (Brown, 1993). With the application of smoke extracts, these negatively photoblastic seeds germinated under light (Brown and van Staden, 1997). Aqueous smoke solutions at high concentrations may inhibit seed germination, but they are not toxic to seeds. Seeds did not germinate when treated with high concentrations of smoke, but they germinated when smoke was diluted with water (Brown and van Staden, 1997). Depending on species, sensitivity to active compounds in smoke may vary, and a high concentration of smoke may have

no effect on germination (Brown and van Staden, 1994; Jager *et al*., 1996). The potential for smoke to promote germination at optimal concentrations and to inhibit germination at high concentrations suggest that inhibitors may also be present in smoke (Drewes *et al*., 1995).

3.0 MATERIALS AND METHODS

3.1 Species studied

Eleven species were studied under field and laboratory conditions, including northern wheatgrass (*Agropyron dasystachyum* [Hook.] Scribn cv. Elbee), western wheatgrass (*Pascopyrum smithii* [Rydb] cv. Walsh), needle-and-thread grass (*Hesperostipa comata* [L.] Trin. & Rupr. [collected from Last Mountain Lake, Saskatchewan, Accession #S0996]), orchardgrass (*Dactylis glomerata* [L.] cv. Kootenay), green needle grass (*Stipa viridula* [Trin.] [collected from Last Mountain Lake, Saskatchewan, Accession #S0940]), lettuce (*Lactuca sativa*[L.] cv. Grand Rapids), kura clover (*Trifolium ambiguum* [M.] Bieb cv. Endura), plains rough fescue (*Festuca hallii* [Vasey] Piper [collected from Kernen Prairie, Saskatchewan]), cicer milkvetch (*Astragalus cicer* [L.] cv. Windsor), Altai wildrye (*Elymus angustus* [Trin.] cv. Prairieland), and Russian wildrye (*Elymus junceus* [Fisch.] cv. Tetracan).

Dactylis glomerata, Elymus angustus, Elymus junceus, and *Trifolium ambiguum* are native to Europe and Asia. *Pascopyrum smithii, Agropyron dasystachum, Festuca hallii, Hesperostipa comata,* and *Stipa viridula* are native to the semi-arid grasslands of western North America. *Lactuca sativa* was studied because it responds to a wide range of aqueous smoke concentrations and can serve as a quick bioassay to detect the effect of smoke compounds on seed germination (Drewes *et al*., 1995). Seeds of *Agropyron dasystachyum, Pascopyrum smithii, Dactylis glomerata, Elymus angustus, Elymus junceus, Astragalus cicer, and Trifolium ambiguum,* were provided by Agriculture Canada, while seeds of *Festuca hallii, Hesperostipa comata,* and *Stipa viridula* were collected from native stands. *Lactuca sativa* was purchased from Early's Home and Garden Center in Saskatoon, SK.

Agropyron dasystachyum, Pascopyrum smithii, Hesperostipa comata, Dactylis glomerata, and *Stipa viridula* have seed dormancy, poor seedling vigour, and limited germination (Frank and Larson, 1970; Asay and Jensen, 1996; Probert, 2000; USDA-NRCS, 2002; Waldron *et al*., 2006; Qiu *et al*., 2008). Similarly, seeds of *Trifolium ambiguum, Astragalus cicer, Elymus angustus,* and *Elymus junceus* have dormancy that hinders germination and stand establishment (USDA-NRCS, 2002). *Astragalus cicer* seeds have hard seed coats, often requiring chemical or mechanical scarification for germination (Pelikan, 1994). Germination and dormancy-breaking requirements for the species studied are summarized in Table 3.1.

Table 3.1 Germination and dormancy-breaking requirements of 11 species studied

Species	Temperature and light requirements for the germination of non-dormant seeds	Temperature and seed treatments that break seed dormancy	References
Agropyron dasystachyum	20°/30°C (16 h/8 h)	15°/25°C, 15°/30°C, 20°/30°C (16 h/8 h)	Young and Evan s (1980), AOSA (1981), ISTA (1985)
Dactylis glomerata	15°/25°C; 20°/30°C (16 h/8 h)	15°/25°C (16 h/8 h), 10-25°C, 11/21°C (24 h) darkness	Qiu *et. al.* (2008), Probert *et.al.* (1988), ISTA (1985)
Elymus angustus	20°C light/darkness	19/22°C (12 h/12 h)	Berdahl and Ries (2002)
Elymus junceus	20°C light/darkness	19/22°C (12 h/12 h)	Berdahl and Ries (2002)
Festuca hallii	13-18°C light/darkness or darkness	25°C (12 h/12 h); 20°C (12 h/12 h or 24 h darkness)	Ersin *et al.* (2009)
Hesperostipa comata	15°/25°C; 20°/30°C (16 h/8 h)	15°/30°C, and 20°/30°C (16 h/8 h)	Nakamura (1962), ISTA (1985)
Pascopyrum smithii	15°/25°C; 20°/30°C (16 h/8 h)	15°/30°C, Pre-chill, Potassium nitrate; 15-20°C	Vivian (1976) Nakamura (1962), ISTA (1985)
Stipa viridula	15°/30°C (16 h/8 h)	25°/15°C (16 h/8 h), 20°/15°C (16 h/8 h), 20°/15°C (16 h/8 h)	Fulbright *et al.* (1983), AOSA (1981)
Astragalus cicer	18°C light/darkness or darkness	24°C after 50% H_2S0_4 treatment	Basalma *et al*. (2008), Acharya *et al.* (2006)
Trifolium ambiguum	15°C light/darkness or darkness	24-25°C	Taylor and Smith (1997)
Lactuca sativa	10/22 °C (16 h/8 h) 15°C (24 h darkness)	HCN applied for 1-22 h at 25°C, after a 2 h soak at 5°C enhanced germination in darkness	Hendericks and Taylorson (1975), Toshihito *et. al.* (1998), Khan and Zeng (1985)

3.2 Construction of combustion chamber and preparation of aqueous smoke solutions

Aqueous smoke solutions were produced by burning dry wheat straw (*Triticum aestivum* cv. Unity) or prairie hay collected from a Fescue Prairie dominated by *Festuca hallii* (plains rough fescue). A combustion chamber was constructed by assembling a wooden board, an electric ring heater, a 75 L metal garbage can, silicon tubing, and an air supply hose with a pressure gauge attached (Fig. 2). The electric ring heater was firmly fitted to the wooded board, leaving room for the power cord to exit from under the board. Two holes were drilled on opposite sides of the 75L metal garbage can; one directly connected to a pressure gauge linked to an air supply hose and the other connected to a silicon tubing.

Wheat straw or prairie hay was initially weighed into 1.6 kg samples, and then split into eight subsamples of 200 g each. One-by-one, subsamples were put in a 10 L metal container and placed on the electric ring heater. The 75 L metal garbage can was then inverted and placed on the wooden board, such that it enclosed the ring heater and the 10 L metal container containing plant materials. Electric power was supplied to the ring heater, and air was also pumped into the combustion chamber through the air hose and pressure gauge at 70-140 KPa. Smoke generated from the eight subsamples was continuously passed through the attached silicon tubing and bubbled into 4 L of distilled water in a flask (Fig. 3.1). About 20-30 minutes were required to completely smoulder each 200 g subsample. Four replicates each of stock solution (1/1 v/v dilution) for wheat straw and prairie hay were produced for each run of the experiments. Temperatures in the combustion chamber averaged 165°C (SE=5.0) during smouldering of the fuel.

Figure 3.1 Experimental set up for producing aqueous smoke solutions. One by one, eight subsamples of wheat straw or prairie hay (200 g each) were smouldered in a 10 L metal container placed on an electric heater that is fitted to wooded board. A 75 L metal garbage can is inverted to rest on the wooded board, such that it enclosed the ring heater and the 10 L metal container containing plant materials. Air at 70-140 kPa was forced into the combustion chamber. Smoke produced was continuously passed through silicon pipe and bubbled into 4 L of distilled water. It took about 20-30 minutes to smoulder each 200 g subsample.

3.3 Germination test

Aqueous smoke solutions prepared from burning wheat straw or prairie hay were taken as the stock solution (1/1v/v). From this stock solution, three serial dilutions were made including 1/1000v/v, 1/100v/v, and 1/10v/v. Distilled water (0/1v/v) and non-primed, dry seeds were also included in the treatments as control for the priming treatments and to evaluate the effects of priming, respectively. For each species, 50 seeds were counted and placed in 50 mL centrifuge tubes. The tubes were held in a vertical position, and perforated paper boxes. seeds were then primed by adding 10 mL of distilled water, 1/1000v/v, 1/100v/v, 1/10v/v, or 1/1v/v aqueous smoke concentrations, after which, each centrifuge tube was sealed with a cap and kept in darkness for 24 h at 20^{o}C.

Subsequently, seeds were transferred to 10 cm petri dishes lined with two layers of Whatman #1 filter paper and dried for 7 d at 20^{o}C in darkness. Seeds were dried because this procedure would need to be done before seeds are planted using conventional seeders. Each petri dish containing 50 seeds was moistened with 5 mL of distilled water, and incubated at 10/0°C or

25/15°C alternating temperatures under 12 h light/12 h darkness or 24 h darkness. Depending on the light treatment, Petri dishes were either placed in transparent or non-transparent ziplock bags before placing them in incubators. Germination of *Lactuca sativa*, *Astragalus cicer,* and *Trifolium ambiguum* was recorded at 1, 2, 4, and then 7-d intervals for 49 d, but counting at 7-d intervals for 49 d was used for the other species. A green safe light was used while checking germination of seeds incubated in darkness to avoid exposure to light (Drewes *et al.,* 1995). Seeds were considered germinated when the radicle was ≥ 2 mm in length. Seeds were visually examined for fungal infections during germination checks, and a 0.05% benomyl solution was applied if infections were present. Distilled water was added to keep the filter paper moist. Germinated seeds were counted, transferred to a new petri dish and seedlings were allowed to grow for 7 d under 12 h:12 h light/darkness at 25/15°C. Total seedling lengths (the lengths of radicle + the length of the hypocotyl) were measured after 7 d.

A factorial experiment was used in a randomized-complete-block-design within species using four replicates, two incubation temperature treatments (10/0°C and 25/15°C), two light treatments (24 h darkness and 12 h light/12 h darkness), six priming treatments (1/1000v/v, 1/100v/v, 1/10v/v, 1/1v/v, distilled water, and dry), two fuel materials (wheat straw and prairie hay) used for smoke generation, and the experiment was repeated with four new replicates of stock solutions. Replicates were started at 2 to 3-week intervals.

3.4 Seeding Experiment in the Field

The objective of the study was to investigate the effects of seed priming on seedling emergence and standing crop in the field. The study site was located at the University of Saskatchewan, (Lat. 52° 8' 6.9", Long. 106° 37' 18.8") with an elevation of 504 m above sea level (Environment Canada, 2013). This study site is in the Saskatoon Plain within the Moist

Mixed Grassland Ecoregion of Saskatchewan (Acton *et al*., 1998). The soil is a Dark Brown Chernozem of the Elstow Association with a silty loam/loam texture (Acton and Ellis, 1978), on level topography. The Moist Mixed Grassland Ecoregion is characterized by a sub-humid semi-arid continental climate with short, warm summers, and long, cold winters (Acton *et al*., 1998). The long-term average annual temperature for Saskatoon is 2.2^{o}C (Environment Canada, 2013), while the long-term average temperatures in May, June, July, and August are 11.5^{o}C, 16.0^{o}C, 18.2^{o}C, and 17.3^{o}C, respectively (Environment Canada, 2013). In the year of this study, average temperatures were 10.1^{o}C in May, 15.8^{o}C in June, 19.7^{o}C in July, and 17.3^{o}C in August. The long-term average annual precipitation for Saskatoon is 350 mm; the long-term average precipitation in May, June, July, and August is 49.4 mm, 61.1 mm, 60.1 mm, and 38.8 mm, respectively (Environment Canada, 2013). Precipitation totalled 108 mm in May, 121.1 mm in June, 80.9 mm in July, and 48.5 mm in August (Environment Canada, 2013).

This study was started on 16 May 2012 and terminated on 28 August 2012; *Lactuca sativa* was not included. Six replicates of 250 seeds were counted for the eight grasses and two legumes. The seeds were primed in 24 h darkness at 20^{o}C using 1/100v/v aqueous smoke solutions generated from wheat straw, prairie hay, and distilled water following the same procedures described earlier. Three lots of 250 seeds each were treated as non-primed controls. The 1/100v/v dilution of the aqueous smoke solution was chosen because maximum germination was observed at this concentration in preliminary studies. After priming, seeds were dried at 20^{o}C for 7 d in 24 h darkness, and placed in paper envelopes.

Forty-four plots measuring 2 m x 2 m were established with each plot consisting of 6 rows with 30 cm spacing. A 60 cm buffer was created around plots. Seeds were sown in 2 m rows within plots as a randomized-complete-block-design with the priming treatments of wheat

straw, prairie hay, distilled water, and no priming (control) replicated four times within species. Non-primed seeds were also sown in the two outer rows of each plot to ensure that seedlings emerging in the four priming treatments would have equal competition on both sides of the row. Seedlings emerging were recorded weekly, and plots were weeded as needed during the experiment. Plots were irrigated when necessary to increase seedling emergence. Ten weeks after seeding, a 1 m long section was centred in each of the seeded rows, and the above-ground mass (standing crop) of plants was clipped at ground level. These samples were placed in paper bags, dried at 80 ^{o}C for 48 h, and weighed.

3.5 Calculating germination rate using Chapman-Richard's growth function

The Chapman-Richards growth function has been widely used to define sigmoid curves (Roman *et al*., 2000) and it takes the form:

$$g = a\,(1-e^{-bt})^{c} \quad (3.1)$$

where *g* = germination percentage, *t*= time, *a* = the asymptote, *b* = the rate parameter, and *c*=the shape parameter (Qiu *et al.*, 2006). The parameters *a*, *b* and *c* are constants. A sigmoid growth form has an asymptote (parameter *a*) for the maximum germination percentage. The *b* and *c* parameters define the shape of the curve. The Chapman-Richards function can well fit a cumulative germination time course, which is a sigmoid curve characterised by a lag phase, in which no germination occurs, and an increasing approximately linear phase that increases germination rate as maximum germination percentage is reached (Durmur *et al*., 1990).

In this study, the Chapman-Richards growth function was used to derive the days to 50% of total germination (T_{50}):

$$T_{50} = (-1/b)\log(1- [g/2a]^{1/c}) \quad (3.2)$$

where g = final germination, *a* = the asymptote, *b* = the rate parameter, and *c*=the shape parameter and T_{50}= days to 50% of total germination.

3.6 Procedure used for viability testing and estimate of dormancy

Seeds were tested for viability using Tetrazolium Chloride. For each species, 5 replicates of 50 seeds were primed in distilled water for 5 h. Seeds were then removed from the solution, cut laterally using a razor blade, stained with 0.1% Tetrazolium Chloride solution (Grabe, 1970), and left for 18 h at 20°C. Staining patterns and intensity of colouration were observed and viability was interpreted (Hampton *et al.*, 1999). Where seeds stained evenly, they were assumed viable.

Within species, average germination percentages of non-primed, dry seeds were subtracted from viability percentages to give the dormancy for each species. Seed viability was based on results from Tetrazolium Chloride tests (n=50). When negative numbers were obtained (actual germination > viability), these values were adjusted to zero.

3.7 Data Analysis

Differences in germination among treatments were tested with analysis of variance in a randomized-complete-block design for a factorial experiment using the linear mixed model procedure on R.i386.3.0.2 statistical package (R Development Team, 2011). In a linear mixed model, the fixed and random effects contribute linearly to the response function (R Development Team, 2011; Pinheiro, 2008). A linear mixed model is maximal when it contains all factors and interactions that are of interest (R Development Team, 2011). Within species, a maximal model was fixed that included either total germination, germination rate, or seedling lengths as the dependent variable, and in each case, the main effects and all possible interactions of priming, temperature, light, smoke type were used as independent variables. Replicates and runs were factored into the model as random effects.

When dependent variables varied significantly among priming treatments ($P \leq 0.05$), means were compared using contrasts that included: 1) non-primed vs. primed in distilled water, 2) non-primed vs. primed in 1/1000 v/v, 1/100 v/v, 1/10 v/v, and 1/1v/v aqueous solutions of smoke; 3) seeds primed in distilled water vs. seeds primed in 1/1000 v/v, 1/100 v/v, 1/10 v/v, and 1/1v/v aqueous solutions of smoke; 4) seeds primed in 1/1000v/v aqueous solutions of smoke vs. primed in 1/100v/v, 1/10v/v, 1/1v/v aqueous solutions of smoke; 5) seeds primed in 1/100v/v aqueous solutions of smoke vs. primed in 1/10v/v, 1/1v/v aqueous solutions of smoke, and; 6) seeds primed in 1/10v/v aqueous solutions of smoke vs. primed in 1/1v/v aqueous solutions of smoke.

Contrasts of means were also used to compare treatments when dependent variables varied among interactions of priming x temperature or priming x light ($P \leq 0.05$); means of priming treatments were compared within each temperature (10/0°C or 25/15°C) or light treatments (24 h darkness or 12 h light/12 h darkness). Dependent variables varying significantly among the temperature x light treatments ($P \leq 0.05$), were compared between 10/0°C and 25/15°C; within 24 h darkness, and 12 h light/12 h darkness. Means were also compared between 24 h darkness and 12 h light/12 h darkness; within 10/0°C, and 25/15°C. Dependent variables varying significantly among the priming x temperature x light interaction ($P \leq 0.05$) were compared among priming treatments as explained earlier, but within each light treatment and at each temperature. When dependent variables varied between temperature or light treatments, it meant means of seeds incubated at 10/0°C were significantly different from 25/15°C, and means of seeds incubated in 24 h darkness were significantly different from 12 h light/ 12 h darkness.

Differences in emergence and standing crop among treatments in the field study were also tested with Analysis of Variance for a randomized-complete-block design using the linear mixed

model procedure on R.i386.3.0.2 statistical package (R Development Team, 2011). A maximal model was fixed for each species, with the dependent variables of seedling emergence, seedling emergence rates, and standing crop, while the independent variable was priming treatment. When dependent variables varied significantly among priming treatments ($P \leq 0.05$), means were compared with contrasts that included: 1) non-primed seeds vs. primed in distilled water ; 2) non-primed seeds vs. primed in aqueous solutions of smoke made from wheat straw; 3) non-primed seeds vs. primed in aqueous solutions of smoke made from prairie hay; 4) primed in distilled water vs. primed in aqueous solutions of smoke made from wheat straw, and; 5) primed in distilled water vs. primed in aqueous solutions of smoke made from prairie hay. Statistical significance was assumed at $P \leq 0.05$ in all cases.

4.0 RESULTS

4.1 Seed Germination and Seedling Growth

Priming seeds in aqueous smoke solutions significantly affected ($P \leq 0.05$) total germination, germination rate, and seedling lengths in a species dependent manner. Total germination did not vary significantly ($P \geq 0.05$) with the smoke type from which aqueous smoke solutions was made, but germination rate and seedling lengths were significantly affected by smoke type.

4. 2 *Lactuca sativa*

Seed germination of *Lactuca sativa* (88%, SE=1.4 viable, and 1%, SE=0.5 dormant), responded to priming treatments, smoke type, and the interactions of temperature x light, and priming x temperature. Total germination in priming treatments (72%, SE=2.1) was significantly less than control (95%, SE=1.0) (Fig. 4.1a). Priming seeds in the 1/1v/v dilution reduced germination by 85% and 94%, relative to distilled water and the non-primed control, respectively. Priming seeds in distilled water or the 1/10v/v dilution also reduced germination by 8% as compared with the non-primed control. Total germination was 2% greater in light at 10/0 ^{o}C as compared with darkness (Fig. 4.1b).

