Postfire growth of seeded and planted big sagebrush—strategic designs for restoring greater sage-grouse nesting habitat

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Wildfires change plant community structure and impact wildlife habitat and population dynamics. Recent wildfire-induced losses of big sagebrush (Artemisia tridentata) in North American shrublands are outpacing natural recovery and leading to substantial losses in habitat for sagebrush-obligate species such as greater sage-grouse. Managers are considering restoration strategies that include planting container-grown sagebrush to improve establishment within areas using more conventional seeding methods. Although it is thought that planting sagebrush provides initial structural advantages over seeding, empirical comparisons of sagebrush growth are lacking between individuals established postfire using both methods. Using a Bayesian hierarchical approach, we evaluated sagebrush height and canopy area growth rates for plants established in 26 seeded and 20 planted locations within the Great Basin. We then related recovery rates to previously published nesting habitat requirements for sage-grouse. Under average weather conditions, planted or seeded sagebrush will require 3 or 4 years, respectively, and a relatively high density (≥2 plants/m²) to achieve the minimum recommended canopy cover for sage-grouse (15%). Sagebrush grown in warmer and drier conditions met this cover goal months earlier. Although planted sagebrush reached heights to meet sage-grouse nesting requirements (30 cm) 1 year earlier than seeded plants, seeded individuals were approximately 19 cm taller with 410 cm² more canopy area than planted sagebrush after 8 years. However, big sagebrush establishment from seed is unreliable. Strategically planting small, high-density patches of container-grown sagebrush in historic sage-grouse nesting habitat combined with lower density seedings in larger surrounding areas may accelerate sage-grouse habitat restoration.

Key words: Artemisia tridentata, canopy area, density, growth rate, height, high-density patches

Implications for Practice

- Transplants of big sagebrush can achieve the minimum height and cover requirements for greater sage-grouse nesting habitat nearly 1 year faster than seeded individuals, but high plant densities (≥2 plants/m²) may be required to create the necessary nesting cover.
- Strategically planting high-density patches of container-grown sagebrush within historical nesting areas may benefit sage-grouse populations in locations where large wildfires have removed most or all big sagebrush plants.
- Combining high-density planted patches with seedings (possibly over multiple years), or with less dense planted patches that cover larger areas, will likely facilitate achieving landscape habitat requirements for greater sage-grouse, as well as habitat for other sagebrush obligate species.

Introduction

Ecosystem disturbances, invasive species, and climate change may result in major shifts in plant community composition, structure, and function across the globe (Nolan et al. 2018).
For some shrubland ecosystems, natural disturbances like wildfire may cause these shifts by removing dominant woody species and altering the dominance hierarchy toward herbaceous plants that tolerate fire. Time required for a return to shrub dominance differs depending on the plant community, species’ resistance to fire (i.e., the ability to survive fire or root-sprout), and natural fire regimes (Pyke et al. 2010). For example, burned sites in chaparral vegetation can return to shrub communities within a decade because of the shrubs’ rapid resprouting ability (Keeley et al. 2012), whereas shrublands in the semiarid intermountain region of western North America may require a century for the fire-intolerant big sagebrush (Artemisia tridentata Nutt., Asteraceae) to recover dominance (Miller et al. 2013).

The speed of recovery to big sagebrush dominance after a wildfire depends in part on: (1) wildfire size; (2) the number and distribution of unburned patches of sagebrush within the wildfire perimeter; and (3) sagebrush seed availability and its distribution across the burn area (Baker 2011). On average, wildfires in big sagebrush ecosystems combat all plants on 80% of the area within the wildfire perimeter, and introductions of invasive annual grasses into these plant communities have likely led to fewer or smaller unburned patches within these wildfires (Baker 2013). Big sagebrush is incapable of regrowth from wood older than 1 year (Cook & Stoddart 1960), therefore, seed banks or seed dispersal are necessary for natural recovery.

