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# High-Severity Burning Increases Jack Pine Seedling Biomass Relative to Low-Severity Prescribed Fires

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**Within the state of Wisconsin, there is a gradient of serotiny in *Pinus banksiana* Lamb. (jack pine). With prescribed burning becoming more common in Wisconsin, understanding the dynamic and variable effects of burning on soil properties and their interactions with post-fire plant communities is critical. Our objective was to isolate and examine how fire effects on soil properties affect *P. banksiana* seed germination and seedling growth and establishment. We investigated these effects in two pot experiments and an intact paired core experiment, maintained in a greenhouse for 19 to 24 wk. Soils from the O and A horizons were collected from Coon Fork Barrens, Eau Claire County, WI, before and after a prescribed fire, and O horizon soil was burned in the laboratory to mimic a high-severity wildfire. In the intact core experiment, seed germination and seedling aboveground mass were not affected by prescribed burning. In the pot experiments, jack pine seedlings produced more biomass in laboratory-burned soils than prescribed-burned soils, and seedlings from northwest seed lots consistently had a higher frequency of establishment compared to those from central seed lots. For the low-severity prescribed fire considered in this study, effects on measured soil properties were minimal, and did not result in any improvement to seedling establishment. For soil properties to play an important role in promoting jack pine seedling growth, hotter fires may be required, while lower-severity fires will require other effects- such as seed release, changes to moisture dynamics, or competition- to affect jack pine germination and establishment.**

Fire is a natural disturbance in many ecosystems of the Great Lakes Region, and can dramatically affect vegetation structure (Miesel et al., 2012). Fundamental to overall ecosystem functions and processes, soil is also affected by fire (Neary et al., 2008). Many effects of fire on soil are immediate and well-correlated with burn severity (Keeley, 2009). One of the most immediate effects is the combustion of biomass, which results in the formation of ash and the loss of organic matter (Certini, 2005). Organic matter is lost from the soil surface between 200 and 315°C, temperatures commonly reached during a fire (Knicker, 2007). Organic nitrogen (N) compounds can also persist after a low intensity fire (Certini, 2005), and different studies have reported both increases and decreases in total soil N after fires (Wan et al., 2001). However, the form of organic N compounds also may be modified into more plant available forms such as ammonium ($NH_4^+$) and nitrate ($NO_3^-$) (Knicker, 2007). In such cases, post-fire processes including nitrification, leaching, microbial immobilization, and plant uptake of N affect the net fluxes of mineral N in the soil (Wan et al., 2001). In contrast to organic matter, inorganic compounds are often comparatively preserved post-fire. Phosphorous (P), calcium (Ca), magnesium (Mg), and potassium (K) are generally volatilized at higher temperatures than for C and N (Knicker, 2007), and thus tend to be relatively enriched compared to C and N in the soil post-fire (Neary et al., 2008). Although some portion is still lost, what remains may be transformed into different

## Core Ideas

- **Prescribed fire did not affect jack pine seed germination or seedling establishment.**
- **Severely burned soil had 10-fold the available P and significantly lower organic matter and higher pH.**
- **Jack pine seedlings produced about twice as much biomass in severely burned soil.**
- **Regional genetic differences in jack pine may alter seedling establishment.**

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chemical states (Gray and Dighton, 2006). This fire-affected soil with an altered nutrient composition represents the new seedbed and medium for growth of plants that colonize burned areas.

In ecosystems where fire is an important disturbance agent, species selection will favor those that display adaptive traits, especially related to reproduction. For example, jack pine (*Pinus banksiana* Lamb.) is favored in areas affected by infrequent, high severity crown fires (Miesel et al., 2012). Jack pine trees may retain up to 10 cohorts of serotinous cones in the canopy, with seed dispersal occurring after cones open as a result of fire (Greene et al., 2013). Jack pine is also adapted to xeric, nutrient poor sites where seeds germinate and seedlings establish on exposed mineral soil, providing better access to water and decreased drought stress compared to that on thicker, high porosity seedbeds (Greene et al., 2013).

Genetic differences in jack pine are reflected in range-wide patterns of morphological variation linked to geographic clines (mainly associated with climatic gradients) (Saenz-Romero and Guries, 2002). Phenological traits such as growth rate vary and are correlated with the photoperiod, length, and temperature of the growing season (Rudolph et al., 1957; Yeatman and Teich, 1969; Yeatman, 1965). Traits such as seed weight, seedling height, dry root mass, and dry shoot mass also vary in a gradient, generally increasing with a longer, warmer growing season at the geographic location from which the seed is sourced (Yeatman and Teich, 1969; Saenz-Romero and Guries, 2002).

One of the principle genetic differences among jack pine seed sources is variation in the quantity of serotinous cones that trees produce. In Wisconsin, where fire was a part of the pre-settlement environment (Myer, 2017), Radeloff et al. (2004) documented a gradient of serotiny at the stand level in jack pine trees in the northwest part of the state. The proportion of cones that were serotinous was greater in northern sites of the study area (83 ± 13.5%) compared to the southern sites (9 ± 3.7%). The authors attributed this difference to three distinct fire regimes in the area pre-settlement: (i) frequent, non-lethal ground fires in the south, (ii) non-frequent, lethal crown fires in the center, and (iii) medium frequency, lethal, crown fires in the north. Likely reflecting similar processes, jack pine cones sourced from central Wisconsin have a lower percent of serotinous cones (~65%) compared to cones sourced from northwest Wisconsin (~85%) (J.J. Auer, pers. comm., 2016).

Many studies have suggested that prescribed fire—the intentional use of fire for a pre-planned area for a specific management goal—can increase conifer recruitment (Certini, 2005; Hiers et al., 2007; Williams et al., 2012). Prescribed fire exposes new seedbeds, increases nutrient availability immediately post-fire, and creates opportunities for seed establishment (Chapin et al., 2014). Because the frequency of fires in the jack pine barrens has been reduced in Wisconsin in the last 150 yr, it has become more common for land managers of the Wisconsin Department of Natural Resources (WI DNR) to use prescribed fire to help restore or maintain historical forest structure and function (Witecha, 2018). Benefits of prescribed fire are not limited to increasing abundance of jack pines, but also its associated plant community, most notably the wild lupine (*Lupinus perennis* L.). The world's largest population of the endangered Karner blue butterfly (*Lycaeides melissa samuelis*) thrives on the wild lupine in Wisconsin's jack pine barrens (Myer, 2017).

Knowing how frequency of serotiny could influence jack pine establishment in soils affected by low-intensity prescribed fire may assist managers in planning prescribed burns. For example, are the genetic and/or phenotypic differences in jack pines with serotinous cones vs. those without serotinous cones largely limited to the release of seeds, or do the seedlings from these trees also perform differently once sprouted in the post-fire soil? Furthermore, are these potential interactions modified by burn severity? This research investigates the question: How does burning affect *P. banksiana* seed germination frequency, seedling height, and biomass production? We predicted that the more severely burned the soil is, the higher the germination frequency would be, and that seedlings would grow taller and produce more biomass. To specifically isolate and examine the effects of fire on soil properties in determining jack pine seedling growth (excluding effects such as changes to water status, competition, or release of seeds with fire), we used three greenhouse experiments. In Experiment 1, we asked whether seedling growth differed in pre-burn, post-burn, and extreme laboratory-burn soils, using seed from two regions of Wisconsin in a pot experiment. Then, to determine whether the observed differences between seed sources were consistent across seed lots, we designed a second pot experiment to test this: in Experiment 2, we asked whether seedlings from the northwest region of Wisconsin consistently established better than those from the central region, using four different seed lots for each of the two regions in a pot experiment. Finally, in Experiment 3, we wanted to determine whether there were differences in seed germination and seedling establishment in visibly burned vs. visibly not burned microsites within the fire, at field bulk densities, and with local seed. We conducted a soil core incubation experiment using paired intact cores and seed collected from the study site.