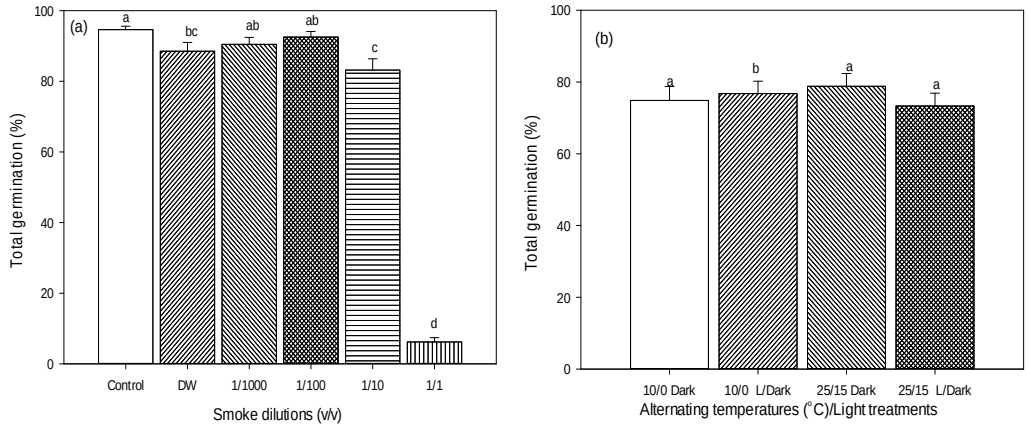

Figure 4.1 (a & b) Total germination for *Lactuca sativa* seeds after priming in serial dilutions made from aqueous smoke solutions and incubating at 10/0^{o}C and 25/15^{o}C in 24 h darkness or 12 h light/12 h darkness; **(a)** Means with different letters indicates total germination of primed seeds were significantly different (P≤0.05). DW=Distilled water **(b)** Means with different letters within each temperature treatment were significantly different (P≤0.05). Bars represent (±) standard error.

Germination rate was affected by the interaction of priming x temperature. Seeds germinated slower after priming in the 1/1v/v dilution at 10/0^{o}C in contrast with distilled water and the non-primed control (Fig. 4.2), but at 25/15^{o}C, seeds germinated faster after priming in the 1/1000v/v dilution relative to distilled water.

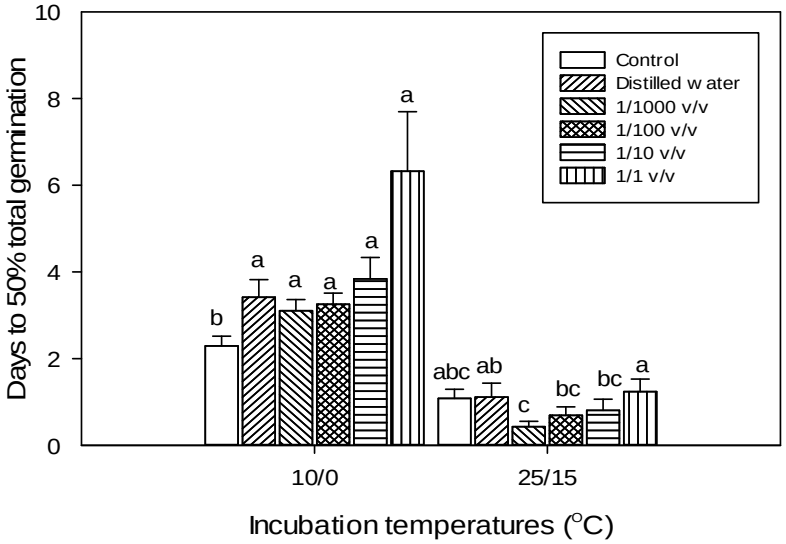

Figure 4.2 Days to 50% of total germination for *Lactuca sativa* seeds after priming in serial dilutions from aqueous smoke solutions and incubating at 10/0°C or 25/15°C in 24 h darkness or 12 h light/12 h darkness. Means with different letters indicates days to 50% total germination of primed seeds were significantly different (P≤0.05) within temperatures. Bars represent (±) standard error.

Seedling lengths were affected by priming treatments and smoke type. Seedlings were 55% shorter after priming in the 1/10v/v or 1/1v/v smoke dilutions (Table 4.1) relative to the non-primed control. Seedling lengths varied between smoke types with an average of 12 mm (SE=1.5) and 22 mm (SE =2.0) in the prairie hay and the wheat straw smoke types, respectively.

Table 4.1 Seedling lengths for *Lactuca sativa* after priming in serial dilutions from aqueous smoke solutions and incubating in 24 h darkness or 12h light/ 12 h darkness. Standard error estimate of overall variation in data = 1.5.

Dilution	Seedling length (mm)	SE
Control	20 a	3.2
Distilled water	12 ab	2.8
1/1000v/v	20 a	2.8
1/100v/v	18 ab	2.7
1/10v/v	9 b	2.4
1/1v/v	9 b	4.1

Means with different letters indicates seedling lengths were significantly different (P ≤ 0.05).

4.3 *Astragalus cicer*

With 74% viability (SE=3.5) and 40% (SE=2.2) dormancy, seed germination of *Astragalus cicer* responded to priming treatments, and the interacting effects of temperature x light, and priming x smoke type. Overall total germination in priming treatments (33%, SE=1.0) (Fig. 4.3a) was significantly different from the non-primed control (35%, SE= 2.3). Total germination was also 20% greater in light at 10/0^{o}C than in 24 h darkness; however, at 25/15^{o}C, total germination was 5% greater in 24 h darkness than in light (Fig. 4.3b).

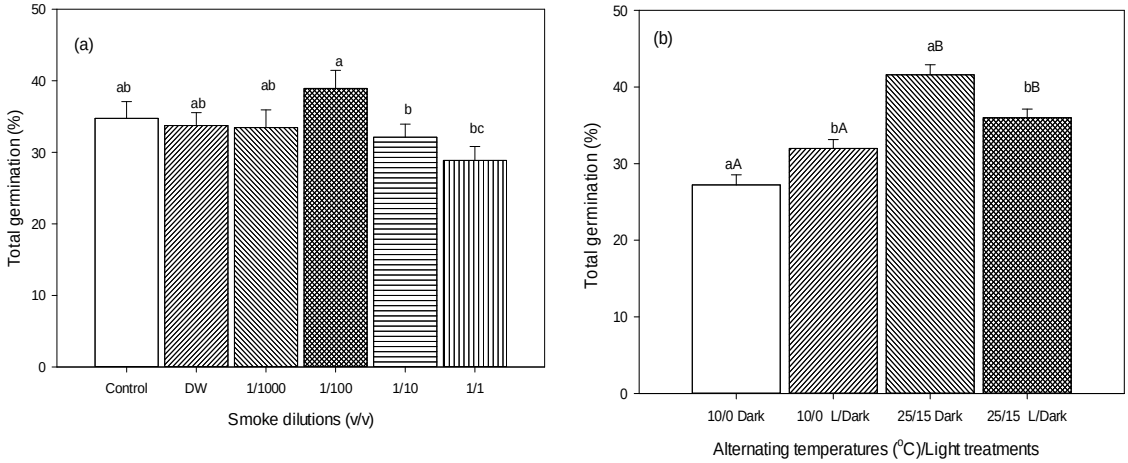

Figure 4.3 (a & b) Total germination for *Astragalus cicer* seeds after priming in serial dilutions made from aqueous smoke solutions and incubating at 10/0^{o}C and 25/15^{o}C in 24 h darkness or 12 h light/12 h darkness **(a)** Means with different letters indicates total germination of primed seeds were significantly different (P≤0.05). DW=Distilled water **(b)** Means with a different lower case letters within a temperature were significantly different (P≤0.05). Means with represent (±) standard error.

Germination rate was related to the interacting effects of incubation temperature and light (Fig. 4.4). At 10/0 ^{o}C, germination was faster in 12 h light/12 h darkness as compared with 24 h darkness, but germination was generally more rapid at 25/15 ^{o}C than at 10/0 ^{o}C under both light treatments.

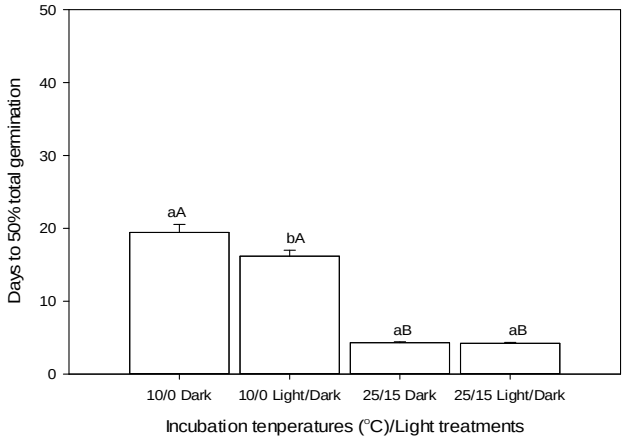

Figure 4.4 Days to 50% of total germination for *Astragalus cicer* after priming seeds in serial dilutions made from aqueous smoke solutions and incubating at 10/0^{o}C or 25/15^{o}C in 24 h darkness or 12 h light/12 h darkness. Means with a different lower case letters within a temperature were significantly different (P≤0.05). Means with the same capital letters within light treatments were not significantly different (P>0.05). Bars represent (±) standard error.

Seedling lengths were affected by the temperature x light and the priming x smoke type interactions. Seedlings were shorter after priming in 1/10v/v and 1/1v/v aqueous smoke solutions made from prairie hay as compared with distilled water and non-primed control (Table 4.3). However, seedlings were generally longer after priming in smoke solutions produced from wheat straw. Seedlings were also longer in 24 h darkness at 25/15 ^{o}C, relative to12 h light/12 h darkness (Table 4.4), but within 12 h light/12 h darkness, seedlings were longer at 10/0 ^{o}C than at 25/15 ^{o}C.

Table 4.3 Seedling lengths for *Astragalus cicer* after priming in serial dilutions of aqueous smoke solutions made from prairie hay or wheat straw and incubating in 24 h darkness or 12h light/12 h darkness. Standard error estimate of overall variation in data = 0.9.

Fuel type	Dilution	Seedling length (mm)	SE
Prairie hay	Control	13 a[1]	2.7
	Distilled water	15 a	3.6
	1/1000v/v	18 a	4.6
	1/100v/v	10 ab	2.2
	1/10v/v	4 b	1.3
	1/1v/v	4 b	1.0
Wheat straw	Control	13 a	2.7
	Distilled water	15 a	3.6
	1/1000v/v	11 a	2.5
	1/100v/v	17 a	3.8
	1/10v/v	13 a	2.7
	1/1v/v	11 a	2.6

[1]Means with different letters indicates that seedling lengths were significantly different ($P \leq 0.05$) within fuel type treatments.

Table 4.4 Seedling lengths for *Astragalus cicer* after priming in serial dilutions of aqueous smoke solutions and incubating at 10/0°C or 25/15°C in 24 h darkness or 12 h light/12 h darkness. Standard error estimate of overall variation in data =1.7.

Temperature (°C)	Light treatment	Seedling length (mm)	SE
10/0	24 h darkness	10 aA[1]	1.8
	12 h light/12 h darkness	14 aA	3.2
25/15	24 h darkness	15 aA	3.2
	12 h light/12 h darkness	9 bB	2.4

[1]Means with a different lower case letters within a temperature were significantly different ($P \leq 0.05$). Means with different capital letters within each light treatment were significantly different ($P \leq 0.05$).

4.4 *Trifolium ambiguum*

Germination of *Trifolium ambiguum* seeds (97%, SE=1.3 viable and 59%, SE=1.1 dormant), responded to priming treatments, and the interactions of temperature x light, priming x smoke type, and priming x temperature x light treatments. Total germination in priming treatments (31%, SE=1.0) was significantly less than the non-primed control (38%, SE=1.1) (Fig. 4.5). Except for the 1/1v/v dilution which reduced germination by about 38% relative to distilled water and the non-primed control, priming seeds had no effect on total germination.

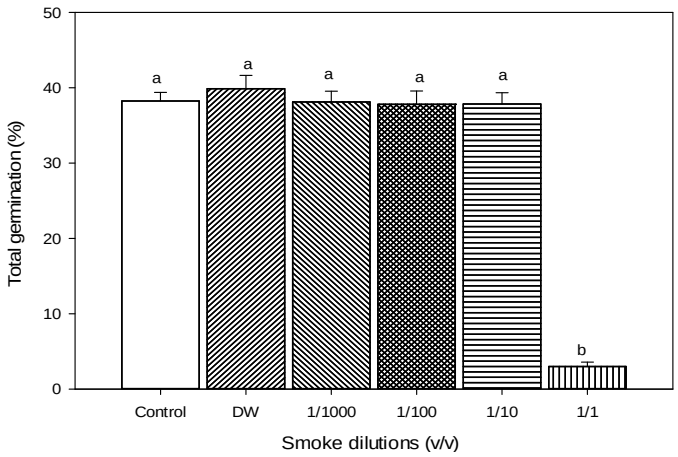

Figure 4.5 Total germination for *Trifolium ambiguum* after priming seeds in serial dilutions of aqueous smoke solutions. Means with different letters indicates total germination of primed seeds were significantly different ($P \leq 0.05$). DW=Distilled water. Bars represent (±) standard error.

Germination rate was significantly affected by priming treatments and by the interaction of incubation temperatures and light treatment. Priming seeds in the 1/1v/v dilution increased germination rate relative to distilled water and the non-primed control (Fig. 4.6 a). Seeds incubated in 12 h light/12 h darkness at 10/0 ^{o}C germinated faster than in 24 h darkness (Fig. 4.6 b). Seeds incubated at 25/15 ^{o}C generally germinated faster than at 10/0 ^{o}C.

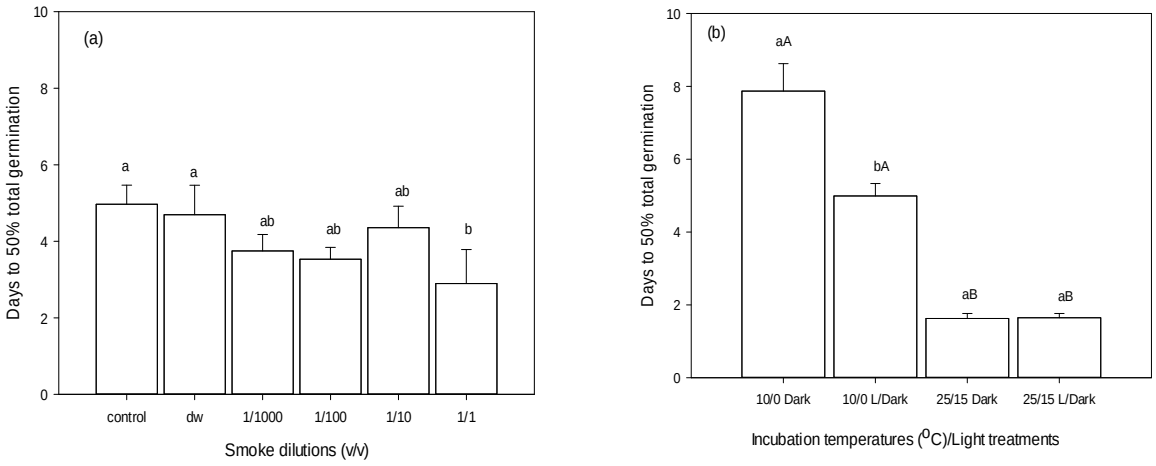

Figure 4.6 (a & b) Days to 50% total germination for *Trifolium ambiguum* seeds after priming in serial dilutions from aqueous smoke solutions and incubating at 10/0^{o}C or 25/15^{o}C in 24 h darkness or 12 h light/12 h darkness **(a)** Means with different letters indicates days to 50% total germination of primed seeds were significantly different (P≤0.05). DW=Distilled water**. (b)** Means with a different lower case letters within a temperature were significantly different (P≤0.05). Means with different capital letters within each light treatment were significantly different (P>0.05). Bars represent (±) standard error.

Seedling lengths responded to the interactions of priming x fuel type, and priming x temperature x light treatments. Priming seeds in the 1/1v/v aqueous smoke solution made from prairie hay reduced seedling lengths by 100% relative to distilled water and the non-primed control, while priming in the 1/10v/v dilution reduced seedling lengths by 67% as compared with the control (Table 4.5). Seedlings were generally longer after priming in smoke solutions produced from wheat straw. Incubating seeds in 24 h darkness at 10/0^{o}C reduced seedling lengths in distilled water, the 1/10v/v and the 1/1v/v dilutions as compared with the non-primed control, while incubating in the 1/1000v/v and 1/100v/v dilutions increased seedling lengths relative to distilled water (Table 4.6). Conversely, priming seeds in the 1/1v/v dilution, reduced seedling lengths in 12 h light/12 h darkness at 25/15^{o}C.

Table 4.5 Seedling lengths for *Trifolium ambiguum* after priming in serial dilutions of aqueous smoke solutions made from prairie hay or wheat straw and incubating in 24 h darkness or 12h light/ 12 h darkness. Standard error estimate of overall variation in data = 0.7.

Fuel type	Dilution	Seedling length (mm)	SE
Prairie hay	Control	12 a[1]	2.7
	Distilled water	7 ab	2.7
	1/1000v/v	12 a	2.1
	1/100v/v	11 a	2.4
	1/10v/v	4 bc	1.3
	1/1v/v	0 c	0.2
Wheat straw	Control	12 a	2.7
	Distilled water	7 a	2.7
	1/1000v/v	12 a	3.3
	1/100v/v	10 a	2.0
	1/10v/v	14 a	3.5
	1/1v/v	10 a	3.6

[1]Means with different letters indicates that seedling lengths were significantly different ($P \leq 0.05$) within fuel type treatments.

Table 4.6 Seedling lengths for *Trifolium ambiguum* after priming in serial dilutions of aqueous smoke solutions and incubating at 10/0°C or 25/15°C in 24 h darkness or 12 h light/12 h darkness. Standard error estimate of overall variation in data = 0.8.

Temperature (°C)	Light treatment	Dilution	Seedling length (mm)	SE
10/0	24 h darkness	Control	18 a[1]	3.0
		Distilled water	4 c	2.1
		1/1000v/v	14 ab	2.9
		1/100v/v	14 ab	2.6
		1/10v/v	9 bc	2.5
		1/1v/v	4 c	3.2
	12 h light/12 h darkness	Control	8 a	3.6
		Distilled water	18 a	5.5
		1/1000v/v	15 a	6.1
		1/100v/v	14 a	3.5
		1/10v/v	9 a	4.6
		1/1v/v	10 a	6.6
25/15	24 h darkness	Control	9 a	2.3
		Distilled water	5 a	1.9
		1/1000v/v	10 a	3.3
		1/100v/v	9 a	3.5
		1/10v/v	13 a	6.1
		1/1v/v	4 a	2.7
	12 h light/12 h darkness	Control	13 a	5.4
		Distilled water	2 b	1.0
		1/1000v/v	10 ab	2.8
		1/100v/v	5 ab	2.3
		1/10v/v	6 ab	3.1
		1/1v/v	2 b	1.9

[1]Means with different letters indicates that seedling lengths were significantly different ($P \leq 0.05$) within temperatures and light treatments.

4.5 *Elymus angustus*

Seeds of *Elymus angustus* were 82% viable (SE=4.2) with 70% dormancy (SE=1.0), and their germination was affected by priming treatments, temperature, smoke type, and the interactions of priming x light, priming x temperature, and temperature x light. Priming seeds in the 1/1000v/v dilution improved total germination in 12 h light/12 h darkness by 25% compared with the non-primed control (Fig 4.7), but the 1/1 v/v dilution reduced total germination by 98% relative to distilled water and the non-primed control. Priming seeds in the 1/100v/v dilution improved germination in 24 h darkness by 29% compared with the non- primed control, but 1/1v/v and 1/10v/v dilutions reduced germination by 98% and 40%, respectively, relative to

distilled water. Priming seeds in distilled water also increased germination by 100% relative to the non-primed control. Total germination was about 20% higher at 10/0^{o}C than at 25/15^{o}C.

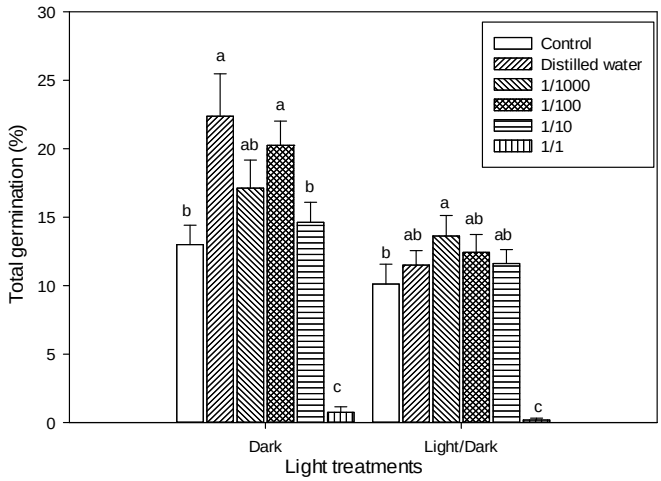

Figure 4.7 Total germination for *Elymus angustus* seeds after priming in serial dilutions made from aqueous smoke solutions and incubating at 10/0^{o}C and 25/15^{o}C. Means with different letters indicates total germination of primed seeds were significantly different (P≤0.05) within each light treatment. Bars represent (±) standard error.

