Research Article

Smoke Water and Heat Influence Emergence of Shortgrass Prairie Species

Robert D. Cox*, Yi-Fang Chou, and David B. Wester[1]

Department of Natural Resources Management, Texas Tech University,
2903 15th Street, Lubbock, Texas 79409, USA

[1] Current address: Department of Animal, Rangeland and Wildlife Sciences and
Caesar Kleberg Wildlife Research Institute, Texas A&M University,
MSC 228, Kingsville, Texas 78363, USA

* Corresponding author: Tel.: +1-806-742-2841; e-mail: robert.cox@ttu.edu

ABSTRACT

Exposure to smoke can influence the germination of seeds in many fire-prone ecosystems, but this effect is not well studied in grasslands. Smoke treatments such as smoke water could be useful as management and restoration tools if the response of target species in natural settings is well understood. We tested eight species native to the southern High Plains region in Texas, USA, that were already known to respond to smoke water in the laboratory, for their responses in a less controlled glasshouse environment. We exposed seeds to smoke water, heat, or a combination of the two, sowed them into greenhouse flats, and observed and recorded emergence. Emergence of nearly all species was influenced by smoke water, with most species experiencing either lower emergence or longer times for emergence when exposed to high-concentration smoke water. Smoke water exposure enhanced emergence of broom snakeweed (*Gutierrezia sarothrae* [DC.] A. Gray) seeds, with more than twice as many treated seeds emerging than untreated seeds (germination of control seeds = 26% ± 4.39% SE; germination of treated seeds = 69% ± 4.62%

RESUMEN

La exposición al humo puede influenciar la germinación de semillas en muchos ecosistemas propensos al fuego, aunque este efecto no ha sido bien estudiado en pastizales. Los tratamientos con humo pueden ser exitosos como herramientas de manejo o de restauración, si la respuesta de las especies clave en ambientes naturales está bien entendida. Nosotros probamos ocho especies nativas de la región de las planicies altas de Texas, EEUU, que era conocido respondían al humo y posterior humidificación en laboratorio por su respuesta en ambientes poco controlados en invernaderos. Nosotros expusimos semillas a humo, calor, y a una combinación de ambos, y luego fueron sembradas en bandejas planas en invernadero, observando y registrando su emergencia. La emergencia de casi todas las especies fue influenciada por el humo, con la mayoría de las especies mostrando una baja emergencia o mucho tiempo para emerger cuando estuvieron expuestas a una alta concentración de humo. El humo aumentó la emergencia de semillas de hierba de la serpiente o hierba de San Nicolás (*Gutierrezia sarothrae* [DC.] A. Gray) a más del doble en semillas tratadas con humo que en aquellas sin tratar (germinación de semillas en el control = 26% ±

SE). Because many species displayed different results in the glasshouse as compared to the laboratory, smoke treatments should be tested in the field before being used on a larger scale. Doing so will allow a better understanding of how target species might respond to smoke treatments with more realistic soils, fluctuating temperatures, and other complications encountered in the field.

4.39% ES; germinación de semillas tratadas = 69% ± 4.62% ES). Dado que distintas especies pueden mostrar dispares resultados en el invernáculo cuando se las compara con el laboratorio, el tratamiento con humo debe probarse a campo antes de ser usado a gran escala. El hacer esto permitirá conocer mejor cómo las especies clave podrían responder en suelos reales, con temperaturas fluctuantes, y otras complicaciones que se encuentran en condiciones de campo.

Keywords: greenhouse, liquid smoke, smoke-stimulated germination, southern High Plains

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INTRODUCTION

The effect of smoke on seed germination has received attention in several ecosystems around the world (de Lange and Boucher 1990, Egerton-Warburton 1998, Keeley and Fotheringham 2000, Read *et al.* 2000, van Staden *et al.* 2004), and is especially well studied in fire-prone, mediterranean-climate ecosystems such as those in Australia, South Africa, and California (see Keeley and Fotheringham 2000, Jefferson *et al*. 2014 for reviews). This effect has received much less attention in other fire-prone ecosystems such as grasslands. Nevertheless, several species native to the southern High Plains in Texas, USA, recently have been shown to be responsive to smoke treatments, including smoke water and aerosol smoke (Jefferson *et al*. 2008, Chou *et al.* 2012*,* Schwilk and Zavala 2012). Because the response of these species was observed in the laboratory, their response in less controlled conditions, such as when sown in soil, is unknown. Fire has historically played an important role in the Great Plains grasslands, and is still used as a management treatment, so fire cues such as smoke and heat might be useful as on-the-ground restoration treatments. Therefore, understanding how seeds of grassland species respond to smoke in more natural settings is important.

