

Synthesis

Natural Regeneration Processes in Big Sagebrush (*Artemisia tridentata*)

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Abstract

Big sagebrush, *Artemisia tridentata* Nuttall (Asteraceae), is the dominant plant species of large portions of semiarid western North America. However, much of historical big sagebrush vegetation has been removed or modified. Thus, regeneration is recognized as an important component for land management. Limited knowledge about key regeneration processes, however, represents an obstacle to identifying successful management practices and to gaining greater insight into the consequences of increasing disturbance frequency and global change. Therefore, our objective is to synthesize knowledge about natural big sagebrush regeneration. We identified and characterized the controls of big sagebrush seed production, germination, and establishment. The largest knowledge gaps and associated research needs include quiescence and dormancy of embryos and seedlings; variation in seed production and germination percentages; wet-thermal time model of germination; responses to frost events (including freezing/thawing of soils), CO₂ concentration, and nutrients in combination with water availability; suitability of microsite vs. site conditions; competitive ability as well as seedling growth responses; and differences among subspecies and ecoregions. Potential impacts of climate change on big sagebrush regeneration could include that temperature increases may not have a large direct influence on regeneration due to the broad temperature optimum for regeneration, whereas indirect effects could include selection for populations with less stringent seed dormancy. Drier conditions will have direct negative effects on germination and seedling survival and could also lead to lighter seeds, which lowers germination success further. The short seed dispersal distance of big sagebrush may limit its tracking of suitable climate; whereas, the low competitive ability of big sagebrush seedlings may limit successful competition with species that track climate. An improved understanding of the ecology of big sagebrush regeneration should benefit resource management activities and increase the ability of land managers to anticipate global change impacts.

Key Words: recruitment, sagebrush steppe, Sage-Grouse habitat, seedlings, seeds

INTRODUCTION

Plant communities dominated by *Artemisia tridentata* Nuttall (Asteraceae), big sagebrush, have occupied large areas in western North America since at least the last glacial maximum (Bartlein et al. 1998) and as early as 12×10⁶ yr ago in the Snake River Plain, Idaho (Bartlein et al. 1998; Davis and Ellis 2010). Many bird, mammal, reptile, and other species evolved with dependency on big sagebrush (West and Young 1999; Rowland et al. 2006). Consequently, big sagebrush provides crucial habitat and food for these sagebrush-obligate and -associated species, many of which are currently vulnerable and of conservation concern (Connelly et al. 2004; Rowland et al. 2006). Big sagebrush is well recognized for providing crucial habitat for game species including *Centrocercus urophasianus* (Greater Sage-Grouse) and *Antilocapra americana* (pronghorn), and recent attention has focused on the value of big sagebrush as habitat for nongame species, such as *Oreoscoptes*

montanus (Sage Thrasher) or *Sceloporus graciosus* (sagebrush lizard) (Hanser et al. 2011). Additionally, big sagebrush-dominated systems provide other ecosystem services including nutrient and water cycling, carbon storage in soils, and microhabitats for a diverse set of herbaceous plant species (West and Young 1999).

Big sagebrush-dominated ecosystems are of major economic importance for the western United States. They are used for livestock grazing, renewable and nonrenewable energy extraction, and recreation. Much of historical big sagebrush vegetation has been removed, modified, or fragmented (Welch 2005; Meinke et al. 2009; Knick et al. 2011; Manier et al. 2013), particularly as a result of agriculture, rangeland brush control (Alley 1956; Sturges 1993; Davies et al. 2012), energy extraction (Walston et al. 2009), and expansion of urban areas and infrastructure corridors (Leu et al. 2008; Manier et al. 2013). Other contemporary factors shaping big sagebrush ecosystems include droughts, climate change, wildfires, tree encroachment (particularly piñon-pine/juniper) at least partially promoted by an absence of fires at higher elevations, and biological invasions, some of which increase fire frequencies at lower elevations (Bradley 2010; Davies et al. 2011; Hanser et al. 2011). Consequently, loss of big sagebrush and reduction of big sagebrush-dominated habitat is a major concern for biodiversity conservation and land management in the western United States (Manier et al. 2013).

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Big sagebrush is a long-lived species that experiences greatest mortality in the seed or seedling stage, which results in episodic regeneration (Perryman et al. 2001). Big sagebrush does not sprout or regenerate vegetatively (Shultz 2006). Taxonomic treatment within this species remains difficult because of genetic, chemical, morphological, and ecological variation across its range, including hybridization among taxa (Bajgain et al. 2011; Garrison et al. 2013). We followed the Flora of North America which recognizes four subspecies: *tridentata*, *vaseyana* (Rydberg) Beetle, *wyomingensis* Beetle & A.M. Young, and *parishii* (A. Gray) H.M. Hall & Clements (Shultz 2006). Other treatments recognize additional/different subspecies, hybrids, and/or varieties (e.g., McArthur and Sanderson 1999). The subspecies align along environmental gradients of elevation, soil moisture, and soil texture, with the exception of subspecies *parishii*, which has a geographic distribution limited to the southwestern part of the range. Subspecies *tridentata* occurs on deep, well-drained soils in valleys of the Great Basin, subspecies *wyomingensis* on drier soils from valleys to plateaus, and subspecies *vaseyana* at higher elevations (Bonham et al. 1991; Shultz 2006).

The annual growth cycle of big sagebrush, which is influenced by winter snow cover, extreme temperatures, and summer drought, can be separated into distinct phases of vegetative growth and formation of reproductive structures (DePuit and Caldwell 1973; Daubenmire 1975; Evans and Black 1993). Vegetative growth (formation and elongation of perennial shoots, development of leaves, and root growth), and thus high levels of transpiration, occurs following snowmelt during spring and early summer when soil water is not limiting. Big sagebrush produces two types of leaves, perennial and ephemeral. Ephemeral leaves are large and maximize carbon gain, whereas perennial leaves last throughout the next winter and facilitate an early start at the beginning of the following growing season (Miller and Shultz 1987). During the summer dry period, ephemeral leaves are shed and annual reproductive structures develop. Reproductive structures are photosynthetically self-sufficient in increasing their biomass (no data available on seed production), allowing exploitation of intermittent summer precipitation events without the need for vegetative growth (Evans et al. 1991). Flowering occurs during late summer and fall, followed by fruit production, and seed dispersal in late fall and early winter. Germination occurs predominantly during late winter and early spring, with primary leaves appearing 6 wk later (Daubenmire 1975).