Big sagebrush seed banks and seed dispersal are unreliable for providing quick plant establishment and cover after wildfires. Seed banks are typically exhausted by summer when wildfires occur (Young & Evans 1989; Meyer 1994; Allen et al. 2008) and those few remaining seeds must be deep enough to survive a fire’s lethal temperatures, but close enough to the soil surface to allow emergence from the soil and survival (McArthur & Stevens 2004; Allen et al. 2008). A fraction of seeds can remain in the seed bank until later years (Wijayratne & Pyke 2012), but such small resulting populations are unlikely to be viable in the long term (Shriver et al. 2019). Cooler and moister sites, like those supporting mountain big sagebrush, tend to foster more resilient communities capable of establishing populations from seed banks; however, it often requires decades to achieve 15% cover (Ziegenhagan & Miller 2009; Baker 2011; Miller et al. 2013; Nelson et al. 2014; Roundy & Madsen 2016; Shriver et al. 2019), a minimum level for nesting habitat of greater sage-grouse (Centrocercus urophasianus; hereafter, sage-grouse), a sagebrush-obligate species (Connelly et al. 2000; Coates et al. 2017).

Without seed banks, remnant unburned sagebrush plants must provide seed sources for recovery. However, annual seed production varies widely from nearly zero in some years to millions of seeds per plant in others (Young et al. 1989; Evans et al. 1991). Maximum seed dispersal is 30 m (Daubenmire 1975; Frischknecht 1978) with most seeds falling to the soil near a plant’s canopy (Young & Evans 1989). Given these constraints on natural recovery of big sagebrush on burned lands, land managers often use active means of sagebrush restoration to prevent loss of habitat for numerous wildlife species, especially those that are sagebrush obligates (Pyke 2011).

Historically, active restoration of vegetation in sagebrush ecosystems, particularly in sagebrush steppe of the Great Basin, has been associated with the U.S. Bureau of Land Management’s (BLM) Emergency Stabilization and Burned Area Rehabilitation program where big sagebrush has increasingly been a component in seed mixtures (Pilliod et al. 2017). However, most studies of management-scale restoration of big sagebrush have found that 1–2 decades posttreatment, sagebrush cover tends to be low to absent, or that cover did not differ from that of unseeded areas within the same wildfire, especially in areas with low annual precipitation (Knutson et al. 2014; Pilliod et al. 2017; Copeland et al. 2018; Shriver et al. 2019). Recently, planting container-grown big sagebrush has become a more common restoration practice in the Great Basin (see table 2 in Pilliod et al. 2017) and these projects yield 15 to 80% survival of plants (Evans & Young 1990; Dettwiler-Robertson et al. 2013; McaDoo et al. 2013; Davidson et al. 2019). However, the higher cost per area of planting big sagebrush has restricted plantings to smaller areas compared to seedings (Welch 2005).

Natural resource managers are presented with these trade-offs when restoring big sagebrush habitat for sagebrush-obligate wildlife (Pyke 2011; Arkle et al. 2014). Sage-grouse, a relatively short-lived sagebrush-obligate bird, is widely thought of as an indicator species for health of sagebrush ecosystems owing to their relatively large annual home ranges (up to 615 km²; Connelly et al. 2011) consisting of a diverse array of plant communities used to meet life-history demands throughout their annual cycle (Rowland et al. 2006; Runge et al. 2019; Pilliod et al. 2020). Sage-grouse have experienced long-term population declines as a result of an array of environmental and anthropogenic stressors. Wildfire is a major driver of sage-grouse declines across larger spatial extents, collectively degrading substantial portions of sagebrush ecosystems (Schroeder et al. 2004; Coates et al. 2016; Doherty et al. 2016). Sage-grouse nest-site vegetation structure, nest selection, and brood survival vary along gradients of ecological site potential (Coates et al. 2017). Despite this variability, established guidelines for nesting habitat suitability (e.g., minimum sagebrush heights >30 cm and canopy cover >15%; Connelly et al. 2000; Coates et al. 2017) could serve as common goals for big sagebrush habitat restoration, especially in areas critical for nesting habitat (e.g., within 5 km of leks; Schroeder & Robb 2003; Connelly et al. 2011; Coates et al. 2013; Foster et al. 2019). The unpredictability of big sagebrush establishment from traditional seeding methods has led agencies to consider and sometimes use combinations of seeding and transplanting of container-grown plants (hereafter, “planting”) for restoration of wildlife habitat (Pilliod et al. 2017).