## MATERIALS AND METHODS

### Field Site and Prescribed Burn

Coon Fork Barrens, in west central Wisconsin, is a 235-ha property in Augusta, WI, owned and managed by Eau Claire County (Myer, 2017). Coon Fork Barrens was designated a State Natural Area in 1996 by the WI DNR. The area features open jack pine barrens with occasional red pine (*Pinus resinosa* Aiton), black oak (*Quercus velutina* Lam.), white oak (*Quercus alba* L.), and bur oak (*Quercus macrocarpa* Michx.) trees. Smaller vegetation cover includes heath-like species such as bracken fern (*Pteridium aquilinum* L.), sweet gale (*Myrica gale* L.), early low blueberry (*Vaccinium angustifolium* Aiton), and Pennsylvania sedge (*Carex pensylvanica* Lam.). There is additionally sand prairie and savanna flora in other open patches, including junegrass [*Koeleria macrantha* (Ledeb.) Schult.], western sunflower (*Helianthus occidentalis* Riddell), prairie coreopsis (*Coreopsis palmata* Nutt.), sky-blue aster (*Aster azureus* Lindl.), prairie goldenrod [*Oligoneuron album* (Nutt.) G.L. Nesom], and rough blazing-star (*Liatris aspera* Michx.). The soil is predominantly from the Simescreek sand series, Frigid, uncoated Typic Quartzipsamments, 0 to 3% slopes (Soil Survey Staff, 2017).

Prescribed fire is used as a management tool at Coon Fork Barrens to help maintain the historical jack pine barrens. The prescribed fire investigated in this study was conducted by the WI DNR at Coon Fork Barrens, Augusta, WI, on 7 Nov. 2016. The burn unit was 14 ha (Fig. 1A). The fire started around noon and lasted 2 h. The burn was carried by short and medium grass species. The management goal of the fire was to help maintain this jack pine barrens by reducing the duff layer so that wild lupine and other native plants can grow without species such as maple establishing and shading them out (N.S. Holoubek, pers. comm., 2018). The prescribed fire was designed to mimic the historical fire regime for a pine barren community in this area (frequent low severity fires every 3 to 10 yr) (Fig. 1B and 1C). Standard and internal protocols were used by the WI DNR to create the desired fire behavior that would result in the target level of heat and relatively low residence time of that heat for the burn unit (N.S. Holoubek, pers. comm., 2018). Although we do not have temperature or residence time for the prescribed fire studied, the WI DNR has data recorded for a similar jack pine barrens community (Crex Meadows, Grantsburg, WI) burned in the spring of 2017. The average soil surface temperature from Crex Meadows was 221 ± 115°C, with a maximum temperature reaching 597°C and a minimum temperature of 60°C (N.S. Holoubek, pers. comm., 2017). The average residence time (number of seconds temperature was greater than 60°C) for Crex Meadows was 166 s (2.77 min), with a maximum residence time of 1019 s (16.98 min) and a minimum residence time of 1 s (N.S. Holoubek, pers. comm., 2017). These data were gathered by the WI DNR using a Campbell Scientific CR21 micrologger with thermocouples (Logan, UT) to measure temperature, with an in-house setup modeled after Sackett and Haase (1992) (N.S. Holoubek, pers. comm., 2018). Note that this study focuses on a small, unreplicated burn. Because the properties and effects of prescribed burns vary substantially with factors such as fuel load, vegetation, moisture, or time of year (Hartford and Frandsen, 1992; Quigley et al., 2019), the implications of the results of this study should be limited to similar fires.

## Field Sample Collection

We established one transect (25 m) in the direction of northeast to southwest through the area to be burned. One hour before the fire, we collected pre-burn soil with a sharp metal shovel and trowel from 30-cm by 30-cm plots every meter along the transect starting at 0 m and divided into the O horizon (~0 to 3 cm) and the A horizon (~3 to 30 cm). Two hours after the prescribed fire, we collected post-burn soil every meter along the transect starting at 0.5 m and divided into O horizon and A horizon. Because the low-intensity fire was patchy, our post-burn pooled sampling approach did include some areas that were only lightly burned. Thus, the pooled soil sample is an integrative representation of the effects of burning across the transect, and not a representation of the effects of fire in the most severely burned patches. We pooled soil from each horizon and burn treatment separately and stored the soil in plastic bags on ice for transport to the laboratory (subsequent sieving and processing described below). This soil was used for the first two experiments (Fig. 2). We took three bulk density cores (85 $cm^3$) with a hammer probe to determine field bulk density. We also collected mature closed cones from the lower branches of three jack pine trees within the burn unit before the fire for use in Experiment 3.

For the third (soil core) experiment, we collected 21 pairs of intact soil cores (42 total) at Coon Fork Barrens 15 d after the prescribed fire (Fig. 2). To control for small-scale site heterogeneity, paired cores were taken in areas that were visibly burned and immediately adjacent to areas (<10 cm apart) that were not visibly burned (Supplemental Fig. S1 and S2). To extract soil cores, we placed a wooden board on top of a section of PVC pipe of 5-cm height and 10-cm inside diameter on top of the soil, and struck the board with a rubber mallet until the soil surface was level with the top of the pipe section. To prevent soil from falling out, we wrapped the bottoms of the cores in cheesecloth and placed them in individual plastic bags for transport back to the laboratory. We also collected complementary paired cores (1.5 cm diameter by 5 cm length), which we used to estimate the thickness of the O horizon in the visibly burned and visibly not burned sites.

## Soil Preparation

For the soil characterization and the two pot experiments, we sieved both O-horizon and A-horizon soils through a 2-mm sieve (Supplemental Fig. S3). For the O horizon, this resulted in the retention of duff along with litter particles >2 mm that were not easily broken up, and the exclusion of the largest litter particles. To create an extreme burned treatment, we burned a subsample of pre-burn moist O-horizon soil in a muffle furnace at 400°C for 10 min, resulting in visibly blackened soil denoted as laboratory-burned soil (Supplemental Fig. S3). The laboratory-burned soil was initially at 16% moisture and lost 27% of its dry mass. Only the O horizon was burned in the laboratory, since it has been noted that often only the top few centimeters of soils are heated during a fire (Neary et al., 2008; Certini, 2005), particularly under higher moisture conditions (Hartford and Frandsen, 1992). That said, in a fire as severe as the one mimicked in the muffle furnace, depending on moisture, fuel load, or other conditions, we might have expected to see meaningful temperature increases in the mineral soil, which we did not attempt to mimic here.

