Forest Ecology and Management 361 (2016) 328–338

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Review and synthesis

A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration

M.D. Petrie [a,b,*], A.M. Wildeman [a], J.B. Bradford [a], R.M. Hubbard [c], W.K. Lauenroth [b]

[a] US Geological Survey, Southwest Biological Science Center, Flagstaff, AZ, United States
[b] Dept. of Botany, University of Wyoming, Laramie, WY, United States
[c] USDA Forest Service, Fort Collins, CO, United States

ARTICLE INFO

Article history:
Received 15 September 2015
Received in revised form 11 November 2015
Accepted 16 November 2015
Available online 7 December 2015

Keywords:
Ponderosa pine
Lodgepole pine
Germination
Regeneration
Climate
Review

ABSTRACT

The persistence of ponderosa pine and lodgepole pine forests in the 21st century depends to a large extent on how seedling emergence and establishment are influenced by driving climate and environmental variables, which largely govern forest regeneration. We surveyed the literature, and identified 96 publications that reported data on dependent variables of seedling emergence and/or establishment and one or more independent variables of air temperature, soil temperature, precipitation and moisture availability. Our review suggests that seedling emergence and establishment for both species is highest at intermediate temperatures (20 to 25 °C), and higher precipitation and higher moisture availability support a higher percentage of seedling emergence and establishment at daily, monthly and annual timescales. We found that ponderosa pine seedlings may be more sensitive to temperature fluctuations whereas lodgepole pine seedlings may be more sensitive to moisture fluctuations. In a changing climate, increasing temperatures and declining moisture availability may hinder forest persistence by limiting seedling processes. Yet, only 23 studies in our review investigated the effects of driving climate and environmental variables directly. Furthermore, 74 studies occurred in a laboratory or greenhouse, which do not often replicate the conditions experienced by tree seedlings in a field setting. It is therefore difficult to provide strong conclusions on how sensitive emergence and establishment in ponderosa and lodgepole pine are to these specific driving variables, or to investigate their potential aggregate effects. Thus, the effects of many driving variables on seedling processes remain largely inconclusive. Our review stresses the need for additional field and laboratory studies to better elucidate the effects of driving climate and environmental variables on seedling emergence and establishment for ponderosa and lodgepole pine.

Contents

* Corresponding author at: US Geological Survey, Southwest Biological Science Center, Flagstaff, AZ, United States.
E-mail address: mpetrie@usgs.gov (M.D. Petrie).

http://dx.doi.org/10.1016/j.foreco.2015.11.028
0378-1127/

1. Introduction

Ponderosa and lodgepole pine forests are dominant ecosystems of western North America (Critchfield and Elbert, 1966; Burns and Honkala, 1990) and provide important ecosystem services including the support of ecological plant and animal diversity, water quality, biogeochemical cycling, and carbon storage (Turner et al., 2013; Wu and Kim, 2013; Hurteau et al., 2014; Rocca et al., 2014). These forests experienced widespread disturbances in the 20th century, and large-scale tree mortality has been observed across much of western North America in response to both enhanced drought severity (Breshears et al., 2005, 2009; Allen et al., 2010; Williams et al., 2013), fire (Savage and Mast, 2005; Parker et al., 2006; Hurteau et al., 2014), and severe insect outbreaks (Parker et al., 2006; Hicke and Jenkins, 2008). Semiarid forests including those of lodgepole and ponderosa pine may be highly impacted by climate change (Diffenbaugh et al., 2008; Allen et al., 2010; Herrero et al., 2013), which is predicted to produce warmer and drier conditions across much of western North America in the coming century (Seager et al., 2007; Gutzler and Robbins, 2011; IPCC, 2013). There is concern that ecological disturbances will be intensified by climate change, resulting in large-scale degradation of and vegetation compositional changes in these forests in the coming decades (Breshears et al., 2005; Aitken et al., 2008; Allen and Breshears, 1998; Allen et al., 2010; Feddema et al., 2013; Hanberry, 2014), altering and possibly reducing the persistence of these forests and the services they provide.

In the 21st century, disturbances such as drought, fire and insect outbreaks are predicted to become more frequent and destructive, and may possibly reduce the persistence of ponderosa and lodgepole pine forests (Savage and Mast, 2005; Parker et al., 2006; Hicke and Jenkins, 2008; Savage et al., 2013; Wu and Kim, 2013). The majority of research on forest persistence has focused on the deleterious effects of mortality events complimented by predictive modeling based on the climate conditions that support mature trees. Yet, the primary mechanism governing the persistence of ponderosa and lodgepole pine forests may actually be the climate-related limitation of forest regeneration after disturbance events have already occurred (Sackett, 1984; Savage et al., 1996, 2013; Kroiss and HilleRisLambers, 2015). Natural variability in climate drivers including precipitation and temperature promotes seedling recruitment events that are highly episodic and that may take decades or longer to occur (Brown and Wu, 2005; Ouzts et al., 2015); In western North America, the majority of forest regeneration in the past 100 years occurred during a small number of time periods that supported seed production, seedling emergence, and seedling establishment (Schubert, 1974; Mast et al., 1999; Brown and Wu, 2005). Forest demographic information during these regeneration events is not widely available, however, and the specific environmental conditions that govern forest regeneration are not completely understood. Because the future persistence of ponderosa and lodgepole pine forests in western North America will be dependent on the ability of these species to regenerate under the changing climatic conditions of the 21st century, it is critical that fine-scale forest demographic information is available to sharpen predictive analytical techniques.

It is clear that adequate moisture availability and above-freezing temperatures support seedling emergence and establishment for both ponderosa and lodgepole pine (International Seed Testing Association, 1985; Kolb and Robberecht, 1996; Coop and Givnish, 2008). Savage et al. (2013) suggest that ponderosa pine seedling emergence requires favorable temperature, evaporation and moisture conditions over a four-year period, including seed production through seedling germination and emergence from the soil, and seedling establishment requires an additional two years of favorable conditions. It is difficult to corroborate Savage et al. (2013)'s requirements with additional studies, however; Puhlick et al. (2012) for example found that ponderosa pine seedling density was closely correlated to annual precipitation, whereas Feddema et al. (2013) used a modeling approach to find that ponderosa pine seedling emergence and establishment was more sensitive to monthly precipitation, especially during the fall prior to seedling emergence. Therefore, although these and other generalities provide a foundation for understanding the relationships between seedling processes and climate and environmental conditions (Schubert, 1974; International Seed Testing Association, 1985; White, 1985), empirical, quantitative information at a finer level of detail would strengthen predictions of future forest demographics, regeneration and persistence.

To better understand how seedling processes – and therefore forest persistence – in ponderosa and lodgepole pine forests may be affected by climatic and environmental conditions in the 21st century, we compiled 96 publications that reported data on seedling emergence and/or establishment in ponderosa pine (*Pinus ponderosa*) and/or lodgepole pine (*P. contorta*), and also one or more driving climate and environmental variables of temperature, precipitation and moisture availability. Our primary objective was to correlate variation in driving, independent variables of temperature, precipitation and moisture availability to dependent variables of seedling emergence and establishment for ponderosa pine and lodgepole pine. In doing so, we also identified what information on seedling emergence and establishment is robust and what information is less-supported, and we investigated the foci of these studies to ascertain the strengths of and deficiencies in the peer-reviewed literature. Because only a small number of peer-reviewed publications have focused on the relationships between climate and environmental drivers and seedling emergence and establishment directly, our analysis included reported data on our driving variables of interest, even when these studies did not explore the influence of these variables. These indirect sources comprise the majority of information on emergence and establishment for ponderosa and lodgepole pine. Our review explores whether or not general assumptions of seedling responses to driving climate and environmental variables are supported by existing data, and also provides additional information on how climate and environmental conditions might govern ponderosa and lodgepole pine persistence in the 21st century.

2. Materials and methods

We conducted a literature search for ponderosa and lodgepole pine publications from 1930 to 2015 that included a United States Department of Agriculture – Forest Service database of 1200 publications, as well as Web of Science, National Agricultural Library (NAL) DigiTop, ProQuest Natural Science Collection, and Elton B. Stephens Co. (EBSCO) Environment Complete databases. We identified publications that reported data for ponderosa pine (*P. ponderosa*) or and/or lodgepole pine (*P. contorta*) seedling emergence and/or establishment, and one or more environmental and climate variables including air temperature [Ta], soil temperature [Ts], precipitation [P], soil moisture [θ] and soil water potential [ψ]. We compiled 96 publications that reported data for ponderosa pine (44 publications) and/or lodgepole pine (59 publications) in western North America and western Europe. Of these, 74 (77%) were laboratory or greenhouse studies, and 22 (23%) were field studies. We extracted data manually from each source; 47 (49%) studies provided only a single data point, and 23 (24%) studies focused on relationships between one or more of our variables of interest and seedling emergence and/or establishment directly. We conducted all analyses and produced all figures using R-project statistical computing software (R Development Core Team, 2015).