Germination rate was affected by the priming x temperature interaction. Seeds germinated faster after priming in the 1/1v/v dilution at both temperatures compared with distilled water and the non-primed control (Fig. 4.8). Priming in distilled water, 1/1000v/v and 1/10v/v dilutions at 25/15^{o}C also enhanced germination rate relative to the non-primed control. Seeds generally germinated faster at 25/15^{o}C than at 10/0^{o}C.

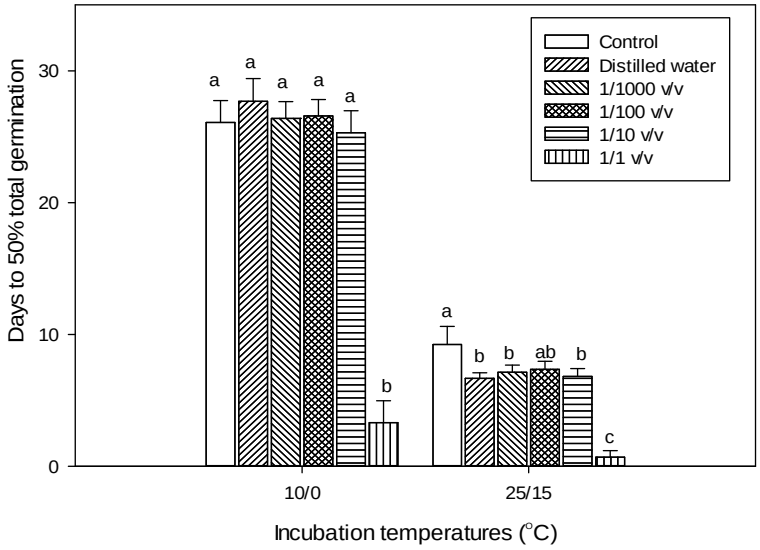

Figure 4.8 Days to 50% total germination for *Elymus angustus* seeds after priming in serial dilutions from aqueous smoke solutions and incubating at 10/0°C or 25/15°C in 24 h darkness or 12 h light/12 h darkness. Means with different letters indicates days to 50% total germination of primed seeds were significantly different ($P \leq 0.05$) within each temperature treatment. Bars represent (±) standard error.

Seedling lengths responded to priming treatments, smoke type, and the temperature x light interaction. Seedlings were shorter than the non-primed control after priming in the 1/1v/v (Table 4.7), but priming in the 1/1000v/v and 1/100v/v dilutions increased seedling lengths in comparison with distilled water. Seedlings were also longer in 12 h light/12 h darkness at 10/0°C 24 h darkness. Conversely, seedlings were longer in 24 h darkness at 25/15°C as compared with 12 h light/12 h darkness (Table 4.8). Seedling lengths were significantly different between smoke types with an average lengths of 17 mm (SE=2.1) for seeds primed in aqueous smoke solutions made from prairie hay, and 26 mm (SE= 2.8) for seeds primed in aqueous smoke solutions made from wheat straw.

Table 4.7 Seedling lengths for *Elymus angustus* after priming in serial dilutions from aqueous smoke solutions and incubating in 24 h darkness or 12h light/ 12 h darkness. Standard error estimate of overall variation in data = 2.8.

Dilution	Seedling length (mm)	SE
Control	25 ab[1]	3.3
Distilled water	15 bc	2.6
1/1000v/v	32 a	4.9
1/100v/v	32 a	4.7
1/10v/v	18 bc	4.6
1/1v/v	8 c	3.5

[1]Means with different letters indicates seedling lengths were significantly different ($P \leq 0.05$)

Table 4.8 Seedling lengths for *Elymus angustus* after priming in serial dilutions of aqueous smoke solutions and incubating at 10/0°C or 25/15°C in 24 h darkness or 12 h light/12 h darkness. Standard error estimate of overall variation in data = 4.9.

Temperature (°C)	Light treatment	Seedling length (mm)	SE
10/0	24 h darkness	13 aA[1]	1.8
	12 h light/12 h darkness	25 bA	5.3
25/15	24 h darkness	32 aA	8.2
	12 h light/12 h darkness	17 bB	5.2

[1]Means with a different lower case letters within a temperature were significantly different ($P \leq 0.05$). Means with different capital letters within each light treatment were significantly different ($P \leq 0.05$).

4.6 *Elymus junceus*

Germination of *Elymus junceus* seeds (83%, SE=3.9 viable and 16%, SE=2.3 dormant), varied with priming treatments, light, temperature, and the interactions of priming x temperature, priming x smoke type, and temperature by light. Total germination of primed seeds (64%, SE=1.9) was significantly less than non-primed seeds (70%, SE= 2.6) (Fig.4.9). Priming seeds in the 1/1 v/v dilution reduced total germination compared with distilled water and the non-primed control; however, priming in distilled water, 1/1000v/v, 1/100v/v, and 1/10v/v dilutions increased germination compared with the non-primed control at 25/15^{o}C. Total germination was significantly different between light treatments with an average of 67% (SE=2.5) in 24 h darkness and 63% in 12 h light/12 h darkness (SE=2.4).

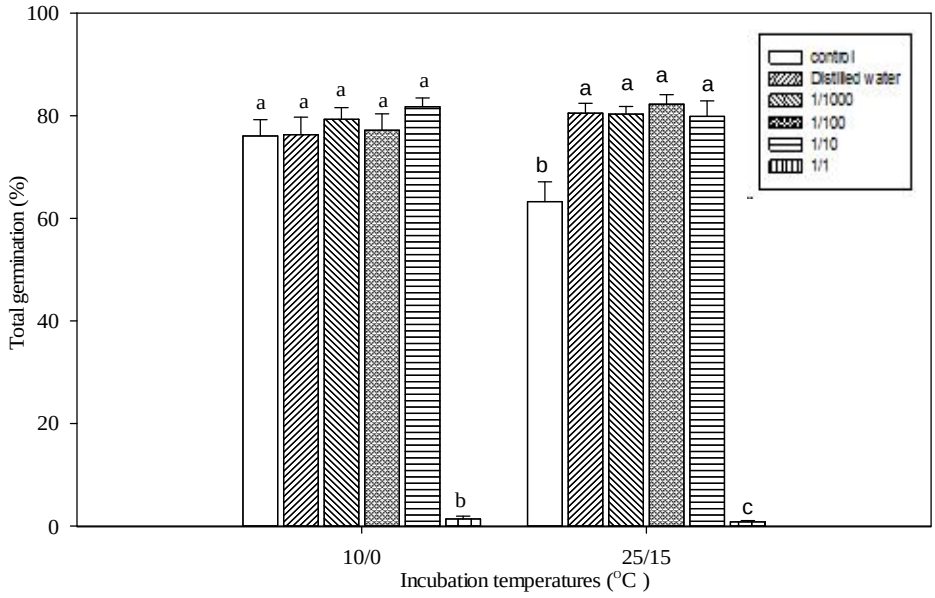

Figure 4.9 Total germination for *Elymus junceus* seeds after priming in serial dilutions from aqueous smoke solutions and then incubating at 10/0^{o}C and 25/15^{o}C in 24 h darkness or 12 h light/12 h darkness. Means with different letters indicates total germination of primed seeds were significantly different (P≤0.05) within each temperature treatment. Bars represent (±) standard error.

Germination rate was affected by priming treatments and by temperature. Germination was more rapid after priming seeds in the 1/1v/v dilution as compared with distilled water and the non-primed control (Fig. 4.10). Seeds also germinated faster at 25/15^{o}C (5 d to 50% germination, SE= 0.3) than at 10/0^{o}C (15 d to 50% germination, SE= 0.7).

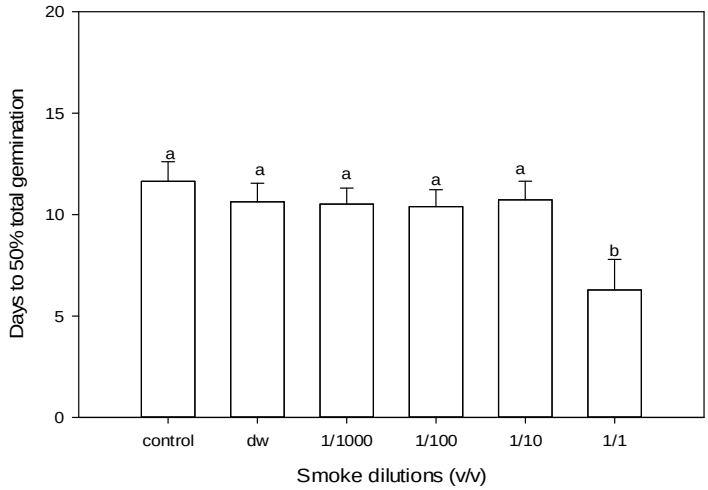

Figure 4.10 Days to 50% total germination for *Elymus junceus* seeds after priming in serial dilutions from aqueous smoke solutions and incubating at 10/0^{o}C or 25/15^{o}C in 24 h darkness or 12 h light/12 h darkness. Means with different letters indicates days to 50% total germination of primed seeds were significantly different (P≤0.05). DW=Distilled water. Bars represent (±) standard error.

Seedling lengths were related to the interacting effects of priming x smoke type, and temperature x light. Seedlings were shorter after priming seeds in distilled water, the 1/10v/v and the 1/1v/v dilutions made from prairie hay relative to the control (Table 4.9). However, seedlings were longer after priming seeds in the 1/1000v/v and the 1/100v/v dilutions made from prairie hay compared with distilled water. Similarly, seedlings were longer after seed priming in the 1/1000v/v, 1/100v/v, and the 1/10v/v dilutions made from wheat straw as compared with distilled water. Seedlings were also longer in 12 h light/12 h darkness at 10/0^{o}C, as compared

with 24 h darkness; seedlings were longer when incubated in 24 h darkness at 25/15^{o}C than when incubated in 12 h light/12 h darkness (Table 4.10).

Table 4.9 Seedling lengths for *Elymus junceus* after priming in serial dilutions of aqueous smoke solutions made from prairie hay or wheat straw and incubating in 24 h darkness or 12h light/ 12 h darkness. Standard error estimate of overall variation in data = 2.1.

Fuel type	Dilution	Seedling length (mm)	SE
Prairie hay	Control	38 a[1]	4.6
	Distilled water	21 b	4.7
	1/1000v/v	45 a	6.5
	1/100v/v	40 a	5.6
	1/10v/v	15 b	4.3
	1/1v/v	0 c	0.1
Wheat straw	Control	38 abc	4.6
	Distilled water	21 c	4.7
	1/1000v/v	44 a	5.2
	1/100v/v	39 ab	5.2
	1/10v/v	42 ab	7.3
	1/1v/v	26 bc	8.8

[1]Means with different letters indicates that seedling lengths were significantly different ($P \leq 0.05$) within fuel type treatments.

Table 4.10 Seedling lengths for *Elymus junceus* after priming in serial dilutions of aqueous smoke solutions and incubating at 10/0°C or 25/15°C in 24 h darkness or 12 h light/12 h darkness. Standard error estimate of overall variation in data = 2.9.

Temperature (°C)	Light treatment	Seedling lengths (mm)	SE
10/0	24 h darkness	26 a[1]	2.8
	12 h light/12 h darkness	35 b	3.5
25/15	24 h darkness	34 a	4.1
	12 h light/12 h darkness	28 a	3.9

[1]Means with a different lower case letters within a temperature were significantly different ($P \leq 0.05$).

4.7 *Dactylis glomerata*

Seeds germination of *Dactylis glomerata* (65%, SE=2.2 viable and 15%, SE=2.5 dormancy) was related to the interactions of priming x temperature, priming x light, priming x smoke type, and priming x temperature x light. Total germination increased after priming seeds in 1/10v/v dilution at 10/0^{o}C as compared with priming in distilled water and the non-primed control (Fig. 4.11a). Total germination was also higher after priming seeds in distilled water, 1/1000v/v, 1/100v/v, and 1/10v/v at 25/15^{o}C, than the non- primed control, but the 1/1 v/v dilution reduced germination relative to distilled water. Total germination increased in 24 h darkness after priming seeds in the 1/10 v/v dilution whereas priming in the 1/1v/v dilution in 12 h light/12 h darkness reduced germination as compared with distilled water and non-primed control (Fig. 4.11b).

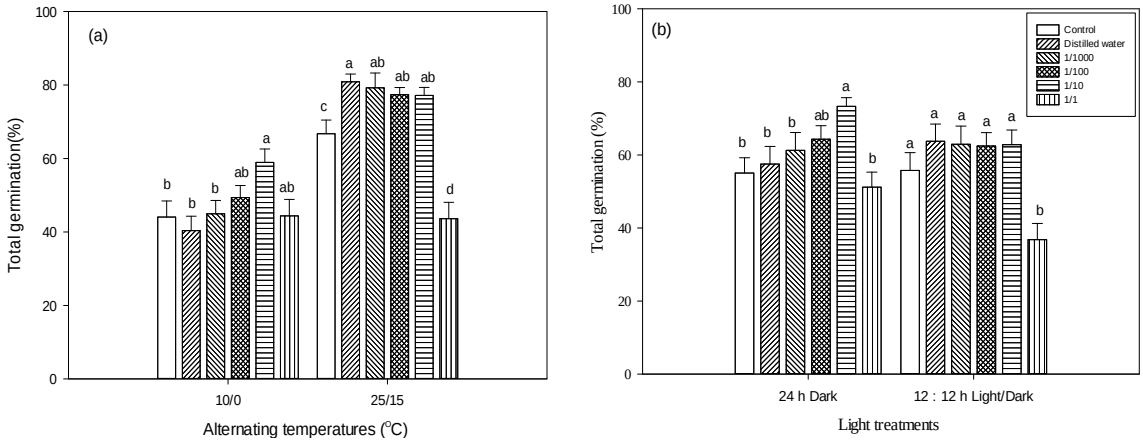

Figure 4.11 (a & b) Total germination for *Dactylis glomerata* seeds after priming in serial dilutions made from aqueous smoke solutions and incubating at 10/0^{o}C and 25/15^{o}C in 24 h darkness or 12 h light/12 h darkness. **(a)** Means with different letters indicates total germination of primed seeds were significantly different (P≤0.05). DW=Distilled water **(b)** Means with different letters within a light treatment were significantly different (P≤0.05). Bars represent (±) standard error.

Germination rate was affected by the priming x temperature x light interaction. Seeds germinated faster at 25/15°C (6 d to 50% germination, SE=0.3) than at 10/0°C (19 d to 50% germination, SE=0.8) (Fig. 4.12). Seeds also germinated faster after priming in distilled water, the 1/100v/v, and the 1/1v/v in 24 h darkness at 10/0°C, but germination was slower after priming in distilled water, 1/1000v/v, and 1/1v/v dilutions in 12 h light/12 h darkness as compared with the non-primed control. Similarly, germination was more rapid after priming seeds in distilled water, the 1/1000v/v, the 1/100v/v, and the 1/10v/v dilution in 12 h light/12 h darkness at 25/15°C, but priming in distilled water and the 1/1000v/v dilution slowed germination in 24 h darkness in relation to the non-primed control. Priming seeds in 1/1v/v dilution reduced germination rate at both temperatures in 24 h darkness.

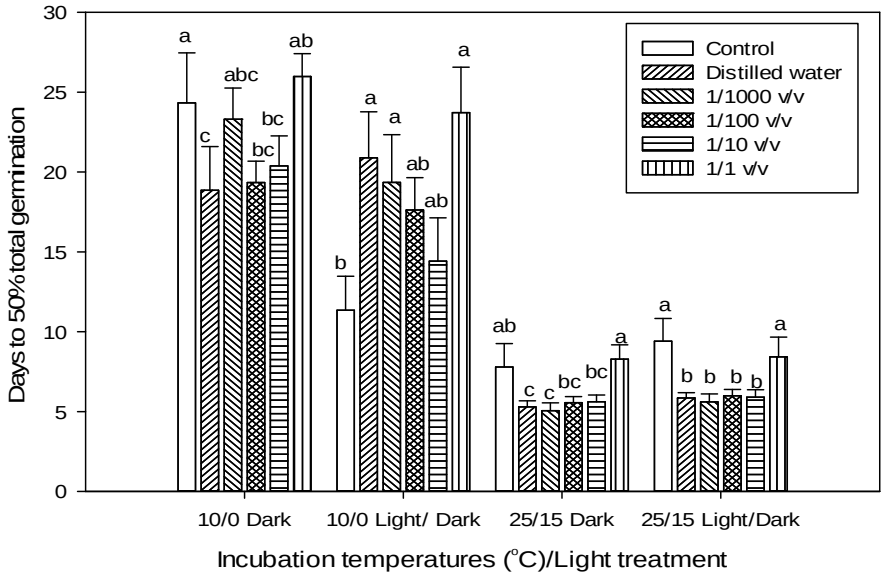

Figure 4.12 Days to 50% total germination for *Dactylis glomerata* seeds after priming in serial dilutions of aqueous smoke solutions and incubating at 10/0°C or 25/15°C in 24 h darkness or in 12 h light/12 h darkness. Means with different letters indicates days to 50% total germination of primed seeds were significantly different ($P \leq 0.05$) within treatments. Bars represent (±) standard error.

Seedling lengths responded to priming x smoke type interaction. Seedlings were shorter after priming seeds in the 1/10v/v and the 1/1v/v aqueous smoke solutions made from prairie hay (Table 4.11), but seedlings were longer after priming seeds in the 1/100v/v aqueous smoke solution made from the wheat straw, compared with priming in distilled water.

Table 4.11 Seedling lengths for *Dactylis glomerata* after priming in serial dilutions of aqueous smoke solutions made from prairie hay or wheat straw and incubating in 24 h darkness or 12h light/ 12 h darkness. Standard error estimate of overall variation in data = 1.3.

Fuel type	Dilution	Seedling length (mm)	SE
Prairie hay	Control	25 a[1]	4.2
	Distilled water	21 a	3.3
	1/1000v/v	29 a	3.3
	1/100v/v	25 a	3.4
	1/10v/v	8 b	2.3
	1/1v/v	8 b	2.6
Wheat straw	Control	25 ab	4.2
	Distilled water	21 a	3.3
	1/1000v/v	29 ab	3.7
	1/100v/v	36 b	5.7
	1/10v/v	29 ab	5.1
	1/1v/v	40 b	3.9

[1]Means with different letters indicates that seedling lengths were significantly different ($P \leq 0.05$) within fuel type treatments.

4.8 *Hesperostipa comata*

Germination of *Hesperostipa comata* seeds (56%, SE=5.4 viable and 38%, SE=1.5 dormant), was significantly affected by priming treatments, smoke type, and the interactions of priming x light, priming x temperature, and temperature x light. Total germination was higher after priming seeds in the 1/10v/v dilution in 12 h light/12 h darkness as compared with distilled water. However, priming seeds in distilled water reduced germination relative to the non-primed control (Fig. 4.13 a). Total germination was reduced by priming seeds in the 1/10 v/v and the 1/1000v/v dilutions in 24 h darkness, relative to the non-primed control. Priming seeds in the 1/1v/v dilution reduced total germination in both light treatments compared with priming in distilled water and the non-primed control. Total germination in priming treatments (12%, SE=0.6) was significantly less than non-primed control (18%, SE= 1.5). Total germination was generally low for this species and was reduced in light at both temperatures when compared with 24 h darkness (Fig 4.13 b).

