

Can biochar be used as a seed coating to improve native plant germination and growth in arid conditions?



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ABSTRACT

Direct seeding is a common large-scale restoration practice for revegetating arid and semi-arid lands, but success can be limited by moisture and temperature. Seed coating technologies that use biochar may have the potential to overcome moisture and temperature limitations on native plant germination and growth. Biochar is a popular agronomic tool for improving soil properties, such as water availability and nutrient retention and has been recently marketed, but not tested, as a seed coating. We analyzed the effect of biochar seed coating thicknesses on the germination and growth of four plant species native to western United States: mountain brome (*Bromus marginatus*), prairie junegrass (*Koeleria cristata*), Wyeth's buckwheat (*Eriogonum heracleoides*), and western yarrow (*Achillea millefolium*). Across different temperature and water potential treatments using environmental chambers and polyethylene glycol (PEG) solutions, biochar coating applied at different thicknesses had either a neutral or negative effect on germination for all species. In the field, biochar seed coatings slightly improved mountain brome root weight and prairie junegrass cover. Our results, alongside the high economic expense of native plant seed and direct seeding operations, suggest that biochar, by itself, may not be an appropriate seed coating for improving native plant establishment.

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1. Introduction

Direct seeding in the western United States is a common restoration practice, but germination and seedling emergence can be major barriers to successful revegetation (Chambers, 2000; James et al., 2011). Seedbed conditions are highly variable for temperature and moisture (Hardegree et al., 2003). Not only do the conditions need to occur that allow seeds to germinate, but for some species the range of temperature and moisture needed for emergence and growth is narrow (Fyfield and Gregory, 1989). Seed coatings that facilitate germination and initial growth may be especially useful in situations where nutrients and water are limited (Taylor and Harman, 1990; Madsen et al., 2012). A recent

tool marketed for restoration is biochar, a fine, carbon rich material that is a byproduct of pyrolysis of materials such as wood, waste organic materials, and agricultural crop residues at temperatures above 400 °C under complete or partial elimination of oxygen (Lehmann, 2007; Beesley et al., 2011). Because of its porous structure, large surface area, and negatively charged surface area (Liang et al., 2006; Downie et al., 2009), biochar has potential to increase water holding capacity and plant-nutrient retention in many soils (Gaskin et al., 2007; Laird et al., 2010; Kammann et al., 2011; Basso et al., 2013) and is commonly used to amend food crop soils (Blackwell et al., 2009). Companies now market biochar as a seed coating to improve germination and growth by increasing water availability and uptake, which appears counterintuitive given the hydrophobicity of biochar (Page-Dumroese et al., 2015). Until now, no research has been conducted or published about the effects of biochar seed coatings on plant germination and growth.

In this study, we evaluate the effect of biochar seed coating at various thicknesses on germination and growth of four native species commonly used for arid and semi-arid land restoration in

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the western U.S. Our goal was to determine the germination of non-coated and biochar-coated seeds in a controlled laboratory setting and under uniform field conditions. We hypothesized that germination of native species treated with biochar coatings would differ from non-coated seeds when exposed to different temperature and water potential conditions and that growth of native species treated with biochar seed coatings would differ from non-coated seeds when sown in a common field.

2. Materials and methods

2.1. Biochar seed coating

Mountain brome (*Bromus marginatus*), prairie junegrass (*Koeleria cristata*), Wyeth's buckwheat (*Eriogonum heracleoides*), and western yarrow (*Achillea millefolium*) seeds (hereafter brome, junegrass, buckwheat, and yarrow) were obtained from Washington State (U.S.A.) (Table 1). These species are adapted to a wide range of climatic and soil conditions making them suitable for revegetating and stabilizing disturbed sites in western North America. The biochar was created by heating ponderosa (*Pinus ponderosa*) and lodgepole (*Pinus contorta*) pine logs at 600 °C for 8 h residence time in a kiln and then crushing the material to a particle size range of 0.42–2 mm. A bench-top rotostat batch mixer equipped with an air dryer for curing was used to combine ingredients (a proprietary blend of biochar, standard alcohol [PVOH] polymer, and seeds). See Table 2 for chemical and physical properties of the biochar, which was applied at 1:1, 2:1, and 4:1 by seed weight. Seeds/kg, viability (tetrazolium chloride test [TZ]), and germination of coated and non-coated seeds were determined (Table 1) following standard seed testing guidelines (AOSA, 2013; ISTA, 2013). Seeds/kg was determined with eight, 100-seed samples. The TZ test was conducted on four, 100-seed samples. Brome, junegrass, and yarrow were germinated at alternating 20 °C (16 h dark)/30 °C (8 h light) and counts finished after 15, 30, and 18 days, respectively. Buckwheat seeds were chilled 28 days in moist conditions and stratified and non-stratified seeds were germinated at

Table 2

Chemical and physical composition of biochar seed coatings produced from beetle-killed ponderosa and lodgepole pine logs. Chemical characteristics of the biochar were performed at the Analytical Sciences Laboratory, University of Idaho, Moscow (U.S.A.) and physical characteristics were performed by the U.S. Environmental Protection Agency in Corvallis, Oregon (U.S.A.).