In regions where rainfall is limited or is concentrated into short periods of time, such as occurs regularly in the southern High Plains, it is important that seeds germinate quickly when soil moisture is available so that they can establish successfully (Read *et al.* 2000). Smoke and heat treatments have the potential to increase germination of desirable species by reducing the time required for germination (Read and Bellairs 1999). In addition, smoke and heat can also increase both the density and richness of seedlings germinating from the seedbank (Read *et al.* 2000).

When applying smoke treatments, two methods are used most often: aerosol and liquid treatments. Aerosol smoke (also: dry smoke, plant-derived smoke, smoke fumigation) can be generated in laboratory settings by burning dry or fresh vegetation (Landis 2000). The active compounds that promote seed germination (karrikins; Chiwocha *et al.* 2009) exist in all plant species and are effective in responsive species, regardless of fuel origin (Jäger *et al.* 1996, Adkins and Peters 2001), although the effect might be slightly different depending on the type of plant fuel used to generate the smoke (Razanamandranto *et al.*

2005). Other active compounds also exist, and not all species are responsive to every promotive compound (Ghebrehiwot *et al.* 2013, Downes *et al.* 2014). The second method of smoke application is the use of smoke water (also: liquid smoke, aqueous smoke; Strydom *et al*. 1996, Read and Bellairs 1999, Clarke *et al.* 2000, Bhatia *et al.* 2005, Abella 2009). Because the active compound in aerosol smoke is water soluble (Flematti *et al.* 2004), liquid smoke can be created as needed by bubbling plant-derived smoke into distilled water (Landis 2000). However, commercial smoke water, advertised especially for germination enhancement, is also available for purchase and might be more effective than aerosol smoke (Dixon and Roche 1995). From the standpoint of evaluating the effect of smoke on seeds, using smoke water has the advantage of not requiring real-time combustion, and can potentially affect larger quantities of seeds at a time (Brown and van Staden 1997).

Heat is another important fire-related cue that can influence seed germination. Exposing seeds to temperatures of 50 °C to 150 °C for 1 min to 60 min has promoted germination of plant species from many families worldwide (Enright and Kintrup 2001, Buhk and Hensen 2006, Thomas *et al.* 2007, Bolin 2009, Tsuyuzaki and Miyoshi 2009). The temperature of the heat treatment does not necessarily correspond to the heat measured during actual wildfires; temperatures of 80 °C to 100 °C are effective for many species (Auld and Ooi 2009), yet typical wildfire temperatures commonly reach higher than 100 °C (Wright and Bailey 1982).

To date, few studies have been done to test the effect of smoke water and heat on species native to the southern High Plains, although fire is an important ecological influence in this ecosystem and such treatments could be used as management and restoration tools. Thus far, studies that have investigated this effect for the region have done so in the laboratory (Chou *et al.* 2012, Schwilk and Zavala 2012).

We selected several species of plants native to the southern High Plains region of Texas that were already known to respond to smoke water in the laboratory (Chou *et al.* 2012), and tested seeds of these species in the glasshouse to determine their germination response to both smoke water and heat, with the objective of understanding their potential field responses to smoke treatments at a broader scale.

METHODS

In a previous laboratory study (Chou *et al.* 2012), we tested seeds of 10 species native to the southern High Plains region for germination response to smoke water, heat, and smoke water and heat in combination. To further characterize the ability of those species to respond to smoke water and heat in more natural conditions, we subsequently tested responsive species (the forbs *Astragalus crassicarpus* Nutt., *Coreopsis tinctoria* Nutt., *Monarda citriodora* Cerv. ex Lag., *Salvia azurea* Michx. ex Lam., *Salvia reflexa* Hornem., *Solanum elaeagnifolium* Cav.; the grass *Digitaria ciliaris* [Retz.] Koeler; and the shrub *Gutierrezia sarothrae* [DC.] A. Gray) in the glasshouse, and report results here.