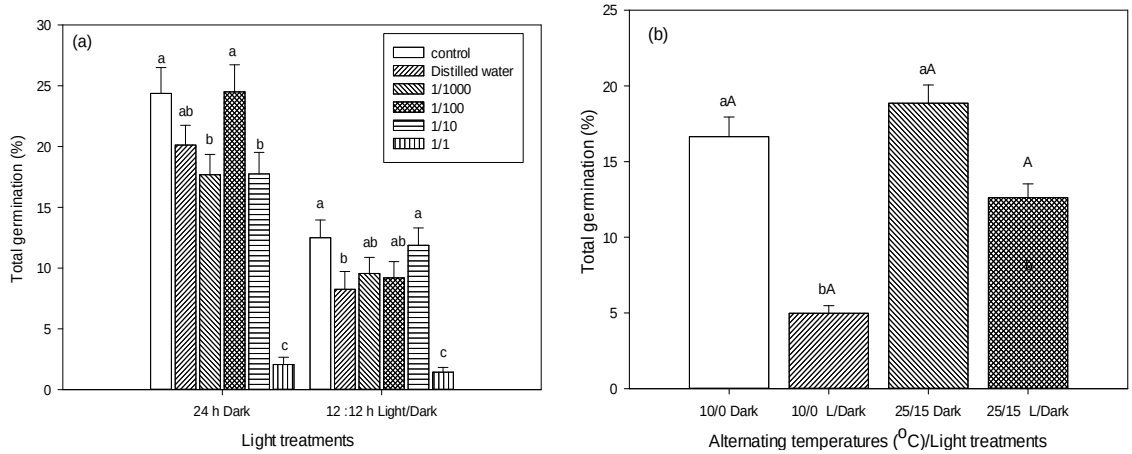

Figure 4.13 (a & b) Total germination for *Hesperostipa comata* seeds after priming in serial dilutions made from aqueous smoke solutions and then incubated at 10/0°C and 25/15°C in 24 h darkness or 12 h light/12 h darkness. **(a)** Means with different letters indicates total germination of primed seeds were significantly different (P≤0.05) within each light treatment (**b)** Means with different letters within each temperature treatment were significantly different (P≤0.05). Bars represent (±) standard error.

Germination rate was affected by the interactions of priming x temperature and temperature x light. Seeds germinated faster at 10/0^{o}C after priming in the 1/1 v/v dilution compared with distilled water and the non-primed control (Fig. 4.14 a). Germination was also faster at 25/15^{o}C after priming in the 1/100 v/v dilution as compared with the non-primed control. Seeds germinated faster in 12 h light/12 h darkness than in 24 h darkness at 10/0^{o}C (Fig. 4.14 b). Conversely, seeds germinated faster in 24 h darkness than in 12 h light/12 h darkness at 25/15^{o}C. Seeds generally germinated faster at 25/15^{o}C (9 d to 50% germination, SE=0.6) as compared with 10/0^{o}C (23 d to 50% germination, SE=1.1).

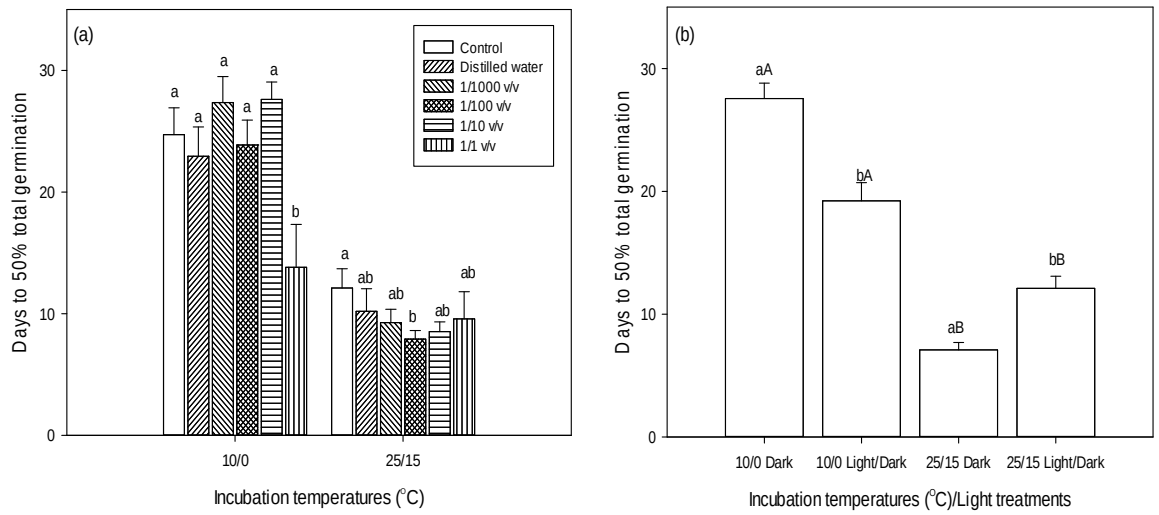

Figure 4.14 (a & b) Days to 50% germination for *Hesperostipa comata* seeds after priming in serial dilutions from aqueous smoke solutions and incubating at 10/0^{o}C or 25/15^{o}C in 24 h darkness or in 12 h light/12 h darkness **(a)** Means with different letters indicates days to 50% total germination of primed seeds were significantly different (P≤0.05) within each temperature treatment **(b)** Means with different letters within each temperature treatment were significantly different (P≤0.05). Bars represent (±) standard error.

Seedling lengths varied with priming treatments, smoke type, and the temperature x light interaction. Seedlings were shorter after priming seeds in distilled water or the 1/1v/v dilution, relative to the non-primed control (Table 4.12). Seedlings were longer after priming in the 1/1000v/v treatment as compared with distilled water. Seeds incubated in darkness produced

longer seedlings as compared with light (Table 4.13). Seedling lengths varied significantly between smoke types with an average of 11 mm for seeds primed in aqueous smoke solutions made from prairie hay (SE=1.4), and 15 mm for seeds primed in aqueous smoke solutions made from wheat straw (SE=1.7).

Table 4.12 Seedling lengths for *Hesperostipa comata* after priming in serial dilutions from aqueous smoke solutions and incubating in 24 h darkness or 12h light/ 12 h darkness. Standard error estimate of overall variation in data = 1.7.

Dilution	Seedling length (mm)	SE
Control	18 ab[1]	2.7
Distilled water	8 c	1.9
1/1000v/v	21 a	3.1
1/100v/v	14 abc	2.6
1/10v/v	12 bc	3.1
1/1v/v	6 c	2.1

[1]Means with different letters indicates seedling lengths were significantly different ($P \leq 0.05$)

Table 4.13 Seedling lengths for *Hesperostipa comata* after priming seeds in serial dilutions of aqueous smoke solutions and the seeds at 10/0°C or 25/15°C in 24 h darkness or 12 h light/12 h darkness. Standard error estimate of overall variation in data = 1.6.

Temperature (°C)	Light treatment	Seedling lengths (mm)	SE
10/0	24 h darkness	10 a[1]	1.6
	12 h light/12 h darkness	10 a	3.3
25/15	24 h darkness	21 a	5.2
	12 h light/12 h darkness	12 b	3.1

[1]Means with different letters within a temperature were significantly different ($P \leq 0.05$).

4.9 *Stipa viridula*

Germination of *Stipa viridula* seeds (77%, SE=2.6 viable and 51%, SE=2.5 dormant), responded to the interactions of priming x light, priming x temperature, priming x smoke type, and temperature x light. Priming seeds in the 1/10v/v dilution in 24 h darkness increased germination by 45% distilled water, but priming seeds in 1/1v/v, 1/100v/v, and 1/1000v/v dilutions in 12 h light/12 h darkness reduced germination compared with priming in distilled water (Fig. 4.15 a). Total germination was generally promoted in darkness with an average of 33% (SE=1.5) relative to 11% in light (SE=0.8). Priming seeds in distilled water, 1/1v/v, 1/100v/v, and 1/1000v/v dilution at 25/15^{o}C reduced germination compared with the non-primed control, but priming seeds in 1/10v/v increased germination compared with distilled water (Fig. 4.15 b). Total germination for seeds incubated at 10/0^{o}C (28%, SE=1.7), was significantly higher than that at 25/15^{o}C (16%, SE=1.0) (Fig. 4.15 c).

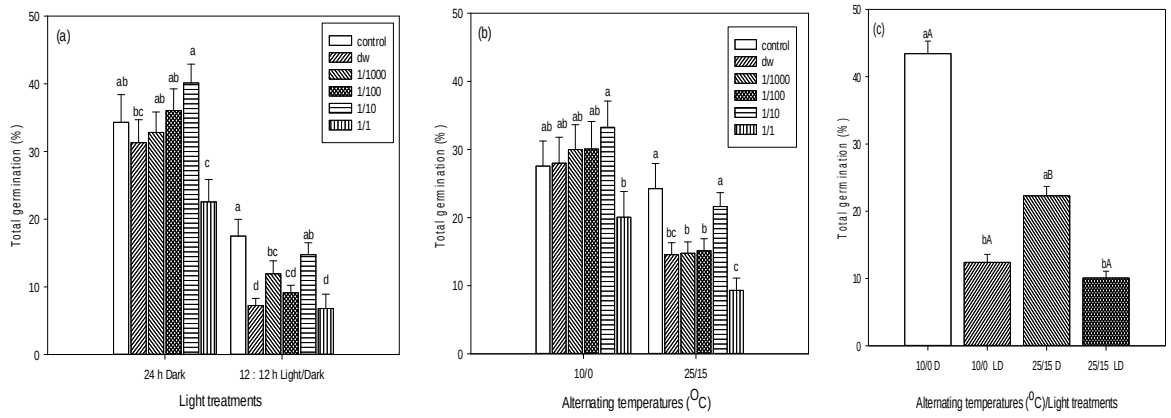

Figure 4.15 (a, b & c) Total germination for *Stipa viridula* seeds after priming in serial dilutions made from aqueous smoke solutions and then incubating at 10/0^{o}C and 25/15^{o}C in 12 light/12 h darkness or 24 h darkness. **(a & b)** Means with different letters indicates total germination of primed seeds was significantly different (P≤0.05) within each light and temperature treatments **(c)** Means with different lower case letters within each temperature treatment were significantly different (P≤0.05). Means with different capital letters within each light treatment were significantly different (P≤0.05). Bars represent (±) standard error.

Germination rate varied with the interacting effects of priming x temperature and temperature x light. Priming seeds in distilled water, the 1/1000v/v, and the 1/100v/v dilutions reduced germination rate at 10/0^{o}C, but priming in distilled water, the 1/10v/v and the 1/1v/v dilutions increased the speed of germination versus the non-primed control (Fig 4.16 a). Compared with the non-primed control, seeds also germinated slower after priming in distilled water, 1/1000v/v, 1/100v/v, and the 1/10v/v dilutions at 25/15^{o}C. Seed priming in the 1/1000v/v dilution also reduced germination rate compared with distilled water. Seeds germinated 25% faster in 12 h light/ 12 h darkness and at 10/0^{o}C, compared with 24 h darkness. Conversely, at 25/15^{o}C, seed germination was 30% faster in darkness than in 12 h light/12 h darkness (Fig. 4.16 b).

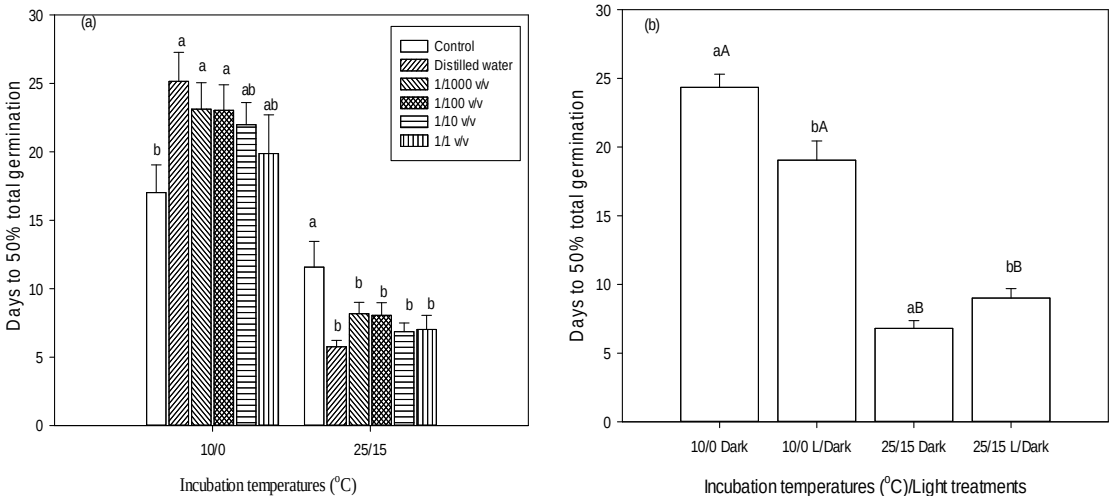

Figure 4.16 (a & b) Days to 50% total germination for *Stipa viridula* seeds after priming in serial dilutions from aqueous smoke solutions and incubating at 10/0^{o}C or 25/15^{o}C in 24 h darkness or in 12 h light/12 h darkness. **(a)** Means with different letters indicates days to 50% total germination of primed seeds were significantly different (P≤0.05) within each temperature treatment **(b)** Means with different lower case letters within a temperature were significantly different (P≤0.05). Means with different capital letters within each light treatment were significantly different (P≤0.05). Bars represent (±) standard error.

Seedling lengths varied with the interacting effects of priming x smoke type and temperature x light. Seedlings were longer after seed priming in the 1/1000v/v dilution in comparison with distilled water, but seedlings were shorter after priming in the 1/1v/v aqueous smoke solutions made from prairie hay, relative to distilled water and the non-primed control (Table 4.14). Incubating seeds at 25/15^{o}C produced seedlings that were longer in 24 h darkness compared with 12 h light/12 h darkness (Table 4.15). Similarly, seeds incubated in 12 h light /12h darkness, produced seedlings that were longer at 10/0^{o}C in relation to 25/15^{o}C.

Table 4.14 Seedling lengths for *Stipa viridula* after priming in serial dilutions of aqueous smoke solutions made from prairie hay or wheat straw and incubating in 24 h darkness or 12h light/ 12 h darkness. Standard error estimate of overall variation in data = 1.2.

Fuel type	Dilution	Seedling length (mm)	SE
Prairie hay	Control	21 abc[1]	4.6
	Distilled water	15 bc	3.9
	1/1000v/v	28 a	5.4
	1/100v/v	17 b	3.2
	1/10v/v	6 cd	1.9
	1/1v/v	3 d	1.5
Wheat straw	Control	21 a	4.6
	Distilled water	15 a	3.9
	1/1000v/v	25 a	3.9
	1/100v/v	23 a	5.1
	1/10v/v	21 a	5.4
	1/1v/v	17 a	5.7

[1]Means with different letters indicates that seedling lengths were significantly different ($P \leq 0.05$) within fuel type treatments.

Table 4.15 Seedling lengths for *Stipa viridula* after priming in serial dilutions of aqueous smoke solutions and incubating at 10/0°C or 25/15°C in 24 h darkness or 12 h light/12 h darkness. Standard error estimate of overall variation in data = 3.1.

Temperature (°C)	Light treatment	Seedling length (mm)	SE
10/0	24 h darkness	15 aA[1]	1.7
	12 h light/12 h darkness	20 aA	4.9
25/15	24 h darkness	24 aA	5.4
	12 h light/12 h darkness	12 bB	3.8

[1]Means with a different lower case letters within a temperature were significantly different ($P \leq 0.05$). Means with different capital letters within each light treatment were significantly different ($P \leq 0.05$).

4.10 *Agropyron dasystachyum*

Seeds of *Agropyron dasystachyum* were 69% viable (SE=3.1) and 12% dormant (SE=1.9). Germination was significantly affected by temperature, and the interacting effects of priming x light, priming x temperature, priming x smoke type, and temperature x light. Total germination was generally lower in light than in 24 h darkness (Fig. 4.17 a). Priming seeds in 1/1v/v and 1/100v/v dilution reduced germination in 24 h darkness compared with distilled water and the non-primed control, respectively. Total germination in 12 h light/12 h darkness was reduced after seed priming in the 1/1v/v and the 1/10 v/v dilutions as compared with distilled water. Priming in 1/1v/v dilution reduced seed germination compared with distilled water at 10/0 ^{o}C, but priming in 1/1v/v and 1/100v/v dilutions at reduced germination relative to the non-primed control at the same temperatures (Fig. 4.17 b). Priming seeds in distilled water and the 1/1000v/v dilutions promoted germination at 25/15 ^{o}C compared with the non-primed control, but priming in 1/1v/v, 1/10v/v, and 1/100v/v dilutions reduced germination in relation to distilled water.

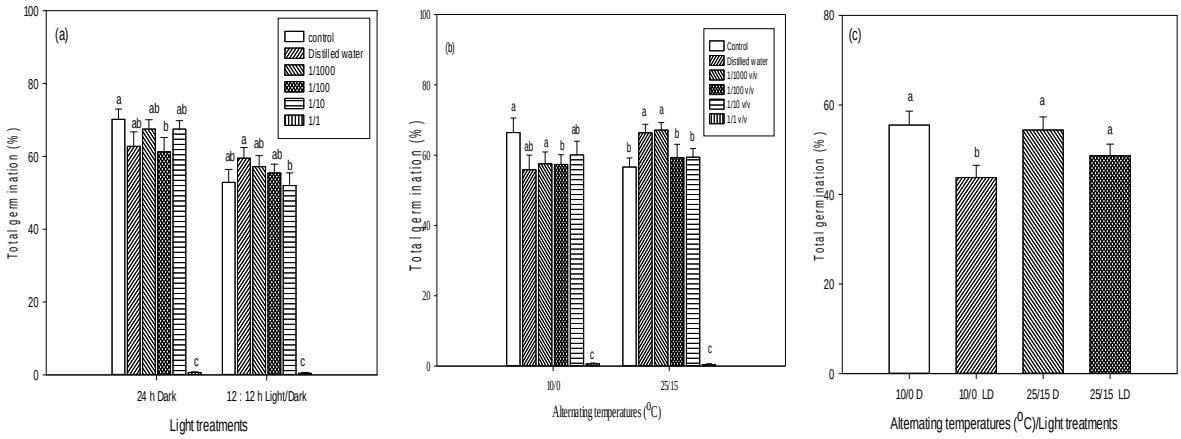

Figure 4.17 (a, b & c) Total germination for *Agropyron dasystachyum* seeds after priming in serial dilutions made from aqueous smoke solutions and incubating at 10/0^{o}C and 25/15^{o}C in 12 light/12 h darkness or 24 h darkness. **(a)** Means with different letters indicates total germination of primed seeds was significantly different (P≤0.05) within each light and temperature treatments **(b & c)** Means with different letters within each temperature treatment were significantly different (P≤0.05). Bars represent (±) standard error.

Germination rate responded to priming x smoke type interaction, and temperature. Priming seeds in the 1/1v/v dilution made from prairie hay increased germination speed compared with distilled water and non-primed control while priming in the 1/1v/v dilution made from wheat straw also increased germination rate relative to distilled water (Fig. 4.18). Germination was also faster after priming seeds in 1/1v/v dilution made from wheat straw in relation to distilled water. Germination was about 65% faster at 25/15^{o}C (5 d to 50% germination, SE=0.3) than at 10/0^{o}C (15 d to 50% germination, SE=0.9).

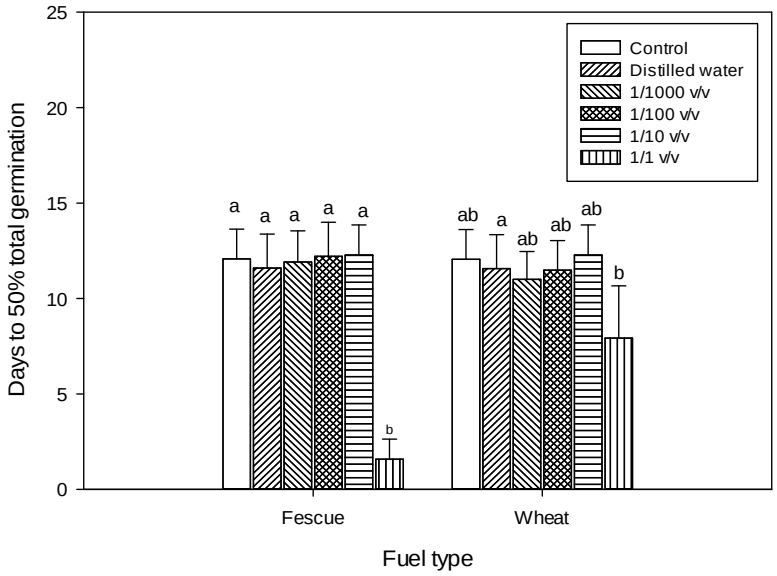

Figure 4.18 Days to 50% total germination for *Agropyron dasystachyum* seeds after priming in serial dilutions made from aqueous smoke solutions of wheat straw or prairie hay and incubated at 10/0^{o}C or 25/15^{o}C in 24 h darkness or in 12 h light/12 h darkness. Means with different letters indicates days to 50% total germination of primed seeds were significantly different (P≤0.05) within fuel type treatments. Bars represent (±) standard error.