The majority of the studies in our review did not investigate the effects of climate and environmental drivers on seedling emergence and establishment directly. We found that a larger number of studies provided usable data indirectly, however, by reporting values for variables such as mean rainfall and air temperature as part of the study. We used these reported data from indirect studies in our investigation alongside data from a smaller number of direct studies. Thus, we combined data from all studies that reported usable data, regardless of whether or not these studies focused on the relationships between climate and environmental drivers and seedling processes directly. We investigated the effects of ten environmental and climate variables: Ta (daily $\bar{x}$, daily maximum, daily minimum), Ts (daily $\bar{x}$, daily maximum, daily minimum), volumetric soil moisture [θ: $m^3\ m^{-3}$], soil water potential [ψ: MPa], and precipitation (total annual and total monthly). We evaluated these relationships using linear correlations when the number of data points from all studies numbered seven or more.

Seedling functions may be defined in a number of ways. Germination in a laboratory, for example, is the emergence of the seedling hypocotyl from the seed coat, whereas germination in a field experiment may not be accounted for until the hypocotyl emerges from the soil surface. These germination events occur over different timescales and at different frequencies. In this study we defined seedling emergence as the final result of all germination phases (Chambers, 2000), and we considered seedling germination in a laboratory and seedling emergence from the soil to be equivalent. We defined seedling establishment as reported seedling survival at any point during the first year and up to a year of age. To be comparable to other studies, we only included studies that reported emergence and establishment data as a percentage of total seeds or seedlings, or studies with data that could be converted to a percentage.

3. Results

3.1. Literature review

We investigated seedling emergence and establishment for ponderosa and lodgepole pine from 96 primary sources, comprised of 74 laboratory and greenhouse studies (e.g. 'greenhouse' in text) and 22 field measurement and experimental studies (e.g. 'field' in text) (Fig. 1a). A total of 34 studies (35%) reported emergence or establishment data for ponderosa pine, and 62 studies (65%) reported data for lodgepole pine (Fig. 1a). A total of 53 (55%) of these studies reported data on seedling emergence, 27 studies (28%) reported data on seedling establishment, and 16 studies (17%) reported data on both variables (Fig. 1b).

Although all of the greenhouse and field studies in our review reported data on climate and environmental variables, only a relatively small number of studies investigated or manipulated any of these variables directly (23 total; 24% of all studies; Fig. 2a). The majority of greenhouse studies reported average values of climate and environmental variables, and we found only a single field study that evaluated any of these variables as a driver of seedling emergence or establishment (Rother et al., 2015) (Fig. 2). The timescales of studies focused on seedling emergence versus those focused on seedling establishment differed in their timescales of analysis; of published values, seedling emergence studies focused primarily on periods shorter than one month in duration (62% of published values; Fig. 3a), and seedling establishment studies focused primarily on periods longer than one year (59% of published values; Fig. 3b). 21% of studies did not report the timescale

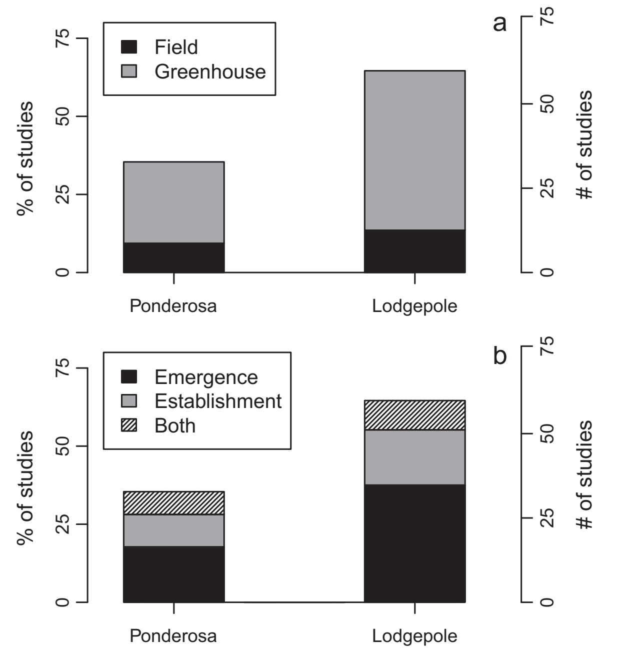

Fig. 1. Percentage and total number of studies focused on ponderosa and lodgepole pine (Panel a), greenhouse and field studies (Panel b), and on seedling emergence and establishment (Panel c).

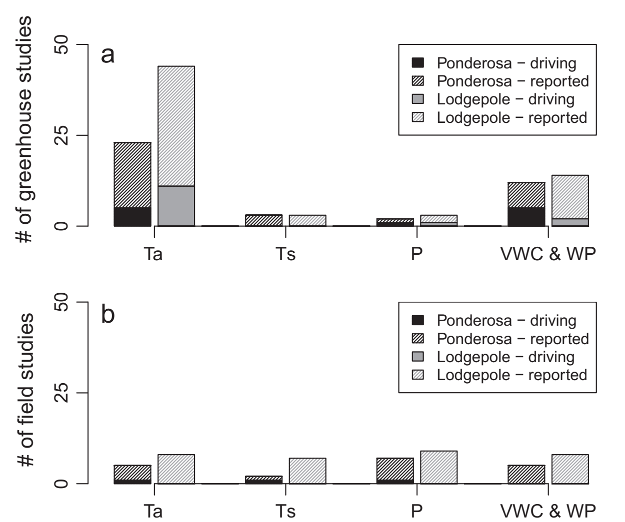

Fig. 2. Number of studies focused on climate variables of air temperature [Ta], precipitation [*P*], soil temperature [Ts] and soil moisture and soil water potential [VWC & WP] for seedling emergence (Panel a) and seedling establishment (Panel b) for ponderosa and lodgepole pine. 'Driving' variable studies specifically manipulated or evaluated the role of a driving climate variable on seedling emergence or establishment, whereas 'Reported' variable studies reported data for a driving climate variable without investigating its influence.

over which they investigated or reported seedling emergence and establishment (Fig. 3).

3.2. Summary of climate effects on seedling emergence and establishment from the literature

Seedling emergence in ponderosa and lodgepole pine is reported to be highest when Ta is between 20 to 30 °C during summer (International Seed Testing Association, 1985). We found that both greenhouse and laboratory studies maintained Ta in this

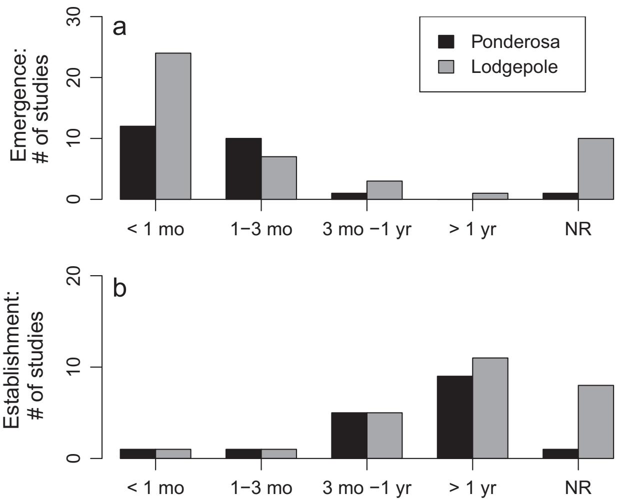

Fig. 3. Number of studies focused on different timescales of seedling emergence (Panel a) and establishment (Panel b) for ponderosa and lodgepole pine for periods of less than one month [<1 mo] to periods of over one year [>1 yr]. The value 'NR' stands for 'Not Reported.

range (Downie and Wang, 1992; Li et al., 1994; Page-Dumroese et al., 2002; Wang et al., 1992; Wang, 2003; Simpson et al., 2004; Teste et al., 2011). A constant Ta of 20 to 25 °C was often considered ideal for ponderosa and lodgepole pine emergence (Weber and Sorensen, 1990; Ohlson and Zackrisson, 1992; Fay and Mitchell, 1999; Pasquini et al., 2008), and emergence rates for ponderosa pine were found to decline when Ta was above or below approximately 20 °C (Weber and Sorensen, 1990). A number of studies found that seedling emergence for both ponderosa and lodgepole pine increased as mean Ta increased up to 25 °C, at which point emergence decreased (Haasis and Thrupp, 1931; Ackerman and Farrar, 1965; Peterson, 1970; Kaufmann and Eckard, 1977; Kamra, 1980; Weber and Sorensen, 1990; Jones and Gosling, 1994). Similarly, lower minimum Ta (>∼15 to 20 °C) increased emergence in lodgepole pine (Holmes and Buszewicz, 1955; Ackerman and Farrar, 1965; Kamra, 1980; Tanaka et al., 1986; Jones and Gosling, 1994). Higher maximum Ta was found to reduce emergence in both ponderosa and lodgepole pine (Wright, 1931; Ackerman and Farrar, 1965; Peterson, 1970; Knapp and Anderson, 1980; Hall, 1984; Tanaka et al., 1986). Based on this information, emergence in ponderosa and lodgepole pine is likely to increase with increasing Ta up to a mean or maximum Ta 25 to 30 °C, beyond which emergence may decline.