To understand population dynamics of species with the greatest mortality early in life (Type III survivorship curve), we need to know the controls over reproduction and offspring survival (Fenner 2002). These controls change in relative importance throughout the lifespan; for instance, long-lived plants can show marked differences in environmental tolerance between adults and young individuals, with younger stages typically having a narrower tolerance (Grubb 1977). Changes in environmental controls including higher temperatures and more frequent drought periods and severe precipitation events, as anticipated with climate change (IPCC 2014; Maloney et al. 2014), may impact population dynamics and potentially promote local extinction because of a failure to regenerate following adult removal. Impacts on regeneration may be of greater importance, if regeneration is episodic even under

current climatic conditions (Jackson et al. 2009) as displayed by big sagebrush. Therefore, characterizing environmental controls on early life stages is relevant both for understanding natural regeneration and for improving success of seeding applications in land management practices.

Population dynamics illustrate that in the absence of migration, both mortality of adult individuals and regeneration failure can lead to a loss of big sagebrush. Reduction or removal of big sagebrush stands due to land uses and management practices such as shrub control, as well as to increased fire cycles associated with invasive annual grasses, emphasizes the importance of regeneration as the critical component for restoration and reclamation (Lysne 2005; Madsen et al. 2013; McAdoo et al. 2013). Moreover, following energy extraction, vegetation must have a sufficient density of big sagebrush to meet legal requirements (Williams et al. 2002; Schuman et al. 2005; Steward 2006). Despite established reseeding and transplant techniques, restoration success of big sagebrush is often low, slow, or expensive (Lambert 2005; Shaw et al. 2005; Davies et al. 2013; McAdoo et al. 2013). Despite a considerable body of literature on big sagebrush germination and seedling ecology, we lack a comprehensive synthesis of either natural big sagebrush regeneration requirements or big sagebrush revegetation practices (Hardegee et al. 2011). This limited knowledge is also an obstacle to anticipating the consequences of increasing disturbance frequency and global change on big sagebrush ecosystems.

The overall objective for this article is to address one of these needs by synthesizing knowledge about natural big sagebrush regeneration. Our manuscript may serve as a basis for a future synthesis of revegetation practices for big sagebrush regeneration that should promote using science to address management challenges (Hardegee et al. 2011). By regeneration, we refer to the processes of seed production, germination, and survival of seedlings, particularly through the first year. Our specific objectives are to: 1) identify and characterize the controls of big sagebrush seed production and germination, 2) identify and characterize the controls of big sagebrush establishment, 3) recognize the largest knowledge gaps in regeneration and derive associated research needs, and 4) discuss the potential impacts of global change on sagebrush regeneration.

LITERATURE SEARCH AND RETRIEVAL

We accumulated a body of literature by querying SCI Web of Science on 2 March 2012 and by locating gray literature that was either cited or appeared in Internet searches. If sufficient information is available, this synthesis distinguishes among subspecies of big sagebrush, otherwise we report information for big sagebrush in general. However, this synthesis will not cover the subspecies *parishii* because of its limited geographic range. We selected literature from SCI Web of Science in three stages: First, we queried titles, keywords, and abstracts for the search term (“big sagebrush” or “*Artemisia tridentata*”), which resulted in 827 publications. Second, we queried this set by (“seed production” OR “seed mass” OR “seed weight” OR “seed” OR “seedling” OR “germination” OR “regeneration” OR “establishment”), which resulted in 197 entries. Third, a manual review of abstracts for these publications yielded 58

publications. Most publications not meeting these criteria focused on germination or regeneration of a different species associated with big sagebrush habitat. Additionally, we located 66 publications, mostly gray literature, through Internet searches or as citations for a total of 124 publications. We had access to complete texts of every publication except one (Shepherd 1937).

From these publications, we extracted information on seed mass, seed production and dispersal, and on relationships involving germination and seedling growth with biotic and abiotic environmental factors or disturbances. We built data sets accumulating data on seed mass (Table S1; available online at <http://dx.doi.org/10.2111/REM-D-13-00079.s1>) and seed production (Table S2; available online at <http://dx.doi.org/10.2111/REM-D-13-00079.s2>), as well as results from controlled lab and field experiments. The latter related conditions of stratification, mean winter temperature of parent population, and incubation temperature, light, and water potential to 1) germination percentage (Table S3; available online at <http://dx.doi.org/10.2111/REM-D-13-00079.s3>) and to 2) time to germinate (Table S4; available online at <http://dx.doi.org/10.2111/REM-D-13-00079.s4>). Further, we built data sets describing relationships between 3) seedling age and rooting depth (Table S5; available online at <http://dx.doi.org/10.2111/REM-D-13-00079.s5>), 4) seedling survival and soil water potential (Table S6; available online at <http://dx.doi.org/10.2111/REM-D-13-00079.s6>), and 5) seedling survival and cold temperatures (Table S7; available online at <http://dx.doi.org/10.2111/REM-D-13-00079.s7>).

Studies examining big sagebrush germination and seedling survival were published as early as 1937, almost as early as other publications on big sagebrush (Fig. 1). The number of publications focusing on germination and seedlings has continuously increased, including recently, indicating a consistent interest in big sagebrush regeneration ecology. Noteworthy are periods in the 1950s and late 1980s to early 1990s with more frequent publications. Eradication of big sagebrush from rangelands was of high concern in the 1950s, whereas several symposia during the 1980s and 1990s focused research on ecological understanding of controls on germination and seedling growth. Germination and seedling studies dominated overall publication on big sagebrush until the 1970s.

GERMINATION

Research identified five relevant processes for big sagebrush germination: 1) availability of seeds, 2) release of dormancy, 3) germination rate (here, the number of germinated seeds per time unit), 4) germination percentage (here, the fraction of germinated seeds of a seed sample expressed in percent), and 5) growth to the surface (i.e., emergence).

Availability of Seeds

Availability of seeds in a big sagebrush stand depends on amount of seed production, timing and distance of seed dispersal, and seedbank dynamics. Big sagebrush reaches maturity and begins producing seeds after 2–3 yr under ideal conditions (Daubenmire 1975; Young et al. 1989; Welch et al. 1990), but maturity can take up to 20 yr (Weldon et al. 1958).