Seedling lengths were significantly affected by the interactions of priming x smoke type and temperature x light. Seedling lengths were reduced after priming seeds in 1/1v/v aqueous smoke solutions made from prairie hay, relative to distilled water and the non-primed control (Table

4.16). Priming seeds in distilled water and the 1/10v/v dilution also reduced seedling lengths compared with the non-primed control, but the 1/1000v/v dilution increased seedling lengths compared with distilled water. Seeds primed in 1/1000v/v and 1/100v/v aqueous smoke solution made from wheat straw had longer seedlings compared with distilled water. Seedlings were also longer in 12 h light/12 h darkness at 10/0 ^{o}C than in 24 h darkness at the same temperature (Table 4.17).

Table 4.16 Seedling lengths for *Agropyron dasystachyum* after priming in serial dilutions of aqueous smoke solutions made from prairie hay or wheat straw and incubating in 24 h darkness or 12h light/12 h darkness. Standard error estimate of overall variation in data = 2.0.

Fuel type	Dilution	Seedling length (mm)	SE
Prairie hay	Control	35 a[1]	4.9
	Distilled water	22 bc	4.9
	1/1000v/v	37 a	3.7
	1/100v/v	30 ab	5.3
	1/10v/v	12 c	3.5
	1/1v/v	0 d	0.0
Wheat straw	Control	35 ab	4.9
	Distilled water	22 b	4.9
	1/1000v/v	43 a	5.9
	1/100v/v	44 a	7.2
	1/10v/v	42 ab	9.1
	1/1v/v	30 ab	9.0

[1]Means with different letters indicates that seedling lengths were significantly different ($P \leq 0.05$) within fuel type treatments.

Table 4.17 Seedling lengths for *Agropyron dasystachyum* after priming in serial dilutions of aqueous smoke solutions and incubating at 10/0°C or 25/15°C in 24 h darkness or 12 h light/12 h darkness. Standard error estimate of overall variation in data = 3.1.

Temperature (°C)	Light treatment	Seedling length (mm)	SE
10/0	24 h darkness	24 a[1]	2.9
	12 h light/12 h darkness	34 b	6.3
25/15	24 h darkness	34 a	7.7
	12 h light/12 h darkness	27 a	6.3

[1]Means with a different lower case letters within a temperature were significantly different ($P \leq 0.05$).

4.11 *Pascopyrum smithii*

With 80% viability (SE=3.6) and 58% dormancy (SE=2.9), seed germination of *Pascopyrum smithii* was affected by light, temperature, and the interactions of priming x temperature, priming x light, priming x smoke type, and temperature x light. Total germination was generally lower in light as compared with 24 h darkness (Fig. 4.19 a). Seeds incubated at 25/15^{o}C in 24 h darkness had 45% higher germination than at 10/0^{o}C. Germination of primed seeds was significantly less than the non-primed control in the two light and temperature treatments. Germination was reduced by 85% in 24 h darkness and 12 h light/12 h darkness after priming seeds in the 1/1v/v dilutions. Priming seeds in 1/1000v/v, 1/100v/v, and 1/10v/v dilutions at 10/0^{o}C increased germination compared with distilled water (Fig. 4.19 b), but priming seeds in distilled water, 1/1v/v, 1/10v/v, 1/100v/v, and 1/1000v/v dilutions reduced total germination in comparison with the non-primed control. Priming in 1/1v/v dilution reduced germination at 25/15^{o}C by 80% relative to distilled water and the non-primed control, and at 10/0^{o}C, it reduced total germination by over 82% as compared with the non-primed control.

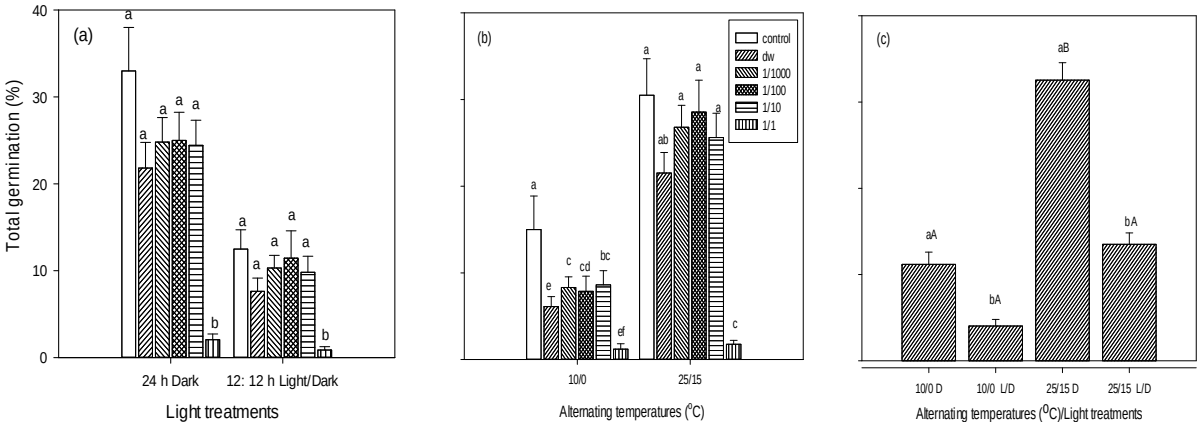

Figure 4.19 (a, b, & c) Total germination for *Pascopyrum smithii* seeds after priming in serial dilutions made from aqueous smoke solutions and then incubated at 10/0^{o}C or 25/15^{o}C in 12 light/12 h darkness or 24 h darkness **(a & b)** Means with different letters indicates total germination of primed seeds was significantly different (P≤0.05) within each light and temperature treatments **(c)** Means with different lower case letters within each temperature

treatment were significantly different (P≤0.05). Means with different capital letters within each light treatment were significantly different (P≤0.05). Bars represent (±) standard error.

Germination rate varied with the priming x temperature interaction. Priming seeds in the 1/1v/v dilution at 10/0 ^{o}C increased germination rate as compared with distilled water and the non-primed control (Fig. 4.20 a). Seed priming in distilled water also increased germination rate by 5 d to 50% germination at 25/15 ^{o}C compared with the non-primed control. Seed germination was 50% faster in light at 10/0 ^{o}C as compared with 24 h darkness (Fig. 4.20 b). The days to 50% germination was 2d less in 24 h darkness at 25/15 ^{o}C, than in 12 h light/12 h darkness (9 d).

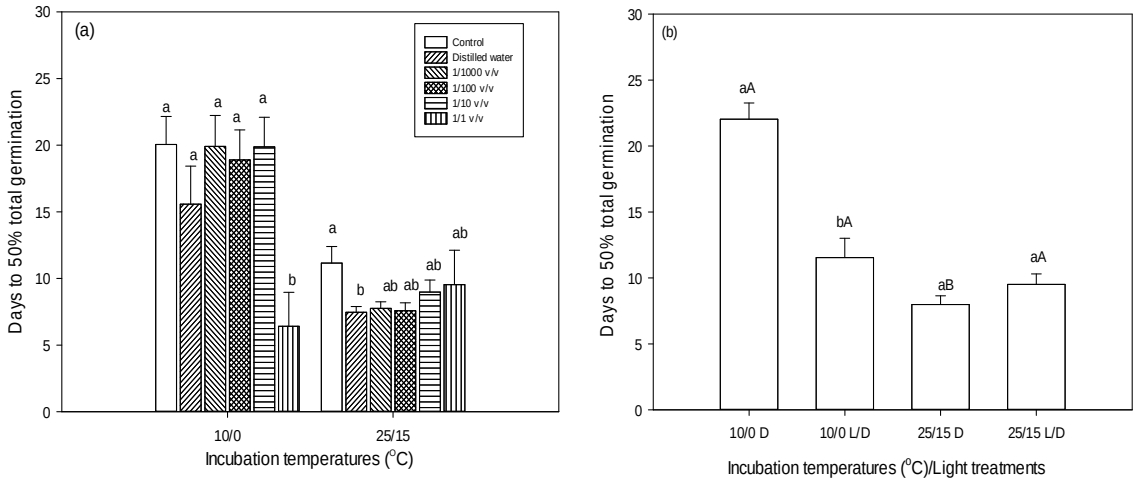

Figure 4.20 (a &b) Days to 50% total germination for *Pascopyrum smithii* seeds after priming in serial dilutions from aqueous smoke solutions and incubating at 10/0^{o}C or 25/15^{o}C in 24 h darkness or in 12 h light/12 h darkness **(a)** Means with different letters within each temperature treatment were significantly different (P≤0.05) **(b)** Means with different lower case letters within a temperature were significantly different (P≤0.05). Means with different capital letters within each light treatment were significantly different (P≤0.05). Bars represent (±) standard error.

Seedling lengths were affected by the priming x smoke type interaction, temperature and light. Seedling lengths reduced after priming seeds in 1/10v/v and 1/1v/v aqueous smoke solutions made from prairie hay, relative to the non-primed control (Table 4.18). Seedlings were longer after priming seeds in 1/100v/v and 1/1000v/v dilutions relative to distilled water.

Seedling lengths averaged 9 mm (SE=0.9) in 24 h darkness, significantly less than the average of 22 mm (SE =1.5) in 12 h light/12 h darkness. Seedling lengths also averaged 14 mm (SE=2.0) at 10/0°C, which was greater than the 24 mm (SE=2.3) at 25/15°C.

Table 4.18 Seedling lengths for *Pascopyrum smithii* after priming in serial dilutions of aqueous smoke solutions made from prairie hay or wheat straw and incubating in 24 h darkness or 12h light/ 12 h darkness. Standard error estimate of overall variation in data = 1.5.

Fuel type	Dilution	Seedling length (mm)	SE
Prairie hay	Control	21 ab[1]	4.7
	Distilled water	13 bc	3.9
	1/1000v/v	25 a	5.0
	1/100v/v	25 a	4.7
	1/10v/v	9 cd	2.6
	1/1v/v	0 d	0.0
Wheat straw	Control	21 a	4.7
	Distilled water	13 a	3.9
	1/1000v/v	25 a	4.5
	1/100v/v	27 a	6.8
	1/10v/v	29 a	7.1
	1/1v/v	20 a	7.4

[1]Means with different letters indicates seedling lengths were significantly different ($P \leq 0.05$) within fuel type treatments.

4.12 *Festuca hallii*

Seed germination of *Festuca hallii* (59%, SE=2.2 viable and 29%, SE=2.3 dormant), responded to the interacting effects of priming x temperature x light, priming x temperature, and temperature x light. Total germination was generally lower at 10/0^{o}C (15%, SE=1.5), than at 25/15^{o}C (36%, SE=2.0) (Fig. 4.21). Total germination of primed seeds was significantly less than the non-primed control under both light and temperature treatments. Priming in the 1/1v/v and the 1/100v/v dilutions in 24 h darkness at 10/0^{o}C reduced germination by 85% and 25%, respectively, compared with the non-primed control. Priming in 1/1v/v dilution also reduced germination by 90% in relation to distilled water. Priming in the 1/1v/v and 1/1000v/v dilutions in 12 h light/12 h darkness at 10/0^{o}C reduced total germination by 90% and 50%, respectively, versus the non-primed control. Priming seeds in 1/1 v/v dilution also reduced total germination by 80% compared with distilled water. Priming in distilled water and 1/100v/v dilutions at 25/15^{o}C in 24 h darkness increased total germination by 30% and 36%, respectively, relative to the non-primed control. Seed priming in 1/10 v/v and 1/1v/v dilutions reduced germination in comparison with distilled water and the non-primed control. Priming seeds in 1/1000v/v dilution in 12 h light/12 h darkness at 25/15^{o}C increased germination by about 50% relative to the non-primed control, but priming in 1/10v/v and 1/1v/v reduced germination in comparison with distilled water.

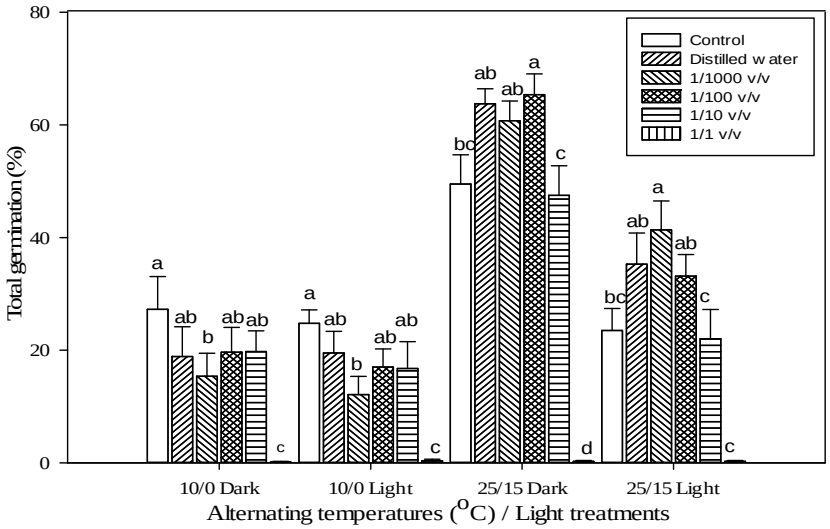

Figure 4.21 Total germination of *Festuca hallii* seeds after priming in serial dilutions of aqueous smoke solutions and incubating at 10/0°C or 25/15°C in 24 h darkness or in 12 h light/12 h darkness. Means with different letters were significantly different (P≤0.05) within each treatment.

Germination rate varied with the priming x temperature interaction. Seeds germinated faster after priming in the 1/1v/v dilution at 10/0 °C, than in distilled water and the non-primed control, but at 25/15 °C, seed germinated faster only in comparison with distilled water (Fig. 4.22). Priming seeds in distilled water, 1/1000v/v, 1/100v/v, 1/10v/v, and 1/1v/v dilutions at 25/15 °C, all increased germination rate as compared with the non-primed control.

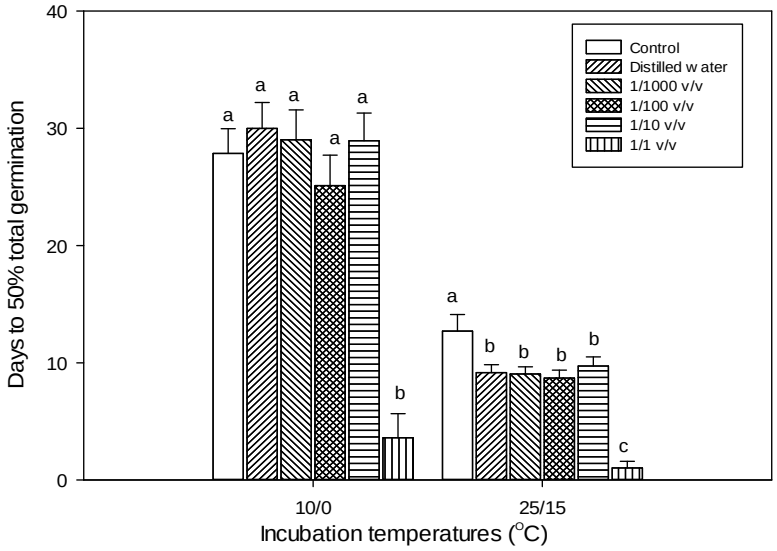

Figure 4.22 Days to 50% total germination for *Festuca hallii* seeds after priming in serial dilutions from aqueous smoke solutions and incubating at 10/0°C or 25/15°C in 24 h darkness or in 12 h light/12 h darkness. Means with different letters indicates days to 50% total germination were significantly different ($P \leq 0.05$) within each temperature treatment.

Seedling lengths were significantly affected by the interactions of priming x temperature and temperature x light. Seedling lengths were reduced by priming seeds in distilled water or aqueous smoke solutions (1/1000v/v, 1/100v/v, 1/10v/v or 1/1v/v) at 10/0 °C, compared with the non-primed control (Table 4.19). Light also increased seedling lengths by 40% relative to 24 h darkness (Table 4.20).

Table 4.19 Seedling lengths for *Festuca hallii* after priming in serial dilutions of aqueous smoke solutions and incubating at 10/0°C or 25/15°C in 24 h darkness or 12h light/ 12 h darkness. Standard error estimate of overall variation in data =0.8.

Temperature (°C)	Dilution	Seedling length (mm)	SE
10/0	Control	19 a[1]	2.9
	Distilled water	5 b	1.6
	1/1000v/v	9 b	2.0
	1/100v/v	7 b	2.1
	1/10v/v	6 b	2.2
	1/1v/v	3 b	1.7
25/15	Control	13 ab	2.1
	Distilled water	11 ab	4.4
	1/1000v/v	18 a	2.3
	1/100v/v	15 a	2.7
	1/10v/v	11 a	2.9
	1/1v/v	6 b	2.8

[1]Means with different letters indicates seedling lengths were significantly different ($P \leq 0.05$) within each temperature treatment.

Table 4.20 Seedling lengths for *Festuca hallii* after priming in serial dilutions of aqueous smoke solutions and incubating at 10/0°C or 25/15°C in 24 h darkness or 12 h light/12 h darkness. Standard error estimate of overall variation in data =1.7.

Temperature (°C)	Light treatment	Seedling lengths (mm)	SE
10/0	24 h darkness	6 a[1]	1.1
	12 h light/12 h darkness	11 b	2.8
25/15	24 h darkness	14 a	2.9
	12 h light/12 h darkness	10 a	3.2

[1]Means with a different lower case letters within a temperature were significantly different ($P \leq 0.05$).

4.13 Seedling emergence in the field

Total seedling emergence of all species in the field did not vary among the four priming treatments (Fig. 4.23). Seedling emergence, however, trended toward being greater in smoke treated seeds of *Agropyron dasystachyum*, *Dactylis glomerata*, *Elymus angustus*, *Hesperostipa comata*, *Pascopyrum smithii*, and *Trifolium ambiguum* relative to control. For all species, the rate of seedling emergence was not significantly different among priming treatments (Fig. 4.24), but *Agropyron dasystachyum*, *Astragalus cicer*, *Dactylis glomerata*, *Elymus junceus*, *Hesperostipa comata*, and *Stipa viridula* showed a trend of emerging about 1 to 4 d faster to 50% germination after priming seeds in smoke solutions, relative to priming in distilled water and the non-primed control (Fig. 4.24).

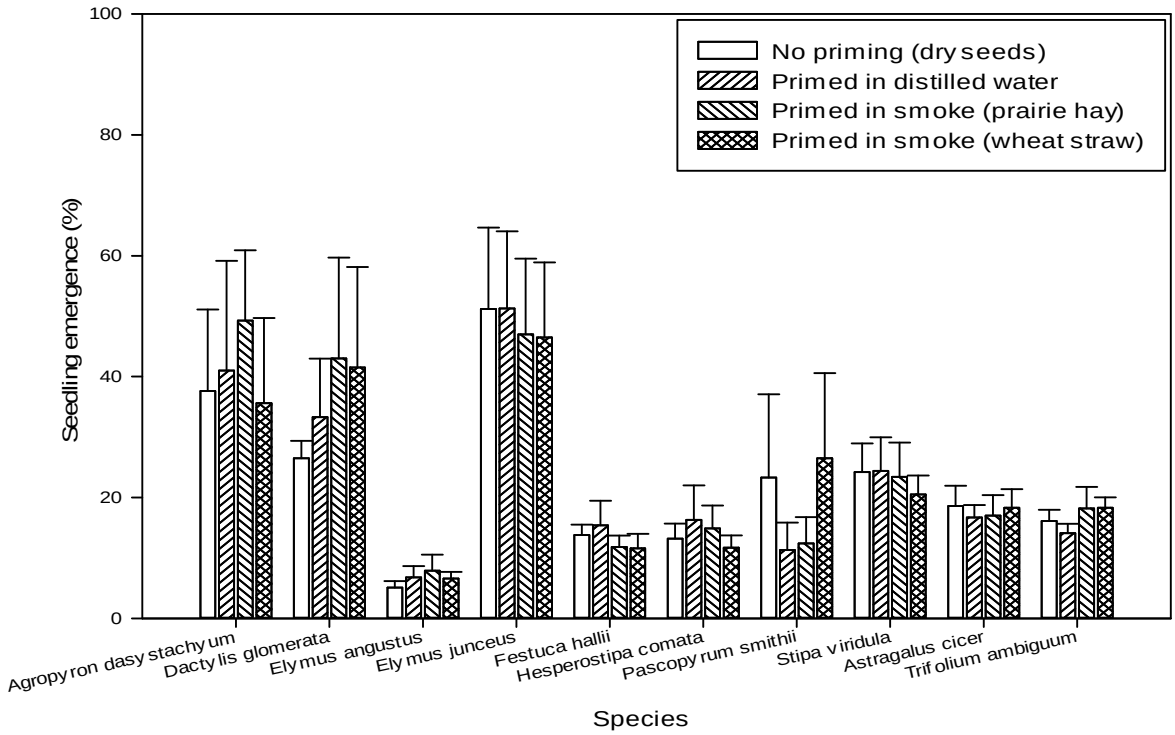

Figure 4.23 Seedling emergence for ten species after priming seeds in serial dilutions of aqueous smoke solutions. All means are not significantly different within species. Bars represent (±) standard error.

