



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

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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.

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* Corresponding author at: US Geological Survey, Southwest Biological Science Center, Flagstaff, AZ, United States.

E-mail address: mpetrie@usgs.gov (M.D. Petrie).

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 complemented 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; Pubhlick 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: T_a (daily \bar{x} , daily maximum, daily minimum), T_s (daily \bar{x} , daily maximum, daily minimum), volumetric soil moisture [θ : $\text{m}^3 \text{m}^{-3}$], 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 (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

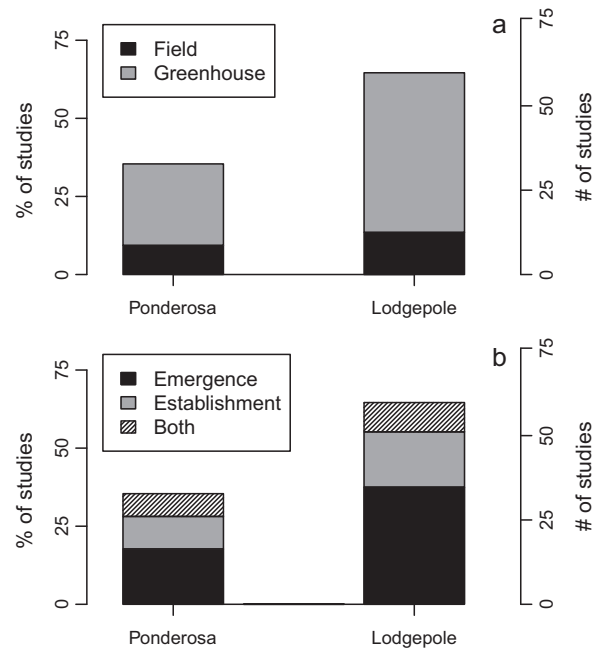


Fig. 1. Percentage and total number of studies focused on ponderosa and lodgepole pine (Panel a), greenhouse and field studies (Panel b), and on seedling emergence and establishment (Panel c).

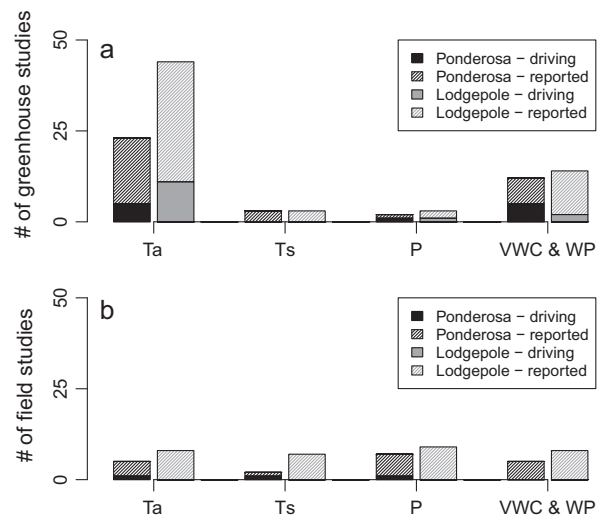


Fig. 2. Number of studies focused on climate variables of air temperature [T_a], precipitation [P], soil temperature [T_s] and soil moisture and soil water potential [VWC & WP] for seedling emergence (Panel a) and seedling establishment (Panel b) for ponderosa and lodgepole pine. 'Driving' variable studies 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 T_a is between 20 to 30 °C during summer (International Seed Testing Association, 1985). We found that both greenhouse and laboratory studies maintained T_a in this