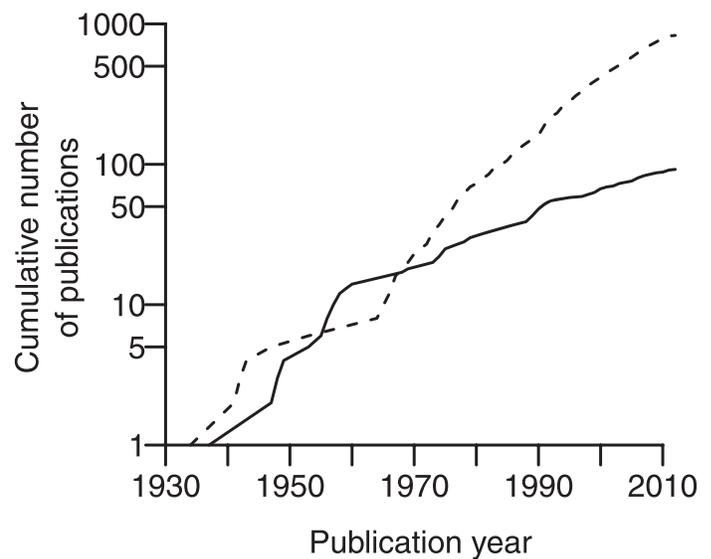


Figure 1. Cumulative fraction of publications concerning big sagebrush (dashed line, $n=827$) and those which include data on seeds, germination, seedlings or regeneration of big sagebrush (solid line, $n=92$) by 2 March 2012 (for further details, see Available Literature section).

After maturity, big sagebrush individuals produce reproductive structures in most or all years; however, production of number of seed stalks, seed heads, and total number of seeds can vary among years and sites (e.g., Young et al. 1989), including seed viability and germination percentage (see below). Seed production is influenced by maternal conditions. For instance, shrub biomass characteristics explained most of the variation in seed production among individuals (Young et al. 1989). Moisture availability has been suggested to positively influence seed production (Welch 1997; Booth and Bai 2000; Booth et al. 2003), but no definitive experiment has been carried out. Subspecies can differ in seed production, although with no conclusive results. For instance, subspecies *vaseyana* produces more seeds than *tridentata* in some instances (Young et al. 1989) and the opposite occurs in other studies (Graham et al. 1995). Two of the largest controls on seed production are herbivory and diseases. Strong positive effects of an order of magnitude have been found upon release from insect (Takahashi and Huntly 2010) and mammalian (e.g., pronghorn, mule deer, elk) herbivores (Rodriguez and Welch 1989; Wagstaff and Welch 1991; Hoffman and Wambolt 1996; Booth et al. 2003), as well as from pathogens (Welch and Nelson 1995).

Big sagebrush in natural populations produces an annual output (cleaned seeds) between 0 and $2.6 \text{ g} \cdot \text{plant}^{-1}$ with a median of $1 \text{ g} \cdot \text{plant}^{-1}$ (based on 25 observations; Table S2, available online at <http://dx.doi.org/10.2111/REM-D-13-00079.s2>). Plants in experimental settings can produce more seeds (range from 0 to $137 \text{ g} \cdot \text{plant}^{-1}$ with a median of $11 \text{ g} \cdot \text{plant}^{-1}$) prompting formulation of a hypothesis of resource limitation to seed production in natural populations. Most studies have not measured seed viability, seed mass, and shrub density in combination with produced seed mass to get stand seed number output. Big sagebrush seed mass varies widely; we found a range from 1800 to 10000 seeds $\cdot \text{g}^{-1}$ with a median of 4100 seeds $\cdot \text{g}^{-1}$ among 36 observations in natural populations (original data referenced

in Table S1, available online at <http://dx.doi.org/10.2111/REM-D-13-00079.s1>). A median individual would thus produce annually 4 100 seeds, albeit with a much higher potential of up to $\sim 10^6$ seeds (Goodwin 1956). Assuming a density of 0.5 and 1 plant $\cdot \text{m}^{-2}$ (corresponding to an average density found in communities with subspecies *wyomingensis* [lower value] and subspecies *vaseyana* [higher value] in eastern Oregon; Davies and Bates 2010), a stand of median big sagebrush individuals would produce $20\text{--}41 \times 10^6$ seeds $\cdot \text{ha}^{-1}$ annually. The higher estimate is comparable to 50×10^6 seeds $\cdot \text{ha}^{-1}$ that was reported as a mean of 5 stands (Young et al. 1989).

Seed dispersal from stands at high elevations or with low soil moisture occurs earlier than at low elevations or with high soil moisture (Goodwin 1956). There is no consensus on the duration of seed dispersal and subspecies may differ: some studies reported completion within 8 wk after seed maturity for subspecies *vaseyana* (Young and Evans 1989), completion by January (Goodwin 1956), or by end of winter for subspecies *tridentata* (Young and Evans 1989). However, most seeds are dispersed during September to November (Goodwin 1956; Mueggler 1956; Bartolome and Heady 1978; Young and Evans 1989).

Seeds are dispersed as achenes primarily by wind, despite a lack of structures supporting dispersal (Blaisdell 1953; Mueggler 1956; Welch 2005). Hydrochory and epizoochory in fur of wildlife or livestock may explain infrequent long-distance dispersal events (Goodwin 1956). Endozoochory is not believed to be important because postpassage viability after livestock ingestion is near zero (Whitacre and Call 2006). Seed dispersal distance is a function of wind speed, prevailing wind direction, length of flower stalks (wind whips stalks and ejects seeds; Young and Evans 1989) and snow (seeds blown across snowpack during winter storms; Blaisdell 1953). The majority of seeds reach a distance of $< 1\text{--}2$ m from the maternal plant (Goodwin 1956; Welch 2005) with an observed maximum at 33 m (Goodwin 1956; Daubenmire 1975). Unsuitability of big sagebrush seeds for long-distance dispersal by wind and the importance of appropriate placement in suitable microsites may also be demonstrated by the low success of aerially broadcasted seeds of subspecies *wyomingensis* in restoration areas (Lysne and Pellant 2004; Lysne 2005). However, aerial seeding of subspecies *vaseyana* after fire has been successful and may be attributed to higher precipitation associated with this subspecies, compared to sites with attempted aerial seeding of subspecies *wyomingensis* (Davies et al. 2014).

The importance of seedbank for big sagebrush regeneration was initially controversial, but has recently been resolved by studies differentiating seed persistence at different soil depths. Some studies reported no or very few viable seeds by the summer following dispersal (Hassan and West 1986; Young and Evans 1989; Boudell et al. 2002). Other studies concluded that big sagebrush seeds can persist in the seedbank (Wijayratne and Pyke 2009; Wijayratne and Pyke 2012) for at least 2–3 yr (Mueggler 1956; Ziegenhagen and Miller 2009). This apparent discrepancy is explained by soil depth: although few seeds remain viable at the surface and in the litter layer, seeds buried deeper than 3 cm retain 30–40% viability after 2 yr (Wijayratne 2011; Wijayratne and Pyke 2012). These seeds also contribute to postfire regeneration (Mueggler 1956) if

seeds are moved closer to the surface (see Seedling Emergence section); for instance, by small, local-scale soil disturbance (see Disturbance Regimes Affecting Seedlings section).