Planted big sagebrush may provide an advantage in achieving structural habitat (i.e., height and cover) more quickly than seeded plants, largely because planted individuals have at least an initial year of growth before being planted into the field. If planted and seeded sagebrush individuals are planted or sown in the same year, achieved adequate density, and have similar age-specific growth rates, then planted individuals might achieve height and cover habitat goals more quickly than seeded individuals. However, studies of other species found that the initial size advantage of planted individuals only lasted a few years,
with some species exhibiting slower growth rates when planted than when seeded (McCreary 1995; Welch 1997; Young & Evans 2005). Growth rates of planted and seeded big sagebrush individuals in management-scale projects are unknown.

We hypothesized that the initial size advantage of planted big sagebrush will allow areas to meet minimum nesting habitat goals (i.e. ≥15% cover and plants ≥30 cm tall) for sage-grouse sooner than in seeded areas. In addition, we hypothesized that the growth rate of seeded big sagebrush is greater than that of planted individuals during the first 10 years of life, ultimately leading to seeded plants catching, and potentially surpassing, the growth of planted individuals. We discuss our findings as they relate to restoring nesting habitat for sage-grouse, including establishment probabilities, big sagebrush density, and the strategic placement of these two forms of big sagebrush restoration across lands recently burned in wildfires.

**Methods**

**Study Area**

Sites were selected subjectively through a stepwise process in 2015. Initially, we identified all possible postfire BLM restoration projects conducted in the Great Basin that were either seeded or planted with Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis Beetle and Young) or mountain big sagebrush (A. tridentata ssp. vaseyana (Rydb.) Beetle) (Pilliod & Welty 2013). Projects containing both seeding and planting on the same area were eliminated from further consideration. Restoration practitioners may have used a variety of container types for planted individuals among sites, but typically these plants were 1- to 2-year-old nursery-grown plants grown in cone-tainers (e.g. 3.8 cm diameter and 21 cm depth) and planted using standard techniques (Shaw 2004).

We stratified these sites into age-since-planting or -seeding and into categories of sagebrush ecosystem resilience and resistance (R&R) by categorizing the potential dominant soil temperature and moisture regimes within the project’s restoration area (Maestas et al. 2016). Resistance to annual grass invasion and resilience to disturbance and stress (Chambers et al. 2014), when coupled with soil temperature and moisture, are recognized as strong drivers influencing sagebrush establishment (Shriver et al. 2018, 2019). Applying these criteria resulted in 26 seeded and 20 planted sites with similar R&R classes, elevations, and climates (Figs. 1 and 2; Tables 1 and 2). Planted plots were less likely to occur in moderate to high R&R categories because seedings were considered more likely to be successful (and thus more cost-effective) in these cooler and moister environments and because these locations tend to occur at higher elevations with steeper slopes where planting is more difficult (Chambers et al. 2014). Despite this trend, plots from one of the planted sites were at the highest elevations (Table 2). This appears to cause a skewed distribution of planted plot elevations since other quantiles show lower elevation for planted than seeded plots. Long-term mean monthly air temperatures were similar between seeded and planted plots, but long-term mean winter precipitation was slightly greater on planted plots, which were also slightly drier in summer months, perhaps due to the greater range of elevations among planted sites (Fig. 2). The sites ranged in time-since-seeding or -planting from 2 to 10 and 2 to 13 years, respectively.

**Sampling**

Plots within each site were sampled in locations with successfully established big sagebrush plants to facilitate growth rate comparisons. We identified potential plot locations within big sagebrush patches (approximately 1 ha or larger) using two sources: (1) visual inspection of images from the National Agriculture Imagery Program (U.S. Department of Agriculture, Farm Service Agency), and (2) discussions with local BLM staff who knew locations of established and surviving big sagebrush. Field crews verified that these areas had big sagebrush and then navigated to a point randomly placed near the center of the patch using GPS devices. Crews then established a 50-m radius plot and determined if there were at least 10 big sagebrush individuals from the initial seeding or planting in the plot. Plant size and structural cues (e.g. main stem diameter, numbers of branching main stems) were used to subjectively categorize big sagebrush individuals into: (1) unburned residual plants; (2) plants from the original seeding or planting; or (3) offspring from plants in the original seeded or planted individuals. If plots had residual plants, crews rejected the plot and went to the next potential plot location. If plots had at least 10 plants from the original seeding or planting, the plot was retained and heights (cm) of each individual big sagebrush were measured from the soil surface of the main stem to the highest portion of nonreproductive growth. Two canopy diameters were also measured (the longest diameter and the longest diameter that was perpendicular to the first diameter) and used to estimate canopy area using the formula of an ellipse.