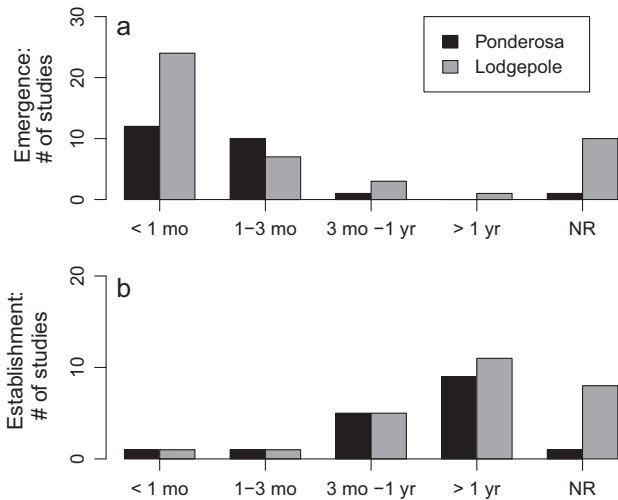


Fig. 3. Number of studies focused on different timescales of seedling emergence (Panel a) and establishment (Panel b) for ponderosa and lodgepole pine for periods of less than one month [<1 mo] to periods of over one year [>1 yr]. The value 'NR' stands for 'Not Reported'.

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 T_a 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 T_a 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 T_a 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 T_a (>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 T_a 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 T_a up to a mean or maximum T_a 25 to 30 °C, beyond which emergence may decline.

Similar to reported relationships for seedling emergence, higher mean and minimum daily T_a may increase establishment of ponderosa pine, and may also reduce establishment as daily maximum T_a 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 T_a , 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 T_a increased establishment (Cochran and Berntsen, 1973; Shepperd and Noble, 1976; Noble et al., 1979; Seidel, 1986; Lopushinsky et al., 1992). Although higher daily T_a may support greater emergence of ponderosa and lodgepole pine, none of the studies in our review reported a relationship between maximum T_s 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 $T_a > 25$ to 30 °C (Table 1, Figs. 4a, c and 5a), and also had higher % seedling emergence as daily minimum T_a and T_s increased (Table 1, Figs. 4b and 5b). Increasing maximum $T_a > 25$ °C strongly reduced seedling emergence from 65% to 27% (Fig. 4c). Increasing daily minimum T_a from ~ 0 to 20 °C increased ponderosa pine emergence from 14% to 70% (Fig. 4b), yet increasing \bar{T}_a from ~ 20 to 25 °C decreased ponderosa pine emergence from 69% to 58% (Fig. 4a). Lodgepole pine emergence increased from 10% to 69% as \bar{T}_s 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 T_a and T_s : establishment increased as daily \bar{T}_a increased from ~ 15 to 25 °C (Fig. 4e), and also increased as minimum T_s and lower than average maximum T_s increased up to 10 and 15 °C, respectively (Fig. 4g and h). Establishment decreased as maximum daily T_a increased beyond 25 °C (Fig. 4f). Lodgepole pine establishment also increased as minimum T_s 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 [T_a], soil temperature [T_s], 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.

	\bar{x}	T_a		\bar{x}	T_s		\bar{x}	\bar{x}	P	P
		min	max		min	max				
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