Big sagebrush can produce large numbers of seeds; however, under specific conditions seed availability may drop below a level where stand-replacing recruitment is successful. For instance, seed consumption can remove large numbers of seeds and heavy herbivory can drastically limit seed production (e.g., Rodriguez and Welch 1989). This is because flowering stems originate from buds on the distal portion of branches (Bilbrough and Richards 1991) that are easily reached by browsing, and because big sagebrush does not allocate additional resources to new stem growth in response to browsing (Bilbrough and Richards 1993). Interannual variability in climatic conditions can also cause a zero or small seed crop (e.g., Young et al. 1989). This does not cause complete regeneration failure over long periods of time, but rather contributes to strongly episodic regeneration (Perryman et al. 2001). Limited seed dispersal by wind and a limited seedbank can severely limit the availability of seeds for big sagebrush re-establishment in large disturbed areas such as the interior of burns (e.g., Mueggler 1956; Johnson and Payne 1968), in areas of shrub die-off (e.g., Cárdenas et al. 1997), and restoration areas (Chambers 2000; Lysne and Pellant 2004; Lysne 2005). Nevertheless, because big sagebrush produces large numbers of seeds during average conditions, seed production is generally not a limiting stage in regeneration of established big sagebrush stands (e.g., Wagstaff and Welch 1991).

Release of Dormancy

Dormancy and low germination rates in cold temperatures are strategies to avoid unfavorable conditions, which include germination during early winter thaw events or underneath snow cover (Meyer and Monsen 1991). Dormancy of big sagebrush seeds can be broken in four ways: cold stratification, removal of pericarp, dry storage, or light.

The effect of cold stratification depends on mean winter temperature experienced by the mother plant (Meyer et al. 1990; Meyer and Monsen 1991; Meyer and Monsen 1992). Seeds from sites with low mean winter temperatures germinated more slowly, particularly in the dark at 1°C (simulating snow cover), and responded less to short chills than seeds from warm sites. It is unclear whether these relationships were independent of subspecies identity or showed additional maternal effects besides mean winter temperature (Meyer and Monsen 1992). However, these responses may help explain varying germination reports among subspecies, particularly subspecies *vaseyana*, which regularly occurs at colder sites than other subspecies. Most studies found that 2–4 mo of cold stratification were required to entirely break dormancy (McDonough and Harniss 1974a; Eddleman 1977; Romo 1985; Meyer and Monsen 1991). Dormancy is also broken by experimental removal of the pericarp. In situ, the pericarp may be eroded and end dormancy by spring as a result of weathering during the winter and consumption by soil biota (McDonough and Harniss 1974b; Meyer et al. 1990). After-ripening of seeds in dry storage for 4 to 12 mo has been observed in big sagebrush; it can remove or reduce stratification requirements (Eddleman 1977; Romo 1985; Meyer et al. 1990) and increase

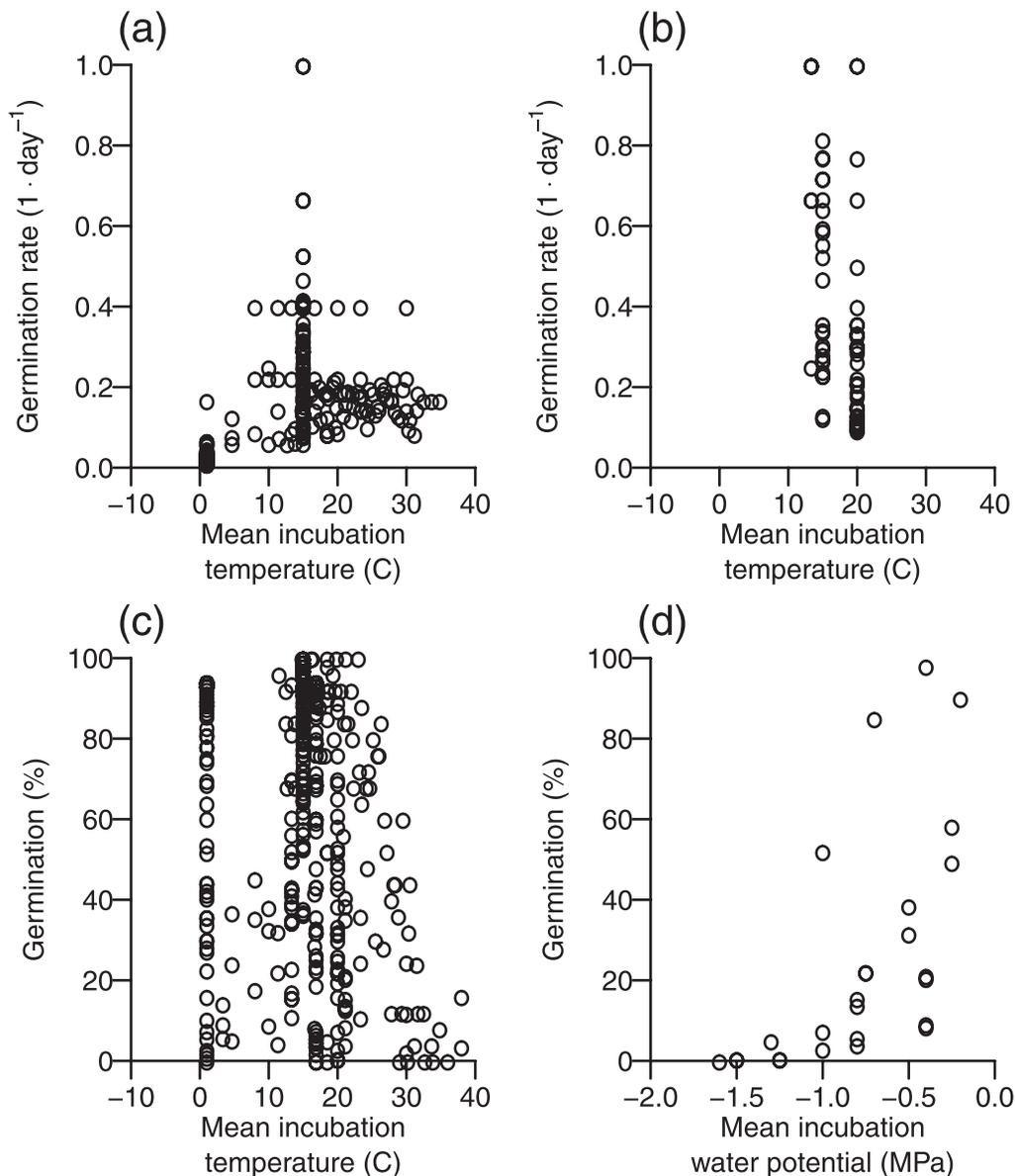


Figure 2. (a) Relationship between big sagebrush germination rate (day^{-1}) and incubation temperature with $n=284$ literature reports (original data referenced in Table S4; available online at <http://dx.doi.org/10.2111/REM-D-13-00079.s4>) including experiments without stratification and (b) experiments with stratification ($n=71$). (c) Relationships between big sagebrush germination percentage (%) and incubation temperature with $n=430$ unique literature reports (Table S3; available online at <http://dx.doi.org/10.2111/REM-D-13-00079.s3>) and (d) water potential with $n=26$ literature reports (Table S3; available online at <http://dx.doi.org/10.2111/REM-D-13-00079.s3>). Note: all values at 1°C in (c) are results from the only long-term germination study lasting 84 d to simulate conditions underneath snow cover (Meyer et al. 1990).