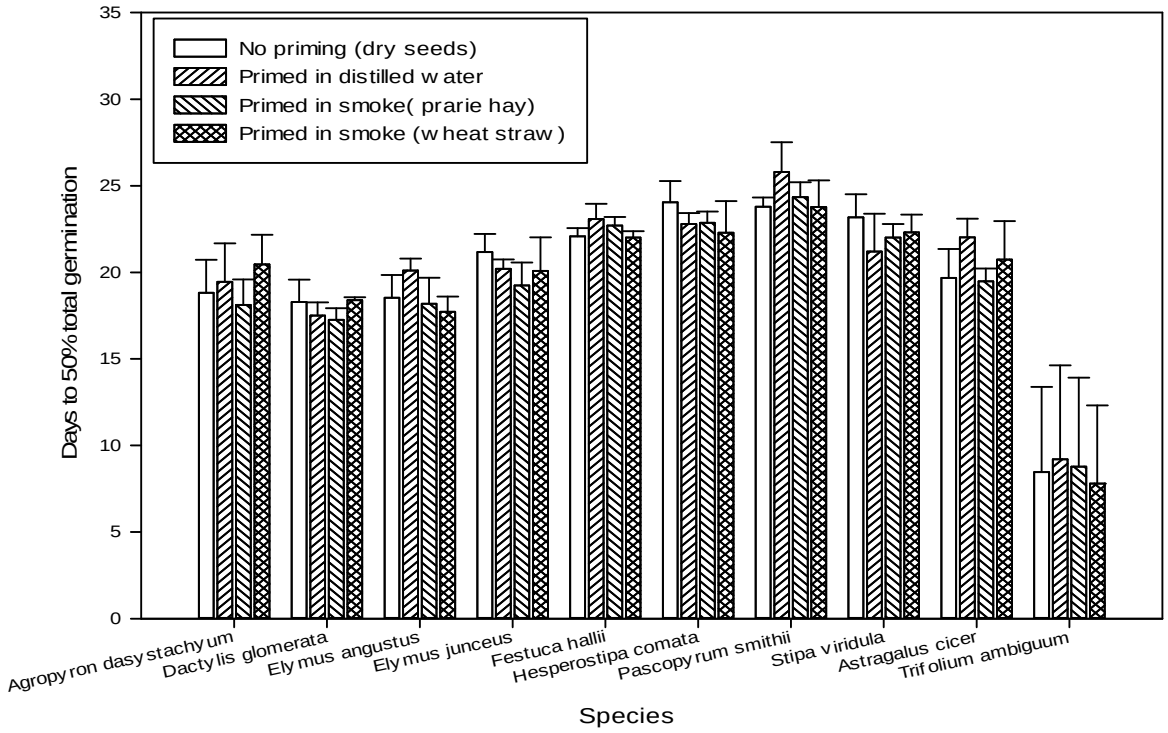

Figure 4.24 Days to 50% germination for ten species after priming seeds in serial dilutions of aqueous smoke solutions. All means are not significantly different within species. Bars represent (±) standard error.

4.14 Standing crop in the field

Except for *Dactylis glomerata*, standing crop was not significantly different among priming treatments. Priming seeds of *Dactylis glomerata* in aqueous smoke solutions made from wheat straw or prairie hay increased standing crop by 57% and 45%, respectively, as compared with priming seeds in distilled water and the non-primed control (Fig. 4.25). *Agropyron dasystachyum*, *Astragalus cicer*, *Elymus angustus*, *Pascopyrum smithii*, *Stipa viridula*, and *Trifolium ambiguum* showed a trend of increased standing crop in the priming treatment involving aqueous smoke solutions, relative to control.

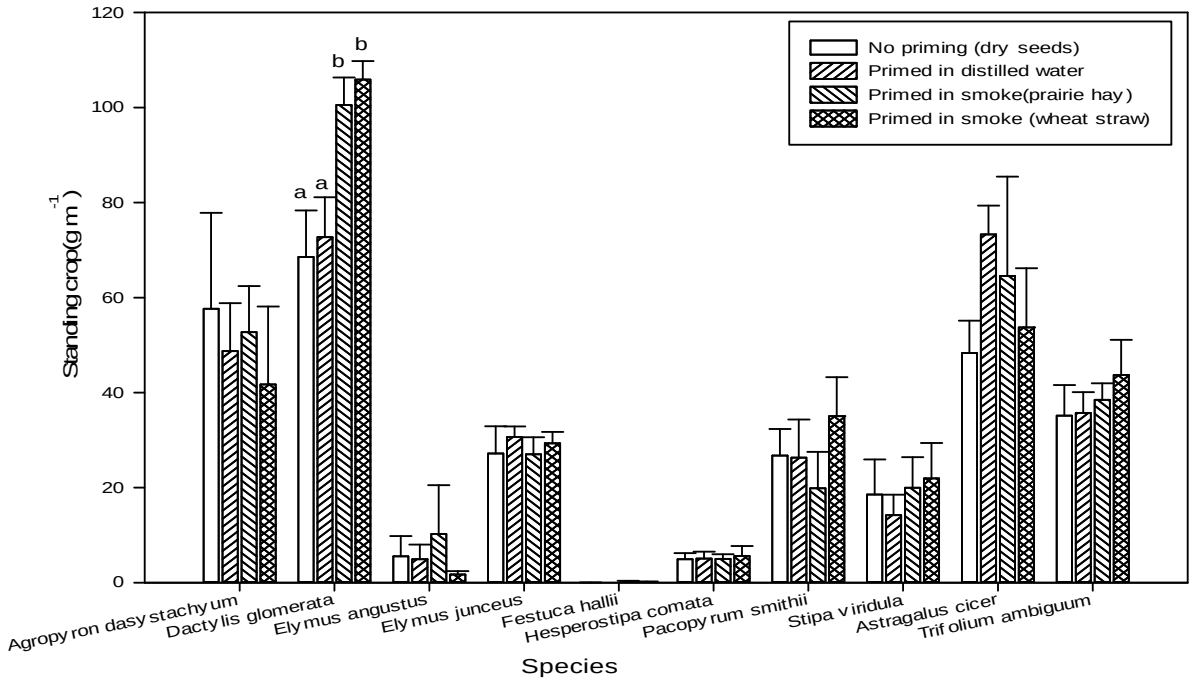

Figure 4.25 The standing crop for 10 species studied after priming seeds in serial dilutions of aqueous smoke solutions, "b" indicates the standing crop of seedlings from *Dactylis glomerata* seeds primed in aqueous solutions made from wheat straw or prairie hay was significantly different ($P \leq 0.05$) from distilled water and the dry (non-primed) control. All other means are not significantly different within species. Bars represent (±) standard error.

5.0. DISCUSSION

Responses observed in these studies indicates that priming seeds in aqueous smoke solutions made from wheat straw or prairie hay has the potential to stimulate germination in some plant species. Priming seeds in aqueous smoke solutions significantly affected seed germination, seedling growth, and standing crop of some species through an independent or interacting effect of light, incubation temperatures, or smoke type.

5.1 Enhancing Effects of Aqueous Smoke Solutions on Seed Germination and Seedling Growth

Priming seeds in aqueous smoke solutions significantly affected total germination, germination rates and seedling lengths of *Astragalus cicer*, *Elymus junceus*, *Elymus angustus*, *Hesperostipa comata*, *Lactuca sativa*, and *Trifolium ambiguum*. Low concentrations of aqueous smoke solutions had no effect on total germination of *Lactuca sativa*, *Astragalus cicer*, and *Trifolium ambiguum*, but at high concentrations, total germination was reduced by about 30% in *Trifolium ambiguum* and 70% in *Lactuca sativa.* Ana and Bradford (1992) reported that priming seeds in water for 1 h, followed by drying, did not affect the germination of *Lactuca sativa*. On the other hand, high concentrations of aqueous smoke solutions slowed the germination of *Trifolium ambiguum* and *Elymus junceus* by 2 and 3 d to 50% of germination, respectively. Priming in low concentrations of aqueous smoke solutions also increased the seedling lengths of *Elymus angustus* by 28% and those of *Hesperostipa comata* by 100%. Karrikinolide, a compound isolated from smoke, may stimulate germination in responsive species by acting like cytokinin, and auxin plant hormones when used for seed priming at low concentrations (Jain *et al*., 2008b). Reduced total germination at high concentrations of aqueous smoke solutions observed in *Lactuca sativa* and *Trifolium ambiguum* agrees with Kulkarni *et al*. (2007) in which

high concentrations of aqueous smoke solutions reduced seed germination of *Acacia robusta*. This reduction may either be due to the presence of inhibiting or toxic compounds in smoke at high concentrations (Dixon and Roche 1995) or different compounds becoming active at different concentrations (Boucher and Meets, 2004). The compounds in smoke at high concentrations may have also modified seed membrane permeability, impeding water uptake and mobilization of energy reserves (van Staden *et al*., 1995). However, it is possible that such effects may be neutralized upon dilution (Brown and van Staden, 1997). Prolonged smoke treatment may also inhibit seed germination (Drewes *et al*. 1995). *Astragalus cicer* did not respond to priming of seeds in aqueous smoke solutions, agreeing with observations for other legumes; seed germination of *Cochlospermum planchonii, Cassia mimosoides,* and *Tephrosia pedicellata* was not responsive to priming in aqueous smoke solutions (Dayamba *et al*., 2008). Priming seeds in aqueous smoke solutions may not affect germination in some species of *Amaryllidaceae* (Brown *et al*., 2003, Jager *et al.,* 1996), because of physical dormancy caused by a hard seed coat. Therefore, pre-treating seeds of *Astragalus cicer* using treatments such as scarification to reduce physical dormancy may be necessary before priming in aqueous smoke solutions. High concentrations of aqueous smoke solutions increased germination rates of *Trifolium ambiguum* and *Elymus junceus* irrespective of its negative effect on total germination. It should be noted that rapid germination was related to low total germination; at high concentrations of aqueous smoke solutions, only a few seeds germinated, but they germinated more rapidly relative to the non-primed control. Smoke treatment of seeds also promoted germination rate, but not total germination of arable species (Adkins and Peters, 2001).

Priming seeds in low concentrations of aqueous smoke solutions increased seedling lengths for *Elymus angustus* and *Hesperostipa comata*. However, seedling lengths for these

grasses were reduced at high concentrations, confirming that high concentrations of aqueous smoke solutions may reduce seedling growth due to the presence of inhibiting compounds (Light *et al.*, 2002). Under natural environmental conditions, these inhibiting compounds may be diluted or washed away by rain without affecting their potential to stimulate germination (Baldwin *et al.*, 1994). Generally, priming seeds in low concentrations of aqueous smoke solutions increased germination of *Trifolium ambiguum*, *Elymus angustus*, *Hesperostipa comata*, and *Elymus junceus.*

5.2 Light Interaction with Aqueous Smoke Solutions in Stimulating Seed Germination and Seedling Growth

Light can break dormancy and germination can be improved or accelerated by exposing seeds to light (Farmer, 1997). Priming seeds in aqueous smoke solutions interacted with light on the germination of *Elymus angustus, Hesperostipa comata, Stipa viridula, Dactylis glomerata, Agropyron dasystachyum,* and *Pascopyrum smithii.* Dormant seeds are metabolically active and have the potential to respond to light signals that can stimulate germination (Bewley, 1997). Priming seeds in aqueous smoke solutions increased total germination of *Dactylis glomerata*, *Stipa viridula,* and *Elymus angustus* in darkness, but not in light. Fulbright *et al.* (1983) reported 15 to 25% higher germination in darkness than in light for *Stipa viridula* at temperatures below 20°C. This increased germination in darkness indicates buried seeds of *Dactylis glomerata*, *Stipa viridula,* and *Elymus angustus* may germinate after treatment or fire as reported for *Stylidium affine* and *Hibbertia commutata* (Tieu *et al.*, 2001).

When incubated in light, total germination of *Elymus angustus*, *Hesperostipa comata,* and *Stipa viridula* was improved after priming seeds in aqueous smoke solutions, but total germination of *Dactylis glomerata* did not change. Light is a critical determinant of seed

germination in some species (Shinomura *et al*., 1996), including *Dactylis glomerata* (Qiu *et al*., 2008), and it may interact with the compounds in smoke (Brown *et al*., 1994) to improve germination. However, the active ingredients in smoke could have impeded light-promoting effects on germination of *Dactylis glomerata*. Depending on light, the compounds in aqueous smoke solutions may have affected the germination of *Elymus angustus, Hesperostipa comata, Stipa viridula, Dactylis glomerata, Agropyron dasystachyum,* and *Pascopyrum smithii by* activating hormones (Kulkarni *et al*., 2007). Compounds in aqueous smoke solutions may have also activated the phytochrome system leading to increased sensitivity of seeds to light and GA (gibberrelic acid) (van Staden *et al*., 1995), and decreased sensitivity to ABA (abscisic acid) (Grappin *et al*., 2000). Increased GA and decreased ABA are necessary to stimulate seed germination in many species (Grappin *et al*., 2000). Biosynthesis of GA is also regulated by light and temperature (Yamaguchi *et al*., 1998).

Total germination for *Elymus angustus* was higher in darkness than in light, and priming in aqueous smoke solutions improved germination in light, and in dark treatments. Seeds of *Syncarpha vestita* are negatively photoblastic, germinating in darkness, but requiring the application of smoke extract to germinate in light (Brown, 1993, 1997). Smoke treatment may have increased the sensitivity to light of *Elymus angustus* seeds during germination. This increase in total germination was also observed in *Stipa viridula* in which germination increased from 30% in darkness to 100% in light. Total germination of *Dactylis glomerata* increased in darkness, but not in light. Similarly, total germination in *Agropyron dasystachyum* and *Pascopyrum smithii* was higher in darkness relative to light, suggesting that the active compounds in aqueous smoke solutions may have partially replaced a light requirement for seed germination. Brief exposure of seeds to light reduced germination of *Pascopyrum smithii* at

15/25°C (Qiu *et al*., 2008). However, germination of *Pascopyrum smithii* was independent of light with less than 2% difference between light and dark treatments, indicating that aqueous smoke solutions partially replaced a light requirement for germination and increased sensitivity to light (Hardegree, 1994).

Generally, priming seeds in aqueous smoke solutions may partially substitute a light requirement for germination as observed in *Dactylis glomerata, Agropyron dasystachyum, Elymus angustus, Stipa viridula, Hesperostipa comata,* and *Pascopyrum smithii.* The interaction observed between priming of seeds and light treatments during incubation indicates smoke may stimulate germination in these species over a wide range of light conditions. Priming seeds in distilled water or aqueous smoke solutions interacted with light to improve germination in *Elymus angustus, Stipa viridula, Dactylis glomerata,* and *Hesperostipa comata*.

5.3 Aqueous Smoke Solutions and Temperature Interactions Affecting Seed Germination and Seedling Growth

Priming seeds in aqueous smoke solutions interacted with temperature to affect total germination of *Stipa viridula, Dactylis glomerata, Elymus junceus, Agropyron dasystachyum,* and *Pascopyrum smithii.* Seed priming also interacted with incubation temperatures to affect the germination rates of *Lactuca sativa, Elymus angustus, Stipa viridula, Festuca hallii, Pascopyrum smithii,* and *Hesperostipa comata,* and seedling lengths of *Festuca hallii.* Optimum temperatures for germination of *Stipa viridula* are 20^{o}C and 20/15^{o}C (16 h/8 h alternation) (Fulbright *et al*., 1983). In the present study, priming seeds in 1/10v/v concentration of aqueous smoke solutions improved total germination of *Stipa viridula* at 10/0^{o}C, but not in the other concentrations tested at 10/0^{o}C and at 25/15^{o}C. Together this response suggests a narrow window of smoke concentrations for smoke action, and the need for a precise balance between smoke

concentrations and temperature in this grass. The narrow window of smoke concentrations for smoke action observed at 10/0^{o}C could also mean the compounds in smoke may alter the temperature requirements for seeds germination after alleviating dormancy. Spring seeding of *Stipa viridula* may be desirable due to its high germination at low temperatures. Fall seeding may also be desirable, in which case seeds may over-winter and germinate in spring. Alternating temperatures may stimulate germination through the activation of important physiological processes within seeds (Robert and James, 1998; Qiu *et al.*, 2008).

Total germination in *Dactylis glomerata* increased after priming seeds in aqueous smoke solutions or distilled water and incubating them at 10/0^{o}C or 25/15^{o}C. This response indicates compounds in aqueous smoke solutions stimulate seed germination of this grass over a wide range of alternating temperatures. Alternating temperatures reportedly increase germination of *Dactylis glomerata* (Pannangpetch and Bean, 1984; Qiu *et al.*, 2008). Priming seeds in interaction with temperature may have altered the state of dormancy in *Dactylis glomerata* seeds, allowing them to germinate over a wider range of temperatures. Seeds with less dormancy can germinate over a broader range of temperatures than those with deeper dormancy (Batlla *et al.*, 2003). This response is important because temperatures fluctuate under field conditions, and exposing seeds, such as those of *Dactylis glomerata* to fluctuating temperatures can be a critical requirement for breaking dormancy (Benech-Arnold *et al*., 2000). Alternating temperatures (16/27^{o}C) reduced germination of *Elymus junceus* relative to constant temperature (21^{o}C) (McElgunn, 1974). However, in the present study, total germination of *Elymus junceus* increased at 25/15^{o}C after priming seeds in low concentrations of aqueous smoke solutions, but high concentrations reduced total germination at 10/0^{o}C and 25/15^{o}C. This response indicates alternating temperature may not constrain germination of *Elymus junceus* following priming in

optimal concentrations of aqueous smoke solutions. A similar response was observed for *Agropyron dasystachyum*, in which total germination was promoted at 25/15°C after priming seeds, but germination was reduced at 10/0°C. Total germination of *Pascopyrum smithii* was also reduced at 10/0°C after priming seeds in distilled water or aqueous smoke solutions. At higher concentrations of aqueous smoke solutions, priming of seeds reduced total germination of *Agropyron dasystachyum* at 10/0°C and that of *Pascopyrum smithii* at 25/15°C. These responses underscore the role of temperature in the seed germination of *Elymus junceus, Agropyron dasystachyum*, and *Pascopyrum smithii*, and they suggest high concentrations of aqueous smoke solutions interact with temperature and may inhibit germination. Inhibition of germination could be caused by inhibiting actions of some compounds in smoke. Total germination of *Pascopyrum smithii* at 10/0°C was reduced after priming seeds in distilled water or aqueous smoke solutions.

Priming seeds in low concentrations of aqueous smoke solutions accelerated the germination of *Lactuca sativa, Stipa viridula,* and *Festuca hallii* at 25/15°C. Seed priming in low concentrations of aqueous smoke solutions also increased the speed of germination for *Hesperostipa comata* at 10/0°C. Priming seeds in high concentrations of aqueous smoke solutions appears to have increased the germination speed of *Hesperostipa comata, Pascopyrum smithii,* and *Festuca hallii* at 10/0°C. Seeds of *Festuca hallii* germinate over a wide range of temperature (Qiu *et al*., 2008), but mostly at constant temperatures (Romo *et al*., 1991).

Priming seeds in high concentrations of aqueous smoke solutions also accelerated the germination of *Pascopyrum smithii* and *Festuca hallii* at 25/15°C, but not for *Lactuca sativa*. The toxic effects likely posed by high concentrations of aqueous smoke solutions, may have slowed germination by either inhibiting physiological processes or killing the seeds of *Lactuca sativa*. Priming seeds also reduced seedling lengths for *Festuca hallii* at 10/0°C.