Similar to reported relationships for seedling emergence, higher mean and minimum daily Ta may increase establishment of ponderosa pine, and may also reduce establishment as daily maximum Ta surpasses 25 to 30 °C (Cochran and Berntsen, 1973; Shepperd and Noble, 1976; Noble et al., 1979; Seidel, 1986; Lopushinsky et al., 1992). Lower minimum Ta, which may occur during winter in the field or as part of a manipulative experiment, reduced the establishment of ponderosa and lodgepole pine seedlings (Cochran and Berntsen, 1973; Lopushinsky et al., 1992), and higher minimum Ta increased establishment (Cochran and Berntsen, 1973; Shepperd and Noble, 1976; Noble et al., 1979; Seidel, 1986; Lopushinsky et al., 1992). Although higher daily Ta may support greater emergence of ponderosa and lodgepole pine, none of the studies in our review reported a relationship between maximum Ts and seedling establishment.

A small number of studies have investigated the effect of precipitation and moisture availability on seedling emergence and establishment. Ohlson and Zackrisson (1992) and Varmola et al. (2000) found that, in multi-year studies, higher mean annual precipitation supported lodgepole pine emergence and establishment. Shepperd and Noble (1976) and Noble et al. (1979) found that higher monthly precipitation increased emergence and establishment for lodgepole and ponderosa pine, respectively. Generally, higher soil moisture availability measured as volumetric soil moisture [θ] or soil water potential [ψ: MPa] increased seedling emergence (Brayshaw, 1953; Holmes and Buszewicz, 1955; Larson and Schubert, 1969; Djavanshir and Reid, 1975; Kaufmann and Eckard, 1977; Elena Fernandez et al., 2014), and Moore and Kidd (1982) found that declining ψ from −4 to −8 MPa greatly reduced ponderosa pine seedling emergence. When experimentally manipulated, drier conditions inhibited seedling establishment in lodgepole pine (Cochran and Berntsen, 1973; Bulmer and Simpson, 2005) and in ponderosa pine (Pinto et al., 2012; Rother et al., 2015).

3.3. Data review

Ponderosa pine and lodgepole pine had lower % seedling emergence as Ta > ∼25 to 30 °C (Table 1, Figs. 4a, c and 5a), and also had higher % seedling emergence as daily minimum Ta and Ts increased (Table 1, Figs. 4b and 5b). Increasing maximum Ta > 25 °C strongly reduced seedling emergence from 65% to 27% (Fig. 4c). Increasing daily minimum Ta from ∼0 to 20 °C increased ponderosa pine emergence from 14% to 70% (Fig. 4b), yet increasing $\overline{Ta}$ from ∼20 to 25 °C decreased ponderosa pine emergence from 69% to 58% (Fig. 4a). Lodgepole pine emergence increased from 10% to 69% as $\overline{Ts}$ increased from 5 to 20 °C (Fig. 5b). Increasing ψ, MAP and monthly P increased lodgepole pine emergence (Fig. 5c–e). Lodgepole pine seedling emergence was much lower when data were comprised solely of field studies (Fig. 5d) compared to those comprised solely of greenhouse studies (Fig. 5c and e).

Ponderosa pine establishment was highly sensitive to variation in Ta and Ts: establishment increased as daily $\overline{Ta}$ increased from ∼15 to 25 °C (Fig. 4e), and also increased as minimum Ts and lower than average maximum Ts increased up to 10 and 15 °C, respectively (Fig. 4g and h). Establishment decreased as maximum daily Ta increased beyond 25 °C (Fig. 4f). Lodgepole pine establishment also increased as minimum Ts and lower than average maximum

Table 1
R^2 correlation statistic for ponderosa pine (PP) and lodgepole pine (LP) seedling emergence and establishment response to environmental and climate variables of air temperature [Ta], soil temperature [Ts], volumetric soil moisture [θ], soil water potential [ψ], and precipitation [P]. Bold values indicate significance of the R^2 correlation statistic at $p < 0.05$. Relationships listed as NA did not have enough data points for the regression analysis, those listed as NS were not significant, and a dash (–) indicates that no data were available.

	Ta			Ts			θ	ψ	P	P
	$\bar{x}$	min	max	$\bar{x}$	min	max	$\bar{x}$	$\bar{x}$	annual	monthly
PP emergence	**0.14**	**0.46**	**0.26**	–	–	–	–	**0.39**	NA	NS
PP establishment	**0.05**	NS	**0.17**	NA	**0.13**	**0.13**	NA	NS	**0.10**	NS
LP emergence	NS	NS	**0.22**	**0.49**	–	–	NA	**0.69**	**0.42**	**0.66**
LP establishment	NA	NS	NS	NS	**0.05**	**0.14**	**0.09**	NS	NS	**0.31**