For those species that responded to the interaction of smoke water and heat in the previous laboratory study, we applied both treatments and their combinations. For those that responded to only smoke water or heat, we applied all levels of the effective treatment only (Table 1). As described in Chou *et al.* (2012), we exposed seeds to four concentrations of commercial smoke water, diluted in distilled water (control of 0, 1:100, 1:10, and 1:5), and three levels of heat (no heat, 50 °C, and 80 °C). The treatments were organized as a completely randomized factorial experiment, replicated four times (in time), with 25 seeds for each replicate.

For smoke water treatment, we soaked seeds of each species in their respective smoke

Table 1. Species and treatments applied during glasshouse emergence experiments for species native to the southern High Plains region, Texas, USA. Nomenclature follows USDA NRCS (2012).

Family	Species	Treatments
Asteraceae	*Coreopsis tinctoria*	Smoke
	Gutierrezia sarothrae	Smoke
Fabaceae	*Astragalus crassicarpus*	Smoke × heat
Lamiaceae	*Monarda citriodora*	Smoke
	Salvia azurea	Smoke × heat
	Salvia reflexa	Smoke × heat
Poaceae	*Digitaria ciliaris*	Smoke
Solanaceae	*Solanum elaeagnifolium*	Smoke × heat

water-distilled water solution separately for 20 hr at room temperature, using the commercially available aqueous smoke solution Regen 2000® (Grayson Co., Bayswater, Australia), which recommends dilution at 1:10. To apply the heat treatment, seeds were placed in a preheated oven for 5 min at the prescribed temperature, and then cooled to room temperature. Seeds in the unheated control were not heated in the oven. When both smoke water and heat were applied, seeds were first treated with heat and then with smoke water after cooling.

After treatment, we sowed seeds of each species on top of sterile potting soil and covered them with a 1 mm layer of soil in a 12 cm × 12 cm paperboard glasshouse tray. Trays with seeds were randomly and evenly arranged on only one bench in the glasshouse. We applied distilled water to moisten the soil. We checked trays daily for emergence and once we observed a seedling emergence, we removed and recorded it. The experiment ran until emergence ceased (up to 45 days, depending on the species). During the experiment, glasshouse temperatures ranged from 24 °C to 30 °C.

We calculated emergence capacity (EC, also emergence, %) and mean emergence time (MET, days) for each species and treatment as:

$$EC = 100\frac{\sum n_i}{N} \text{ , and} \quad (1)$$

$$MET = \frac{\sum t_i n_i}{\sum n_i} \text{ ,} \quad (2)$$

where n_i is the number of seeds germinating at each i day, N is total number of seeds sown, and t_i is the number of days from the date of sowing until all emergence ceased (Bewley and Black 1994).

We analyzed EC with Proc Glimmix in SAS (SAS Institute, Cary, North Carolina, USA) using a logit link function to model a binomial response variable. When we identified a significant difference between treatments, we conducted pair-wise comparisons with the *t*-test at the 0.05 level of significance. Significant differences in MET among smoke water, heat, and their interactions were tested with either a two-way ANOVA or one-way ANOVA, depending on the number of factors tested (smoke water or heat or both). We used Levene's test (Levene 1960) and the Shapiro-Wilk test (Shapiro and Wilk 1965) to test homogeneity of variances across treatments and normality of experimental errors within each treatment, respectively, for MET. We also used the Brown and Forsythe (1974) test when variances were heterogeneous.

RESULTS

Of the eight species tested, only *Monarda citriodora* did not respond to smoke water

(data not shown). Smoke water affected other species positively or negatively, depending on species, although germination of most species was inhibited. When treated with high-concentration (1:5) smoke water, *Coreopsis tinctoria* displayed approximately 14% (± 3.47% SE) emergence, compared to almost 80% (± 4.14% SE) emergence with no smoke water (Figure 1a). High-concentration (1:5) smoke water similarly suppressed the emergence capacity in *Digitaria ciliaris* (32% ± 4.66% SE emergence compared to 50% ± 5.00% SE emergence in untreated controls; (Figure 1b). *Gutierrezia sarothrae,* on the other hand, displayed a significant effect of promotion of EC as smoke water concentration increased, so that treatment by 1:100, 1:10, and 1:5 concentrations of smoke water increased the EC from the 26% (± 4.39% SE) of the control to 45% (± 4.98% SE), 59% (± 4.92% SE) , and 69% (± 4.62% SE), respectively (Figure 1c). Emergence of *Salvia azurea,* however, was inhibited by higher smoke water concentrations, with the highest concentration treatment (1:5) essentially eliminating emergence of this species (Figure 1d).