5.4 Plant Materials from Which Aqueous Smoke Solutions Were Generated Affected Seedling Growth

Seedling lengths for *Hesperostipa comata*, *Lactuca sativa*, and *Elymus angustus* were reduced by priming seeds in aqueous smoke solutions made from prairie hay as compared with wheat straw. Seeds of *Stylidium affine* had higher germination in response to aqueous smoke solutions made from *Avena fatua* hay relative to aqueous smoke solutions derived from cellulose (Downes *et al*., 2013). However, since it was not the objective of the present study to investigate if aqueous smoke solutions made from prairie hay or wheat straw contain different active compounds; further research is needed in this area to identify the compounds involved.

Priming seeds of *Astragalus cicer* and *Trifolium ambiguum* in aqueous smoke solutions made from prairie hay reduced seedling lengths relative to wheat straw smoke solutions, but seedlings of *Pascopyrum smithii* and *Stipa viridula* were longer with prairie hay smoke solutions. Lengths of seedlings produced after priming seeds in aqueous smoke solutions made from wheat straw were not significantly different for *Pascopyrum smithii* and *Stipa viridula*. Seedling lengths of *Elymus junceus* and *Agropyron dasystachyum* increased after priming seeds in aqueous smoke solutions made from both prairie hay and wheat straw. Both smoke sources affected seedling lengths of *Elymus junceus* and *Agropyron dasystachyum*, but aqueous smoke solutions from wheat straw increased seedling growth of *Astragalus cicer and Trifolium ambiguum.* Priming seeds in high concentrations of aqueous smoke solutions generally depressed seedling growth for all species. These varied responses to priming seeds in different aqueous smoke solutions further strengthen existing evidence (Brown and van Staden, 1994; Jager *et al*., 1996) that responses to smoke are complex and species specific.

5.5 Treating Seeds with Aqueous Smoke Solutions increased Standing Crop, but not Seedling Emergence

Within species, priming seeds did not cause significant differences in seedling emergence among treatments in the field. However, an increasing trend of greater seedling emergence after priming seeds in aqueous smoke solutions was noted for *Elymus angustus*, *Trifolium ambiguum*, *Dactylis glomerata*, *Hesperostipa comata*, *Agropyron dasystachyum*, and *Pascopyrum smithii*. Of the ten species tested in the field, seed priming increased standing crop for *Dactylis glomerata*. Germination of *Dactylis glomerata* also responded positively to priming seeds in aqueous smoke solutions in the laboratory. This similarity in laboratory and field performance indicates *Dactylis glomerata* may be a fire and smoke dependent species consistent with observations of increased germination of *Dactylis glomerata* after fires (Perez-Fernandez and Rodriguez-Echeverria, 2003). Seed priming treatments did not cause any significant changes in the emergence rates of any species in the field, unlike under controlled conditions in the laboratory, but *Agropyron dasystachyum, Astragalus cicer*, *Dactylis glomerata*, *Elymus junceus*, *Hesperostipa comata*, and *Stipa viridula* showed a trend of emerging about 1 to 4 d faster to 50% germination after priming seeds in smoke solutions, relative to priming in distilled water and the non-primed control. Different responses in the field and the laboratory may be attributed to changes in soil temperature and moisture (Roman *et al*., 1999; Shrestha *et al*., 1999), physical constraints of the soil (Vleeshouwers, 1997; Vleeshouwers and Kropff, 2000), seed burial depth (Qi and Redmann, 1992; Vleeshouwers, 1997; Qaderi *et al*., 2002), and water stress (Helms *et al*., 1996).

To my knowledge, this is the first study in Canada to evaluate the effects of aqueous smoke solutions derived from wheat straw or prairie hay on seed germination, seedling lengths, field

emergence, and yield of grasses and legumes. The responses observed in this study, suggests that priming seeds in different concentrations of aqueous solutions of smoke act independently or in a dependent manner with temperature and light to affect seed germination and seedling growth. The compounds in smoke can break seed dormancy and alter the physiological mechanisms and processes that lead to germination. The responses observed in this study may cause changes in recruitment which in turn can alter plant community composition and structure. Priming seeds of *Agropyron dasystachyum, Dactylis glomerata, Elymus angustus, Elymus junceus*, and *Festuca hallii* with aqueous smoke solutions could be a potential way to increase germination and emergence in the field. The use of alternating temperatures in this study may explain why total germination observed for *Lactuca sativa* after priming in aqueous smoke solutions was not in accordance with previous reports in which aqueous smoke solutions improved germination at constant temperatures (Drewes *et al*., 1995). It is not unusual that seeds of *Astragalus cicer* were not responsive to priming with aqueous smoke solutions. This observation may be linked to a previous conclusion that smoke treatment has not been successful in stimulating the germination of seeds that are physically dormant (Razanamandranto *et al*., 2005; Dayamba *et al*., 2008). The present studies involved the use of alternating temperature which generally stimulates germination; however, alternating temperature do not always stimulate germination (Ellern and Tadmor, 1966), and *Astragalus cicer* reportedly responds to 10^{o}C and 20^{o}C constant temperatures (Young *et al*., 1969).

6.0 CONCLUSIONS

The effects of priming seeds in aqueous smoke solutions on total germination was generally not dependent on whether the fuel was wheat straw and prairie hay. Different concentrations of aqueous smoke solutions did, however, affect germination rates and seedling growth. Germination of *Agropyron dasystachyum, Dactylis glomerata, Elymus angustus, Elymus junceus,* and *Festuca hallii* increased after priming of seeds with distilled water, 1/10v/v, 1/100v/v, or 1/1000v/v dilutions of aqueous smoke solutions. Seed priming in aqueous smoke solutions partially substituted a light requirement for germination in *Pascopyrum smithii, Festuca hallii, Hesperostipa comata, Dactylis glomerata, Agropyron dasystachyum, Stipa viridula,* and *Elymus angustus*. Priming seeds of *Astragalus cicer, Trifolium ambiguum, Hesperostipa comata, Stipa viridula,* and *Pascopyrum smithii* with distilled water or aqueous smoke solutions did not promote or inhibit total germination. However, except for *Pascopyrum smithii,* and *Lactuca sativa,* priming seeds of *Astragalus cicer, Trifolium ambiguum, Stipa viridula, Agropyron dasystachyum, Dactylis glomerata, Elymus angustus, Elymus junceus, Festuca hallii,* and *Hesperostipa comata* in distilled water and (or) aqueous smoke solutions resulted in optimum germination (Table 4.21).

Table 4.21 Summary of optimum germination conditions determined from this study for the 11 species studied.

Species	Optimum temperature requirement (°C)	Optimum light requirement	Optimum seed priming treatment (v/v)[1]
Agropyron dasystachyum	25/15	24 h darkness	1/1000
Dactylis glomerata	25/15	24 h darkness	Distilled water, 1/1000
Elymus angustus	10/0	24 h darkness	Distilled water, 1/100
Elymus junceus	25/15	24 h darkness	1/100
Festuca hallii	25/15	24 h darkness	1/10
Hesperostipa comata	25/15	24 h darkness	1/100
Pascopyrum smithii	25/15	24 h darkness	Dry, 1/100
Stipa viridula	10/0	24 h darkness	1/10
Astragalus cicer	25/15	24 h darkness	1/100
Trifolium ambiguum	10/0	24 h darkness	Distilled water, 1/1000
Lactuca sativa	25/15	24 h darkness	Dry, 1/100

[1]Seeds were primed in aqueous smoke solutions prepared from burning wheat straw or prairie hay, and incubated at 10/0^{o}C or 25/15^{o}C in 24 h darkness or in 12 h light/12 h darkness. Three serial dilutions of aqueous smoke solutions (1/1000v/v, 1/100v/v, and 1/10v/v) were made from the stock solution (1/1v/v). Distilled water (0/1v/v) and non-primed, dry seeds were included in the treatments as control.

Priming seeds in aqueous smoke solutions increased the rate of germination *in Trifolium ambiguum, Elymus junceus, Lactuca sativa, Elymus angustus, Stipa viridula, Hesperostipa comata, Pascopyrum smithii, Festuca hallii,* and *Dactylis glomerata*. Germination rates of *Astragalus cicer* and *Agropyron dasystachyum* were not affected after priming seeds in aqueous smoke solutions, but *Astragalus cicer* germinated faster depending on the interaction of incubation temperature and light. Priming seeds in aqueous smoke solutions improved seedling growth of *Elymus angustus* and *Hesperostipa comata,* but it reduced seedling lengths of *Lactuca sativa, Festuca hallii,* and *Trifolium ambiguum.*

Seed priming in aqueous smoke solutions made from wheat straw increased seedling lengths for *Lactuca sativa, Elymus angustus,* and *Hesperostipa comata*. On the other hand, priming seeds in aqueous smoke solutions made from prairie hay increased seedling lengths of *Pascopyrum smithii,* but it reduced seedling lengths for *Astragalus cicer, Trifolium ambiguum,* and *Dactylis glomerata*. Seedling lengths of *Elymus junceus* and *Agropyron dasystachyum*

increased after priming in aqueous smoke solutions of prairie hay or wheat straw. Seedling lengths for *Stipa viridula* only responded to temperature by light interaction. Stimulating germination through smoke treatments could be a useful pre-sowing treatment. Therefore, understanding the responses of different species to such treatments and other environmental factors is crucial.

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8.0 APPENDIX

8.1 Appendix A

Analysis of variance (ANOVA) tables for the effects of aqueoussmoke solutions on total germination of the 11 species studied in the laboratory

Table A1: ANOVA table for the effects of aqueous smoke solutions on total germination of *Lactuca sativa*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	3610.66	≤.0001
dilution	5	329	282.906	≤.0001
type	1	329	1.749	0.1869
temp	1	329	0.019	0.8909
light	1	329	1.151	0.2841
dilution : type	5	329	1.433	0.2119
dilution : temp	5	329	1.728	0.1277
type : temp	1	329	0.04	0.8419
dilution : light	5	329	0.283	0.9223
type : light	1	329	1.588	0.2085
temp : light	1	329	4.932	0.027
dilution : type : temp	5	329	0.579	0.716
dilution : type : light	5	329	0.311	0.9062
dilution : temp : light	5	329	0.696	0.6271
type : temp : light	1	329	0.971	0.325
dilution:type:temp:light	5	329	0.115	0.9889

Table A2: ANOVA table for the effects of aqueous smoke solutions on total germination of *Astragalus cicer*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	107.39138	≤.0001
dilution	5	329	3.30997	0.0062
type	1	329	0.00244	0.9606
temp	1	329	90.65032	≤.0001
light	1	329	1.29121	0.2567
dilution : type	5	329	1.26347	0.2794
dilution : temp	5	329	1.85717	0.1014
type : temp	1	329	0.00045	0.9831
dilution : light	5	329	0.3183	0.9019
type : light	1	329	3.44554	0.0643
temp : light	1	329	37.27157	≤.0001
dilution : type : temp	5	329	0.68835	0.6326
dilution : type : light	5	329	0.69106	0.6305
dilution : temp : light	5	329	0.33719	0.8902
type : temp : light	1	329	2.01251	0.157
dilution:type:temp:light	5	329	0.35623	0.8781

Table A3: ANOVA table for the effects of aqueous smoke solutions on total germination of *Trifolium ambiguum*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	521.9389	≤.0001
dilution	5	329	104.7596	≤.0001
type	1	329	1.1541	0.2835
temp	1	329	3.492	0.0626
light	1	329	1.6202	0.204
dilution:type	5	329	0.4171	0.8368
dilution:temp	5	329	0.1056	0.991
type:temp	1	329	0.0431	0.8356
dilution:light	5	329	0.46	0.8059
type:light	1	329	1.761	0.1854
temp:light	1	329	0.2465	0.6199
dilution:type:temp	5	329	0.1769	0.9711
dilution:type:light	5	329	0.3946	0.8524
dilution:temp:light	5	329	0.3725	0.8674
type:temp:light	1	329	0.8313	0.3626
dilution:type:temp:light	5	329	0.1753	0.9717

Table A4: ANOVA table for the effects of aqueous smoke solutions on total germination of *Elymus angustus*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	410.882	≤.0001
dilution	5	329	31.5466	≤.0001
type	1	329	0.4103	0.5222
temp	1	329	14.1522	0.0002
light	1	329	28.5788	≤.0001
dilution:type	5	329	0.2443	0.9425
dilution:temp	5	329	2.0127	0.0764
type:temp	1	329	0.6089	0.4358
dilution:light	5	329	3.0022	0.0115
type:light	1	329	0.049	0.825
temp:light	1	329	2.546	0.1115
dilution:type:temp	5	329	0.467	0.8008
dilution:type:light	5	329	0.7255	0.6047
dilution:temp:light	5	329	0.6044	0.6966
type:temp:light	1	329	0.0001	0.9907
dilution:type:temp:light	5	329	0.0418	0.999

Table A5: ANOVA table for the effects of aqueous smoke solutions on total germination of *Elymus junceus*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	2637.1073	≤.0001
dilution	5	329	322.0772	≤.0001
type	1	329	0.0413	0.839
temp	1	329	0.3374	0.5617
light	1	329	8.1015	0.0047
dilution:type	5	329	0.2382	0.9454
dilution:temp	5	329	3.3687	0.0056
type:temp	1	329	0.3374	0.5617
dilution:light	5	329	0.9916	0.4228
type:light	1	329	0.0076	0.9306
temp:light	1	329	0.216	0.6425
dilution:type:temp	5	329	0.4845	0.7878
dilution:type:light	5	329	0.5264	0.7563
dilution:temp:light	5	329	0.3688	0.8699
type:temp:light	1	329	0	1
dilution:type:temp:light	5	329	0.0747	0.996

Table A6: ANOVA table for the effects of aqueous smoke solutions on total germination of *Dactylis glomerata*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	294.68857	≤.0001
dilution	5	329	13.29206	≤.0001
type	1	329	0.0149	0.9029
temp	1	329	161.16298	≤.0001
light	1	329	2.5891	0.1086
dilution:type	5	329	0.30845	0.9077
dilution:temp	5	329	9.85258	≤.0001
type:temp	1	329	0.56942	0.451
dilution:light	5	329	2.91324	0.0137
type:light	1	329	0.34591	0.5568
temp:light	1	329	0.44332	0.506
dilution:type:temp	5	329	0.96552	0.439
dilution:type:light	5	329	0.16821	0.9742
dilution:temp:light	5	329	0.60461	0.6964
type:temp:light	1	329	0.15959	0.6898
dilution:type:temp:light	5	329	0.41871	0.8356

Table A7: ANOVA table for the effects of aqueous smoke solutions on total germination of *Hesperostipa comata*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	138.08511	≤.0001
dilution	5	329	36.92032	≤.0001
type	1	329	0.02071	0.8857
temp	1	329	38.29571	≤.0001
light	1	329	126.30314	≤.0001
dilution:type	5	329	0.13081	0.9853
dilution:temp	5	329	2.08461	0.067
type:temp	1	329	0.06179	0.8038
dilution:light	5	329	7.20575	≤.0001
type:light	1	329	0.02071	0.8857
temp:light	1	329	11.66028	0.0007
dilution:type:temp	5	329	0.2787	0.9247
dilution:type:light	5	329	1.99423	0.0791
dilution:temp:light	5	329	0.80755	0.5449
type:temp:light	1	329	0.26035	0.6102
dilution:type:temp:light	5	329	0.24885	0.9402

Table A8: ANOVA table for the effects of aqueous smoke solutions on total germination of *Stipa viridula*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	102.0796	≤.0001
dilution	5	329	9.46841	≤.0001
type	1	329	0.30664	0.5801
temp	1	329	92.18157	≤.0001
light	1	329	313.09006	≤.0001
dilution:type	5	329	0.35279	0.8803
dilution:temp	5	329	2.28589	0.046
type:temp	1	329	0.17426	0.6766
dilution:light	5	329	2.37367	0.039
type:light	1	329	0.02097	0.8849
temp:light	1	329	59.17957	≤.0001
dilution:type:temp	5	329	0.3838	0.8598
dilution:type:light	5	329	0.35907	0.8763
dilution:temp:light	5	329	1.29327	0.2664
type:temp:light	1	329	0.08891	0.7658
dilution:type:temp:light	5	329	0.11242	0.9896

Table A9: ANOVA table for the effects of aqueous smoke solutions on total germination of *Agropyron dasystachyum*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	336.0024	≤.0001
dilution	5	329	164.3211	≤.0001
type	1	329	1.0235	0.3124
temp	1	329	1.4673	0.2266
light	1	329	31.1081	≤.0001
dilution:type	5	329	0.3258	0.8973
dilution:temp	5	329	3.8184	0.0022
type:temp	1	329	2.3434	0.1268
dilution:light	5	329	3.1777	0.0081
type:light	1	329	0.0937	0.7597
temp:light	1	329	3.6743	0.0561
dilution:type:temp	5	329	1.1261	0.3462
dilution:type:light	5	329	0.1567	0.9779
dilution:temp:light	5	329	1.1635	0.3269
type:temp:light	1	329	0.1198	0.7295
dilution:type:temp:light	5	329	0.2355	0.9467

Table A10: ANOVA table for the effects of aqueous smoke solutions on total germination of *Pascopyrum smithii*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	59.50332	≤.0001
dilution	5	329	25.8959	≤.0001
type	1	329	2.97219	0.0856
temp	1	329	175.01351	≤.0001
light	1	329	126.07588	≤.0001
dilution:type	5	329	1.19294	0.3123
dilution:temp	5	329	6.9717	≤.0001
type:temp	1	329	0.60395	0.4376
dilution:light	5	329	4.96004	0.0002
type:light	1	329	0.02881	0.8653
temp:light	1	329	26.01559	≤.0001
dilution:type:temp	5	329	0.19701	0.9635
dilution:type:light	5	329	0.03436	0.9994
dilution:temp:light	5	329	1.68357	0.138
type:temp:light	1	329	0.14754	0.7011
dilution:type:temp:light	5	329	0.21858	0.9545

Table A11: ANOVA table for the effects of aqueous smoke solutions on total germination of *Festuca hallii*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	91.02353	≤.0001
dilution	5	329	54.31603	≤.0001
type	1	329	1.17055	0.2801
temp	1	329	207.2034	≤.0001
light	1	329	66.36788	≤.0001
dilution:type	5	329	0.41392	0.839
dilution:temp	5	329	16.13436	≤.0001
type:temp	1	329	0.75164	0.3866
dilution:light	5	329	3.0089	0.0114
type:light	1	329	0.3204	0.5718
temp:light	1	329	48.20416	≤.0001
dilution:type:temp	5	329	0.18031	0.9699
dilution:type:light	5	329	1.25544	0.283
dilution:temp:light	5	329	2.36278	0.0398
type:temp:light	1	329	1.17055	0.2801
dilution:type:temp:light	5	329	0.75521	0.5827

8.2 Appendix B

Analysis of variance (ANOVA) tables for the effects of aqueoussmoke solutions on the days to 50% germination of the 11 species studied inthe laboratory

Table B1: ANOVA table for the effects of aqueous smoke solutions on the days to 50% germination of *Lactuca sativa*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	35.51545	≤.0001
dilution	5	329	5.10083	0.0002
type	1	329	0.9662	0.3264
temp	1	329	100.37156	≤.0001
light	1	329	0.00572	0.9398
dilution:type	5	329	1.77146	0.1182
dilution:temp	5	329	3.52519	0.0041
type:temp	1	329	0.3659	0.5457
dilution:light	5	329	0.45766	0.8076
type:light	1	329	1.04195	0.3081
temp:light	1	329	0.9662	0.3264
dilution:type:temp	5	329	0.66347	0.6514
dilution:type:light	5	329	0.44251	0.8186
dilution:temp:light	5	329	0.10091	0.9919
type:temp:light	1	329	1.04195	0.3081
dilution:type:temp:light	5	329	1.54706	0.1747

Table B2: ANOVA table for the effects of aqueous smoke solutions on the days to 50% germination of *Astragalus cicer*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	64.915	≤.0001
dilution	5	329	0.4168	0.837
type	1	329	0.0093	0.9232
temp	1	329	439.0321	≤.0001
light	1	329	6.293	0.0126
dilution:type	5	329	1.2333	0.2931
dilution:temp	5	329	0.1484	0.9804
type:temp	1	329	0.0838	0.7724
dilution:light	5	329	0.6862	0.6342
type:light	1	329	0.0209	0.885
temp:light	1	329	5.9744	0.015
dilution:type:temp	5	329	1.3335	0.2496
dilution:type:light	5	329	0.3987	0.8496
dilution:temp:light	5	329	0.4729	0.7964
type:temp:light	1	329	0.0209	0.885
dilution:type:temp:light	5	329	0.4344	0.8245