## Soil Characterization

For chemical characterizations, we sent sieved, air dried, and ground soil samples to the University of Wisconsin-Madison Soil and Forage Analysis Laboratory in Marshfield, WI for determination of pH (1:1 soil/water) (ASTM, 1995), plant available P (Bray I) (Bray and Kurtz, 1945), plant available K (Bray I) (Bray and Kurtz, 1945), organic matter (loss on ignition) (Ball, 1964), exchangeable sodium (1 M $NH_4OAc$) (Thomas, 1982), $NO_3$–N (2 M KCl) (Tucker, 2009), and $NH_4$–N (2 M KCl) (Tucker, 2009)

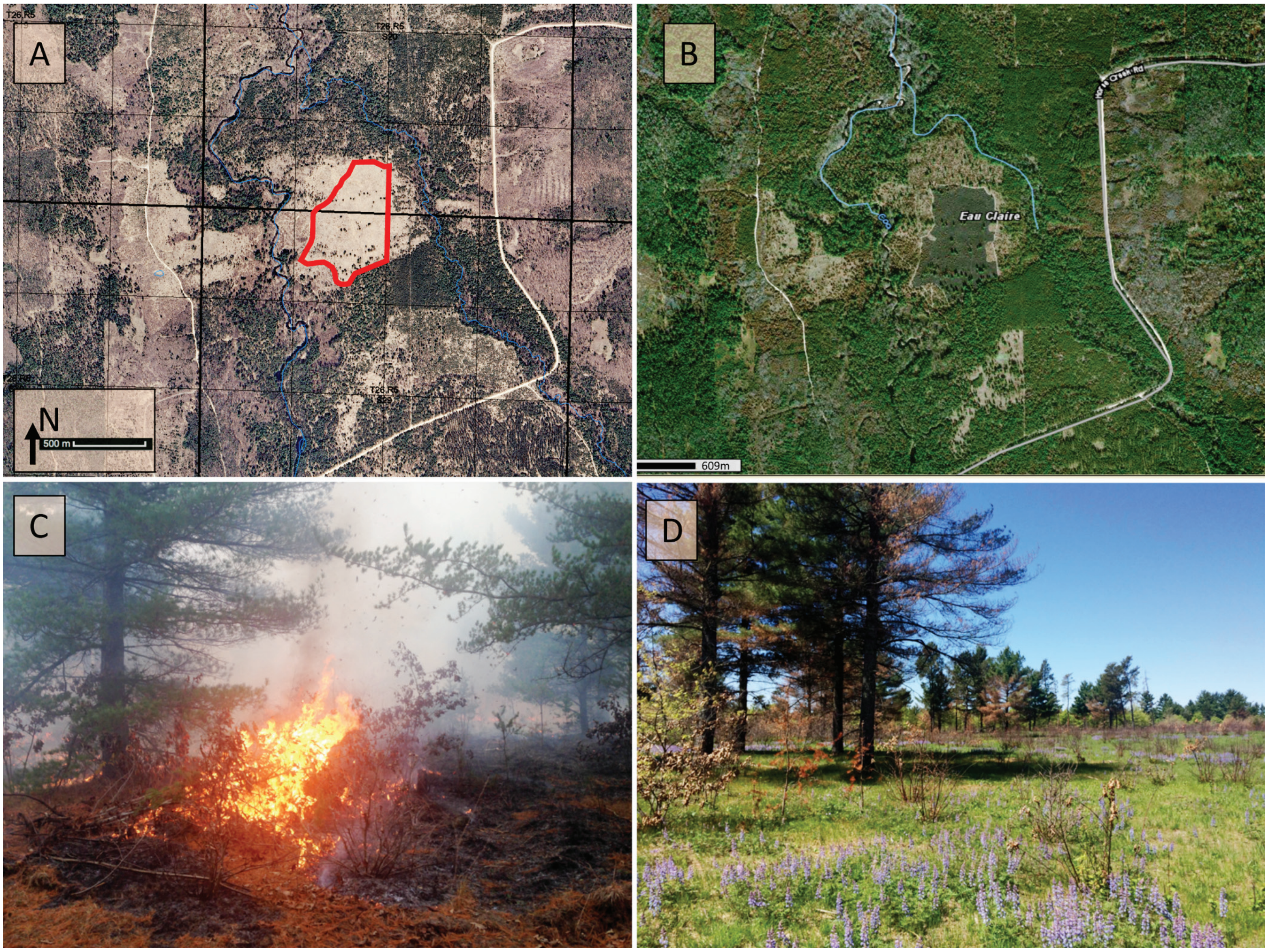


**Fig. 1. (A) Map from the Coon Fork Barrens including the 14-ha burn area outlined in red, T26N, R5W, Sections 20 and 29 (photo courtesy of Dean Edlin, WI DNR). (B) Map of field site post-prescribed fire (Soil Survey Staff, 2017). (C) Prescribed fire at Coon Fork Barrens in November 2016. (D) Coon Fork Barrens 6 mo after the prescribed fire in June 2017; Note wild lupine in the foreground and background.**

in triplicate. We used a DELTA Professional Handheld XRF Analyzer (Olympus, Waltham, MA) for Mining and Exploration (Geochemical mode) for total elemental analysis on dried, sieved soil samples, taking five scans for each soil treatment. We analyzed total C and N using flash combustion in a ThermoFisher Scientific Flash EA 1112 Flash Combustion Analyzer (Waltham, MA). We analyzed particle size using a Beckman Coulter LS230 (Brea, CA) with a 5% solution of $(NaPO_3)_6$.

## Experiment 1: Pot trial—Growth of seedlings from two different regions of Wisconsin in burned and not burned soils

In Experiment 1, we asked whether seedling growth differed in pre-burn, post-burn, and extreme laboratory-burn soils, using seed from two different regions of Wisconsin, in a pot experiment. We planted pre-germinated jack pine seeds from northwest Wisconsin or central Wisconsin (details below) in pre-burn soil, post-burn soil, or laboratory-burn soil in Deepots D40H (Stuewe & Sons, Inc., Tangent, OR) (656 mL, 2.5 cm diameter, 10 cm height). To keep the soil from falling out, we inserted peat to a depth of 1 cm in the bottom of each pot to plug the bottom hole. For each treatment, we packed ten pots (pre- and post-burn soils) or five pots (laboratory-burn soils, due to limited quantities) to field bulk density with sieved A-horizon soil, up to 3 cm from the top of the pot. For the pre- and post-burn soils, we filled the remaining 3 cm with sieved O-horizon soil. For the laboratory-burn soils, we added a mass of laboratory-burned O-horizon soil that would be equivalent to what would remain if the 3 cm of unburned O horizon were subjected to the laboratory-burned treatment (Fig. 2). We watered the pots to field capacity for 2 wk prior to planting and maintained them in a greenhouse with an 18-h photoperiod. We defined field capacity in our study as the amount of water that remains after saturated soils are freely drained by gravity.

To test whether seed from different regions had different responses to burned soils, we obtained jack pine seeds from the WI DNR from two different regions: northwest Wisconsin (~85% serotinous) and central Wisconsin (~65% serotinous) (J.J. Auer, pers. comm., 2016) (Supplemental Table S1, seed lots H15 and G15). To isolate the post-germination effects of soils on the seedlings, we pre-germinated the seeds before planting. Seeds were disinfested according to Smith et al. (2015). Briefly, we placed seeds in a plastic vial and stirred them in 10% hydrogen peroxide for 4 h,