**Analyses**

We attempted to identify big sagebrush subspecies using field-based morphometrics, but when we compared our field crew’s subspecies identification of the same individual plants that underwent genetic analyses for subspecies identification, we found poor correspondence (M.J. Germino, personal observation), convincing us to combine subspecies for analyses. Misidentification of subspecies using morphometrics appears to be related to hybridization or polyploid formations among and within subspecies that yield overlapping subspecies structures (Richardson et al. 2012; Garrison et al. 2013).

Plots, rather than sites, were used as experimental units because plots within sites had similar variation in environmental conditions to the variation of sites across the Great Basin. This similarity in environmental variation is because most of these wildfires and their associated treated areas spanned a wide range of environmental conditions (e.g. soils, elevations, temperatures, and precipitations across thousands of hectares). In addition, this allowed us to retain plot-level mean annual temperature and precipitation (MAT and MAP; 30-year
averages using PRISM 2010) in our models to examine them as covariates. We present the site-level analyses and model results in the supporting information (Supplement S1, Figs. S1-S3).

We fit a Bayesian hierarchical regression using JAGS (Plummer 2003) in R (version 3.6.0; R Core Team 2019) to quantify differences in size (canopy area and height) and growth trajectories of planted and seeded big sagebrush. Hierarchical regression allows us to share information across plots through partial pooling, thus maximizing data and improving overall inference, while also acknowledging that differences among plots (e.g. climate, edaphic effects) are likely to influence the growth, and thus the final sizes, of individuals. The model was:

$$y_{id} \sim N(\beta_0 * I(d) + (\beta_1 * d + \beta_2 * I(d)) * T_d, \sigma^2)$$

Table 1. The number and percentage of plots in Great Basin soil temperature and moisture regimes and their associated resilience and resistance classes from Chambers et al. (2014).

| Temperature-Moisture Regime Class | Resilience | Resistance | Seeded Plots | Planted Plots | % Seeded | % Planted |
|-----------------------------------|------------|------------|--------------|---------------|-----------|-----------|
| Cryic-Xeric                       | Moderately high | High       | 4            | 0             | 3         | 0         |
| Frigid-Xeric                      | Moderately high  | Moderate   | 30           | 14            | 23        | 15        |
| Mesic-Xeric                       | Moderate     | Moderately low | 6    | 15            | 19        | 9         |
| Frigid-Aridic                     | Low         | Moderate   | 25           | 8             | 5         | 16        |
| Mesic-Aridic                      | Low         | Low        | 68           | 54            | 51        | 59        |
| Total                             |             |            | 133          | 91            | 100       | 100       |
Table 2. Elevation distributions of the 1,285 seeded and 1,346 planted big sagebrush plots in the Great Basin, United States.

| Treatment | Minimum | P10th | Median | P90th | Maximum |
|-----------|---------|-------|--------|-------|---------|
| Seeded    | 1,024   | 1,107 | 1,745  | 2,150 | 2,348   |
| Planted   | 721     | 957   | 1,409  | 1,939 | 2,495   |

$$\beta_{1,d} \sim N(\alpha_0 + \alpha_1 MAT_d + \alpha_2 MAP_d, \tau^2)$$

$$I(d) = \begin{cases} 
0 & \text{if } d \text{ is seeded} \\
1 & \text{if } d \text{ is planted} 
\end{cases}$$

where \( y_{i,d} \) is the size of individual \( i \) in plot \( d \), \( T_d \) is the number of years since seeding or planting, \( MAT_d \) and \( MAP_d \) are the plot mean annual temperature and precipitation, respectively (1981–2010; PRISM 2010), and \( \beta \) & \( \alpha \) are fit parameters describing starting sizes, growth rates, and the effects of climate. \( \tau^2 \) is the uncertainty associated with plot-specific growth rates after accounting for \( MAT_d \) and \( MAP_d \), and \( \alpha^2 \) accounts for any remaining uncertainty leading to different size in individual plants. \( MAT_d \) and \( MAP_d \) were centered and standardized for model fitting to improve convergence.