seedling vigor if storage <24 mo (Bai et al. 1997). Light exposure is necessary to break dormancy in seeds that have a thick pericarp, are young, have not been exposed to short chill events, or have mothers from locations with low mean winter temperature (Meyer et al. 1990). All these factors delay germination during unfavorable winter conditions and snow cover, with emergence observed as soon as a few days after snow melt (Payne 1957).

Germination Rate

Germination rate is the third important component of big sagebrush germination and is conditional on dormancy and stratification. Germination rate (i.e., the number of germinated

seeds per time unit) is a function of incubation temperature with a broad near-optimal range of $10\text{--}30^\circ\text{C}$ (Figs. 2A–B; Vleeshouwers and Kropff 2000; Hardegree 2006). Thermal-time models have successfully described germination rates of several sagebrush steppe species (Hardegree 2006; Rawlins et al. 2012a) and have been extended to incorporate water availability in dry environments (Rawlins et al. 2012b). However, no thermal-time model has yet been developed for big sagebrush despite evidence of temperature dependence of germination rate (McDonough and Harniss 1974a; Sabo et al. 1979; Meyer and Monsen 1991; Bai et al. 1997). In addition to temperature, germination rate is positively related to water potential with a 3-fold increase per MPa (Bai et al. 1999), seed

size (Busso et al. 2005), and mean winter temperatures experienced by the maternal plant (Meyer and Monsen 1992).

Germination Percentage

The fourth component of big sagebrush germination, germination percentage (i.e., the fraction of germinated seeds of a seed sample expressed in percent), depends on incubation temperature, soil moisture, light levels, seed size, and conditions of the maternal plant. Large variations in germination percentage can occur in big sagebrush (Payne 1957; Cawker 1980); variations of > 20% among years (e.g., Young et al. 1991) and from 0% to 100% among sites (e.g., Meyer et al. 1990) have been reported, but no systematic variation with subspecies (Meyer et al. 1990; Young et al. 1991). Variation in germination percentage among years or among sites may be related to climatic conditions during seed production (Meyer and Monsen 1992) through maternal effects such as seed mass. Heavier seeds increase percentage germination by 6–9% per mg seed mass (Busso et al. 2005). Seed mass differences are not related to seed moisture content postharvest (Bai et al. 1997), but 85% of seed mass variation among sites and years has been explained by growing season precipitation (March–November) experienced by the mother plant (Busso and Perryman 2005). A broad temperature optimum of 10–30°C makes germination percentage relatively insensitive to temperature and temperature regimes over a wide range (Fig. 2A; Shepherd 1937; McDonough and Harniss 1974a; Eddleman 1979; Sabo et al. 1979; Evans and Young 1986; Young and Evans 1986; Young et al. 1991; Bai et al. 1997). Large variations in temperature response among seeds from different mothers (McDonough and Harniss 1974a) may be explained by a positive correlation between germination and mean January temperature experienced by the mother plant. Water potential during imbibition shows a strong positive relationship with germination percentage (Fig. 2B; Weldon et al. 1959; Sabo et al. 1979; Bai et al. 1999). Light has been reported to have either no (Sabo et al. 1979) or a positive effect on germination percentage (Shepherd 1937; Goodwin 1956; Weldon et al. 1959). Overall, germination percentage is high and not considered to be a limiting factor in big sagebrush regeneration (Harniss and McDonough 1976; Young et al. 1991; Meyer and Monsen 1992).

Seedling Emergence

After appearance of the radicle, a plant must grow to the substrate surface for emergence (Bullied et al. 2013). Thus, germination depth influences both realized emergence and emergence timing (Forcella et al. 2000; Bullied et al. 2013). Seedling emergence as defined in the lab is the phase between germination and appearance of the seedling at the soil surface (Eckert Jr. et al. 1986), whereas seedling emergence as observed in the field has been defined to correspond to the final result of all germination phases together (Chambers 2000). Consequently, laboratory and field experiments measure different stages of the recruitment process.

Big sagebrush seeds require specific microsite conditions including a soil that is easily penetrated by emerging seedlings in spring and a suitable surface roughness for seed positioning after seed dispersal (Young et al. 1990). Positioning of seeds in suitable microsites is promoted by trampling (Eckert Jr. et al.

1986) and by similarity in size between sagebrush seeds and sand grains allowing seeds to ‘winnow’ to shallow soil depths (Young et al. 1990). Big sagebrush seedlings develop hypocotyl hairs to attach the seedling to the substrate and likely to support penetration of the radicle (Young and Martens 1991). However, big sagebrush seeds must be located within 0.5 cm of the soil surface to successfully emerge (Jacobson and Welch 1987; Young and Evans 1989). Similarly, litter from herbaceous (Beetle 1960) and woody species (Horman and Anderson 2003) inhibit germination, but litter or mulch can also promote germination if it also increases soil moisture (Schuman et al. 1998) or protects from frost (Meyer and Monsen 1990). Such requirements indicate that big sagebrush is poor at extending its shoot through soil and litter layers.

ESTABLISHMENT

Research examining big sagebrush seedling growth and establishment has identified three relevant factors: 1) site physical characteristics, 2) site ecological characteristics, and 3) disturbance regimes. We focus here on seedling survival during the first season as an indicator of establishment success. In big sagebrush, most mortality occurs during the first year (Johnson and Payne 1968; Daubenmire 1975; Owens and Norton 1989; Young and Evans 1989; Donovan and Ehleringer 1991; Jones 1991), and this process, rather than adult mortality, regulates population dynamics *via* recruitment success (Cawker 1980). However, stands can also experience high adult mortality as a result of fires, droughts, or pathogens (e.g., Cárdenas et al. 1997). Following adult mortality, big sagebrush stands may be slow to recover abundance because of a lack of seeds (see above) and successful seedling survival. Many studies report that recruitment is episodic (Johnson 1958; Cawker 1980; Evans and Young 1986; Booth and Bai 2000; Maier et al. 2001; Hourihan 2011). For instance, in a field study conducted in Wyoming, mean intervals between recruitment were 1.6–2.3 yr depending on subspecies (Perryman et al. 2001).