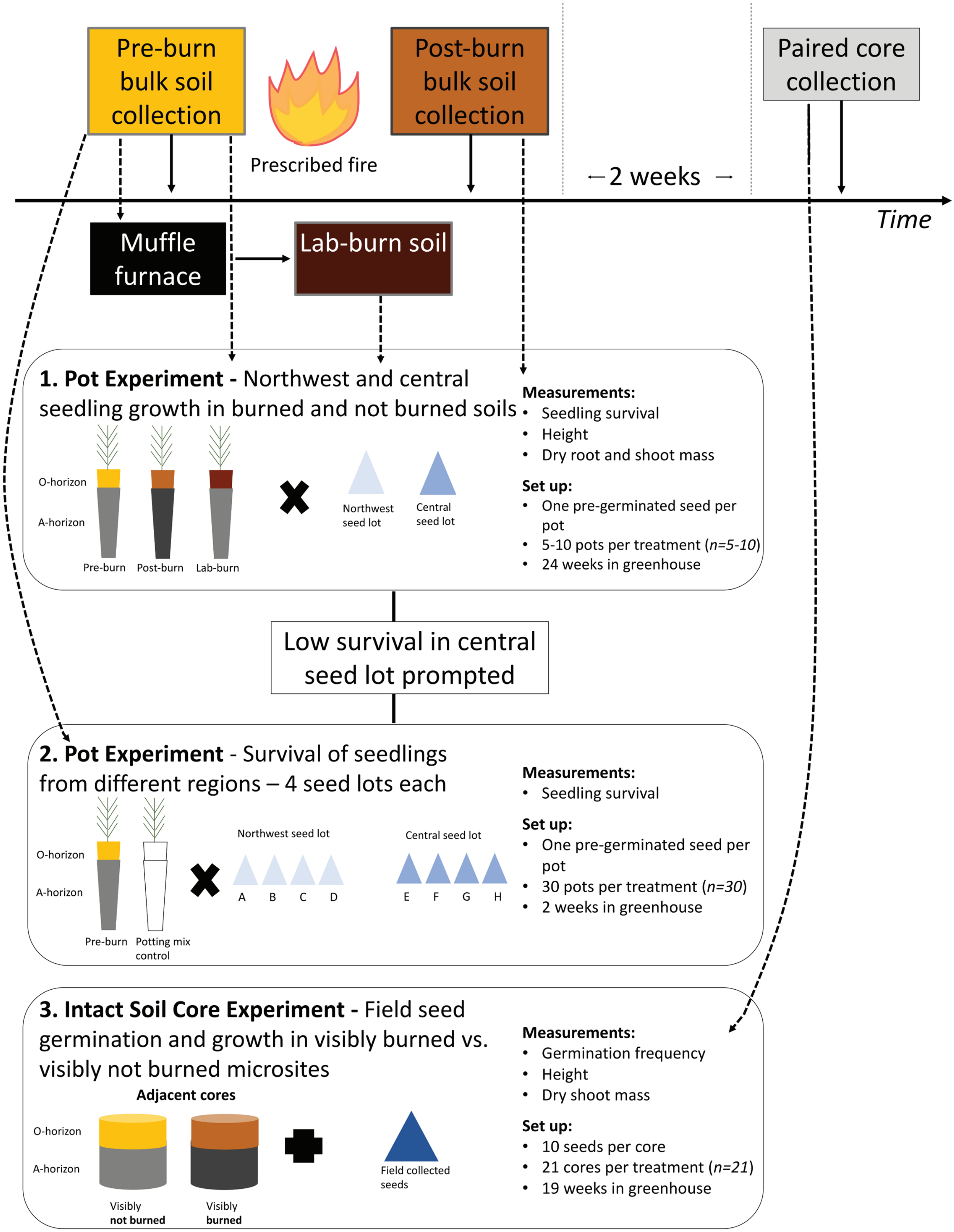


**Fig. 2. Experimental design and timeline of the three experiments carried out. In pot experiment 1, we examined jack pine seedling survival and growth using northwest and central seeds in burned (laboratory and field) and not burned soil. In pot experiment 2, we measured the survival of jack pine seedlings from northwest and central seed regions since central seed regions performed poorly in pot experiment 1. In the intact soil core experiment, we used visibly burned and visibly not burned soil cores from the field to measure jack pine germination and growth.**

before rinsing. We then dried seeds on sterile foil in a laminar flow hood and transferred them to 2% water agar in Petri dishes, which were then incubated in a plant growth chamber at 25°C with an 18-h photoperiod for 14 d. We transplanted the germinated jack pine seeds to the Deepots, with one seedling per pot. For transplanting germinated seeds, we sprayed a glass rod with 70% isopropyl alcohol, air dried it, and then used it to make a hole 1 cm deep in center of the soil surface. We sprayed tweezers with 70% isopropyl alcohol, air dried them, and used them to place one germinated seed in the small hole, radicle down. At the time of planting, the radicles were 3 cm in length or longer. We kept the pots at field capacity by watering to weight every 3 to 4 d and maintained them in the greenhouse for 24 wk. Each week, we took a digital image of each set and recorded heights of germinated seedlings.

After 24 wk, we deconstructed the experiment. We placed the Deepots upright in a large bin of distilled water for 30 min, with water just high enough to cover the soil. We gently extracted surviving seedlings from the soil, patted them dry, and used a paint brush to remove remaining soil from the shoots and roots. We placed seedlings on white paper next to a ruler for a digital image. Using a razor blade, we divided seedlings into roots and shoots and placed each individually into an envelope and dried them at 60°C for 48 h.

To prepare plants for tissue nutrient analysis, we ground each sample of dried roots and shoots separately using a grinding mill (0.6 cm, Thomas Scientific Cyclone Sample Mill, Swedesboro, NJ), including only seedlings that survived for the duration of the experiment. Routine plant tissue analyses for roots and shoots were conducted by the University of Wisconsin-Madison Soil and Forage Analysis Laboratory in Marshfield, WI. Total N was determined using the macro Kjeldahl method (Bradstreet, 1954) and total minerals were determined using nitric acid and hydrogen peroxide digestion (Havlin and Soltanpour, 1980) on an inductively coupled plasma atomic emission spectrometer (Thermo Fisher Scientific iCap 7400 ICP–OES, Waltham, MA).

## Experiment 2: Pot trial—Survival of seedlings from two different regions of Wisconsin in not burned soil

After the first experiment, we needed to determine whether the differences we observed between central vs. northwest seed sources were consistent across seed lots, or just unique to the one seed lot we used from each region. To test this, we designed a second pot experiment comparing four different seed lots for each of the two Wisconsin regions (northwest and central) using the preburn soil from 2.5 (Fig. 2) that had been stored at 4°C in plastic bags. We also used a potting mix treatment as a control (Premier Pro-Mix BX (Pro-Mix, Quakertown, PA); 75 to 85% sphagnum peat moss, with perlite, vermiculite, limestone, and a wetting agent). Although potting mix is an unrealistic growth medium for jack pine trees, our rationale for including it was that if there were differential survival for seed from the two different sources in the potting mix as well as in the soil, then that could strengthen the hypothesis that there may be important differences between the two different seed sources. Second, if the seeds all had poor survival in the potting mix, then that could indicate that some broader contamination or some other problem was affecting the seeds. We packed pots (Ray Leach Cone-tainers, Stuewe & Sons, Inc., Tangent, OR) measuring 3.8 cm in diameter and 13.5 cm in height with a peat plug, and A- and O-horizon soil at field bulk density, as described for the first pot experiment.

We obtained jack pine seeds from four seed lots from northwest Wisconsin and four seed lots from central Wisconsin from the WI DNR and prepared and germinated them for planting as described above (seed lots from the years 2012, 2013, 2014, and 2015 for the northwest and central seeds; Supplemental Table S1). We transplanted one germinated jack pine seed to each pot, as described above, using 30 pots for each seed lot. We maintained pots at field capacity in the greenhouse for 2 wk. After each week, we recorded a digital image, the number of surviving seedlings, and the height of surviving seedlings. We determined mean seed size by taking the mass of 100 seeds from each seed lot.

## Experiment 3: Intact soil cores—Germination of seeds and growth of seedlings from visibly burned vs. visibly not burned microsites

In Experiment 3, we wanted to determine whether there were differences in seed germination and seedling establishment in visibly burned vs. visibly not burned microsites within the fire, at field bulk densities, and with local seeds. We conducted a soil core incubation experiment using paired intact cores and seeds collected at the study site. We placed intact soil cores in PVC cylinders in clear food-grade plastic containers (53 cm by 31 cm by 15 cm) with five cores per container. We grouped soil cores into plastic containers by whether they were visibly burned or not visibly burned, leaving the cheesecloth on the bottom of each soil core. We watered soil cores to field capacity in a greenhouse with an 18-h photoperiod for 2 wk prior to planting. Cores were spaced in a way so as to not affect the moisture content of each other.