Volatile matter (%)	16.8
Fixed carbon (%)	77.7
Ash content (%)	5.5
Carbon (%)	86.0
Nitrogen (%)	0.18
Calcium (mg/mL)	5100
Magnesium (mg/mL)	930
Potassium (mg/mL)	2400
Phosphorus (μg/g)	280
Sulfur (μg/g)	120
Chromium (μg/g)	110
Copper (μg/g)	30
Iron (μg/g)	13,000
Manganese (μg/g)	480
Zinc (μg/g)	53

alternating 15 °C (16 h dark)/25 °C (8 h light) and counted for 30 days. After analysis, buckwheat seeds required further cleaning on a gravity table to remove inert matter.

2.2. Germination experiment

Seeds were germinated using the water potential control system developed by Hardegree and Emmerich (1992) under three constant temperatures replicated in environmental chambers (Hardegree and Burgess, 1995). The water potential control system consists of a membrane-bottom germination cup, the bottom of which is in contact with a solution reservoir of polyethylene glycol (PEG). PEG was mixed with water to yield osmotic solutions with a water potential of −0.033, −0.5, and −1.0 MPa. These solutions were mixed separately for each temperature to account for the thermal dependence of PEG-solution water potential (Michel and

Table 1

Mean characteristics (standard deviation) of non-coated and biochar-coated seeds of four native species acquired in Washington State and used in the germination and field study. Viability (tetrazolium chloride test [TZ]), germination, and seeds/kg of non-coated and biochar-coated seeds were determined at the U.S. National Seed Laboratory (Macon, Georgia), generally following established International Seed Testing Association (ISTA, 2013) and Association of Official Seed Analysts (AOSA, 2013) guidelines. Wyeth's buckwheat germination was determined for non-stratified and stratified (chilled 28 days) seeds.

	Purity %	Viability (TZ) %	Germination %	Seeds/kg
Mountain brome				
Moses Lake, WA				
Non-coated	99.7	81.8 (14.7)	79	95,678 (1102)
1:1		81.3 (15.9)	73	58,043 (525)
2:1		82.8 (13.3)	89	38,146 (124)
4:1		85.5 (10.4)	81	22,050 (226)
Prairie junegrass				
Eltopia, WA				
Non-coated	98.4	80.0 (8.1)	63	4,027,723 (52,644)
1:1		76.0 (16.1)	63	2,296,662 (36,453)
2:1		77.8 (7.2)	70	1,832,234 (31,554)
4:1		67.0 (8.7)	74	1,115,655 (31,451)
Wyeth's buckwheat				
Moses Lake, WA			Non-strat, strat	
Non-coated	75.7	54.0 (2.9)	9, 16	369,797 (2798)
1:1		45.5 (14.1)	6, 11	251,924 (3283)
2:1		35.5 (9.3)	6, 13	180,347 (3018)
4:1		23.3 (9.0)	0, 5	112,479 (2967)
Western yarrow				
Moses Lake, WA				
Non-coated	98.7	89.8 (10.2)	91	4,641,311 (98,942)
1:1		93.0 (5.9)	86	2,568,930 (112,269)
2:1		86.3 (11.2)	89	1,598,317 (38,327)
4:1		88.5 (10.7)	88	1,183,714 (29,974)

Radcliffe, 1995). The temperature and water potential treatments represent the range typically found in seedbed microclimates of the western U.S. (Hardegree et al., 2010). In March 2013, 30 seeds (15 seeds for brome) were germinated under all treatment combinations of species ($n = 4$), water potential ($n = 3$), temperature ($n = 3$), and biochar ($n = 4$). Using a randomized complete block design, vials ($n = 1296$) were arranged within 18 environmental chambers controlled at 6, 12, and 18 °C (6 blocks per temperature) with lights 12 h/day (Hardegree and Burgess, 1995). Vials were placed in the environmental chambers for acclimation prior to adding seeds. To prevent fungal growth, seeds were dusted with the fungicide Captan 50–WP (N-trichlorormethylthio-4-cyclohexene-1,2-dicarboximide). Germination was assessed daily up to 32 days. When the radicle extended greater than or equal to 2 mm, seeds were considered germinated, counted, and removed from the vials.