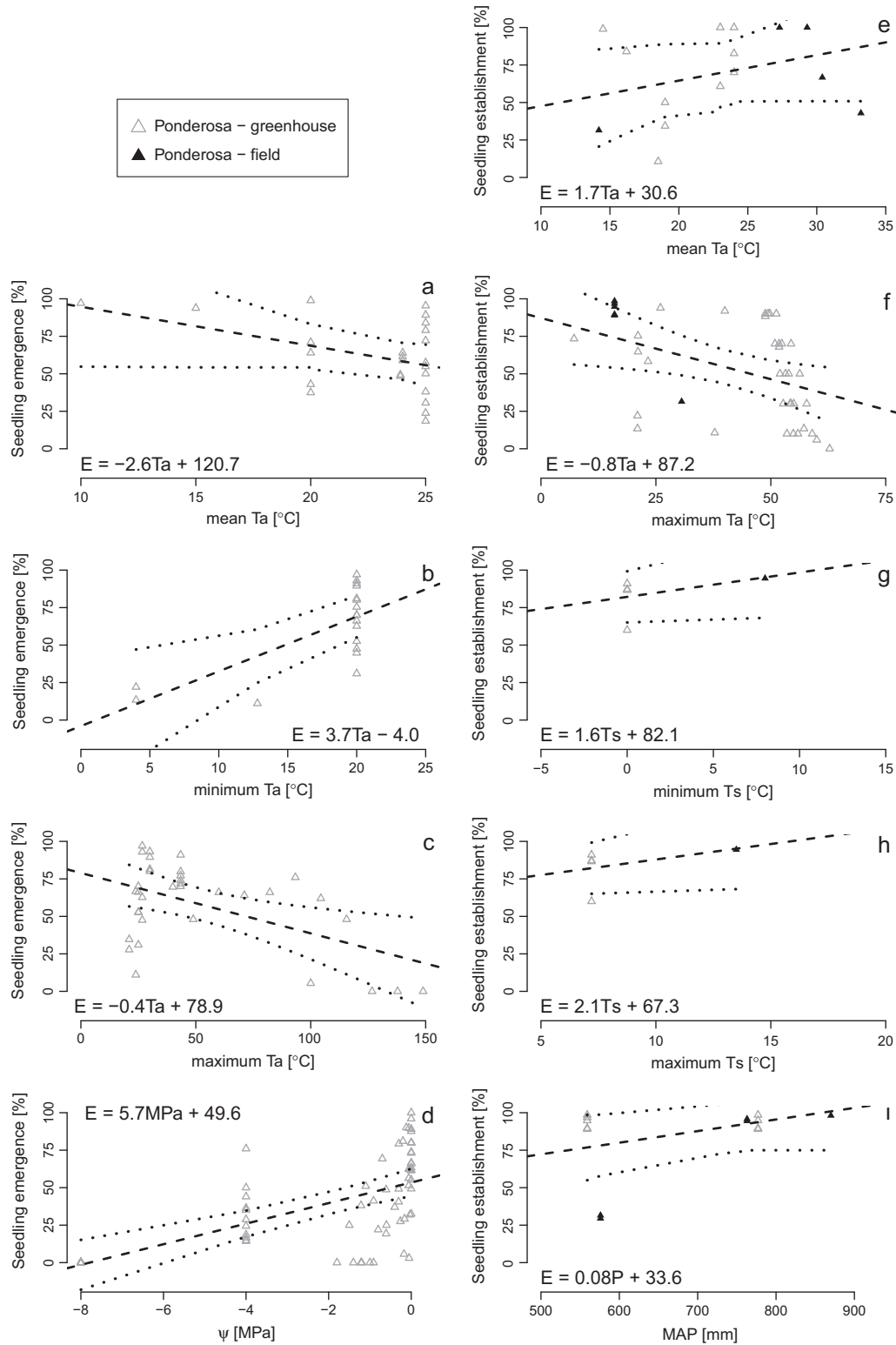


Fig. 4. Linear regression analysis of ponderosa pine seedling emergence and mean air temperature [Ta] (Panel a: Wright, 1931; Brayshaw, 1953; Djavanshir and Reid, 1975; Rietveld, 1975; Harrington, 1977; Van Haverbeke and Peterson, 1989; Weber and Sorensen, 1990; Bai et al., 2004), minimum Ta (Panel b: 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.