To open the field-collected, closed jack pine cones, we heated them in an oven at 100°C for 30 min to open the cones, which was expected to be more than sufficient to open them, but not to affect viability (Beaufait, 1960). Using tweezers, we gently extracted seeds from the cones and evenly distributed ten seeds on surface of the soil of each core. This seeding density was based on the recommendation from the WI DNR Division of Forestry, Reforestation Program. We maintained the soil cores at field capacity in the greenhouse for 19 wk. Each week, we recorded a digital image, the number of seedlings present, and their height.

After 19 wk, we deconstructed the soil core experiment. We cut the seedlings at the soil line and placed seedlings from each core into paper envelopes and dried at 60°C for 48 h. We determined mean dry mass by dividing the total dry mass by the number of individual surviving seedlings at the end of the experiment.

## Data Analysis

We used paired and unpaired *t* tests for two-factor comparisons and multivariate ANOVA tests for multi-factor comparisons,

**Table 1. Properties (means ± SD) of soil sampled before (pre-burn) and after (post-burn) prescribed burn at Coon Fork Barrens and also after burning at 400°C for 10 min in a laboratory muffle furnace (laboratory-burn).**

| Soil property | Pre-burn O horizon | Post-burn O horizon | Laboratory-burn O horizon | Pre-burn A horizon | Post-burn A horizon |
|---|---|---|---|---|---|
| **Soil pH, organic matter, and texture ($n$ = 3)** | | | | | |
| pH | 4.8 ± 0.1 b† | 4.7 ± 0.1 b | 6.4 ± 0.1 a | 5.1 ± 0.1 A‡ | 5.2 ± 0.1 A |
| O horizon (mm; $n$ = 10) | 26 ± 11 a | 28 ± 6 a | NA | NA | NA |
| Organic matter (%) | 5.0 ± 0.2 a | 6.0 ± 1 a | 2.0 ± 0.1 b | 2.0 ± 0.1 A | 2.0 ± 0.1 A |
| Total C (g kg soil$^{-1}$) | 22.2 ± 1.21 b | 35.17 ± 8.2 a | 4.78 ± 0.19 c | 2.9 ± 0.2 B | 11.0 ± 1.2 A |
| Total N (g kg soil$^{-1}$) | 0.95 ± 0.03 b | 1.6 ± 0.4 a | 0.5 ± 0.1 b | 0.21 ± 0.07 B | 0.58 ± 0.03 A |
| C to N ratio | 24 ± 1 a | 22 ± 1 a | 11 ± 1 b | 14 ± 3 B | 19 ± 1 A |
| Sand (%) | 81 ± 2 a | 80 ± 3 a | 85 ± 2 a | 80 ± 2 A | 83 ± 2 A |
| Silt (%) | 4 ± 3 a | 4 ± 2 a | 4 ± 2 a | 4 ± 3 A | 4 ± 2 A |
| Clay (%) | 12 ± 2 a | 14 ± 3 a | 10 ± 2 a | 14 ± 3 A | 13 ± 3 A |
| **Plant-available nutrients and exchangeable Na ($n$ = 3)** | | | | | |
| $NO_3$–N (mg kg soil$^{-1}$) | 1.7 ± 0.1 a | 1.6 ± 0.1 a | 1.5 ± 0.6 a | 1.5 ± 0.2 A | 1.3 ± 0.2 A |
| $NH_4$–N (mg kg soil$^{-1}$) | 13.9 ± 6.9 a | 15.0 ± 7.3 a | 28.4 ± 3.0 a | 6.1 ± 0.7 A | 7.2 ± 0.9 A |
| Plant available K (mg kg soil$^{-1}$) | 64 ± 3 a | 59 ± 2 a | 58 ± 5 a | 27 ± 2 A | 28 ± 1 A |
| Plant available P (mg kg soil$^{-1}$) | 8 ± 1 b | 8 ± 0.1 b | 88 ± 5 a | 6 ± 1 A | 6 ± 1 A |
| Exchangeable Na (mg kg soil$^{-1}$) | 4 ± 0.3 a | 4 ± 1 a | 4 ± 0.1 a | 3 ± 0.1 A | 2 ± 1 A |
| **Elemental composition (XRF) ($n$ = 5)** | | | | | |
| Al (g kg soil$^{-1}$) | 19.1 ± 1.6 a | 16.7 ± 1.1 b | 22. 0 ± 2.7 a | 23.8 ± 0.8 A | 21.8 ± 2.7 A |
| Ca (g kg soil$^{-1}$) | 4. 2 ± 0.9 a | 3.4 ± 1.5 a | 3.2 ± 1.9 a | 0.8 ± 0.4 A | 0.3 ± 0.1 A |
| Fe (g kg soil$^{-1}$) | 8.1 ± 0.9 a | 7.6 ± 1.1 a | 9. 0 ± 2.6 a | 9.1 ± 1.0 A | 9.3 ± 1.0 A |
| Mg (g kg soil$^{-1}$) | 23.3 ± 3.6 a | 21.5 ± 4.2 a | 26.5 ± 3.7 a | 22.1 ± 4.7 A | 24.3 ± 3.2 A |
| Mn (mg kg soil$^{-1}$) | 663 ± 71 a | 609 ± 50 a | 844 ± 313 a | 758 ± 78 A | 748 ± 89 A |
| P (mg kg soil$^{-1}$) | 939 ± 132 a | 759 ± 175 a | 833 ± 283 a | 385 ± 70 A | 331 ± 74 A |
| S (mg kg soil$^{-1}$) | 957 ± 112 a | 789 ± 243 a | 353 ± 188 b | b.d.l.§ | b.d.l. |
| Si (g kg soil$^{-1}$) | 201 ± 19 b | 212 ± 17 b | 237 ± 23 a | 234 ± 16 A | 239 ± 9 A |

† Values followed by different lowercase letters indicate significant differences between O-horizon samples.
‡ Values followed by different uppercase letters indicate significant differences between A-horizon samples.
§ b.d.l., below detection limit.

using Tukey's HSD to test for significant differences between treatments when the ANOVA was found to be significant, in R version 3.4.4 (R Core Team, 2018). In the case of unbalanced design, we used least squares means (*lsmeans* package [Lenth, 2016]) instead of ANOVA. We used the packages *ggplot2* (Wickham, 2009) and *vegan* (Oksanen et al., 2016) for data visualization and analysis, respectively, with an $\alpha$ value of 0.05 for all statistical analyses.

# RESULTS

## Soil Analysis

The prescribed burn did not significantly alter the thickness of the O horizon ($p$ = 0.13). The prescribed burn did not affect most of the measured soil chemical properties when comparing by horizon, including pH, total organic matter, or plant-available P (Table 1). However, numerous chemical properties of laboratory-burned O horizon were significantly different from both the pre- and post-burn O-horizon soils (Table 1). This included a pH increase of 1.6 units, the loss of more than half of its organic matter, almost twice as much $NH_4$–N, and ten-fold more plant available P in the laboratory-burned O-horizon soil as compared with the pre-burn or post-burn O-horizon soils (Table 1).

The post-burn O horizon had significantly more total C than both pre-burn and laboratory-burn soils (Table 1). Laboratory-burned soil also had significantly more total C compared to the pre-burn soil (Table 1). The post-burn O-horizon soil also had significantly more total N when compared to the pre-burn O-horizon and laboratory-burn soil (Table 1).