2.3. Field experiment

Species were seeded into a field at the U.S. Forest Service nursery in Coeur d'Alene, Idaho (U.S.A.) in October 2012. The nursery (47°43'2"N, 116°49'34"W, 688 m elevation) is on an outwash terrace of glaciofluvial deposits. Soil is described as the Marble series soil (mixed, mesic, Lamellic Xeropsammets); a coarse sandy loam to a depth of 44 cm with an overall depth to gravel of 107 cm having a plow layer pH of 6.9 (Soil Survey Staff, 2011) and an organic matter content of 2.5% determined by loss-on-ignition at 375 °C for 8 h. Mean annual precipitation is 642 mm and mean annual air temperature is 8.9 °C (WRCC, 2015). Treatments (non-coated and biochar-coated seeds) were sown with a J.E. Love/Øyjord seeder (J.E. Love Co., Garfield, Washington, U.S.A.) into a formed nursery bed. In seven rows 15 cm apart, brome and buckwheat were sown at 100 seeds per row per meter (700 seeds/m²) and junegrass and yarrow were sown at 165 seeds per row per meter (1155 seeds/m²). For each species, the non-coated and biochar-coated seed treatments were replicated 3 times across a uniform nursery bed; each replication was 1.2 m wide × 3 m long. The center 1 m² of each replication was hand-weeded throughout the season. In July 2013, species cover (%) was estimated in three, 30 × 30-cm quadrats for each non-coated and biochar-coated seed replication using digital images ($n = 9$). Aboveground and belowground biomass were collected within one, 30 (wide) × 30 (long) × 20 (deep)-cm quadrat for each non-coated and biochar-coated seed replication in September 2013 ($n = 3$). Biomass was sorted into roots and shoots by species, replication, and biochar coating treatment, oven-dried at 60 °C, and weighed. Biomass variables estimated were shoot, root, and total (shoots and roots) weight, shoots and roots per plant, total shoots and roots per species, and shoot-to-root ratio. To evaluate potential differences in seed production and weight, we collected brome seeds (the only species to set seeds) from 3 replicates of each treatment ($n = 3$) growing within the hand-weeded quadrats in July 2013. Seeds, operationally processed at the U.S. Forest Service Bend Pine Seed Extractory (Bend, Oregon, U.S.A.) following established AOSA (2013) and ISTA (2013) standard guidelines, were cleaned to ensure that the resulting seeds were filled (x-ray, %) and free of debris (purity > 95%) before determining moisture content (%) and seeds/kg. Thus, our comparison of seeds/kg among treatments was based on clean, filled seeds having similar water content.

2.4. Data analysis

For the laboratory experiment, we aggregated all of the vial replications within a block (environmental chamber) to obtain maximum percentage germination among all treatments for brome (100%), buckwheat (23.3%), junegrass (83.3%), and yarrow

(96.7%). The maximum percent germination was used as a scaling factor to estimate cumulative germination capacity (GC). This scales each species seedlot to a 0–100% germination range. The GLIMMIX procedure in SAS was used to identify significant main effects and two- and three-way interactions for GC among water potential, temperature, and biochar seed coatings (fixed effects) ($\alpha = 0.05$) (SAS Institute, 2006). Seventeen vials were omitted before analysis because of observer error, mold, and a faulty environmental chamber temperature. Block (environmental chamber) was treated as a random factor. Germination was compared for each species, but not among, species. Residuals were assessed for meeting the assumptions of generalized linear mixed models (GLMM). Treatment differences were evaluated using Tukey–Kramer LSD, means adjusted for multiple comparisons. When two- and three-way interactions were significant, we evaluated biochar differences within the treatment combinations (i.e. within 18 °C and –0.033 MPa).

To identify significant main effects of biochar seed coatings (fixed factor) on cover, biomass, and brome seed characteristics in the field experiment, we used the GLIMMIX procedure in SAS ($\alpha = 0.05$). Species were analyzed separately. Treatment differences were evaluated using Tukey–Kramer LSD, means adjusted for multiple comparisons.

3. Results

3.1. Germination experiment

For brome, germination capacity differed across temperature, water potential, and biochar treatments ($F_{[12, 67]} = 3.03$, $P = 0.0019$). At 6 °C and –1.0 MPa, the thickest biochar coating (4:1) had a lower germination ($\bar{X} = 24.8\%$, $SE = 4.0$) than 2:1 (53.6%, 4.0) and non-coated (51.0%, 4.0) seeds (Fig. 1) but was similar to seeds coated 1:1 (35.8%, 4.0). The non-coated, 1:1, and 2:1 behaved similarly — steady increase in germination capacity from 18 days until peaking above 35% by 32 days (Fig. 1). The 4:1 coated seeds did not start germinating until 16 days at 0.7% and peaked at 25% by the end of the study. Germination capacity of biochar treatments did not differ at 12 (90.9%, 1.3) and 18 °C (90.7%, 1.3); germination means >80% were unaffected by water potential and biochar at these temperatures.