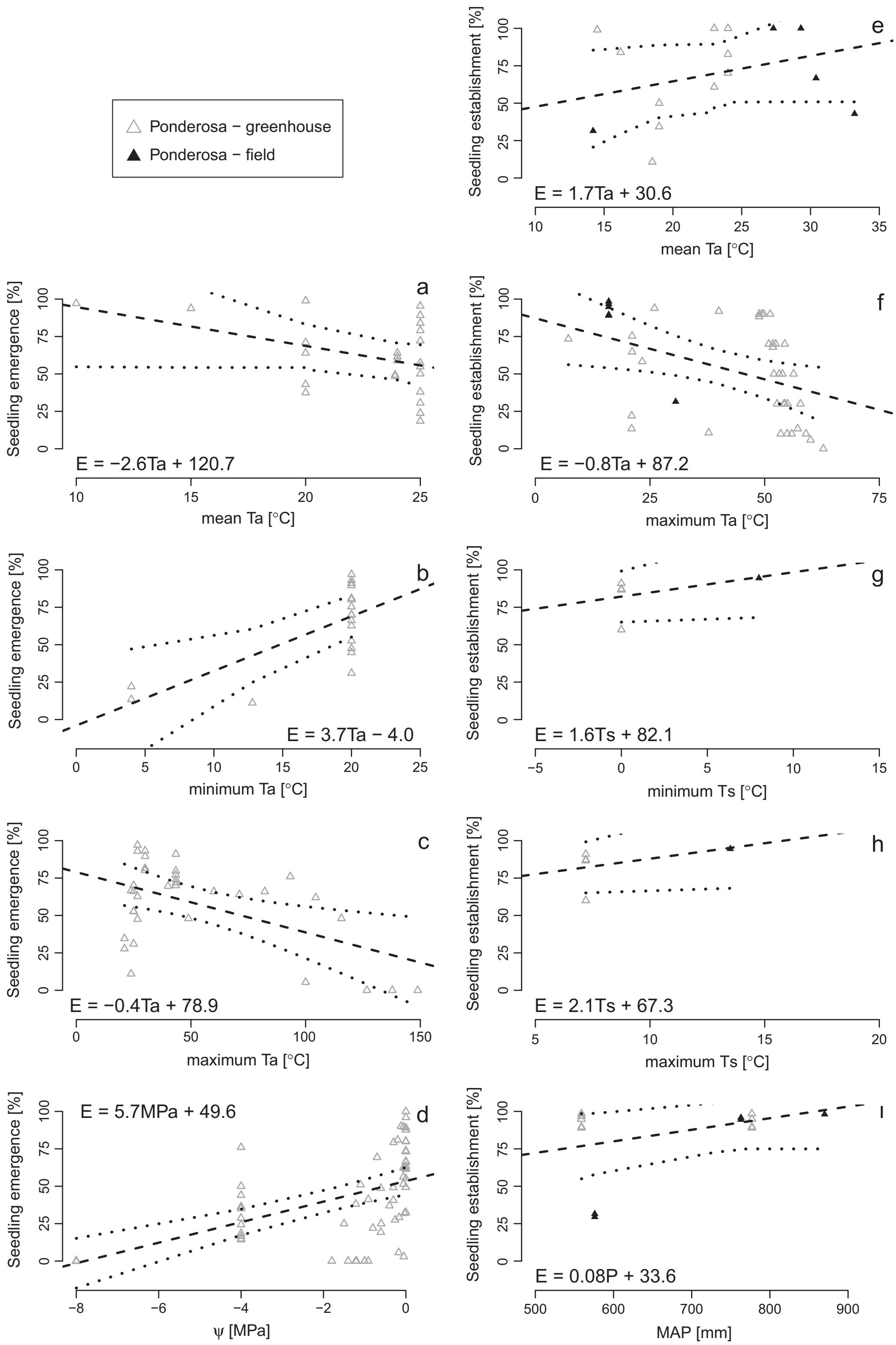

Fig. 4. Linear regression analysis of ponderosa pine seedling emergence and mean air temperature [Ta] (Panel a: Wright, 1931; Brayshaw, 1953; Djavanshir and Reid, 1975; Rietveld, 1975; Harrington, 1977; Van Haverbeke and Peterson, 1989; Weber and Sorensen, 1990; Bai et al., 2004), minimum Ta (Panel b: Lavender, 1955; Heidmann, 1962; Peterson, 1970; Cochran, 1973; Jenkinson, 1977; Noble et al., 1979; Li et al., 1994; Pasquini et al., 2008), maximum Ta (Panel c: Wright, 1931; Lavender, 1955; Heidmann, 1962; Larson and Schubert, 1969; Peterson, 1970; Cochran and Berntsen, 1973; Cochran, 1973; Jenkinson, 1977; Noble et al., 1979; Li et al., 1994; Pasquini et al., 2008), and soil water potential [ψ] (Panel d: Brayshaw, 1953; Larson and Schubert, 1969; Djavanshir and Reid, 1975; Rietveld, 1975; Moore and Kidd, 1982), and also seedling establishment and mean Ta (Panel e: Jenkinson, 1974; Heidmann and Thorud, 1976; Seidel, 1986; Coop and Givnish, 2008; Pinto et al., 2011; Pinto et al., 2012; Rother et al., 2015), maximum Ta (Panel f: Stone and Jenkinson, 1970; Cochran, 1973; Lopushinsky and Beebe, 1976; Noble et al., 1979; Seidel, 1986; Coop and Givnish, 2008; Pinto et al., 2012), minimum soil temperature [Ts] (Panel g: Stone and Jenkinson, 1970; Cochran and Berntsen, 1973; Cochran, 1973; Lopushinsky and Beebe, 1976; Noble et al., 1979; Coop and Givnish, 2008), maximum Ts (Panel h: Stone and Jenkinson, 1970; Cochran and Berntsen, 1973; Cochran, 1973; Lopushinsky and Beebe, 1976; Noble et al., 1979; Seidel, 1986; Coop and Givnish, 2008; Pinto et al., 2012) and mean annual precipitation [P] (Panel i: Lopushinsky and Beebe, 1976; Noble et al., 1979; Chen, 1997; Fan et al., 2002; Coop and Givnish, 2008; Pinto et al., 2011; Pinto et al., 2012). All relationships are significant at $p < 0.05$. The linear regression and 95% confidence interval are illustrated by the dotted lines.

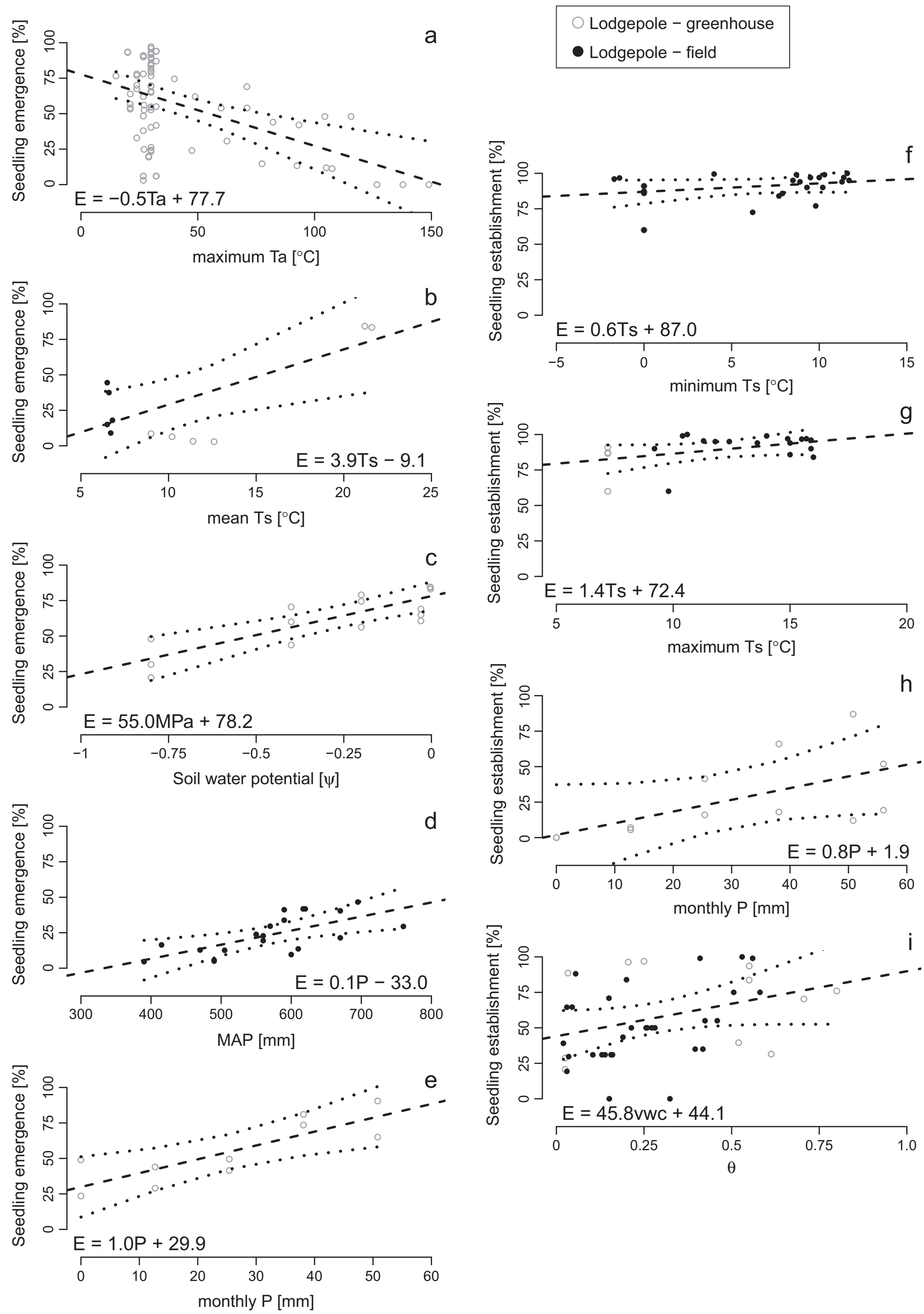

Fig. 5. Linear regression analysis of lodgepole pine seedling emergence and maximum air temperature [Ta] (Panel a: Wright, 1931; Crossley, 1955; Holmes and Buszewicz, 1955; Timonin, 1964; Ackerman and Farrar, 1965; Ackerman and Gorman, 1969; Minore, 1972; Cochran and Berntsen, 1973; Cochran, 1973; Shepperd and Noble, 1976; Hellum and Pelchat, 1979; Hellum and Barker, 1980; Kamra, 1980; Knapp and Anderson, 1980; Wang, 1980; Hellum and Dymock, 1986; Hall, 1984; Tanaka et al., 1986; Downie and Wang, 1992; Wang et al., 1992; Woodard, 1983; Woodard and Cummins, 1987; Jones and Gosling, 1994; Li et al., 1994; Wang, 2003; Simpson et al., 2004; El-Kassaby et al., 2008; Aoki et al., 2011; Teste et al., 2011), seedling emergence and soil water potential [ψ] (Panel b: Page-Dumroese et al., 2002; Wright et al., 1998; Pinto et al., 2009), seedling emergence and mean annual precipitation [*P*] (Panel c: Kaufmann and Eckard, 1977; Pinto et al., 2009), seedling emergence and monthly *P* (Panel d: Ohlson and Zackrisson, 1992; Page-Dumroese et al., 2002), seedling establishment and monthly *P* (Panel e: Shepperd and Noble, 1976), seedling establishment and volumetric soil moisture [θ] (Panel f: Timonin, 1964; Etter, 1969; Minore, 1972; Cochran and Berntsen, 1973; Cochran, 1973; Shepperd and Noble, 1976; Coutts and Philipson, 1978; Chakravarty and Sidhu, 1987; Sidhu and Chakravarty, 1990; Coates et al., 1991; Lopushinsky et al., 1992; Van den driessche, 1992; Chakravarty et al., 1999; Hawkins et al., 2003), (Panel g: Timonin, 1964; Etter, 1969; Minore, 1972; Cochran and Berntsen, 1973; Cochran, 1973; Shepperd and Noble, 1976; Lotan and Perry, 1977; Coutts and Philipson, 1978; Chakravarty and Sidhu, 1987; Sidhu and Chakravarty, 1990; Lopushinsky et al., 1992; Chakravarty et al., 1999; Hawkins et al., 2003), (Panel h: Timonin, 1964; Etter, 1969; Shepperd and Noble, 1976; Lotan and Perry, 1977; Bulmer and Simpson, 2005; Johnstone and Chapin, 2006), and (Panel i: Coates et al., 1991; Van den Driessche, 1996; Wright et al., 1998; Bulmer and Simpson, 2005; Dehlin et al., 2008). All relationships are significant at $p < 0.05$. The linear regression and 95% confidence interval are illustrated by the dotted lines.

Ts increased up to 10 and 15 °C, respectively (Fig. 5f and g). Ponderosa pine establishment increased from 78% to ~100% as MAP increased from 550 mm to 850 mm (Fig. 5e). Lodgepole pine establishment increased from 37% to 78% as soil water potential increased from −0.75 to 0.0 MPa (Fig. 5h), and also increased from 44% to 78% as θ increased from 0.0 to 0.75 (Fig. 5i).

4. Discussion

4.1. Climate and environmental controls on emergence and establishment

From the studies we analyzed in this review, it is clear that driving variables of air and soil temperature, precipitation and moisture availability affect seedling emergence and establishment for ponderosa and lodgepole pine. Generally, both information reported in the literature and our analysis of reported data suggest that seedling emergence and establishment are highest at moderate ranges of air and soil temperature, and when precipitation and moisture availability are at or above average local values (Figs. 4 and 5). Yet, very little primary information exists on the relationships between driving climate and environmental variables and seedling processes, and it is difficult to determine clear driver and response relationships for seedling emergence and establishment solely based on data available from these primary sources. We believe this is in part due to the variety of settings of these studies (field, greenhouse, laboratory), especially the low number of field investigations (Fig. 1a). Despite this shortcoming, the majority of studies did report data for emergence and establishment at relevant timescales; the majority of emergence studies focused on the first 0 to 3 months of seedling fecundity (91%; Fig. 3a), and establishment studies focused on periods from 3 months to > 1 year in duration (88%; Fig. 3b). Because climate and environmental variables will likely play an important role in future scenarios of forest regeneration in coming decades, it is critical to better understand these relationships, and to continue conducting research at the timescales at which seedling emergence and establishment occur.