Site Physical Characteristics Affecting Big Sagebrush Seedlings

Characteristics Defining Favorable Conditions for Seedling Growth. Conditions for growth of big sagebrush seedlings are influenced by snow cover, soil water potential, and soil temperature. There is a dearth of studies on this topic, but two provide insights into minimal favorable temperatures for growth. Seedlings exposed to simulated spring temperature regimes sustained growth under below-average temperatures (with no differences among the three subspecies), albeit with reduced biomass accumulation compared to warmer temperature regimes (Harniss and McDonough 1975). However even short frost periods can limit seedling growth; i.e., a 1-hr treatment at –5°C stopped growth for the 4-wk duration of an experiment in two subspecies, *vaseyana* and *tridentata* (Lambrecht et al. 2007). Seedlings of subspecies *vaseyana* were more sensitive to freezing temperatures when water stressed, whereas subspecies *tridentata* showed no increased susceptibility (Lambrecht et al. 2007), indicating that interactions of stressors may be particularly relevant for growth of big sagebrush seedlings.

Conditions Allowing Seedling Survival. Survival conditions are influenced by duration of snow cover, minimum and maximum temperatures, duration of saturated soil water conditions, and duration and severity of dry soils. Snow cover can have positive and negative effects on seedlings. While snow cover can reduce seedling exposure to extreme low temperatures in early spring at high elevations (Loik and Redar 2003), prolonged snow cover can increase seedling mortality (e.g., in *vaseyana* at higher elevations; Maier et al. 2001). Low temperatures cause membrane damage and decrease photosystem II function in seedling leaves and low temperatures of -13°C to -15°C can influence seedling survival (Loik and Redar 2003). Studies correlating seedling establishment with long-term mean temperature patterns report a range of relationships: positive (Cawker 1980), negative (Cawker 1980; Schuman et al. 1998), and no correlation (DiCristina et al. 2006). Such conflicting observations could indicate that either local and microsite temperature or, alternatively, temperature variation is more relevant for big sagebrush seedlings than mean temperature conditions.

Soil water is one of the most important factors influencing seedling survival, but excessively wet or dry conditions both cause big sagebrush seedling mortality. Seedlings are reported to survive saturated soil conditions for up to 3 wk (Daubenmire 1975). Mortality due to low availability of soil water was observed after 4 d in soils of -1.5 MPa (Daubenmire 1975). However, another study suggested that while 50% of seedlings survived drying soils at -3.3 MPa, no seedlings survived soil water potentials less than -3.7 MPa (Stahl et al. 1998). A few studies report no relationship or a negative relationship between seedling survival and soil water availability or precipitation. For instance, Maier et al. (2001) demonstrated that above-average spring precipitation following seedling emergence can reduce survival in subspecies *vaseyana*. This effect arose because at the elevation of the study site, spring precipitation occurred as snow, which prolonged snow cover and reduced seedling survival. Most studies agree, however, that soil water availability is one of the most important factors determining seedling survival, underscoring the crucial positive role of precipitation (Lommasson 1948; Young and Evans 1973; Cawker 1980; Owens and Norton 1989; Young et al. 1990; Jones 1991; Owens and Norton 1992; Schuman et al. 1998; Maier et al. 2001; Ziegenhagen and Miller 2009; Hourihan 2011).

Aboveground and Belowground Growth. Aboveground seedling growth contrasts with patterns of root growth. Maximum aboveground growth rates are roughly 2.4 – 5.7 $\text{mm} \cdot \text{d}^{-1}$, and subspecies *wyomingensis* attains maximal rates earlier than *vaseyana* or *tridentata* (Booth et al. 1990). However, another study found no subspecies differences in above- or belowground growth (Harniss and McDonough 1975). Shoot growth of seedlings is reduced during taproot growth (Daubenmire 1975). Seedlings focus root growth on the taproot and produce only few short lateral roots (Wijayratne 2011). A very wide range of root elongation rates (between 0.7 – 21.4 $\text{mm} \cdot \text{d}^{-1}$) has been reported (Daubenmire 1975; Wijayratne 2011) and may vary with temperature. Subspecies differ in root elongation rates as well as in total root length measured. Subspecies *wyomingensis* elongated roots faster and longer early in the

growing season than *vaseyana* or *tridentata* (Welch and Jacobson 1988).

Seedling growth rates are modulated by available resources such as soil water, CO_2 concentrations, and nutrient availability during periods of favorable conditions (see sections above). Seedlings adjust root growth rates to water stress, including up to 75% reduction during drought; growth rates recovered to control levels within a few days of resumption of well-watered conditions (Bassirirad and Caldwell 1992). Seedling growth thus involves several strategies to avoid drought, particularly during summer, including rapid early-season growth of aboveground and belowground biomass, and emphasis on taproot growth. Measured growth responses of above- and belowground biomass of big sagebrush seedlings in experimentally elevated atmospheric CO_2 concentrations show no consensus: above- and belowground biomass do not respond (Lucash et al. 2005); only belowground biomass increased (Klironomos et al. 1996); only aboveground biomass increased in combination with high nutrient availability (Johnson and Lincoln 1991). Field experiments also indicate that big sagebrush seedlings may benefit from high nutrient availability when neighboring plants are far away (DiCristina and Germino 2006); whereas, other studies found no positive effect of high nutrients on seedling growth (Klironomos et al. 1996). Relationships between seedling growth and resources other than water likely involve complex interactions, and detection is difficult, because big sagebrush seedlings grow relatively slowly and many experiments are of short duration.