The model has two biological components. First, we used an intercept term (\( \beta_0 \)) describing the starting size of a plant in the year of seeding or planting. The starting size was assumed to be 0.0 cm for seeded plants, while \( \beta_0 \) was a parameter fit to the data to describe the mean starting size of all planted individuals, since individuals were planted by different crews in different years and initial sizes were unknown. Second, a plot-specific mean annual growth rate, \( \beta_{1,d} \), was estimated and allowed to consistently differ in seeded and planted plots based on \( \beta_2 \), which describes the average difference between growth rates of seeded and planted individuals. We report the posterior probability of seeded and planted individuals having the same growth rate given the same MAT and MAP based on the overlap of \( \beta_2 \) with 0. Plot-specific starting sizes (intercepts) or nonlinear relationships are not identifiable given that size measurements were only taken at one time in each plot. Our simplification that starting sizes do not vary, on average, across plots while growth rates do was based on our knowledge that planted individuals typically come from common container stock or are grown using similar methods and thus have similar starting sizes, while plot characteristics (climate, soils, etc.) influencing a growth rate can vary substantially. Still, we can estimate our uncertainty in the starting size of planted individuals as the posterior of \( \beta_0 \). Sagebrush heights were untransformed and provided a linear size-time relationship, but canopy area was square-root-transformed to linearize the size-time relationship.

We used two metrics to summarize differences in sizes and growth rates in planted and seeded individuals. First, the posterior distribution of \( \beta_2 \) summarizes the average difference in growth rates between seeded and planted individuals. If the 95% Bayesian credible intervals (CrI) estimates of \( \beta_2 \) did not overlap zero, we concluded that growth rates were significantly different on average between planted and seeded plants. Second, assuming plants were grown in the same plot (i.e. same \( \beta_{1,d} \), we calculated the posterior distribution for the number of years required for seeded and planted individuals to reach the same size, on average as \( \beta_0 - \beta_2 \), by iterating through all of the Markov chain Monte Carlo draws of \( \beta_0 \) and \( \beta_2 \). This approach provides robust estimates of uncertainty by integrating over the posterior distribution of both starting sizes of planted individuals (\( \beta_0 \)) and the average growth rate differences in seeded and planted individuals (\( \beta_2 \)). If long-term average temperature and precipitation at the plot were significant, then we evaluated these responses across a range of temperature and moisture regimes described by R&R categories (Chambers et al. 2014; cool, moist sites = High R&R; warm, dry sites = Low R&R). We ran the model using precipitation and temperature for the 90% quantile for precipitation and 10% quantile for temperature (High R&R) and contrasted the results with those from 10% quantile for precipitation and 90% quantile for temperature (Low R&R).

**Results**

Planted individuals had greater height and canopy area than seeded big sagebrush for the first approximately 4–5 years (Fig. 3, 4B). After year 5, canopy area of the two forms of big sagebrush continued to increase and diverge slightly through year 8 (\( \bar{x}_{\text{planted}} = 2,460 \text{ cm}^2; \bar{x}_{\text{seeded}} = 2,870 \text{ cm}^2 \)). Canopy area growth rates, however, were greater for seeded than planted individuals over these same times (45 vs. 38 cm²/year; Fig. 4A).

Height growth rates were also greater for seeded than planted individuals (Fig. 4A) with seeded individuals growing nearly 5 cm taller than planted individuals each year prior to year 5.

Figure 2. Monthly mean temperature (solid lines; primary y-axis) and monthly mean precipitation (thick dashed lines; secondary y-axis) of the 30-year averages (1981–2010) for plots at seeded (orange) and planted (blue) sites across the Great Basin, United States (PRISM 2010). Thin dashed lines indicate the first and third quartile for values across all seeded plots. Corresponding values for planted sites were omitted for clarity.
By year 5, seeded big sagebrush exceeded heights of planted individuals (Fig. 4B) and by year 8 seeded plants were expected to be nearly 19 cm taller than the planted big sagebrush.