Smoke water treatment also prolonged MET of most species. Moderate (1:10) concentration smoke water prolonged the MET of *Astragalus crassicarpus* (9 days ± 0.26 days SE, compared to 7 days ± 0.26 days SE for the control; Figure 2a). When treated with the 1:5 concentration of smoke water, *Coreopsis tinctoria* also emerged at a slower rate (11 days ± 0.94 days SE) than the control (7 days ± 0.21 days SE), but the 1:100 concentration of smoke water actually shortened the MET of this species to 5 days (± 0.24 days SE; Figure 2b). Effects on the MET of *Digitaria ciliaris* were only significantly different between the 1:5 and the 1:10 and 1:100 treatments; no treatment differed from the control (Figure 2c). Similar to the results for *Coreopsis tinctoria*, higher smoke water concentration pro-

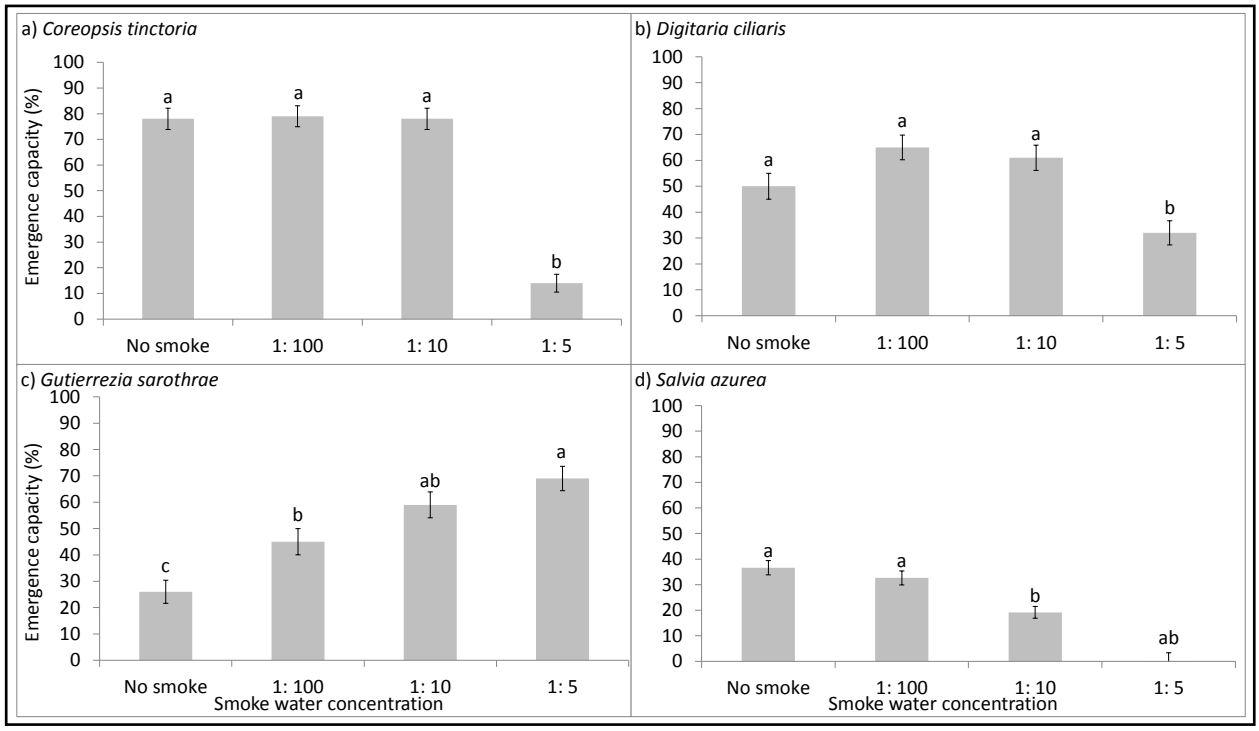

Figure 1. Main effect of smoke water on the emergence capacity (%) of a) *Digitaria ciliaris,* b) *Coreopsis tinctoria,* c) *Gutierrezia sarothrae,* and d) *Salvia azurea* (mean ± SE) in the glasshouse. Means followed by the same letters are not significantly different (0.05 level).