Ponderosa and lodgepole pine seedlings had similar and differing sensitivities to driving climate and environmental variables. Ponderosa pine seedlings were more sensitive to Ta and Ts than to other variables (Table 1, Fig. 4), whereas lodgepole pine seedlings were more sensitive to Ts, precipitation and moisture availability (Table 1, Fig. 5). Yet, we found that emergence of ponderosa pine may be greatly reduced at low ψ (Fig. 4d), suggesting that ponderosa pine is also sensitive to moisture availability. Because only 23 studies focused on driving climate and environmental variables, however, it is unclear if these species-specific differences indicate actual differences in ponderosa and lodgepole pine seedlings (Fig. 2). Furthermore, only one of these studies occurred in the field (Rother et al., 2015), and this study did not evaluate lodgepole pine (Fig. 2). On average, we observed lower lodgepole pine seedling emergence in field studies (Fig. 5d) compared to greenhouse studies (Fig. 5c and e), suggesting that the relationships we found in greenhouse studies may be artificially inflated. In greenhouse studies, temperature and moisture availability are usually maintained at levels that do not limit seedling processes, and additional stressors such as low bare soil availability, soil water repellency and vegetation competition are expelled from the seedling environment. For example, in Figs. 4b and 5a, greenhouse temperature was held constant in many studies, resulting in a large amount of data points from 20 to 30 °C. We believe that the varying results and inconclusive correlations that we observed in this review (e.g. Table 1) suggest uncertainty in the information available for seedling emergence and establishment, and the high degree of variability in these results and in available data sources stresses the need to further investigate the emergence and establishment requirements for ponderosa and lodgepole pine.

Our results do corroborate a number of studies that focused on temperature effects on seedling emergence and establishment. Similar to our findings, Weber and Sorensen (1990) and McTague and Tinus (1996) reported that seedling emergence and establishment rates declined when Ta > 25 °C, and Jones and Gosling (1994) and Beardmore et al. (2008) reported that very low Ta (<0 to 25 °C) may also decrease emergence in lodgepole pine. Many studies report that both emergence and establishment for ponderosa and lodgepole pine may be highest at intermediate (~20 to 30 °C) temperatures (Haasis and Thrupp, 1931; Wright, 1931; Ackerman and Farrar, 1965; Cochran and Berntsen, 1973; Shepperd and Noble, 1976; Kaufmann and Eckard, 1977; Noble et al., 1979; Kamra, 1980; Seidel, 1986; Weber and Sorensen, 1990; Lopushinsky et al., 1992; Jones and Gosling, 1994; Hawkins et al., 2003; Coop and Givnish, 2008). We found high Ta to decrease emergence for both ponderosa pine and lodgepole pine (Figs. 4c and 5a), and to decrease ponderosa pine establishment (Fig. 4f). Increasing Ta and Ts from 5 to 20 °C increased emergence in both species (Figs. 4b and 5b), and also increased establishment (Figs. 4e, g, h and 5f and g). Although increasing $\overline{Ta}$ from ~20 to 25 °C decreased ponderosa pine emergence (Fig. 4a), the data largely show that Ts and Ta ~20 to 25 °C is likely the most favorable range for seedling emergence and establishment for ponderosa and lodgepole pine.

A good deal of research suggests that higher precipitation at monthly to annual timescales supports greater seedling emergence and establishment (Lotan and Perry, 1976; Shepperd and Noble, 1976; Noble et al., 1979; Lopushinsky et al., 1992; Ohlson and Zackrisson, 1992; Fries, 1993; Chen, 1997; Burton et al., 2000; Zabowski et al., 2000; Fan et al., 2002; Page-Dumroese et al., 2002; Coop and Givnish, 2008; Dehlin et al., 2008; Page-Dumroese et al., 2008; Pinto et al., 2011), and higher moisture availability supports greater seedling emergence (Brayshaw, 1953; Holmes and Buszewicz, 1955; Larson and Schubert, 1969; Djavanshir and Reid, 1975; Moore and Kidd, 1982). Our results corroborate these findings, and show that lodgepole pine seedling emergence and establishment may be especially sensitive to ψ and P at monthly to annual timescales (Fig. 5), which supports the findings of Feddema et al. (2013). Coincidently, we also found that higher annual P increased ponderosa pine seedling establishment (Fig. 4i), which supports the somewhat contradictory findings of Puhlick et al. (2012). Although ponderosa and lodgepole pine may actually have different sensitivities to rainfall and moisture, and the timescales over which these processes occur remain unclear, our results suggest that higher rainfall and moisture availability supports higher seedling success for both species.

4.2. Emergence and establishment in the 21st century

Seedling success is limited to a narrow range of temperature and precipitation-driven controls (Savage et al., 2013), and these drivers have limited regional forest regeneration in western North America to a small number of favorable periods over the past 100 years (Schubert, 1974; Mast et al., 1999; Brown and Wu, 2005). In this review, we found that seedling processes for ponderosa pine were more sensitive to fluctuations in temperature (Fig. 4), whereas these processes in lodgepole pine were more sensitive to fluctuations in precipitation and soil moisture (Fig. 5). Despite these relationships, temperature, precipitation and moisture availability are inextricably linked (Laio et al., 2002; Porporato et al., 2004), and both temperature and moisture availability will likely have a strong influence on future emergence and establishment for ponderosa and lodgepole pine. As an example of these interactions, Brandes and Wilcox (2000) found that soil moisture availability governed the seasonal pattern of evapotranspiration in a ponderosa pine forest in New Mexico, and potential evaporation (which is largely governed by temperature and vapor pressure deficit) was consistently of high enough magnitude that variation in potential evaporation did not influence rates of evapotranspiration and moisture availability. Yet, increasing average temperatures have been found to shift the timing of evapotranspiration towards earlier dates in spring, thus reducing moisture availability and increasing ecosystem sensitivity to precipitation in late spring and summer (D'Odorico et al., 2000; Schwartz et al., 2006; Petrie et al., in press). As a result of the interactions of temperature, precipitation and moisture availability, we hypothesize that change to any of these variables is likely to influence seedling processes for ponderosa and lodgepole pine.

Favorable periods for forest regeneration may be further restricted by disturbances including windfall, fire, insect invasion, and competition (Sackett, 1984; Savage et al., 1996; Parker et al., 2006; Allen et al., 2010; Williams et al., 2013; Savage et al., 2013). We found that very high air temperatures (>75 °C), such as those produced by fire, reduced seedling emergence and establishment (Figs. 4c, f and 5a). It is well-documented that ponderosa and lodgepole pine seedling viability is severely affected by very high temperatures (White, 1985; Brown and Wu, 2005), although fire events may also support seedling emergence in subsequent years (Edwards et al., 2015). In the 21st century, increasing maximum temperatures of fire events as a result of higher fuel loads and drier average conditions may limit forest regeneration by reducing seed fecundity (Battaglia et al., 2009). Additionally, while we found that temperatures >15 °C support seedling emergence and establishment (Figs. 4b, e, g, h and 5b), these conditions also support higher insect survival (Parker et al., 2006). It is critical for tree seedlings to emerge in a bare-soil environment before shallow-rooted woody and herbaceous species are established (International Seed Testing Association, 1985; Elliott and White, 1987; Wagner et al., 1989; Stone and Wolfe, 1996), and plant community composition, productivity, and growing season dynamics will likely all be influenced by changes in climate, making the influence of biotic and abiotic disturbances increasingly complex in the future.

The effect of a shift towards a warmer and drier climate in western North America may be a reduction in the range and persistence of many forests (Johnstone and Chapin, 2003; Aitken et al., 2008). Species Distribution Models (SDMs) are often used to investigate the future persistence and geographic ranges of ponderosa pine and lodgepole pine (Johnstone and Chapin, 2003; Coops et al., 2005; Aitken et al., 2008; Lintz et al., 2013), yet our results suggest SDMs may overestimate the range and persistence of these forests because they focus on the current climatic and environmental conditions of mature forests instead of the climatic and environmental conditions that support forest regeneration (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005). Many SDM techniques are critiqued for oversimplifying ecosystem responses to geographic barriers, no-analog vegetation communities, and novel climate conditions, yet SDMs do provide valuable information on potential ecosystem responses and we believe they can be a valuable analysis tool when focused on the correct demographic processes (Pearson and Dawson, 2003; Guisan and Thuiller, 2005). For example, a SDM technique from Bell et al. (2014) suggests that the geographic range of ponderosa pine may contract or shift as suitable climates for mature trees and seedlings diverge in the coming century. Better forest demographic information, especially information on how climate drivers affect seedling emergence and establishment, would greatly enhance the ability of SDM techniques to predict the persistence of ponderosa and lodgepole pine forests in the 21st century. We believe that it is critical that scientific understanding of forest regeneration moves beyond the impact of climate drivers and towards a complete understanding of how climate drivers, ecological disturbances and forest demographic processes interact to impact the effects of a changing climate on ponderosa and lodgepole pine forest persistence.