Site Ecological Characteristics Affecting Seedlings

Competition is an important factor that affects big sagebrush seedling success. While some studies found no or few competitive effects (Bleak and Miller 1955; Johnson and Payne 1968), most studies reported either decreased seedling survival or complete sagebrush seedling exclusion by herbaceous species (Booth 1947; Eddleman 1979; Owens and Norton 1989; Young and Evans 1989; Reichenberger and Pyke 1990; Wagstaff and Welch 1990; Jones 1991; Schuman et al. 1998; DiCristina and Germino 2006; DiCristina et al. 2006; Ziegenhagen and Miller 2009; Wijayratne 2011). Furthermore, intraspecific competitive effects, particularly shallow root competition by established big sagebrush on seedling roots, may be more severe than interspecific effects (Reichenberger and Pyke 1990). This may help to explain the rarity of establishment within established stands in the absence of minor soil disturbances (see next section, Disturbance Regimes Affecting Seedlings). Big sagebrush seedlings experience most of the negative consequences of competition during spring and early summer; this coincides with the time soil water is most often not limiting and seedlings assimilate most of their carbon (DiCristina et al. 2006; Wijayratne 2011). This suggests that sagebrush seedlings are competing for resources other than soil water, perhaps nutrients (but see Blaisdell 1953; DiCristina and Germino 2006), which are only available during the short period of the growing season when shallow soils are moist (Ryel et al. 2010). Even when springtime competition does not kill seedlings directly, seedling resources or roots may be reduced below levels required to survive dry summer conditions (Wijayratne 2011). Seedlings are most susceptible to negative

competitive effects during the first 1–2 growing seasons (Blaisdell 1949; Owens and Norton 1989; Schuman et al. 1998). Another relevant biotic interaction emerges from the presence of mycorrhizae, which have been reported to allow seedlings to withstand drier soils (Stahl et al. 1998) and to increase establishment success on abandoned ant mounds (Friese and Allen 1993).

Disturbance Regimes Affecting Seedlings. Large-scale disturbances, such as wildfire or intensive land use, generally remove big sagebrush individuals; seeds are the only option for regeneration. Recruitment has been observed during the first few years after fire if and when resources, mainly available soil water following cool-season precipitation recharge of deep soil-water, are not limiting (Ziegenhagen and Miller 2009; Nelson et al. 2014). However, recruitment may be delayed in the absence of a suitable level of available soil water immediately post fire. This phase of abiotic-controlled postfire recruitment is followed by a second phase of reduced establishment due to seedbank depletion and competition (e.g., Blaisdell 1953; DiCristina et al. 2006; Ziegenhagen and Miller 2009). In large areas of complete adult big sagebrush loss, a third phase begins when the first generation of big sagebrush starts to reproduce and produce seeds for further establishment (Ziegenhagen and Miller 2009). Because big sagebrush does not sprout or regenerate vegetatively (Shultz 2006), recovery from such disturbance events must occur through seeds.

Disturbances consisting of modest, localized soil perturbations may enhance recruitment, as evidenced by several studies that found seedlings within established stands only on soils disturbed by rodents (Booth 1947; Beetle 1960). These small and local soil disturbances may promote germination by bringing seeds close to the soil surface, where germination and emergence is most likely (Jacobson and Welch 1987; Young and Evans 1989; Young et al. 1990), as well as by reducing levels of local competition (DiCristina and Germino 2006), particularly from established big sagebrush (Reichenberger and Pyke 1990). An additional link between moderate disturbance and recruitment is that grazing often increases seedling recruitment (Frischknecht and Bleak 1957; Johnson 1958; Owens and Norton 1992; Austin and Urness 1995) and establishment of big sagebrush in stands of crested wheatgrass (Frischknecht and Harris 1968). However, trampling during grazing may kill seedlings, particularly those in unsheltered locations (Owens and Norton 1992). Given sufficient available seeds, small disturbances may interact with abiotic and biotic factors and increase recruitment success when competition is reduced and soil water is available.

KNOWLEDGE GAPS AND RESEARCH NEEDS

Our analysis of the literature uncovered notable knowledge gaps about three types of processes associated with big sagebrush regeneration: 1) processes identified as important in germination and establishment of other species, but not studied in big sagebrush, 2) processes for which there are no or few quantitative or qualitative data, and 3) processes well described qualitatively, but with few quantitative data. Because

big sagebrush is a relatively well-studied species, many of the knowledge gaps are of the third type.

Having no information about a potentially important process is the most severe, as it limits our understanding of the mechanisms of big sagebrush regeneration. We identified two such unknowns: First, it is unknown whether germination continues or the embryo dies once favorable conditions resume following an unsuitable period. Second, it is similarly unknown whether seedlings exhibit quiescence or dormancy during unsuitable growing periods, and whether this is followed by resumption or permanent cessation of growth (e.g., Mok et al. 2012). Understanding these responses is of relevance, for instance, during late spring snow or frost events following onset of germination.

The second type of knowledge gap is due to a lack of both quantitative and qualitative data and includes three points: First, a limited number of studies investigated global change impacts on big sagebrush regeneration, particularly to increases in atmospheric (and soil) CO₂ concentration, nitrogen deposition, and their interactions with climate change—all factors and interactions known to directly and indirectly affect germination and seedling survival in other species (Polley et al. 2002; Classen et al. 2010). Studies on effects of elevated CO₂ concentrations for other species disagree whether above- or belowground growth rates increase or not. Similarly, we found only one study directly addressing how big sagebrush regeneration may respond to projected future climate conditions; e.g., to altered precipitation seasonality (Bates et al. 2006). Bates et al. measured increased reproductive stem biomass of subspecies *wyomingensis* under a precipitation regime shifted to spring/summer; however, no increased regeneration resulted during the duration of the experiment. Several laboratory experiments have explored how germination responds to different temperature or moisture ranges (e.g., McDonough and Harniss 1974a; Young et al. 1991; Meyer and Mosen 1992; Maier et al. 2001), from which extrapolations to climate change conditions may be made. Thus, we hypothesize that climate change will be important for big sagebrush regeneration, but we can only speculate about the magnitude and direction of impacts. Climate change will likely affect regeneration of many or perhaps all dryland species (but see Cipriotti et al. 2008; Mok et al. 2012). Second, with the exception of a few publications describing competitive outcomes and correlation between climate and seedling survival, detailed studies of seedling growth, root elongation, and survival are mostly lacking. Besides some information on how minimum temperature affects growth and survival, we know little about seedling growth responses to temperature, including frost events, water availability, and other factors. Third, overall there is no or little information available to evaluate differences in germination and particularly seedling success among subspecies and ecoregions.

The third type of knowledge gap is the most prevalent for big sagebrush and covers processes for which we know the relative importance and direction of responses, but we lack quantitative data to estimate parameters in a mechanistic model. For instance, a multiyear survival curve has not been established for big sagebrush (for a survival curve during first growing season, see Owens and Norton 1989). We know that survival is lowest during the first year, but not the magnitude of survival increase

in subsequent years. Similarly, we know that seed dispersal occurs in the fall and is likely influenced by temperature or elevation, but we have limited data to estimate parameters of these relationships. Further, variation in both seed production and germination percentage has been observed among years and sites and has been related to site climatic conditions, but we lack mechanistic models to quantify these relationships. Additionally, we have some laboratory observations of germination rate and know that incubation temperature and moisture are important; however, we lack a wet-thermal time model as we have for other species (Rawlins et al. 2012a; Rawlins et al. 2012b). Whereas we have information about minimum soil moisture requirement, we have few observations about seed and seedling responses to saturated soil conditions. Furthermore, limited work suggests that frost during emergence may be important, particularly in combination with other stressors such as low available water, but there are limited data to quantify seedling mortality responses to frost individually and in combination with available water. Additionally, there are no studies that specifically address the mechanical stress of seedbed freeze-thaw events on seedlings. Finally, we know that competition can be crucial for seedling success, but we lack a mechanistic understanding about the resource needs and relative competitive abilities to be able to predict competitive outcomes.