Table B3: ANOVA table for the effects of aqueous smoke solutions on the days to 50% germination of *Trifolium ambiguum*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	64.99239	≤.0001
dilution	5	329	2.29604	0.0451
type	1	329	0.00386	0.9505
temp	1	329	130.45042	≤.0001
light	1	329	11.681	0.0007
dilution:type	5	329	0.16401	0.9756
dilution:temp	5	329	1.22792	0.2956
type:temp	1	329	0.00015	0.9901
dilution:light	5	329	1.03516	0.3968
type:light	1	329	0.1299	0.7188
temp:light	1	329	12.02328	0.0006
dilution:type:temp	5	329	0.02981	0.9996
dilution:type:light	5	329	0.01647	0.9999
dilution:temp:light	5	329	0.90739	0.4764
type:temp:light	1	329	0.06812	0.7943
dilution:type:temp:light	5	329	0.02141	0.9998

Table B4: ANOVA table for the effects of aqueous smoke solutions on the days to 50% germination of *Elymus angustus*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	169.0018	≤.0001
dilution	5	329	52.3103	≤.0001
type	1	329	1.659	0.1986
temp	1	329	551.9359	≤.0001
light	1	329	0.1253	0.7236
dilution:type	5	329	0.6406	0.6689
dilution:temp	5	329	16.1432	≤.0001
type:temp	1	329	0.699	0.4037
dilution:light	5	329	0.8398	0.5222
type:light	1	329	0.1594	0.69
temp:light	1	329	2.3843	0.1235
dilution:type:temp	5	329	0.8558	0.5112
dilution:type:light	5	329	0.4152	0.8381
dilution:temp:light	5	329	0.9874	0.4254
type:temp:light	1	329	0.1149	0.7349
dilution:type:temp:light	5	329	0.7071	0.6185

Table B5: ANOVA table for the effects of aqueous smoke solutions on the days to 50% germination of *Elymus junceus*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	80.66553	≤.0001
dilution	5	329	5.19414	0.0001
type	1	329	0.43568	0.5097
temp	1	329	190.43474	≤.0001
light	1	329	0.58907	0.4433
dilution:type	5	329	0.49901	0.777
dilution:temp	5	329	0.93983	0.4552
type:temp	1	329	0.39609	0.5296
dilution:light	5	329	0.923	0.4661
type:light	1	329	0.04618	0.83
temp:light	1	329	0.79265	0.3739
dilution:type:temp	5	329	0.48205	0.7896
dilution:type:light	5	329	0.05636	0.998
dilution:temp:light	5	329	0.69397	0.6283
type:temp:light	1	329	0.54289	0.4618
dilution:type:temp:light	5	329	0.37323	0.8669

Table B6: ANOVA table for the effects of aqueous smoke solutions on the days to 50% germination of *Dactylis glomerata*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	158.3402	≤.0001
dilution	5	329	4.2741	0.0009
type	1	329	0.0056	0.9405
temp	1	329	375.045	≤.0001
light	1	329	7.3849	0.0069
dilution:type	5	329	0.5067	0.7712
dilution:temp	5	329	2.0522	0.0711
type:temp	1	329	0.002	0.9643
dilution:light	5	329	2.2937	0.0453
type:light	1	329	0.6029	0.4381
temp:light	1	329	13.0567	0.0003
dilution:type:temp	5	329	0.3113	0.9061
dilution:type:light	5	329	0.4386	0.8215
dilution:temp:light	5	329	3.2619	0.0069
type:temp:light	1	329	0.0223	0.8814
dilution:type:temp:light	5	329	0.9664	0.4384

Table B7: ANOVA table for the effects of aqueous smoke solutions on the days to 50% germination of *Hesperostipa comata*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	50.38846	≤.0001
dilution	5	329	3.90586	0.0019
type	1	329	0.50063	0.4797
temp	1	329	169.03462	≤.0001
light	1	329	2.50327	0.1146
dilution:type	5	329	0.90468	0.4781
dilution:temp	5	329	4.31508	0.0008
type:temp	1	329	0.19556	0.6586
dilution:light	5	329	0.39846	0.8498
type:light	1	329	0.66529	0.4153
temp:light	1	329	38.5736	≤.0001
dilution:type:temp	5	329	0.26156	0.9338
dilution:type:light	5	329	1.04071	0.3936
dilution:temp:light	5	329	0.70759	0.6181
type:temp:light	1	329	2.59743	0.108
dilution:type:temp:light	5	329	1.44626	0.2072

Table B8: ANOVA table for the effects of aqueous smoke solutions on the days to 50% germination of *Stipa viridula*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	84.462	≤.0001
dilution	5	329	0.62328	0.6821
type	1	329	0.04774	0.8272
temp	1	329	207.62114	≤.0001
light	1	329	2.68512	0.1022
dilution:type	5	329	0.19359	0.9649
dilution:temp	5	329	3.97862	0.0016
type:temp	1	329	0.19094	0.6624
dilution:light	5	329	0.59094	0.7069
type:light	1	329	0.47366	0.4918
temp:light	1	329	15.46632	0.0001
dilution:type:temp	5	329	0.2924	0.917
dilution:type:light	5	329	0.0517	0.9983
dilution:temp:light	5	329	1.04204	0.3928
type:temp:light	1	329	0.38773	0.5339
dilution:type:temp:light	5	329	0.19089	0.9659

Table B9: ANOVA table for the effects of aqueous smoke solutions on the days to 50% germination of *Agropyron dasystachyum*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	65.44213	≤.0001
dilution	5	329	9.28806	≤.0001
type	1	329	0.66574	0.4151
temp	1	329	183.15799	≤.0001
light	1	329	1.26813	0.2609
dilution:type	5	329	2.23305	0.0508
dilution:temp	5	329	1.55114	0.1735
type:temp	1	329	0.87854	0.3493
dilution:light	5	329	1.19523	0.3112
type:light	1	329	2.14117	0.1443
temp:light	1	329	0.24231	0.6229
dilution:type:temp	5	329	2.01501	0.0761
dilution:type:light	5	329	1.65423	0.1452
dilution:temp:light	5	329	1.47286	0.1982
type:temp:light	1	329	1.52277	0.2181
dilution:type:temp:light	5	329	1.38723	0.2286

Table B10: ANOVA table for the effects of aqueous smoke solutions on the days to 50% germination of *Pascopyrum smithii*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	243.26953	≤.0001
dilution	5	329	4.40745	0.0007
type	1	329	0.0048	0.9448
temp	1	329	58.20165	≤.0001
light	1	329	17.93552	≤.0001
dilution:type	5	329	0.71821	0.6101
dilution:temp	5	329	4.83238	0.0003
type:temp	1	329	0.07138	0.7895
dilution:light	5	329	0.57869	0.7163
type:light	1	329	0.0564	0.8124
temp:light	1	329	32.93688	≤.0001
dilution:type:temp	5	329	0.29226	0.9171
dilution:type:light	5	329	0.19151	0.9657
dilution:temp:light	5	329	0.50114	0.7754
type:temp:light	1	329	0.0141	0.9056
dilution:type:temp:light	5	329	0.31159	0.9059

Table B11: ANOVA table for the effects of aqueous smoke solutions on the days to 50% germination of *Festuca hallii*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	329	91.94562	≤.0001
dilution	5	329	34.37151	≤.0001
type	1	329	0.31559	0.5747
temp	1	329	263.25586	≤.0001
light	1	329	4.60641	0.0326
dilution:type	5	329	0.85188	0.5138
dilution:temp	5	329	8.1931	≤.0001
type:temp	1	329	0.03709	0.8474
dilution:light	5	329	0.35227	0.8807
type:light	1	329	0.34019	0.5601
temp:light	1	329	1.69195	0.1943
dilution:type:temp	5	329	1.49926	0.1895
dilution:type:light	5	329	0.84152	0.521
dilution:temp:light	5	329	0.3832	0.8602
type:temp:light	1	329	1.31185	0.2529
dilution:type:temp:light	5	329	0.39045	0.8553

8.3 Appendix C

Analysis of variance (ANOVA) tables for the effects of aqueoussmoke solutions on the seedlings lengths of the 11 species studied in thelaboratory

Table C1: ANOVA table for the effects of aqueous smoke solutions on the seedlings lengths of *Lactuca sativa*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	141	9.594422	0.0024
dilution	5	141	3.732084	0.0033
type	1	141	7.269913	0.0079
temp	1	141	3.191617	0.0762
light	1	141	0.843952	0.3598
dilution:type	5	141	2.138147	0.0643
dilution:temp	5	141	2.132216	0.065
type:temp	1	141	0.516625	0.4735
dilution:light	5	141	0.691266	0.6309
type:light	1	141	0.497568	0.4817
temp:light	1	141	0.83513	0.3624
dilution:type:temp	5	141	0.361196	0.8743
dilution:type:light	5	141	0.429244	0.8277
dilution:temp:light	5	141	0.501844	0.7745
type:temp:light	1	141	0.000857	0.9767
dilution:type:temp:light	5	141	0.132305	0.9847

Table C2: ANOVA table for the effects of aqueous smoke solutions on the seedlings lengths of *Astragalus cicer*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	141	12.123036	0.0007
dilution	5	141	3.179443	0.0095
type	1	141	3.04222	0.0833
temp	1	141	0.040354	0.8411
light	1	141	0.400795	0.5277
dilution:type	5	141	2.988674	0.0135
dilution:temp	5	141	1.372909	0.238
type:temp	1	141	0.258652	0.6118
dilution:light	5	141	0.092955	0.9932
type:light	1	141	0.205814	0.6508
temp:light	1	141	11.303647	0.001
dilution:type:temp	5	141	0.665485	0.6502
dilution:type:light	5	141	0.53073	0.7527
dilution:temp:light	5	141	1.435565	0.2151
type:temp:light	1	141	0.001082	0.9738
dilution:type:temp:light	5	141	1.260967	0.2842

Table C3: ANOVA table for the effects of aqueous smoke solutions on the seedlings lengths of *Trifolium ambiguum*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	141	14.940174	0.0002
dilution	5	141	2.994778	0.0134
type	1	141	5.176119	0.0244
temp	1	141	9.21444	0.0029
light	1	141	0.000527	0.9817
dilution:type	5	141	2.710835	0.0227
dilution:temp	5	141	0.749151	0.588
type:temp	1	141	1.199665	0.2753
dilution:light	5	141	1.11748	0.3539
type:light	1	141	0.185142	0.6676
temp:light	1	141	2.071894	0.1523
dilution:type:temp	5	141	0.861513	0.5087
dilution:type:light	5	141	0.391662	0.8539
dilution:temp:light	5	141	2.466753	0.0355
type:temp:light	1	141	0.905042	0.3431
dilution:type:temp:light	5	141	0.701189	0.6234

Table C4: ANOVA table for the effects of aqueous smoke solutions on the seedlings lengths of *Elymus angustus*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	141	23.529601	≤.0001
dilution	5	141	7.738749	≤.0001
type	1	141	8.745651	0.0036
temp	1	141	3.580973	0.0605
light	1	141	0.355051	0.5522
dilution:type	5	141	1.520685	0.1871
dilution:temp	5	141	1.53136	0.1838
type:temp	1	141	0.961629	0.3285
dilution:light	5	141	0.910966	0.4759
type:light	1	141	0.730775	0.3941
temp:light	1	141	23.224527	≤.0001
dilution:type:temp	5	141	0.141626	0.9822
dilution:type:light	5	141	0.179822	0.9698
dilution:temp:light	5	141	0.736067	0.5976
type:temp:light	1	141	1.922156	0.1678
dilution:type:temp:light	5	141	0.400089	0.8481

Table C5: ANOVA table for the effects of aqueous smoke solutions on the seedlings lengths of *Elymus junceus*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	141	31.82035	≤.0001
dilution	5	141	10.9327	≤.0001
type	1	141	8.94727	0.0033
temp	1	141	0.01666	0.8975
light	1	141	0.22493	0.636
dilution:type	5	141	3.64305	0.0039
dilution:temp	5	141	0.73736	0.5967
type:temp	1	141	0.77561	0.38
dilution:light	5	141	0.55835	0.7317
type:light	1	141	2.26549	0.1345
temp:light	1	141	7.70405	0.0063
dilution:type:temp	5	141	0.25486	0.9368
dilution:type:light	5	141	0.73813	0.5961
dilution:temp:light	5	141	0.39741	0.85
type:temp:light	1	141	0.11506	0.735
dilution:type:temp:light	5	141	0.16775	0.9741

Table C6: ANOVA table for the effects of aqueous smoke solutions on the seedlings lengths of *Dactylis glomerata*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	141	31.366711	≤.0001
dilution	5	141	6.186317	≤.0001
type	1	141	14.084327	0.0003
temp	1	141	0.161823	0.6881
light	1	141	0.450451	0.5032
dilution:type	5	141	3.079528	0.0114
dilution:temp	5	141	0.748027	0.5888
type:temp	1	141	0.100402	0.7518
dilution:light	5	141	1.293493	0.2701
type:light	1	141	2.632436	0.1069
temp:light	1	141	3.459415	0.065
dilution:type:temp	5	141	0.05154	0.9983
dilution:type:light	5	141	1.112287	0.3566
dilution:temp:light	5	141	0.884394	0.4934
type:temp:light	1	141	0.980581	0.3238
dilution:type:temp:light	5	141	0.206608	0.9593

Table C7: ANOVA table for the effects of aqueous smoke solutions on the seedlings lengths of *Hesperostipa comata*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	141	11.112585	0.0011
dilution	5	141	7.68175	≤.0001
type	1	141	6.306984	0.0132
temp	1	141	13.50334	0.0003
light	1	141	5.853762	0.0168
dilution:type	5	141	1.956031	0.0889
dilution:temp	5	141	1.48309	0.199
type:temp	1	141	0.572002	0.4507
dilution:light	5	141	1.588946	0.167
type:light	1	141	0.800467	0.3725
temp:light	1	141	7.038991	0.0089
dilution:type:temp	5	141	0.169799	0.9734
dilution:type:light	5	141	0.160977	0.9763
dilution:temp:light	5	141	0.179709	0.9698
type:temp:light	1	141	3.147328	0.0782
dilution:type:temp:light	5	141	0.572634	0.7209

Table C8: ANOVA table for the effects of aqueous smoke solutions on the seedlings lengths of *Stipa viridula*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	141	12.086435	0.0007
dilution	5	141	4.918719	0.0004
type	1	141	6.149844	0.0143
temp	1	141	0.205685	0.6509
light	1	141	3.92631	0.0495
dilution:type	5	141	2.37303	0.0421
dilution:temp	5	141	0.977575	0.4337
type:temp	1	141	0.525775	0.4696
dilution:light	5	141	0.739169	0.5953
type:light	1	141	0.605464	0.4378
temp:light	1	141	17.187033	0.0001
dilution:type:temp	5	141	0.108442	0.9903
dilution:type:light	5	141	0.015267	0.9999
dilution:temp:light	5	141	0.362333	0.8736
type:temp:light	1	141	0.403456	0.5263
dilution:type:temp:light	5	141	0.745072	0.591

Table C9: ANOVA table for the effects of aqueous smoke solutions on the seedlings lengths of *Agropyron dasystachyum*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	141	29.312996	≤.0001
dilution	5	141	6.224565	≤.0001
type	1	141	17.909677	≤.0001
temp	1	141	0.220098	0.6397
light	1	141	0.208402	0.6487
dilution:type	5	141	3.036379	0.0124
dilution:temp	5	141	0.377647	0.8634
type:temp	1	141	1.720235	0.1918
dilution:light	5	141	0.601851	0.6986
type:light	1	141	0.04844	0.8261
temp:light	1	141	7.63324	0.0065
dilution:type:temp	5	141	0.226633	0.9504
dilution:type:light	5	141	0.156482	0.9778
dilution:temp:light	5	141	0.288227	0.9189
type:temp:light	1	141	1.556043	0.2143
dilution:type:temp:light	5	141	0.469794	0.7983

Table C10: ANOVA table for the effects of aqueous smoke solutions on the seedlings lengths of *Pascopyrum smithii*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	141	34.58293	≤.0001
dilution	5	141	3.65728	0.0038
type	1	141	6.09369	0.0148
temp	1	141	11.73304	0.0008
light	1	141	12.9759	0.0004
dilution:type	5	141	2.22725	0.0548
dilution:temp	5	141	0.93608	0.4597
type:temp	1	141	0.86306	0.3545
dilution:light	5	141	0.94661	0.453
type:light	1	141	1.19613	0.276
temp:light	1	141	0.96747	0.327
dilution:type:temp	5	141	0.57193	0.7214
dilution:type:light	5	141	0.35439	0.8787
dilution:temp:light	5	141	0.17417	0.9718
type:temp:light	1	141	0.46393	0.4969
dilution:type:temp:light	5	141	0.08945	0.9938

Table C11: ANOVA table for the effects of aqueous smoke solutions on the seedlings lengths of *Festuca hallii*

Source of variation	numDF	denDF	F-value	P-value
(Intercept)	1	141	41.08956	≤.0001
dilution	5	141	5.41137	0.0001
type	1	141	2.60989	0.1084
temp	1	141	8.45207	0.0042
light	1	141	0.11891	0.7307
dilution:type	5	141	1.01714	0.4099
dilution:temp	5	141	2.32189	0.0462
type:temp	1	141	1.2233	0.2706
dilution:light	5	141	0.61294	0.6901
type:light	1	141	0.06317	0.8019
temp:light	1	141	10.50304	0.0015
dilution:type:temp	5	141	0.6244	0.6814
dilution:type:light	5	141	0.14073	0.9825
dilution:temp:light	5	141	1.10946	0.3581
type:temp:light	1	141	0.00014	0.9907
dilution:type:temp:light	5	141	0.38819	0.8563

8.4 Appendix D
Analysis of variance (ANOVA) tables for the effects of aqueous smoke solutions on standing yield of the 10 species studied in the field

Astralagus cicer

Source of variation	Df	Sum Sq	Mean Sq	F value	P value
Replicate	3	3277.8	1092.61	2.0337	0.1797
Smoke treatments	3	1497.9	499.31	0.9294	0.4655
Residuals	9	4835.3	537.25		

Elymus angustus

Source of variation	Df	Sum Sq	Mean Sq	F value	P value
Replicate	3	737.29	245.762	2.5694	0.1192
Smoke treatments	3	149.16	49.721	0.5198	0.6792
Residuals	9	860.84	95.649		

Festuca hallii

Source of variation	Df	Sum Sq	Mean Sq	F value	P value
Replicate	3	0.14188	0.047292	1.7328	0.2296
Smoke treatments	3	0.16187	0.053958	1.9771	0.1880
Residuals	9	0.24563	0.027292		

Stipa viridula

Source of variation	Df	Sum Sq	Mean Sq	F value	P value
Replicate	3	1423.71	474.57	6.9431	0.01021
Smoke treatments	3	129.17	43.06	0.6299	0.61383
Residuals	9	615.16	68.35		

Trifolium ambiguum

Source of variation	Df	Sum Sq	Mean Sq	F value	P value
Replicate	3	1034.24	344.75	6.2198	0.01416
Smoke treatments	3	183.58	61.19	1.1040	0.39691
Residuals	9	498.85	55.43		

Dactylis glomerata

Source of variation	Df	Sum Sq	Mean Sq	F value	P value
Replicate	3	1502.7	500.89	4.1792	0.041318
Smoke treatments	3	4330.7	1443.55	12.0445	0.001671
Residuals	9	1078.7	119.85		

Hesperostipa comata

Source of variation	Df	Sum Sq	Mean Sq	F value	P value
Replicate	3	56.492	18.8306	3.1781	0.07767
Smoke treatments	3	1.142	0.3806	0.0642	0.97746
Residuals	9	53.326	5.9251		

Agropyron dasystachyum

Source of variation	Df	Sum Sq	Mean Sq	F value	P value
Replicate	3	8382.9	2794.31	11.9962	0.001694
Smoke treatments	3	546.7	182.24	0.7824	0.533097
Residuals	9	2096.4	232.93		

Elymus junceus

Source of variation	Df	Sum Sq	Mean Sq	F value	P value
Replicate	3	229.97	76.656	1.5400	0.2702
Smoke treatments	3	36.33	12.111	0.2433	0.8640
Residuals	9	447.98	49.775		

Pascopyrun smithii

Source of variation	Df	Sum Sq	Mean Sq	F value	P value
Replicate	3	1495.91	498.64	3.8862	0.04928
Smoke treatments	3	465.91	155.30	1.2104	0.36069
Residuals	9	1154.78	128.31		