5. Conclusions

In this study we reviewed 96 peer-reviewed publications on ponderosa pine and lodgepole pine seedling emergence and establishment, and investigated how seedling processes are influenced by driving climate and environmental variables of air and soil temperature, precipitation, and moisture availability. Our review suggests that seedling emergence and establishment for both species is highest at intermediate temperatures (20 to 25 °C), and higher precipitation and moisture availability supports higher seedling emergence and establishment at daily, monthly and annual timescales. We found evidence that ponderosa pine seedlings may be more sensitive to temperature fluctuations whereas lodgepole pine seedlings may be more sensitive to moisture fluctuations. However, our findings were limited by the quality of available data – only 23 studies in our review investigated the effects of driving climate and environmental variables directly, and only one of these studies occurred in the field. This review illustrates that lack of data about several key processes and relationships governing forest regeneration limits the ability to make predictive assessments of forest demographics, range and persistence in the coming century, and this review also stresses the need to further evaluate the individual and aggregate effects of driving variables in the field.

Acknowledgments

Portions of this study were funded by a grant from the USDA Forest Service, Western Wildland Environmental Threat Assessment Center. We would like to thank Laura Bojanowski for her help in conducting the literature review. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Ackerman, R., Farrar, J., 1965. The effect of light and temperature on the germination of jack pine and lodgepole pine seeds. University of Toronto Faculty of Forestry Technical Report 5.

Ackerman, R., Gorman, J., 1969. Effect of seed weight on size of Lodgepole pine and white spruce container-planting stock. Pulp Paper Mag. Canada 70, 167–170.

Aitken, S., Yeaman, S., Holliday, J., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol. Appl. 1, 95–111. http://dx.doi.org/10.1111/j.1752-4571.2007.00013.x.

Allen, C., Breshears, D., 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proc. Natl. Acad. Sci. USA 95, 14839–14842. http://dx.doi.org/10.1073/pnas.95.25.14839.

Allen, C., Macalady, A., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D., Hogg, E., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J., Allard, G., Running, S., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684. http://dx.doi.org/10.1016/j.foreco.2009.09.001.

Aoki, C., Romme, W., Rocca, M., 2011. Lodgepole pine seed germination following tree death from mountain pine beetle attack in Colorado, USA. Am. Midl. Nat. 165, 446–451.

Bai, Y., Broersma, K., Thompson, D., 2004. Douglas fir and ponderosa pine seed dormancy as regulated by grassland seedbed conditions. J. Range Manag. 57, 661–667.

Battaglia, M., Smith, F., Shepperd, W., 2009. Predicting mortality of ponderosa pine regeneration after prescribed fire in the Black Hills, South Dakota, USA. Int. J. Wildland Fire 18, 176–190. http://dx.doi.org/10.1071/WF07163.

Beardmore, T., Wang, B., Penner, M., Scheer, G., 2008. Effects of seed water content and storage temperature on the germination parameters of white spruce, black spruce and lodgepole pine seed. New Forest. 36, 171–185.

Bell, D., Bradford, J., Lauenroth, W., 2014. Mountain landscapes offer few opportunities for high-elevation tree species migration. Glob. Change Biol. 20, 1441–1451. http://dx.doi.org/10.1111/gcb.12504.

Brandes, D., Wilcox, B., 2000. Evapotranspiration and soil moisture dynamics on a semiarid ponderosa pine hillslope. J. Am. Water Resour. Assoc. 36, 965–974. http://dx.doi.org/10.1111/j.1752-1688.2000.tb05702.x.

Brayshaw, T., 1953. An approach to the determination of moisture requirements for the germination of seeds of Douglas Fir, Ponderosa Pine and Engelmann Spruce. Research notes: UBC forest club 8.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W. H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. PNAS 102, 15144–15148. http://dx.doi.org/10.1073/pnas.0505734102.

Breshears, D.D., Myers, O.B., Meyer, C.W., Barnes, F.J., Zou, C.B., Allen, C.D., McDowell, N.G., Pockman, W.T., 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. Front. Ecol. Environ. 7, 185–189. http://dx.doi.org/10.1890/080016.

Brown, P., Wu, R., 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. Ecology 86, 3030–3038. http://dx.doi.org/10.1890/05-0034.

Bulmer, C., Simpson, D., 2005. Soil compaction and water content as factors affecting the growth of lodgepole pine seedlings on sandy clay loam soil. Can. J. Soil Sci. 85, 667–679.

Burns, R., Honkala, B., 1990. Silvics of North America: 1. Conifers. Agriculture Handbook, vol. 2. U.S. Dept. of Agriculture, Forest Service, Washington, D.C., p. 654.

Burton, P., Bedford, L., Goldstein, M., Osberg, M., 2000. Effects of disk trench orientation and planting spot position on the ten-year performance of lodgepole pine. New Forest. 20, 23–44.

Chakravarty, P., Khasa, D., Dancik, B., Sigler, L., Wichlacz, M., Trifonov, L., Ayer, W., 1999. Integrated control of Fusarium damping-off in conifer seedlings. J. Plant Dis. Prot. 106, 342–352.

Chakravarty, P., Sidhu, S., 1987. Effect of hexazinone (Prononetm5g) on the seedling growth and mycorrhizal incidence of Pinus-Contorta Var Latifolia and Picea-Glauca. Eur. J. For. Pathol. 17, 282–291.

Chambers, J., 2000. Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. Ecol. Appl. 10, 1400–1413. http://dx.doi.org/10.2307/2641294.

Chen, H., 1997. Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. Can. J. For. Res. 27, 1383–1393.

Coates, K., Emmingham, W., Radosevich, S., 1991. Conifer-seedling success and microclimate at different levels of herb and shrub cover in a Rhododendron-Vaccinium-Menziesia community of South Central British-Columbia. Can. J. For. Res. 21, 858–866.

Cochran, P., 1973. Natural Regeneration of Lodgepole Pine in South-central Oregon. U.S. Dept. of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.

Cochran, P.H., Berntsen, C.M., 1973. Tolerance of lodgepole and ponderosa pine seedlings to low night temperatures. Forest Sci. 19, 272–280.

Coop, J., Givnish, T., 2008. Constraints on tree seedling establishment in montane grasslands of the Valles Caldera, New Mexico. Ecology 89, 1101–1111.

Coops, N., Waring, R., Law, B., 2005. Assessing the past and future distribution and productivity of ponderosa pine in the Pacific Northwest using a process model, 3-PG. Ecol. Model. 183, 107–124. http://dx.doi.org/10.1016/j.ecolmodel.2004.08.002.

Coutts, M., Philipson, J., 1978. Tolerance of tree roots to waterlogging. New Phytol. 80, 71–77.

Critchfield, W., Elbert, L., 1966. Geographic distribution of the pines of the world. U. S. Department of Agriculture, Miscellaneous Publication, vol. 991, pp. 1–97.

Crossley, D., 1955. Viability of the seed of Lodgepole Pine [Pinus contorta var. latifolia] after 20 years in artificial storage. Forest. Chron. 31, 250–251.

Dehlin, H., Peltzer, D., Allison, V., Yeates, G., Nilsson, M., Wardle, D., 2008. Tree seedling performance and below-ground properties in stands of invasive and native tree species. New Zeal. J. Ecol. 32, 67–79.

Diffenbaugh, N.S., Giorgi, F., Pal, J.S., 2008. Climate change hotspots in the United States. Geophys. Res. Lett. 35. http://dx.doi.org/10.1007/s00704-011-0484-y.

Djavanshir, K., Reid, C., 1975. Effect of moisture stress on germination and radicle development of Pinus eldarica Medw. and Pinus ponderosa Laws. Can. J. For. Res. 5, 80–83.

D'Odorico, P., Ridolfi, L., Porporato, A., Rodriguez-Iturbe, I., 2000. Preferential states of seasonal soil moisture: the impact of climate fluctuations. Water Resour. Res. 36 (8), 2209–2219.

Downie, B., Wang, B., 1992. Upgrading germinability and vigor of jack pine, lodgepole pine, and white spruce by the Ids technique. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 22, 1124–1131.

Edwards, M., Krawchuk, M.A., Burton, P.J., 2015. Short-interval disturbance in lodgepole pine forests, British Columbia, Canada: understory and overstory response to mountain pine beetle and fire. For. Ecol. Manage. 338, 163–175. http://dx.doi.org/10.1016/j.foreco.2014.11.011.

El-Kassaby, Y., Stoehr, M., Kolotelo, D., Moss, I., 2008. Seed germination: mathematical representation and parameters extraction. Forest Sci. 54, 220–227.

Elena Fernandez, M., Gyenge, J., Varela, S., de Urquiza, M., 2014. Effects of the time of drought occurrence within the growing season on growth and survival of Pinus ponderosa seedlings. Trees-Struct. Funct. 28, 745–756. http://dx.doi.org/10.1007/s00468-014-0986-1.