Germination capacity of junegrass was influenced more by the interaction between temperature and water potential than by biochar coatings ($F_{[4, 67]} = 34.81$, $P < 0.0001$). Many seeds did not reach 50% germination capacity by the end of the study, especially within the 6 °C treatments and –1.0 MPa treatments (Fig. 2). Within each temperature treatment, germination capacity was greater at –0.033 MPa than at –0.5 and –1.0 MPa by at least 20%.

Buckwheat germination was low ($\bar{X} = 14.4\%$) in comparison to the other species and was influenced by temperature and biochar ($F_{[6, 67]} = 4.87$, $P = 0.0003$) and water potential and biochar ($F_{[6, 67]} = 4.39$, $P = 0.0008$) (Fig. 3a and b). With the exception of 6 °C, biochar had a negative effect on germination at 12 and 18 °C. For the water potential and biochar interaction, biochar coatings had a negative effect on germination at the –0.033 and –0.5 MPa water potentials. Biochar seed coatings had no effect on germination at –1.0 MPa (Fig. 3b).

For yarrow, germination capacity differed among biochar coatings ($F_{[3, 66]} = 8.15$, $P = 0.0001$) (Fig. 4). The non-coated ($\bar{X} = 44.3\%$, $SE = 2.8$) and 1:1 (40.0%, 2.8) biochar-coated seeds had greater germination capacity than the 4:1 biochar-coated seed (32.5%, 2.8). Yarrow seed germination behaved in a similar fashion to junegrass in that many seeds did not achieve 50% germination capacity at the lowest temperature (6 °C) and at the lowest water potential (–1.0 MPa) (Fig. 4).

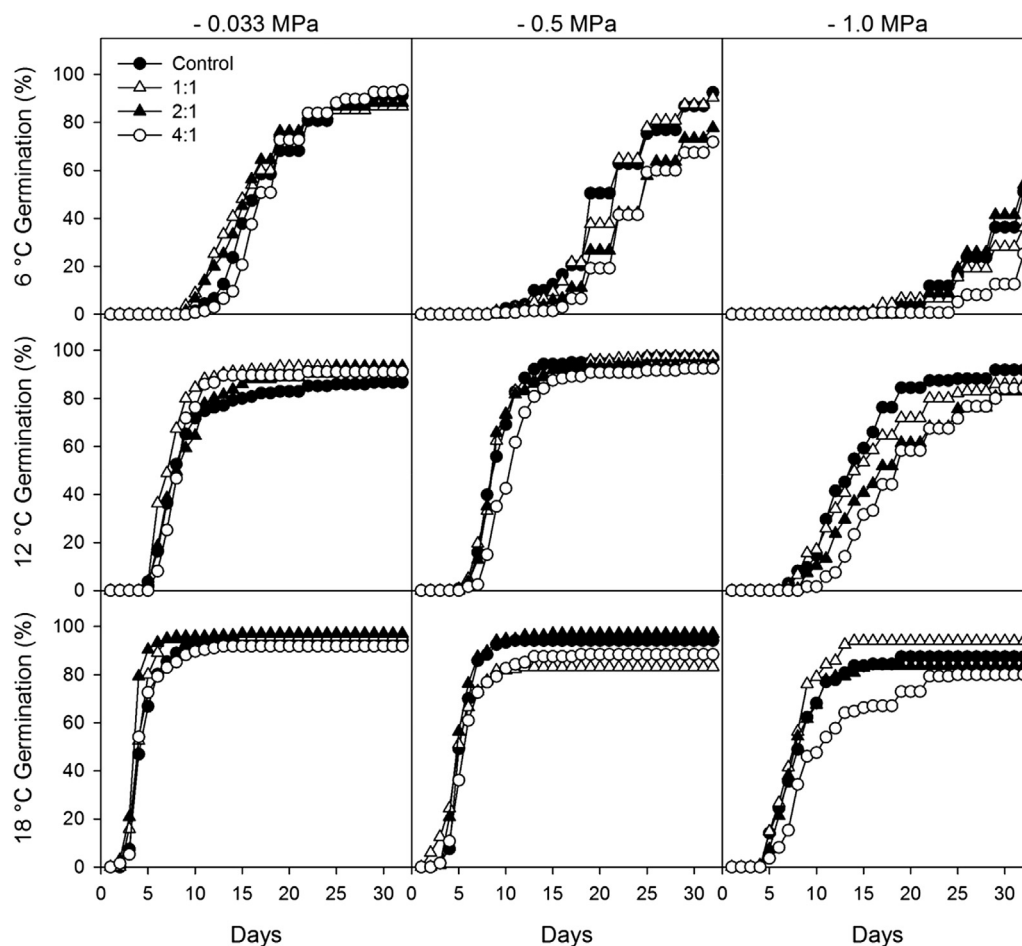


Fig. 1. Effects of temperature, water potential, and biochar seed coating on the cumulative germination of mountain brome (*Bromus marginatus*) after 32 days. At 6 °C and -1.0 MPa, the heaviest biochar seed coating (4:1) had lower germination than non-coated (control) and 2:1 coated seeds.