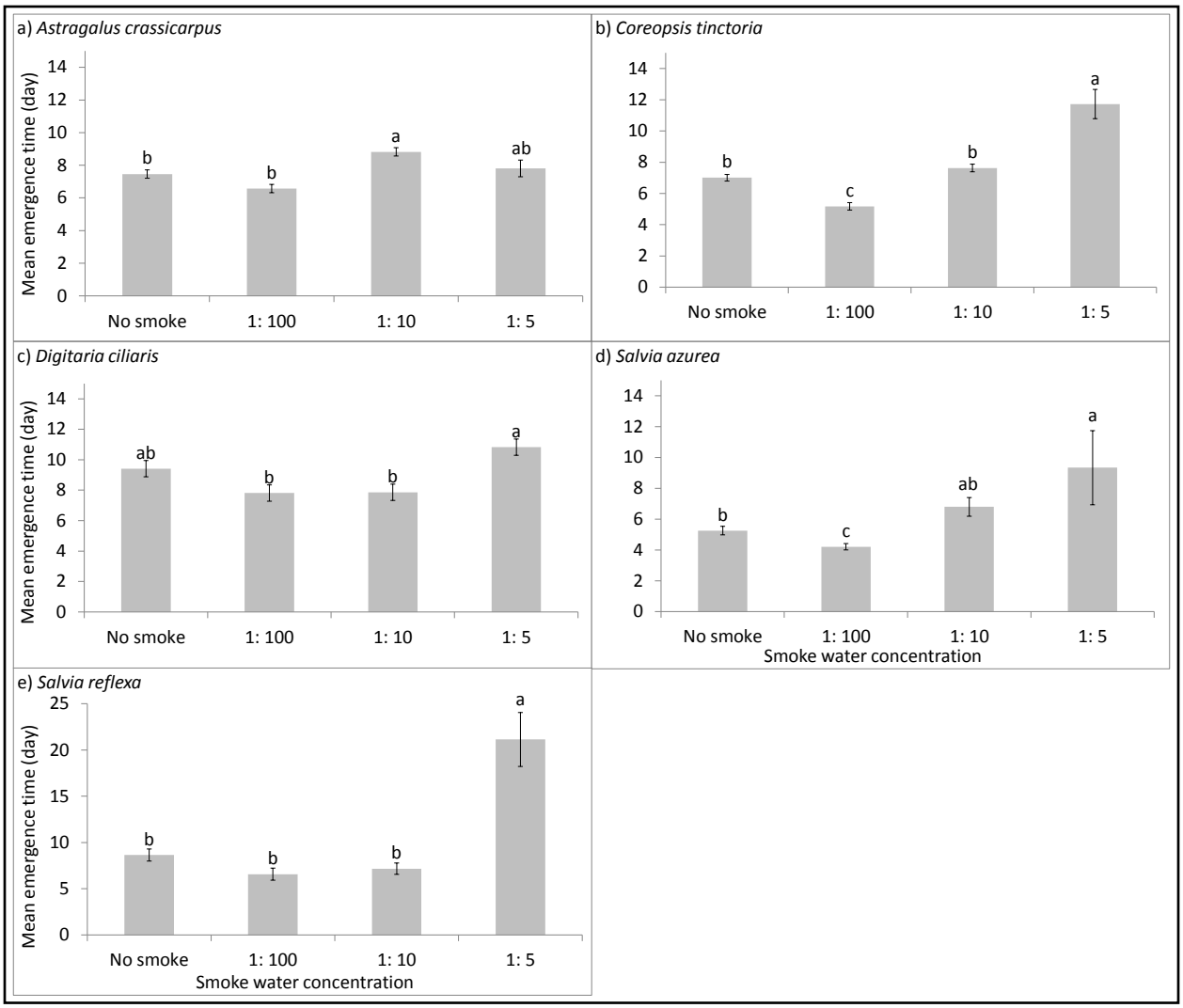

Figure 2. Main effect of smoke water on the mean emergence time (days) of a) *Astragalus crassicarpus,* b) *Coreopsis tinctoria,* c) *Digitaria ciliaris,* d) *Salvia azurea,* and e) *Salvia reflexa* (Mean ± SE) in the glasshouse. Means followed by the same letters are not significantly different (0.05 level).

longed MET of *Salvia azurea* by 9 days (± 2.40 days SE) compared to the control (5 days ± 0.28 days SE), but low-concentration (1:100) smoke water shortened emergence time to 4 days (± 0.21 days SE; Figure 2d). Finally, high-concentration smoke water also prolonged the MET of *Salvia reflexa* (21 days ± 2.91 days SE compared to approximately 9 days ± 0.65 days SE; Figure 2e).