Elliott, K., White, A., 1987. Competitive effects of various grasses and forbs on ponderosa pine-seedlings. Forest Sci. 33, 356–366.

Etter, H., 1969. Growth, metabolic components and drought survival of lodgepole pine seedlings at three nitrate levels. Can. J. Plant Sci. 49, 393–402. http://dx.doi.org/10.4141/cjps69-066.

Fan, Z., Moore, J., Shafii, B., Osborne, H., 2002. Three-year response of ponderosa pine seedlings to controlled-release fertilizer applied at planting. West. J. Appl. Forest. 17, 154–164.

Fay, D., Mitchell, D., 1999. A preliminary study on the mycorrhizal associations of tree seedlings growing on old mine spoil at Avoca, Co. Wicklow. Biol. Environ.-Proc. Roy. Irish Acad. 99B, 19–26.

Feddema, J., Mast, J., Savage, M., 2013. Modeling high-severity fire, drought and climate change impacts on ponderosa pine regeneration. Ecol. Model. 253, 56–69. http://dx.doi.org/10.1016/j.ecolmodel.2012.12.029.

Fries, C., 1993. Development of planted Pinus sylvestris and P. contorta after soil preparation in a northern climate. Scand. J. For. Res. 8, 73–80.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009. http://dx.doi.org/10.1111/j.1461-0248.2005.00792.x.

Guisan, A., Zimmermann, N., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147–186. http://dx.doi.org/10.1016/S0304-3800(00)00354-9.

Gutzler, D., Robbins, T., 2011. Climate variability and projected change in the western United States: regional downscaling and drought statistics. Clim. Dyn. 37, 835–849. http://dx.doi.org/10.1007/s00,382-010-0838-7.

Haasis, F.W., Thrupp, A.C., 1931. Temperature relations of lodgepole-pine seed germination. Ecology 12, 728–744.

Hall, O., 1984. The effects of dry heat on tree seed germination: lodgepole pine, slash pine and douglas fir. Newsl. Assoc. Off. Seed Anal. 58, 117–121.

Hanberry, B., 2014. Compositional changes in selected forest ecosystems of the western United States. Appl. Geography 52, 90–98. http://dx.doi.org/10.1016/j.apgeog.2014.05.004.

Harrington, M., 1977. Response of Ponderosa Pine Seeds to Light, vol. 220, Dept. of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.

Hawkins, B., Guest, H., Kolotelo, D., 2003. Freezing tolerance of conifer seeds and germinants. Tree Physiol. 23, 1237–1246.

Heidmann, L.J., 1962. Longevity of *Ponderosa Pine* seed. Ecology 43, 344.

Heidmann, L.J., Thorud, D.B., 1976. Controlling frost heaving of ponderosa pine seedlings in Arizona.

Hellum, A., Barker, N., 1980. Cone moisture-content influences seed release in lodgepole pine. Can. J. For. Res. 10, 239–244.

Hellum, A., Dymock, I., 1986. Cold stratification for lodgepole pine seed. USDA Forest Service general technical report INT – Intermountain Forest and Range Experiment Station 203, pp. 107–111.

Hellum, A., Pelchat, M., 1979. Temperature and time affect the release and quality of seed from cones of lodgepole pine from Alberta. Can. J. For. Res. 9, 154–159.

Herrero, A., Castro, J., Zamora, R., Delgado-Huertas, A., Querejeta, J., 2013. Growth and stable isotope signals associated with drought-related mortality in saplings of two coexisting pine species. Oecologia 173, 1613–1624. http://dx.doi.org/10.1007/s00442-013-2707-7.

Hicke, J., Jenkins, J., 2008. Mapping lodgepole pine stand structure susceptibility to mountain pine beetle attack across the western United States. For. Ecol. Manage. 255, 1536–1547. http://dx.doi.org/10.1016/j.foreco.2007.11.027.

Holmes, G., Buszewicz, G., 1955. Experiments with cold-wet pretreatment as a method of increasing the germination rate of seed of Douglas Fir, Sitka Spruce and Lodgepole Pine. Report on forest research, London, pp. 1953–1954.

Hurteau, M., Bradford, J., Fule, P., Taylor, A., Martin, K., 2014. Climate change, fire management, and ecological services in the southwestern US. For. Ecol. Manage. 327, 280–289. http://dx.doi.org/10.1016/j.foreco.2013.08.007.

International Seed Testing Association, 1985. International rules for seed testing: rules 1985. Seed Sci. Technol. 13, 299–355.

IPCC, 2013. Climate Change 2013: I. The Physical Science Basis. Cambridge University Press, London.

Jenkinson, J., 1974. Ponderosa pine progenies: differential responses to ultramafic and granitic soils, 14p.

Jenkinson, J., 1977. Edaphic interactions in first-year growth of California ponderosa pine.

Johnstone, J., Chapin, F., 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. Glob. Change Biol. 9, 1401–1409. http://dx.doi.org/10.1046/j.1365-2486.2003.00661.x.

Johnstone, J., Chapin, F., 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems 9, 14–31.

Jones, S., Gosling, P., 1994. Target moisture content prechill overcomes the dormancy of temperate conifer seeds. New Forest. 8, 309–321.

Kamra, S., 1980. Studies on Pinus conforta (Doug, ex Loud.) seed germinated at diferent temperatures. In: Proc. Pinus contorta as an exotic species, pp. 287–289.

Kaufmann, M., Eckard, A., 1977. Water potential and temperature effects on germination of Engelmann Spruce and Lodgepole Pine seeds. Forest Sci. 23, 27–33.

Knapp, A., Anderson, J., 1980. Effect of heat on germination of seeds from serotinous lodgepole pine cones. Am. Midl. Nat. 104, 370–372.

Kolb, P., Robberecht, R., 1996. High temperature and drought stress effects on survival of Pinus ponderosa seedlings. Tree Physiol. 16, 665–672.