3.2. Field experiment

During the study (October 2012–September 2013), total precipitation was 646 mm and mean air temperature was 9.7 °C. During the growing season, specifically April 2013 through September 2013, total precipitation was 256 mm and mean air temperature was 16.1 °C (WRCC, 2015), values equal to or slightly above normal for the area.

Mountain brome cover did not differ among treatments. Cover averaged 30.9% (SD = 7.8) across treatments. Seed yield and characteristics did not differ among treatments. Across treatments, seed purity averaged 98.1% (SD = 1.5), average moisture content was 7.4% (SD = 0.2), and number of seeds/kg was 108,026 (SD = 3842.0). With the exception of root dry weight ($F_{[3, 8]} = 6.85$, $P = 0.0134$), brome biomass did not differ among treatments. Root weight was greater for the 4:1 (19.8 g, SE = 2.0) and 1:1 (17.1 g, 2.0) than the 2:1 (7.7 g, 2.0) biochar-coated seeds, although root weight from non-coated seeds (14.4 g, 2.0) did not differ significantly from the other treatments.

Junegrass cover differed among treatments ($F_{[3, 32]} = 5.46$, $P = 0.0038$) such that cover from the 1:1 treatment was greater than cover from the 2:1 and 4:1 biochar treatments (Fig. 5). Cover from non-coated seed was not different from the other treatments. Because of the junegrass sowing density and vigorous plant growth, we were unable to count individual plants and separate individual shoots and roots. Even so, junegrass biomass did not differ among treatments. Average total biomass and shoot-to-root ratio were

97.9 g (SD = 9.4) and 0.28 (SD < 0.0), respectively.

Western yarrow cover and biomass did not differ among biochar seed coating treatments. Cover within yarrow plots was 79.1% (SD = 4.8) and 20.9% (SD = 4.8), while total biomass and shoot-to-root ratio were 45.3 g (SD = 4.6) and 1.24 (SD = 0.3), respectively. Buckwheat had very low establishment (<5% cover) and we were unable to analyze cover. Buckwheat biomass did not differ among biochar seed coating treatments. Total average buckwheat biomass was 3.1 g (SD = 1.6) and shoot-to-root ratio was 3.3 (SD = 1.3).

4. Discussion

Coating seeds with biochar as a means to improve plant germination and growth is a new practice and our study is the first to examine its effect on native plant species. Based on the reasoning that biochar has the potential to improve water holding capacity (Kammann et al., 2011; Laird et al., 2010), we expected that at low temperatures and low water potentials germination of biochar-coated seeds would perform as well or better than non-coated seeds, but biochar seed coatings did not improve germination of any species. In regards to plant growth, we observed an increase in root dry weight for brome with the thickest biochar coating, and for junegrass, biochar increased cover but only for the thinnest coating, suggesting that too much biochar may limit growth for junegrass. We found that biochar seed coatings did not improve aboveground biomass of any species, which is counter to many other biochar-plant growth studies (see meta-analysis by Biederman and