Heat was not generally effective as a single treatment in this study, although the MET of *Salvia reflexa* was prolonged by moderate (50 °C) and high (80 °C) heat from 6.8 days (± 1.10 days SE) to 10.6 days (± 1.49 days SE) and 10.7 days (± 1.89 days SE), respectively (data not shown). However, smoke water and heat did interact to influence the EC of three species. Medium (1:10) and high (1:5) smoke water concentrations inhibited emergence of *Astragalus crassicarpus* at all heat levels, although the magnitude of the effect varied by heat level (Figure 3a). High-concentration (1:5) smoke water suppressed the EC of *Salvia reflexa* across all levels of heat, while low (1:100) and moderate (1:10) concentrations of smoke water helped to compensate for the de-

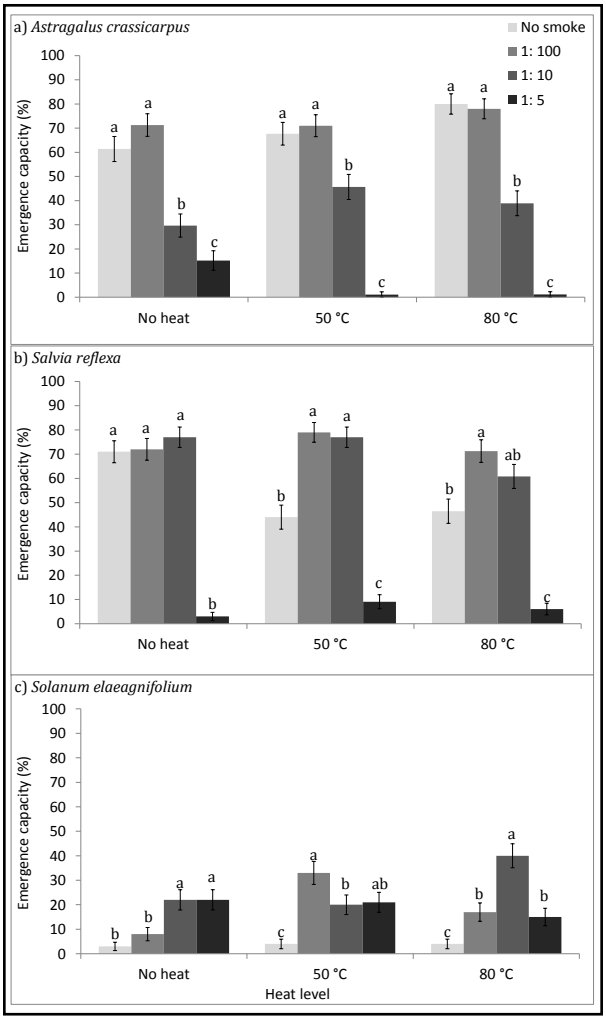

Figure 3. Interaction effects of smoke water and heat on the emergence capacity (%) of a) *Astragalus crassicarpus,* b) *Salvia reflexa,* and c) *Solanum eleagnifolum* (mean ± SE) in the glasshouse. Means followed by the same letters are not significantly different (0.05 level) within groups.

crease of the EC due to the heat (50 °C or 80 °C) (Figure 3b). The interaction effects of smoke water and heat on *Solanum eleagnifolum* were complicated but were promotive in general. The 50 °C and 80 °C heat treatments promoted the EC of this species at 1:100 and 1:10 concentrations of smoke water. Moreover, at least one smoke water treatment enhanced the EC of this species at all levels of heat (Figure 3c).