Assuming average climate conditions for plots, planted big sagebrush attained minimum heights for sage-grouse habitat (30 cm) 3–4 years after planting, about 1 to 2 years earlier than seeded plants (Fig. 3). However, the overall growth rate of big sagebrush, and thus time to reach sage-grouse nesting habitat guidelines varied based on location and climate conditions (i.e. $\beta_1$, $d$). Big sagebrush growing at locations classified as having Low R&R achieved the minimum height for sage-grouse nesting habitat about 1 year sooner than at High R&R sites (Table 3). After 3–4 years (depending on R&R category), both planted and seeded big sagebrush individuals achieved a canopy area of 750 cm$^2$ per individual, which corresponds to the minimum nesting cover guideline of 15% assuming densities of two individuals per m$^2$ (Table 3).

**Discussion**

To our knowledge, this is the first study to empirically relate posttreatment performance of individuals of big sagebrush established from seeds and from container-grown plants and to determine how quickly these plants might achieve minimum wildlife habitat guidelines for nesting sage-grouse. Methods that promote speedy sagebrush recovery are highly beneficial because of multiple unique life-history characteristics of sage-grouse. For example, sage-grouse are a relatively short-lived species (typically <7 years) based on their annual survival of approximately 50% (Connelly et al. 2011) that rely heavily on periods of increased reproduction to maintain populations (Taylor et al. 2012). Additionally, sage-grouse tend to have high fidelity for nesting locations (Schroeder & Robb 2003; Foster et al. 2019), even in areas that have experienced large-scale wildfires (O’Neil et al. 2020). Because populations are largely threatened by habitat loss following wildfires (Coates et al. 2016), expedited restoration of big sagebrush cover, a key

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**Figure 3.** Canopy area (square root) and height of individual big sagebrush (dots; *Artemisia tridentata* ssp. *vaseyana* and *wyomingensis* combined) individuals and the fitted mean assuming average MAT and MAP from across all sampled individuals (solid line ±95% CI dashed lines) relative to the number of years since planted (blue; $n = 1,346$) or seeded (red; $n = 1,285$) at several sites in the Great Basin, United States, in a space-for-time analysis of growth.

**Figure 4.** (A) Posterior distributions for the difference in growth rates (i.e. $\beta_2$ cm/year) between seeded and planted sagebrush individuals for canopy area (in its square-root-transformed values) and height. Values below zero indicate slower growth rates in planted individuals. (B) Posterior distributions for the number of years required for planted and seeded plants to have the same average size (canopy area and height) when holding temperature and precipitation constant. Blue shaded regions cover the 95% CI of each distribution, and the vertical blue line is the median.
component to sage-grouse nesting habitat (Connelly et al. 2000; Coates et al. 2017), is necessary (Pyke 2011). Ideally, restoration actions should result in plant communities that meet nesting habitat guidelines (i.e. sagebrush at least 30 cm tall and providing at least 15% cover) in a timely manner conducive to sage-grouse demography (Connelly et al. 2000; Coates et al. 2017).

Our hypothesis that planted big sagebrush will attain minimum habitat guidelines for sage-grouse more quickly than seeded individuals, given similar climates, was supported for height (1 year earlier, at about 3 vs. 4 years), however, seeded plants eventually grew taller than planted individuals because of their greater growth rate. For canopy cover, however, we found that the guideline of 15% cover for sage-grouse nest sites requires a density of at least 2 plants/m² and nearly 4 years to achieve, but either seeding or planting have the potential of achieving nesting cover in this time frame, assuming equal survival of seeded or planted individuals.

Restoring sage-grouse nesting habitat through seedings of big sagebrush after wildfires has been unlikely and unpredictable (Arkle et al. 2014), due mostly to weather constraints leading to poor initial big sagebrush establishment (Shriver et al. 2018) and demographic processes (i.e. transient dynamics) leading to extirpation of many populations even after they initially establish (Shriver et al. 2019). Poor establishment of seeded sagebrush has also been attributed to competitive suppression of sagebrush seedlings by existing native plants or invasive annual grasses during their first 2 years of growth (Reichenberger & Pyke 1990; Madsen et al. 2016a; Germino et al. 2018).