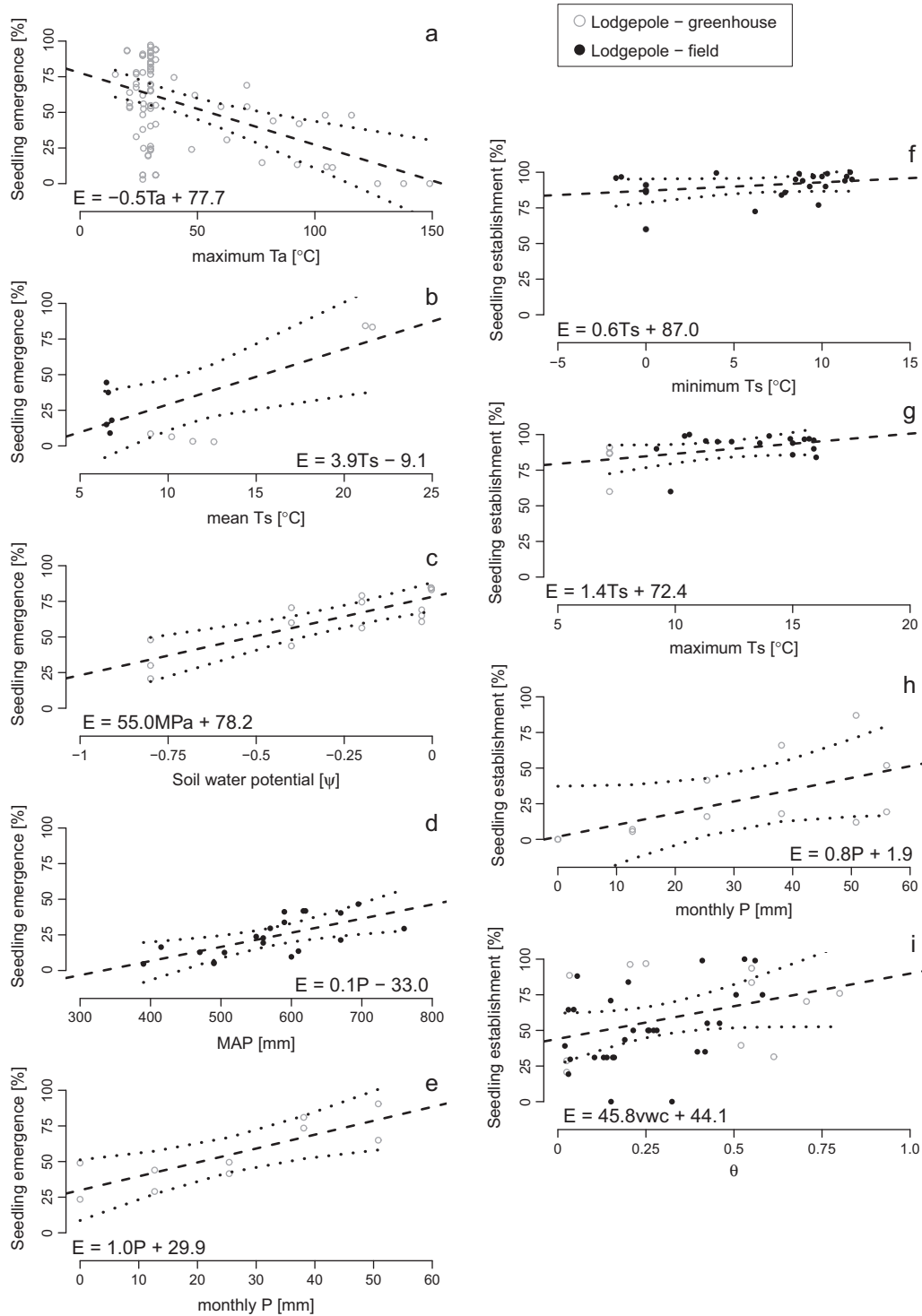


Fig. 5. Linear regression analysis of lodgepole pine seedling emergence and maximum air temperature [T_a] (Panel a: Wright, 1931; Crossley, 1955; Holmes and Buszewicz, 1955; Timonin, 1964; Ackerman and Farrar, 1965; Ackerman and Gorman, 1969; Minore, 1972; Cochran and Berntsen, 1973; Cochran, 1973; Shepperd 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 \bar{T}_a 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). Coincidentally, 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 exam-

ple 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 scien-

tific 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 time-scales. 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.

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