## Experiment 1: Pot trial—Growth of seedlings from two different regions of Wisconsin in burned and not burned soils

By the end of the 24-wk experiment, there were 30% fewer seedlings from seeds sourced from central Wisconsin still alive compared to seeds sourced from northwest Wisconsin when pooling together pre-, post-, and laboratory-burned soil treatments (Table 2). In the first 2 wk, 90% of pre-burn central Wisconsin seedlings died and 70% of post-burn central Wisconsin seedlings died. There was a significant effect of soil burn status on dry root mass ($p$ = 0.024) and dry shoot mass ($p$ < 0.001); seedlings grown in laboratory-burned soil produced more dry root and shoot mass compared to both the pre- and post-burn soils (Fig. 3). The pre-burn and post-burn soils had no significant differences in their dry root and shoot mass (Fig. 3). Seedlings (from northwest seed)

**Table 2. Percentage of established jack pine seedlings grown from one seed lot from central Wisconsin and one seed lot from northwest Wisconsin seed collection areas (Experiment 1). One surface-disinfested, pre-germinated seed of each of the two lots was planted in each of ten pots with either O- or A- horizon pre-burn, post-burn, or laboratory-burn soils in a greenhouse. Establishment was recorded after 24 wk. Germination details are in Supplemental Table S1 (seed lots G15 [Central] and H15 [Northwest]).**

| Treatment | Seed source | Established seedlings, % | Total seedlings planted |
|---|---|---|---|
| Pre-burn soil | Central | 10 | 10 |
| | Northwest | 80 | 10 |
| Post-burn soil | Central | 30 | 10 |
| | Northwest | 80 | 10 |
| Laboratory-burn soil | Central | 100 | 5 |
| | Northwest | 100 | 5 |

grown in laboratory-burned soil had significantly greater root and shoot mass than in all other soils ($p < 0.05$ for both root and shoot; Fig. 3; Fig. 4, Supplemental Fig. S4).

Due to low biomass of individual seedlings, only one pooled sample for each treatment was analyzed for total nitrogen and total elemental plant tissue analysis, which is insufficient to draw strong conclusions. There were generally not extreme differences in total N, P, and K in roots or shoots among soil treatments, with seedlings from the northwest region in the laboratory-burned soil generally having higher total nutrients due to their larger size (Supplemental Table S2). Total N, P, and K concentrations were also comparable among soil treatments across root and shoot tissues. The N to P ratio for shoots ranged from 12.67 to 19.62, for central seedlings in laboratory-burn soil and northwest seedlings in pre-burn soil, respectively (Table 3). The N to P ratio for roots ranged from 7.47 to 18.83, for central seedlings in post-burn soil and northwest seedlings in pre-burn soil, respectively (Table 3).

## Experiment 2: Pot trial—Survival of seedlings from two different regions of Wisconsin

Seedlings from northwest seed lots consistently had a higher survival frequency (95%) compared to those from central seed lots (73%) in pre-burned soil ($p < 0.001$; Fig. 5; Supplemental Table S1). Seedlings produced from seeds sourced from central Wisconsin had significantly lower survival (73%) in the soil than the potting mix control (91%; $p < 0.01$; Fig. 5; Supplemental Table S1). Seedlings germinated from central seeds died more frequently (30% mortality) compared to seedlings germinated from northwest seeds (4% mortality; Fig. 5; Supplemental Table S1).

## Experiment 3: Intact soil cores—Germination of seeds and growth of seedlings from visibly burned vs. visibly not burned microsites

Seeds in most cores germinated during week 3 of the core experiment. By the end of the core experiment (week 19), there were no significant differences in seed germination frequency ($p = 0.583$; Fig. 6A), seedling height ($p = 0.691$; Fig. 6B), or seedling dry aboveground biomass ($p = 0.315$; Fig. 6C) between visibly burned and not visibly burned soil cores.

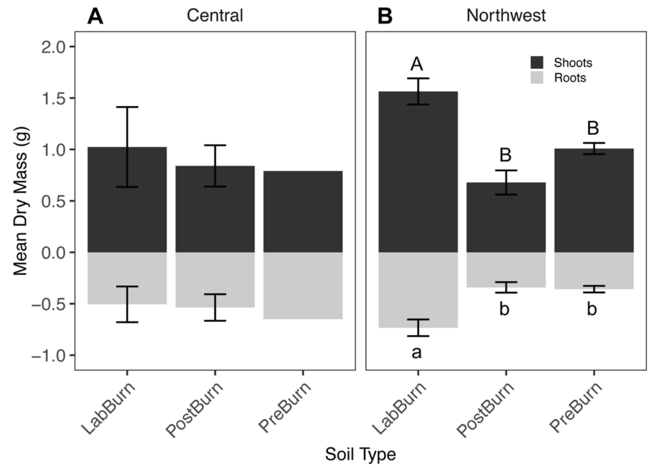


**Fig. 3. Mean dry root and shoot mass from pot experiment one (growth of jack pine seedlings from two different regions of Wisconsin in post-burn, pre-burn, and laboratory-burned soils) at the end of week 24 for seedlings from central (A) and northwest (B) seed sources. Error bars ± 1 SE. Different uppercase or lowercase letters indicate significant differences (lsmeans pairwise comparisons, $p < 0.05$). Central seedlings were not tested for significance due to low survival and error bars are not reported for pre-burn seedlings because $n = 1$; $n = 5/5$ (laboratory-burned), $n = 3/10$ (post-burn), and $n = 1/10$ (pre-burn; Table 2). For seedlings from northwest sources, survival was better; $n = 5/5$ (laboratory-burned), $n = 8/10$ (post-burn), and $n = 8/10$ (pre-burn; Table 2).**

# DISCUSSION

## Jack Pine Produces More Biomass in Laboratory-Burned than Prescribed-Burn Soils

Although seedling biomass in the post-burn soil was not significantly different from the pre-burn soil, jack pine seedlings produced approximately twice as much biomass in the extreme laboratory-burned soil treatment, supporting our hypothesis that more severely burned soils would yield larger seedlings (Fig. 3; Fig. 4). According to the WI DNR Silviculture Handbook, the recommended planting medium for jack pine seeds is bare mineral soil (WI DNR, 2016). With an increased pH and decreased organic matter content, the extreme treatment of the laboratory-burned O-horizon soil more closely resembled bare mineral soil than the post-burn (or pre-burn) soils (Table 1; Moore and Wilson, 2006; Knicker, 2007; WI DNR, 2016). The 10-fold significant increase in available P and increase in $NH_4^+$–N in the laboratory-burn soil are consistent with the observation that high-temperature burns often generate ash that is rich in plant-available nutrients (Gray and Dighton, 2006; Bodí et al., 2014), and suggest an explanation for the observed increase in biomass in the laboratory-burned soils. A previous study of 2-yr-old jack pine seedling tissues found similar macronutrient and micronutrient values in healthy seedlings (Potvin et al., 2014), as did a study that analyzed 1-yr-old jack pine needles (Zhang et al., 2015). Thus, increased nutrient availability in the laboratory-burned O-horizon soil (in particular, P) may have resulted in greater nutrient uptake, as total amount of N, P, K, and other nutrients were higher in plants grown in laboratory-burned soils (due to increased total biomass, not greater concentration in the plant tissues [Table 3; Supplemental Table S3]). In contrast, the effects of the prescribed fire on soil properties were

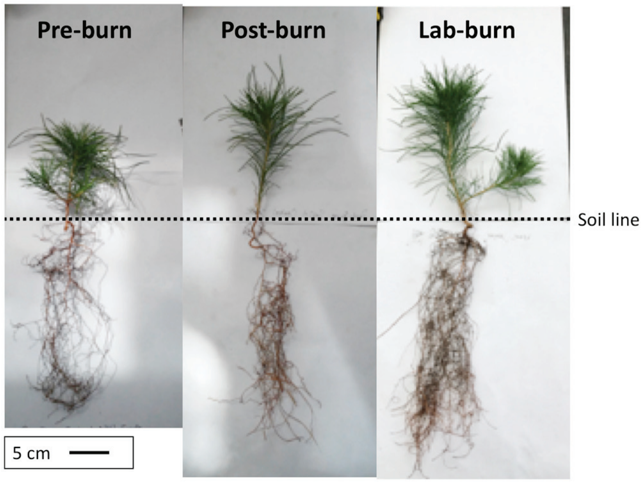


**Fig. 4. Typical jack pine seedlings from northwest seeds at the end of week 24 from pot experiment one (growth of seedlings from two different regions of Wisconsin in pre-burn, post-burn, and laboratory-burned soils).**

generally not detectable, suggesting that the effects of low-severity fires on jack pine seedling establishment are likely due to factors other than changes to soil chemical properties.