Although some studies have demonstrated successful big sagebrush establishment from seeds for various case studies using small research plots (e.g. Schuman & Belden 2002; Hild et al. 2006; Ott et al. 2017), translating this success to larger management-scale projects has been documented, but as a low proportion of implemented efforts (Knutson et al. 2014; Shriver et al. 2019). Publication bias toward restoration success was common until recently (Zedler 2007), and may contribute to a lack of case studies reporting failures (Hardegree et al. 2011). High seeding rates might increase the densities of surviving big sagebrush (Pyke & Archer 1991). However, improved equipment and germination or emergence enhancement techniques (Madsen et al. 2016a, 2016b; Ott et al. 2017; Davies et al. 2018; Hoose et al. 2019) may be necessary to achieve predictable establishment. These new establishment techniques also need to be proven effective in creating predictable densities as quickly as possible and at management-relevant scales.

Restoration projects using planted individuals provide opportunities to avoid this bottleneck.

Planted big sagebrush tend to have better establishment and survival than seeded plants and can achieve 15–30% survival by the third year following planting (Welch 1997; Dettweiler-Robertson et al. 2013; McAdoo et al. 2013; Davidson et al. 2019). In addition, planting pattern and density can be easily manipulated to create cover in targeted locations for nest habitat recovery around known lek sites because sage-grouse typically nest near leks (<5 km; Coates et al. 20013). Previously studied big sagebrush plantings were implemented to provide evenly spaced shrubs across restoration areas and at initial densities between 0.01 and 1.00 plants/m² (Dettweiler-Robertson et al. 2013; McAdoo et al. 2013; Davidson et al. 2019). Given our results and assuming these survival estimates are generalizable, a range of minimal initial planting densities of 4–7 plants/m² in small patches of at least 6 m² could achieve the sage-grouse goal of 15% big sagebrush cover within about 4 years.

Restoration of big sagebrush for sage-grouse nesting habitat might require three levels of sagebrush density. The nest site would be the smallest area, but with the greatest sagebrush density, as described above. These nest patches could be embedded within a larger, less-dense foraging patch of big sagebrush (e.g. 5–10% cover) that is one or more hectares in size. The combination of nesting and foraging patches would mimic combinations of nest sites and non-nest, random locations of big sagebrush cover where Gregg et al. (1994) documented successful nests and broods. The foraging patch, including nesting patches, could be strategically planted within a few kilometers of a recently burned sage-grouse lek and near potential brood-rearing habitat (Ricca & Coates 2020) to quickly achieve nesting habitat. The foraging patch would be surrounded by an even larger and less dense (<5% cover) background restoration area (tens to thousands of hectares or larger). This background area would likely be seeded because of its size, but it may require multiple attempts, especially in warmer and drier environments, to establish big sagebrush (Baker 2011; Shriver et al. 2018). We believe testing this combined seeding and planting technique, with the three sets of big sagebrush densities, is needed to prove this concept, in addition to measures of sage-grouse responses to such restored landscapes.

Warmer and drier sites (lower R&R) tended to achieve minimum heights for sage-grouse nesting approximately 1 year faster than those that were cooler and moister (higher R&R), regardless of restoration method, and minimum cover for sage-grouse nesting

| Restoration Technique | Height | Area |
|-----------------------|--------|------|
|                       | Low R&R | Median | High R&R | Low R&R | Median | High R&R |
| Seeded                | 3.2     | 3.5    | 3.8      | 3.9      | 4.0    | 4.1      |
| Planted               | 2.3     | 2.9    | 3.5      | 3.4      | 3.6    | 3.8      |
sites was achieved slightly faster in these warmer and drier sites. One explanation for this is related to the longer growing season (longer frost-free period) at lower R&R sites (Roundy & Madsen 2016). Winters at cooler and moister sites tend to be snow-covered, reducing the potential for photosynthesis and growth, especially for short-statured, young plants. Big sagebrush is adapted to photosynthesis and grow throughout the year, provided its deep roots are in moist soil with adequate temperatures (Richards & Caldwell 1987), thus giving warmer and drier environments a slight growth rate advantage once sagebrush is established. If climate change increases frost-free periods, then cooler and moister environments may experience improved growth (Roundy & Madsen 2016), whereas warmer and drier sites might have even less frequent opportunities for successful seedling establishment than they currently experience (Shriver et al. 2018).