DISCUSSION

As in previous studies (Keeley and Fotheringham 1998, van Staden *et al.* 2000, Adkins and Peters 2001, Sparg *et al.* 2006), we found that smoke water inhibited the EC of some species (*Coreopsis tinctoria* and *Digitaria ciliaris*), especially at high (1:5) or medium (1:10) concentrations of smoke water. Similarly, the METs of *Coreopsis tinctoria, Gutierrezia sarothrae, Astragalus crassicarpus, Salvia azurea, Salvia reflexa,* and *Digitaria ciliaris* were prolonged by high- (1:5) or medium- (1:10) concentration smoke water, or both. This corresponds well to other examples in which smoke prolonged germination (Drewes *et al.* 1995, Daws *et al.* 2007). Interestingly, while most of these species experienced similar prolonging of germination in the previous laboratory study, *Salvia azurea* was inhibited only when also treated with heat in that same study (Chou *et al.* 2012). In this study, however, high-concentration smoke water inhibited emergence of *Salvia azurea* without heat. Other recent studies also used similar dilution levels as in this study (Norman *et al.* 2006, van Etten *et al.* 2014, Fowler *et al.* 2015).

Although smoke is known to inhibit some species, especially at high concentrations (Drewes *et al.* 1995, Daws *et al.* 2007), it is better known as a germination promoter. We found three species that were promoted by smoke water: *Coreopsis tinctoria, Salvia azurea,* and *Gutierrezia sarothrae.* In this study, these species experienced either increased emergence (*Gutierrezia sarothrae*) or decreased germination time (*Coreopsis tinctoria, Salvia azurea*) when exposed to some (but not all) concentrations of smoke water. This ability of smoke to promote germination in diverse species (Dixon and Roche 1995) has received increasing attention and could be the basis for using smoke or smoke water as a management or restoration tool. For example, smoke water can be sprayed over the soil surface (Abella 2009), thereby stimulating the

germination of selected species. In the case of *Gutierezia sarothrae*, a species that is native but often considered undesirable over much of the western US (Ralphs and McDaniel 2011), smoke treatments could stimulate mass germination, thereby depleting the seedbank of seeds of this plant (Adkins and Peters 2001). Emergent plants could then be treated mechanically or chemically to remove them from the landscape before they produce further seeds. Alternatively, smoke treatment could also be used to treat seeds of desirable species before sowing, perhaps increasing their ability to quickly germinate when sowed under favorable conditions (Baxter and van Staden 1994).

However, before smoke treatments, including smoke water, are used in such a manner in the southern High Plains, their effect on seeds in the field must be further characterized. We observed striking differences between the earlier laboratory study, conducted under tightly controlled conditions, and this glasshouse study, in which conditions were less controlled (i.e., less control over temperatures, light exposure, and contact with soil rather than germination papers as in the laboratory). For example, the mean germination time (MGT) of *Salvia reflexa* did not respond to heat in the laboratory, but MET was retarded by heat (50 °C and 80 °C) in the glasshouse. The measures of MGT and MET are nearly similar measures of seedling development, although MET is used (as we did) when germination cannot be directly observed because seeds are covered with soil. *Astragalus crassicarpus*, *Salvia azurea*, and *Solanum eleagnifolium* all displayed nearly opposite results in the glasshouse as compared to the laboratory. In the glasshouse, smoke water or heat or both might interact with environmental factors such as temperature or soil (Roche *et al.* 1997*b*), and measuring emergence, as we did in this study, rather than germination allows more time for such interactions to occur. In addition, because we used the same seedlots for both the laboratory study (Chou *et al.* 2012) and this study, seed afterripening may have altered some germination responses.

The inconsistent responses to smoke water or heat or both in the glasshouse compared to the laboratory suggest the necessity of testing these methods in the field to determine how factors such as soil (Read and Bellairs 1999), seed aging or ripening (Roche *et al.* 1997*a*), darkness (Tsuyuzaki and Miyoshi 2009), and seasonality (Roche *et al.* 1998) might interact with smoke and heat treatments to affect the germination and produce different results. Likewise, it might be important to consider that different populations of the same species might respond to smoke treatments differently (Thomas *et al.* 2007). For management and conservation of shortgrass prairie, future work should focus on testing the effects of smoke water on soil-stored seedbank germination, seedling density, seedling vigor, and overall species diversity. In addition, understanding the dormancy status and germination process for each species to be tested with smoke water will greatly enhance our ability to predict the outcome of treatment. Finally, we further suggest testing with lower concentrations of Regen 2000® smoke water because, in general, 1:00, 1:10, and 1:5 concentration levels inhibited more than promoted shortgrass prairie species. Other brands of smoke water, or even direct use of the active compound (Flematti *et al.* 2004, Stevens *et al.* 2007) might work even more effectively.

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