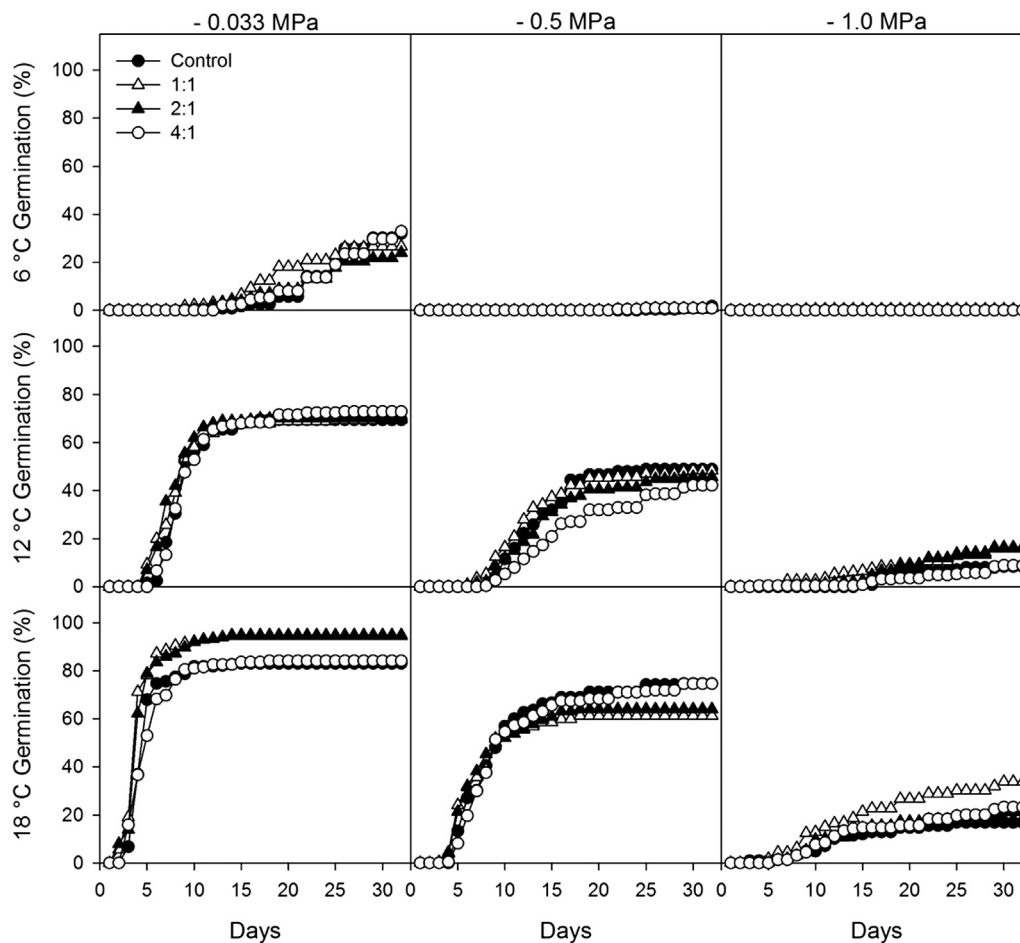


Fig. 2. Effects of temperature, water potential, and biochar seed coating on the cumulative germination of prairie junegrass (*Koeleria cristata*) after 32 days. Biochar seed coatings did not have an influence on germination within each temperature × water potential treatment.

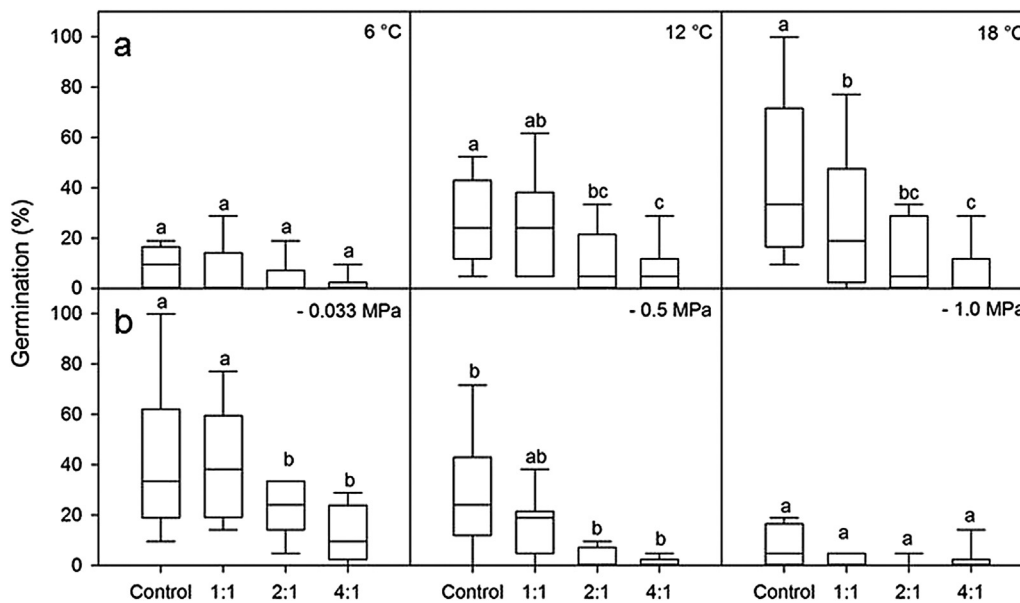


Fig. 3. Effect of temperature (a) and water potential (b) on germination of non-coated (control) and biochar-coated seeds of Wyeth's buckwheat (*Eriogonum heracleoides*). Vertical boxes represent approximately 50% of the observations and lines extending from each box are the upper and lower 25% of the distribution. The horizontal line in the center of each box is the median germination value. Data with different letters are statistically different ($P < 0.05$).