We approached research needs by combining the three levels of knowledge gaps with a ranking of importance of particular processes. However, project-specific research questions will influence importance of a process and will differ among questions. For instance, questions related to regeneration following wildfire will have a greater need to understand the details of seed dispersal and microsites (Baker 2006). On the other hand, questions related to reclamation following surface disturbances, such as during energy extraction practices, will focus more on conditions that influence seedling survival and competitive success (Wijayratne 2011). In the following section, we summarize potential impacts of global change and formulate research needs to address relevant gaps.

POTENTIAL CLIMATE CHANGE IMPACTS ON BIG SAGEBRUSH REGENERATION

Understanding the responses of regeneration to global climate change will require establishing mechanistic relationships between changes in climate, CO₂ concentrations, nitrogen deposition, wildfire, invasive species, and land use and the different aspects of big sagebrush regeneration; i.e., seed availability, germination, emergence and seedling survival. We focus here on climate change impacts due to a lack of studies addressing responses such as those to increased CO₂ concentrations; however, we suggest that such studies are needed to evaluate potential impacts of global change on big sagebrush regeneration.

Across the geographic distribution of big sagebrush, projected climate changes include large increases in mean annual temperatures, small positive or negative changes in annual precipitation with a shift towards increased wintertime precipitation mostly north of 40°N; overall, a regional drying is predicted (IPCC 2014; Maloney et al. 2014). These climatic

changes have a high probability of leading to shifts in geographic distribution of big sagebrush and other species of the intermountain region (Bradley 2010; Schlaepfer et al. 2012b) and may result in nonlinear responses in vegetation activity as a result of decreasing snow cover (Schlaepfer et al. 2012a) and dominance shifts at the sagebrush-conifer ecotone (Bradford et al., 2014).

The most obvious changes in regeneration processes will be increases in incubation temperatures and alteration of the amount as well as seasonality of available water experienced by seeds and seedlings. Laboratory experiments indicate that big sagebrush germination has a broad temperature optimum, and thus changes in temperature may not have a large direct influence on regeneration. Indirectly, however, warmer winters could select for populations with a less stringent requirement of cold winter temperatures to break dormancy. This could increase the risk of mortality during spring frost events, unless frost events become less frequent with warmer temperatures. Similarly, a combination of earlier growing season onset, spring drought, and frost events may combine to reduce seedling survival. In contrast to temperature, available water has a strong direct relationship with germination percentage and seedling survival. Drier conditions and more frequent intra-seasonal dry periods will have a negative effect on both germination and survival. Additionally, drier summers could lead to lighter seeds, which have a lower germination percentage. Furthermore, the short seed dispersal distances characteristic of big sagebrush will impede migration to more suitable climates.

Similar to many other plant species, climate change will likely have its largest influence on future big sagebrush populations by affecting the regenerative niche (Mok et al. 2012). Established individuals can often persist through altered and increasingly unfavorable conditions until an event such as a disturbance eliminates them (Milchunas and Lauenroth 1995; Jackson et al. 2009). However, adult mortality and decreased adult vigor may reduce available seeds such that regeneration fails. Additionally, severe or complete stand die-offs in big sagebrush have been observed (Nelson and Krebill 1981; Hanson et al. 1982; Haws et al. 1990; Cárdenas et al. 1997). Die-off episodes may be multicausal (Wallace and Nelson 1990) and agents may be difficult to determine (Cárdenas et al. 1997), nevertheless, die-offs have been related to insect outbreaks (Haws et al. 1990), fungal pathogens (Nelson and Krebill 1981), and winter frost damage in the absence of a snow cover (Hanson et al. 1982; e.g., Cárdenas et al. 1997). Additional causes attributed to die-offs in other shrub species, particularly shadescale (*Atriplex* sp.), include excessive wet periods (Wallace and Nelson 1990) and high salinity (Weber et al. 1990) in combination with pathogens (Nelson et al. 1990). Such die-offs, as well as mortality due to increased fire frequency, may become more frequent under future climatic conditions and invasions of annual grasses, particularly in the drier parts of big sagebrush distribution, such as at low latitudes and low elevations. Regardless of whether mortality of established big sagebrush individuals as a result of climate change is rapid or delayed, the distribution and abundance of future populations will be ultimately determined by regeneration. If conditions in a portion of the historic range of big sagebrush become

unsuitable to sustain populations from a changing climate, as has been suggested by species distribution models (Bradley 2010; Schlaepfer et al. 2012b), future populations will rely on the entire suite of demographic processes governing regeneration. Thus, our ability to predict future big sagebrush populations depends on our mechanistic knowledge of regeneration, mortality, and migration.

IMPLICATIONS

This is the first synthesis of extant knowledge about natural big sagebrush regeneration. Our synthesis also identifies current gaps in the literature, notably big sagebrush response to interactions between biotic factors and different types of disturbance events, responses to global change including elevated CO₂ concentrations, nitrogen deposition, and climate change, as well as differences in those responses among subspecies and ecoregions. Our synthesis will hopefully provide the foundation and motivation for designing the next generation of experiments and field surveys to fill these knowledge gaps. Most studies included in our synthesis reported germination and seedling responses to abiotic factors under controlled laboratory conditions. The next generation of experiments should focus on increasing our knowledge about big sagebrush seed and seedling responses to conditions experienced in the field in the seedbed and microsites where seedlings establish.

An improved understanding of the ecology of big sagebrush regeneration will benefit resource management activities targeting big sagebrush ecosystems for conservation as critical habitat, strengthen restoration efforts following land uses such as energy extraction, and increase the ability of land managers to anticipate global change impacts. By highlighting the ecological processes underlying big sagebrush regeneration, we hope that our synthesis of natural regeneration promotes a similar effort to characterize the revegetation and seedbed literature on which management actions are designed. For instance, the short seed dispersal distance of big sagebrush may limit its tracking of suitable climate, whereas the low competitive ability of big sagebrush seedlings may limit regeneration in the context of competing species that track climate. While big sagebrush is relatively well studied compared to other rangeland species, addressing the remaining knowledge gaps is important for this widespread species that dominates many ecosystems of the western United States.

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