Kroiss, S., HilleRisLambers, J., 2015. Recruitment limitation of long-lived conifers: implications for climate change responses. Ecology 96, 1286–1297. http://dx.doi.org/10.1890/14-0595.1.
Laio, F., Porporato, A., Ridolfi, L., Rodriguez-Iturbe, I., 2002. On the seasonal dynamics of mean soil moisture. J. Geophys. Res.-Atmos. 107. http://dx.doi.org/10.1029/2001JD001252.
Larson, M., Schubert, G.H., 1969. Effect of osmotic water stress on germination and initial development of ponderosa pine seedlings. Forest Sci. 15, 30–36.
Lavender, D., 1955. Ponderosa pine seed germination after exposure to varying temperatures and humidities. Research Notes, Oregon state board of forestry, 24.
Li, X., Burton, P., Leadem, C., 1994. Interactive effects of light and stratification on the germination of some British-Columbia conifers. Can. J. Bot. 72, 1635–1646.
Lintz, H., Gray, A., McCune, B., 2013. Effect of inventory method on niche models: random versus systematic error. Ecol. Inform. 18, 20–34. http://dx.doi.org/10.1016/j.ecoinf.2013.05.001.
Lopushinsky, W., Beebe, T., 1976. Relationship of shoot-root ration to survival and growth of outplanted Douglas-fir and ponderosa pine seedlings, vol. 274. US Dept. of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.
Lopushinsky, W., Zabowski, D., Anderson, T.D., 1992. Early Survival and Height Growth of Douglas-Fir and Lodgepole Pine-Seedlings and Variations in Site Factors Following Treatment of Logging Residues. USDA Forest Service Pacific Northwest Research Station Research Paper 451, pp. 1–28.
Lotan, J., Perry, D., 1976. Effects of residue utilization on regeneration of lodgepole pine clearcuts, pp. 125–133.
Lotan, J., Perry, D., 1977. Fifth-year seed: seedling ratios of lodgepole pine by habitat type and seedbed preparation technique, vol. 239. Dept. of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.
Mast, J., Fule, P., Moore, M., Covington, W., Waltz, A., 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. Ecol. Appl. 9, 228–239.
McTague, J., Tinus, R., 1996. The effects of seedling quality and forest site weather on field survival of ponderosa pine. Tree Planters' Notes 47, 16–23.
Minore, D., 1972. Germination and early growth of coastal tree species on organic seed beds, p. 18.
Moore, M., Kidd, F., 1982. Seed source variation in induced moisture stress germination of ponderosa pine. Tree Planters' Notes 33, 12–14.
Noble, D., Edminster, C., Shepperd, W., 1979. Effects of watering treatments on germination, survival, and growth of ponderosa pine: a greenhouse study [with respect to natural regeneration success]. Research Note, Rocky Mountain Forest and Range Experiment Station, USDA Forest Service RM-369, 6p.
Ohlson, M., Zackrisson, O., 1992. Tree establishment and microhabitat relationships in North Swedish Peatlands. Can. J. For. Res. 22, 1869–1877.
Ouzts, J., Kolb, T., Huffman, D., Sanchez Meador, A., 2015. Post-fire ponderosa pine regeneration with and without planting in Arizona and New Mexico. Forest Ecology and Management 354, 281–290.
Page-Dumroese, D., Dumroese, R., Carpenter, C., Wenny, D., 2002. Relationship of Seed Microsite to Germination and Survival of Lodgepole Pine on High-elevation Clearcuts in Northeastern Utah. Rocky Mountain Research Station.
Page-Dumroese, D., Kasten Dumroese, R., Jurgensen, M., Abbott, A., Hensiek, J., 2008. Effect of nursery storage and site preparation techniques on field performance of high-elevation Pinus contorta seedlings. For. Ecol. Manage. 256, 2065–2072.
Parker, T., Clancy, K., Mathiasen, R., 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agric. For. Entomol. 8, 167–189. http://dx.doi.org/10.1111/j.1461-9563.2006.00305.x.
Pasquini, N., Defosse, G., Del Longo, O., 2008. Upgrading germinability of ponderosa pine seeds from Patagonia, Argentina, by adjusting prechilling periods and applying the IDS technique. New Forest. 36, 93–102.
Pearson, R., Dawson, T., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob. Ecol. Biogeogr. 12, 361–371. http://dx.doi.org/10.1046/j.1466-822X.2003.00042.x.
Peterson, G., 1970. Seed-protectant chemicals affect germination of ponderosa pine seed. Tree Planters' Notes 21, 25–29.
Petrie, M., Pockman, W., Pangle, R., Limousin, J., Plaut, J., McDowell, N., 2015. Winter climate change promotes altered spring growing season in piñon pine-juniper woodlands. Agricultural and Forest Meteorology, in press.
Pinto, J., Dumroese, R., Cobos, D., 2009. Effects of irrigation frequency and grit color on the germination of lodgepole pine seeds, pp. 52–57.
Pinto, J., Marshall, J., Dumroese, R., Davis, A., Cobos, D., 2011. Establishment and growth of container seedlings for reforestation: a function of stocktype and edaphic conditions. For. Ecol. Manage. 261, 1876–1884.
Pinto, J., Marshall, J., Dumroese, R., Davis, A., Cobos, D., 2012. Photosynthetic response, survival, and growth of three stocktypes under water stress enhanced by vegetative competition. Can. J. For. Res. 42, 333–344.
Porporato, A., Daly, E., Rodriguez-Iturbe, I., 2004. Soil water balance and ecosystem response to climate change. Am. Nat. 164, 625–632.
Puhlick, J., Laughlin, D., Moore, M., 2012. Factors influencing ponderosa pine regeneration in the southwestern USA. For. Ecol. Manage. 264, 10–19. http://dx.doi.org/10.1016/j.foreco.2011.10.002.
R Development Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, <http://www.R-project.org>.
Rietveld, W., 1975. Phytotoxic grass residues reduce germination and initial root growth of ponderosa pine, pp. 15–15.
Rocca, M., Brown, P., MacDonald, L., Carrico, C., 2014. Climate change impacts on fire regimes and key ecosystem services in Rocky Mountain forests. For. Ecol. Manage. 327, 290–305. http://dx.doi.org/10.1016/j.foreco.2014.04.005.
Rother, M., Veblen, T., Furman, L., 2015. A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. Can. J. For. Res. 45, 1607–1616. http://dx.doi.org/10.1139/cjfr-2015-0033.
Sackett, S., 1984. Observations on natural regeneration in ponderosa pine following a prescribed fire in Arizona, vol. 435. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station.
Savage, M., Brown, P., Feddema, J., 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. Ecoscience 3, 310–318.
Savage, M., Mast, J., 2005. How resilient are southwestern ponderosa pine forests after crown fires? Can. J. Res. 35, 967–977. http://dx.doi.org/10.1139/X05-028.
Savage, M., Mast, J., Feddema, J., 2013. Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. Can. J. Res. 43, 570–583. http://dx.doi.org/10.1139/cjfr-2012-0404.
Schubert, G., 1974. Silviculture of southwestern ponderosa pine: the status of our knowledge. USDA Forest Service General Technical Report RM-123.
Schwartz, M., Ahas, R., Aasa, A., 2006. Onset of spring starting earlier across the Northern Hemisphere. Glob. Change Biol. 12, 343–351. http://dx.doi.org/10.1111/j.1365-2486.2005.01097.x.
Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H., Harnik, N., Leetmaa, A., Lau, N., Li, C., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316, 1181–1184. http://dx.doi.org/10.1126/science.1139601.
Seidel, K., 1986. Tolerance of seedlings of ponderosa pine. Douglas-fir, grand fir, and engelmann spruce for high temperatures. Northwest Sci., 60
Shepperd, W., Noble, D., 1976. Germination, survival, and growth of lodgepole pine under simulated precipitation regimes: a greenhouse study, p. 4.
Sidhu, S., Chakravarty, P., 1990. Effect of selected forestry herbicides on ectomycorrhizal development and seedling growth of lodgepole pine and white spruce under controlled and field environment. Eur. J. For. Pathol. 20, 77–94.
Simpson, J., Wang, B., Daigle, B., 2004. Long-term seed storage of various Canadian hardwoods and conifers. Seed Sci. Technol. 32, 561–572.
Stone, E., Jenkinson, J., 1970. Influence of soil water on root growth capacity of ponderosa pine transplants. Forest Sci. 16, 230–239.
Stone, W., Wolfe, M., 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. Vegetatio 122, 1–12. http://dx.doi.org/10.1007/BF00052811.
Tanaka, Y., Kleyn, N., Harper, L., 1986. Seed stratification of engelmann spruce and lodgepole pine – the effect of stratification duration and timing of surface-drying. Forest. Chron. 62, 147–151.
Teste, F., Lieffers, V., Landhausser, S., 2011. Viability of forest floor and canopy seed banks in Pinus contorta Var. Latifolia (Pinaceae) forests after a mountain pine beetle outbreak. Am. J. Bot. 98, 630–637.
Timonin, M., 1964. Interaction of seed-coat microflora and soil microorganisms and its effects on pre-and post-emergence of some conifer seedlings. Can. J. Microbiol. 10, 17–22.
Turner, M., Donato, D., Romme, W., 2013. Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. Landscape Ecol. 28, 1081–1097. http://dx.doi.org/10.1007/s10980-012-9741-4.
Van den driessche, R., 1992. Changes in drought resistance and root-growth capacity of container seedlings in response to nursery drought, nitrogen, and potassium treatments. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 22, 740–749.
Van den Driessche, R., 1996. Drought resistance and water use efficiency of conifer seedlings treated with paclobutrazol. New Forest. 11, 65–83.
Van Haverbeke, D., Peterson, G., 1989. Effect of storage temperature on germination of seeds of twenty sources of ponderosa pine. Research note RM 490 – U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.
Varmola, M., Salminen, H., Rikala, R., Kerkela, M., 2000. Survival and early development of lodgepole pine. Scand. J. For. Res. 15, 410–423.
Wagner, R., Petersen, T., Ross, D., Radosevich, S., 1989. Competition thresholds for the survival and growth of ponderosa pine seedlings associated with woody and herbaceous vegetation. New Forest. 3, 151–170. http://dx.doi.org/10.1007/BF00021579.
Wang, B., 1980. Germination requirements and effect of seed weight on germination and early seedling development on Alberta lodgepole pine.
Wang, B., 2003. Testing of endogenous germination periodicity in Picea glauca, Pinus contorta and Pinus banksiana seeds. Seed Technol 25, 140–148.
Wang, B., Downie, B., Wetzel, S., Palamarek, D., Hamilton, 1992. Effects of cone scorching on germinability, and vigor of lodgepole pine (Pinus-Contorta Var Latifolia) seeds in Alberta. Seed Sci. Technol. 20, 409–419.
Weber, J., Sorensen, F., 1990. Effects of stratification and temperature on seed germination speed and uniformity in central Oregon ponderosa pine (Pinus ponderosa Dougl. ex Laws.). Research paper PNW – U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
White, A., 1985. Presettlement regeneration patterns in a southern ponderosa pine stand. Ecology 66, 589–594. http://dx.doi.org/10.2307/1940407.
Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook,

E.R., Gangodagamage, C., Cai, M., McDowell, N.G., . Temperature as a potent driver of regional forest drought stress and tree mortality. Nat. Clim. Change 3, 292–297. http://dx.doi.org/10.1038/NCLIMATE1693.

Woodard, P., 1983. Germination success of Pinus-contorta Dougl. and Picea-engelmannii Parry on burned seedbeds. For. Ecol. Manage. 5, 301–306.

Woodard, P., Cummins, G., 1987. Engelmann spruce, lodgepole pine and subalpine fir seed germination success on ashbed conditions. Northwest Sci. 61, 233–238.

Wright, E., 1931. The effect of high temperatures on seed germination. J. Forest. 29, 679–687.

Wright, E., Coates, K., Bartemucci, P., 1998. Regeneration from seed of six tree species in the interior cedar-hemlock forests of British Columbia as affected by substrate and canopy gap position. Can. J. For. Res. 28, 1352–1364.

Wu, T., Kim, Y., 2013. Pricing ecosystem resilience in frequent-fire ponderosa pine forests. Forest Policy Econ 27, 8–12. http://dx.doi.org/10.1016/j.forpol.2012.11.002.

Zabowski, D., Java, B., Scherer, G., Everett, R., Ottmar, R., 2000. Timber harvesting residue treatment: Part 1. Responses of conifer seedlings, soils and microclimate. For. Ecol. Manage. 126, 25–34.