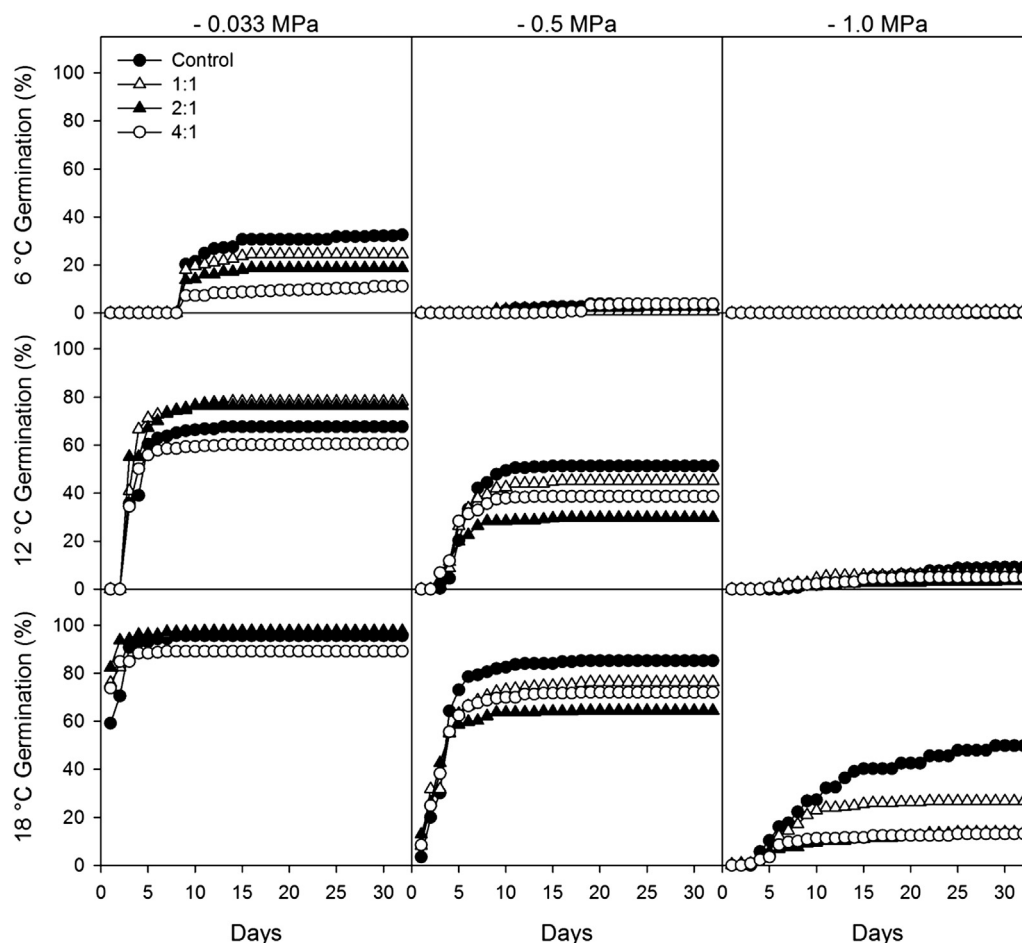


Fig. 4. Effects of temperature, water potential, and biochar seed coating on the cumulative germination of western yarrow (*Achillea millefolium*) after 32 days. Across all temperature and water potential treatments, biochar coatings had a negative effect on germination capacity.

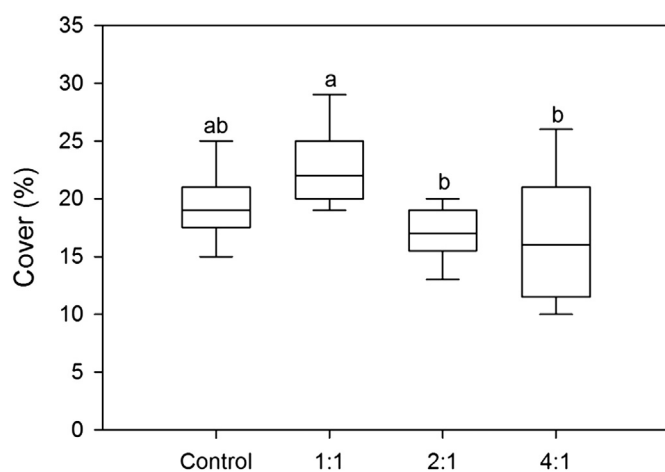


Fig. 5. Cover of biochar and non-coated (control) prairie junegrass seeds (*Koeleria cristata*). Vertical boxes represent approximately 50% of the observations and lines extending from each box are the upper and lower 25% of the distribution. The horizontal line in the center of each box is the median cover value. Data with different letters are statistically different ($P < 0.05$).

Harpole, 2013). Although our field experiment was conducted under very uniform edaphic nursery conditions, the number of replications and number of samples taken in each replication were low.

Thus, future studies with more replication under more diverse outplanting conditions may provide evidence of an effect of biochar on plant growth, particularly if replication is analyzed as a random factor to account for variation in plant growth not caused by the biochar coating treatments.