## Northwest Outperforms Central Seed Sources

Our study of four different seed lots from each region confirmed that the central seedlings' poor survival in the not burned field soil was likely not simply an effect of a low-quality seed lot (Fig. 5). There are three main factors that could be contributing to the differences in seedling establishment between central- and northwest-sourced seeds: (1) seed size, (2) germinative energy, and (3) known genetic differences in jack pine (within populations and between populations). First, seed size has been noted to be a main factor in determining seedling establishment (Dumroese and Wenny, 1987; Chapin et al., 2014). However, the average seed mass between central and northwest seeds used in this study was not significantly different (Supplemental Table S1). Thus, seed size is not likely the reason for the differences observed in this study for seedling establishment.

Second, differences in germinative energy, the capacity of a seed to produce a healthy, vigorous plant (reported as the percentage of seeds that germinate), is another explanation we considered for the differences observed in both pot experiments (Krugman and Jenkinson, 2008). The germination frequencies we observed (70–75% for central; 54–76% for northwest; Supplemental Table S1) were within range of those reported in the Woody Plant Seed Manual (54–72%) (Krugman and Jenkinson, 2008), but lower than what the WI DNR reported for the seed lots used in this experiment (83–85% for central; 89–93% for northwest; Supplemental Table S1). Because we did not observe consistent differences between the central and northwest seeds in germination frequency, germinative energy is not likely to be a complete explanation for the observed differences in seedling success.

Third, there is known genetic variation between and within jack pine populations on a macro-geographical scale (Yeatman and Teich, 1969; Gundale et al., 2005; Greene et al., 2013), and specifically with regard to seedling traits and establishment (Saenz-Romero and Guries, 2002; Wright et al., 2018). Some of the genetic structure of jack pine populations is likely driven by historical post-glacial migration and climatic disturbances (Naydenov et al., 2005). For the present study, the collection region for central seeds is located in an area that had glaciated earlier than the collection region for northwest seeds (Clayton et al., 2006). These differences in glacial succession may have altered the genetic structure between jack pine found in central and northwest regions of Wisconsin, resulting in differences in seedling establishment. In addition to having poorer establishment, seedlings from the central seed lots in this study also had somewhat lower P and K concentrations than those reported in Potvin et al. (2014) and Zhang et al. (2015). The observed differences in seedling establishment between two different regions may be of interest to land managers when considering what seed to use for the restoration or management of jack pine barrens (if the land manager chooses to reseed after the prescribed fire).

**Table 3. Tissue properties for jack pine seedlings grown from one northwest Wisconsin (NW) and one central Wisconsin (C) seed collection areas (Experiment 1, growth of seedlings from two different regions of Wisconsin in burned and not burned soils). There was not enough dry plant tissue for analyses for the central area seed in pre-burn soil because there was only one seedling surviving at the end of the 24 wk ($n$ = 1). No statistics were run. Total mean nutrient contents per plant are reported in Supplemental Table S2.**

| Plant property | NW seed, Pre-burn soil | C seed, Post-burn soil | NW seed, Post-burn soil | C seed, Laboratory-burn soil | NW seed, Laboratory-burn soil |
|---|---|---|---|---|---|
| | | | **Shoots** | | |
| N (%) | 2.55 | 2.25 | 2.23 | 1.9 | 1.7 |
| P (%) | 0.13 | 0.14 | 0.15 | 0.15 | 0.15 |
| N to P ratio | 19.62 | 16.07 | 14.87 | 12.67 | 11.33 |
| K (%) | 0.72 | 0.45 | 0.47 | 0.41 | 0.48 |
| Ca (%) | 0.44 | 0.35 | 0.36 | 0.3 | 0.3 |
| Mg (%) | 0.23 | 0.22 | 0.24 | 0.2 | 0.21 |
| S (%) | 0.16 | 0.14 | 0.15 | 0.14 | 0.14 |
| Zn (mg kg$^{-1}$) | 97 | 96 | 101 | 99 | 97 |
| Mn (mg kg$^{-1}$) | 881 | 698 | 513 | 858 | 923 |
| B (mg kg$^{-1}$) | 21 | 23 | 22 | 56 | 22 |
| Fe (mg kg$^{-1}$) | 58 | 51 | 46 | 41 | 41 |
| Cu (mg kg$^{-1}$) | 6 | 6 | 6 | 5 | 5 |
| | | | **Roots** | | |
| N (%) | 2.26 | 1.27 | 1.72 | 1.7 | 1.89 |
| P (%) | 0.12 | 0.17 | 0.2 | 0.14 | 0.15 |
| N to P ratio | 18.83 | 7.47 | 8.60 | 12.14 | 12.60 |
| K (%) | 0.62 | 0.45 | 0.69 | 0.46 | 0.5 |
| Ca (%) | 0.35 | 0.31 | 0.39 | 0.33 | 0.32 |
| Mg (%) | 0.23 | 0.22 | 0.25 | 0.16 | 0.18 |
| S (%) | 0.16 | 0.19 | 0.23 | 0.17 | 0.2 |
| Zn (mg kg$^{-1}$) | 90 | 207 | 175 | 79 | 84 |
| Mn (mg kg$^{-1}$) | 823 | 453 | 373 | 488 | 573 |
| B (mg kg$^{-1}$) | 37 | 38 | 42 | 33 | 38 |
| Fe (mg kg$^{-1}$) | 661 | 1061 | 1097 | 643 | 803 |
| Cu (mg kg$^{-1}$) | 11 | 23 | 33 | 12 | 13 |

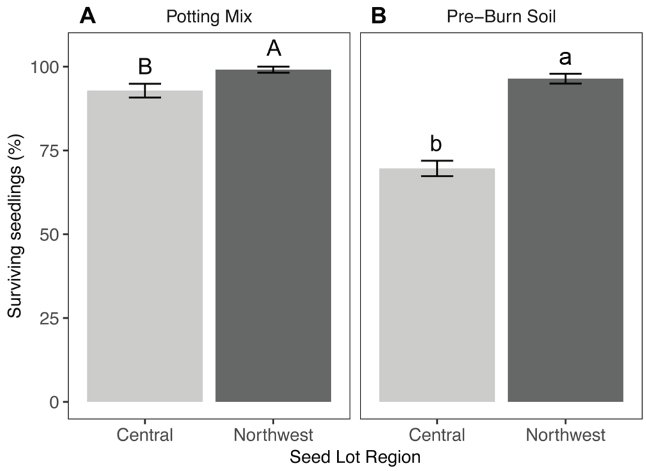


**Fig. 5. Percentage of jack pine seedlings surviving after 2 wk in pot experiment two (survival of seedlings from two different regions of Wisconsin) in potting mix control (A) and pre-burn field soil (B). There were four seed lots from central Wisconsin (light gray) and four seed lots from northwest Wisconsin (dark gray). Error bars ± 1 SE. Different uppercase or lowercase letters indicate significant differences (*t* test, $p < 0.05$). $n$ = 4 seed lots (30 seeds per seed lot). Potting mix was included as a control treatment.**

Different historic fire regimes of central and northwest Wisconsin may also play a role in generating genetic differences in jack pines. Central Wisconsin historically had more frequent, less severe fire compared to the more lethal fires in northern Wisconsin (Radeloff et al., 2004). Although the prescribed fire in this study likely resembled the historical fire regime of central Wisconsin more than that of northwest Wisconsin, central seedlings did not establish well in the pre- or post-burned soils. However, in the laboratory-burned soil, they had the same survival frequency as the northwest seedlings in the packed pot seedling success experiment (Table 2). Central seeds are more likely to be from non-serotinous trees, but, based on the findings here, may still grow larger and survive at higher rates in severely burned soil. Overall, severely burned soils promoted jack pine seedling performance regardless of seed source location.