It is important to note that height and canopy area growth rates of seeded big sagebrush were greater than those of planted individuals, given equal post-planting weather conditions. This was most apparent for height and less so for canopy area. Welch (1997) noted a similar swapping of the structural growth advantage from planted big sagebrush to seeded plants. Other woody plants have demonstrated greater growth rates for seeded over planted individuals (Pinus contorta Douglas ex Loudon—Halter et al. 1993; Quercus sp. L.—McCreary 1995; Young & Evans 2005). Big sagebrush is a tap-rooted species, but there is some evidence that tap-rooted species, and big sagebrush specifically, may lose their tap root dominance if grown in containers (Moore 1985; Welch 1997).

The lower growth rate of planted big sagebrush may be related to a loss or delay in tap root positive geotropism (South et al. 2001). This could make planted individuals susceptible to stresses such as drought, especially if their roots fail to maintain contact with moist soil. Big sagebrush individuals need access to deep soil water for tolerating dryland conditions (Ryle et al. 2004). Sagebrush canopy development and height can be enhanced by access to deep soil moisture (Barnard et al. 2019), but this access will require adequate root development. Studies that combine long-term monitoring of the survival of planted and seeded big sagebrush and their respective water relations may help increase understanding if annual dry periods or prolonged drought threaten the survival of planted individuals more so than seeded big sagebrush.

Land managers often decide not to plant container-grown big sagebrush because implementation costs are higher than seeding (Welch 2005). Costs per surviving planted big sagebrush individual ranges from $285 to $627 per hectare (Dettweiler-Robertson et al. 2013). Costs per successful hectare for seeded big sagebrush are not known, but were estimated between $250 and $700 per hectare for seeded grasses without big sagebrush in the Great Basin (Boyd & Davies 2012). Given the poorer establishment of seeded big sagebrush relative to seeded grasses (Knutson et al. 2014), costs per successful hectare of seeded big sagebrush may be much greater than for planted sagebrush. A controlled economic comparison using management-scale treatments could help managers to make informed decisions.

In summary, restoration practitioners in big sagebrush ecosystems are faced with choices when attempting to maintain wildlife populations and quickly restore habitats after large wildfires. If they opt to do nothing, big sagebrush is unlikely to reestablish quickly enough to sustain sage-grouse populations (Coates et al. 2016; Monroe et al. 2019; Ricca & Coates 2020). Seeding big sagebrush is the least expensive active restoration option to implement, but has the least likelihood of successfully establishing plants, especially at the required densities and in the warmer and drier environments if seeding is only attempted once (Shriver et al. 2018). Annually repeating seedings may increase the likelihood of establishing shrubs (Shriver et al. 2018), but using this method alone to achieve nesting habitat goals for sage-grouse may require too much time and may ultimately lead to extirpation of local sage-grouse populations. Planting container-grown sagebrush may form nesting and foraging patches more quickly in areas of past sage-grouse nesting and brood-rearing (Ricca & Coates 2020). These patches could be set within a larger burned area that is repeatedly seeded until big sagebrush successfully establishes. Selecting areas of high restoration potential (High R&R) may reduce the need to reseed annually to achieve a successful big sagebrush establishment from seeds (Chambers et al. 2014), but this may delay nesting patches reaching minimum nesting conditions by minimally 1 year, if initial seedings are successful. The ultimate question remains, “if we build it, will they come” (a rearrangement of a quote from the 1989 movie “Field of Dreams")? Monitoring both the habitat and the animal will determine if habitats can be restored successfully to be used by and sustained for sagebrush-obligate wildlife.

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Supporting Information
The following information may be found in the online version of this article:

Figure S1. Canopy area (square root) and height of individual big sagebrush (dots; Artemisia tridentata ssp. vaseyana and wyomingensis combined) individuals and the fitted mean assuming average site-level growth rates ($\alpha_t$).

Figure S2. Posterior distribution histograms for model parameters in canopy area model.

Figure S3. Posterior distribution histograms for model parameters in height model.

Supplement S1. Site-level analyses and model results.

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