The species we evaluated are from arid and semi-arid climates and are likely adapted to dry, warm, and cold conditions. Mountain brome, for example, is seeded as an early successional species and valued for its rapid establishment on disturbed sites, winter hardiness, and drought tolerance (Monsen et al., 2004). At the coldest temperature and lowest water potential we saw differences in brome seeds coated with biochar, but the differences were less than positive. In general, temperature may be the dominate factor in seed germination, but in dry conditions, the effects of soil moisture become paramount — the greater the water stress, the less capable the seeds are to germinate at low temperatures (Fyfield and Gregory, 1989). Non-coated seeds can germinate well at 0 to -1.0 MPa (Wuest and Litcher, 2013), but we found that when water was limited (-0.5 to -1.0 MPa), germination capacity alone decreased, an effect amplified for brome seeds coated with biochar. Dry, non-coated seeds usually have very negative water potentials (-350 to -50 MPa) and germination can be blocked if the seed water content is below a critical water potential (Leubner, 2006). The biochar we used may have increased water availability, but perhaps was insufficient to enhance imbibition at the lower water potentials. Volatile organic compounds (VOCs), which occur naturally in soil (Smith and Dowell, 1973) and during pyrolysis (Spokas

et al., 2011), may also affect germination. For example, the VOCs ethylene and propylene are known to stimulate germination (Taylorson, 1979). An evaluation of more than 70 biochars revealed that 97% contained sorbed ethylene + acetylene and propylene (Spokas et al., 2011). Although not measured in this study, the likely presence of ethylene in the biochar tested could improve germination, but as discussed above, we failed to observe any benefit. At least three possible explanations exist. First, the amount of ethylene produced during pyrolysis, in general, is maximized at a temperature of 350 °C and is about ten-times higher than that generated at the temperature used to create the biochar in this study (600 °C) (Spokas et al., 2011), so the amount of ethylene created may have been insufficient to invoke response. Second, even if the amount was adequate, the release of sorbed ethylene, which varies by biochar type (Fulton et al., 2013), may have been too slow. And third, germination of some species is known to be reduced by the presence of ethylene (Taylorson, 1979).

Most research has evaluated biochar as a soil amendment rather than a seed coating, and results have been mixed: increasing plant growth in some studies (Chan et al., 2008; Kammann et al., 2011) and hindering growth in others (Deenik et al., 2010; Solaiman et al., 2012). Variability in biochar type and application rate and mode (e.g. top-dressing, tilled, pellets), as well as environmental setting, can play a factor in plant response (Lehmann, 2007; Van Zwieten et al., 2010; Barrow, 2012; Solaiman et al., 2012). When applied to coarse- to medium-textured, unproductive soils at rates less than 100 t ha⁻¹, biochar can improve nutrient supply, water holding capacity, and water availability (Chan et al., 2008; Jeffery et al., 2011). In addition, biochar added to the soil is more effective for improving soil moisture conditions (i.e. water repellency) when mixed into the profile rather than surface applied (Page-Dumroese et al., 2015). Biochar's ability to absorb water and adsorb nutrients is also contingent upon its chemical and physical properties, a function of pyrolysis temperature (e.g. pH and surface area increase with temperature to a point) (Downie et al., 2009; Lehmann, 2007). In forest soil applications, for example, biochar produced at 550–650 °C was better than other temperatures for absorbing water (Kinney et al., 2012). And in a study of different types, biochar, in general, enhanced water storage capacity of soils but it varied with feedstock type and pyrolysis temperature (Novak et al., 2012). We tested only one type of biochar, but our methods provide a framework for evaluating other types and modes of application. Biochar can be designed with characteristics specific to intended objectives, goals, and environmental settings (Novak et al., 2009; Novak and Busscher, 2013). Given enough completed studies and data, decision frameworks could help practitioners decide whether or not to use biochar and what type is appropriate based on initial soil properties and other environmental conditions (Beesley et al., 2011).

5. Conclusions

Biochar has potential to improve soil properties that benefit plant germination and growth, such as water holding capacity and nutrient retention (Basso et al., 2013; Gaskin et al., 2007; Laird et al., 2010), but we found that biochar seed coatings had either a neutral or negative effect on native plant germination and growth when exposed to different temperature and moisture conditions. Biochar's negative impact on germination capacity for brome, buckwheat, and yarrow is cause for concern and given biochar production costs that range between \$51 to \$3747/ton (Meyer et al., 2011), seed coating technologies that add extra cost and weight, thereby reducing seeds/kg, and native seed costs that can exceed \$60 million per year for federal lands in the U.S. (U.S. Government, 2014), biochar may not be an appropriate seed coating for

improving native plant establishment on arid and semi-arid lands. However, if biochar can be tailored to improve plant establishment through a seed coating versus widespread soil application, we need to better understand its water potential properties, physiological interface with seed coats, and sorbed VOCs and their potential to impact germination.

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