## Seed Germination and Seedling Aboveground Mass was Not Affected by Prescribed Burning in Intact Soil Cores

Our goal in the intact soil core experiment was to best represent the natural soil and seeds available at Coon Fork Barrens (but excluding the effects of climate in this greenhouse study). The lack of differences in the germination frequency, survival frequency, height, or dry aboveground biomass of jack pine seeds planted in visibly burned vs. not visibly burned soil cores (Fig. 6) suggest that jack pine germination and establishment may not be improved by changes in soil properties due to low-intensity prescribed fire that is designed to create more openness for native prairie plants. This is not surprising, given that this low-intensity prescribed burn seemed to have little impact on fundamental soil chemical properties belowground. In addition to having minimal effects on soil chemical properties, low-intensity ground fires may not produce flames and heat that are sufficient to liberate

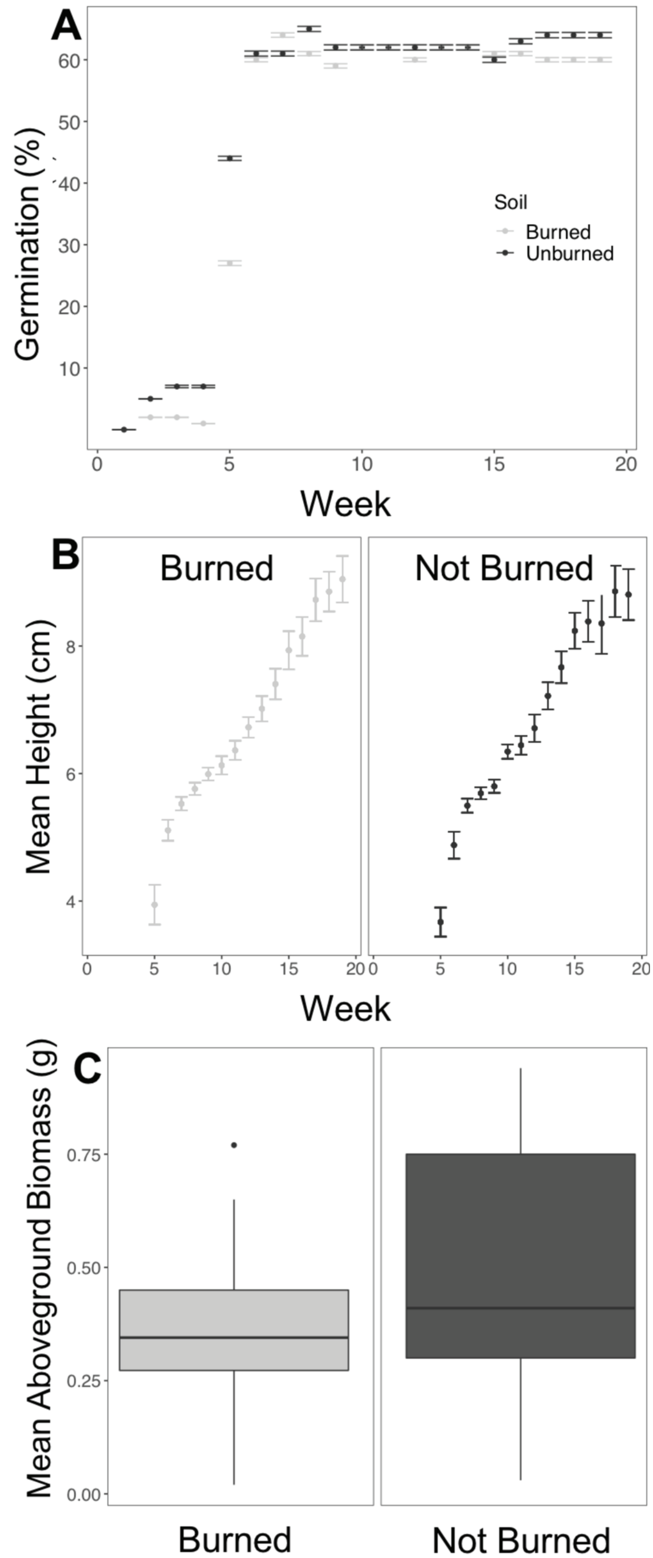


**Fig. 6. Results from soil core Experiment 3. (A) Number of individual jack pine seeds germinated over 19 wk maintained in the greenhouse. Error bars represent ± 1 SE. $n$ = 21. (B) The mean height of jack pine seedlings over 19 wk maintained in the greenhouse. Error bars represent ± 1SE. $n$ = 21. (C) The mean aboveground dry mass of jack pine seedlings at the end of week 19.**

seeds enclosed in serotinous cones in tree crowns (Saenz-Romero and Guries, 2002; Radeloff et al., 2004; WI DNR, 2016), which would mean the efficacy of only using low-intensity prescribed fires to regenerate jack pine may be limited. However, other effects of fire, such as seed release, changes to moisture dynamics, or competition were not tested in this study, and could be expected to have effects on jack pine germination and establishment.

## CONCLUSIONS

Small differences in abiotic and biotic factors may be causing genetic differences among jack pine populations in Wisconsin, which resulted in the observed lower survival frequency overall for seeds from seed lots sourced from central Wisconsin as compared to those from northwest Wisconsin. Studies designed to fully characterize the nature and extent of these differences, as well as the ecological implications of these differences between populations, could be a useful next step.

Land managers in Wisconsin are interested in using prescribed fires to help restore or maintain the jack pine barrens, a fire-dependent ecosystem. Prescribed fire may affect jack pine seedling germination and establishment through numerous mechanisms. For the low-severity prescribed fire considered in this short-term study (24 and 19 wk), effects on measured soil properties were minimal, and did not result in any improvement to seedling establishment, suggesting that the effects of low-severity fires on seedling establishment are likely due to factors other than changes to soil chemical properties. However, the extreme laboratory-burned treatment did result in significant changes to soil chemical properties, including pH, available P, and organic matter content. Thus, for soil properties to play an important role in promoting jack pine seedling growth, hotter fires may be required, while lower-severity fires will require other effects, such as seed release, changes to moisture dynamics, or competition to affect jack pine germination and establishment. Additionally, there are likely interactions with burn severity and burn return interval, which could alter the cumulative effects of fire on soil physical, chemical, and biological properties (Neary et al., 1999; Certini, 2005; Knelman et al., 2015; Sawyer et al., 2018; Alcañiz et al., 2018). Before recommending the integration of our findings into management practices, they should be complemented by further field studies, where the effects of existing seed banks, post-fire seed release, changing water dynamics and other microclimatic effects, competition from other plants, and other possible effects of fire that were not included in this study could be accounted for.

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## SUPPLEMENTAL MATERIAL

Supplemental material associated with the manuscript is available with the online version of this article. Code and data associated with the manuscript are available at www.github.com/WhitmanLab/Jack_Pine.

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