

Making a stand: five centuries of population growth in colonizing populations of *Pinus ponderosa*

MARK R. LESSER¹ AND STEPHEN T. JACKSON

Program in Ecology (Department of Botany), University of Wyoming, 1000 E. University Avenue, Laramie, Wyoming 82071 USA

Abstract. The processes underlying the development of new populations are important for understanding how species colonize new territory and form viable long-term populations. Life-history-mediated processes such as Allee effects and dispersal capability may interact with climate variability and site-specific factors to govern population success and failure over extended time frames. We studied four disjunct populations of ponderosa pine in the Bighorn Basin of north-central Wyoming to examine population growth spanning more than five centuries. The study populations are separated from continuous ponderosa pine forest by distances ranging from 15 to >100 km. Strong evidence indicates that the initial colonizing individuals are still present, yielding a nearly complete record of population history. All trees in each population were aged using dendroecological techniques. The populations were all founded between 1530 and 1655 cal yr CE. All show logistic growth patterns, with initial exponential growth followed by a slowing during the mid to late 20th century. Initial population growth was slower than expectations from a logistic regression model at all four populations, but increased during the mid-18th century. Initial lags in population growth may have been due to strong Allee effects. A combination of overcoming Allee effects and a transition to favorable climate conditions may have facilitated a mid-18th century pulse in population growth rate.

Key words: *Allee effects; Bighorn Basin, Wyoming, USA; climate variability; colonization; demographic stochasticity; demography; growth rate; invasion; Pinus ponderosa.*

INTRODUCTION

Establishment and expansion of colonizing populations is a central problem in population ecology, and is essential for estimating the speed at which species can migrate into new territory, and for understanding the processes that control recruitment and expansion patterns at the population level (Hamrick 2004, Caplat et al. 2008). These processes are important for understanding primary successional patterns (Fastie 1995), invasion biology (Shigesada and Kawasaki 1997), and the fine-scale dynamics underlying migration patterns observed in paleoecological records (Jackson and Overpeck 2000). Knowledge of population-level processes is also essential for parameterizing process-based species distribution models and population viability models (Morris and Doak 2002, Caplat et al. 2008). Furthermore, current and projected rates of climate change have the potential to induce much more dramatic and immediate responses than those of the recent past (Davis and Shaw 2001, Rosenzweig et al. 2007, Williams et al. 2007). An understanding of the rates and mechanisms governing migration is needed to predict

how species will respond both ecologically and biogeographically to climate change.

Most range expansions ultimately involve development and persistence of disjunct, colonizing populations (Stacey and Taper 1992, Bruna 2003). The formation and success of new populations are influenced by life-history traits of a species, including generation time and dispersal capability (Clark et al. 1999, Nathan et al. 2002). The strength of Allee effects, or the effects of small population size on individual fitness, also plays a major role in the success of new populations (Allee 1931, Taylor and Hastings 2005). In plant populations, Allee effects are most often manifested in pollination or fertilization failure at low population densities or sizes (Yamanaka and Liebhold 2009). When Allee effects are strong, stochastic demographic events, such as immigration or chance matings between in situ individuals, can contribute to population growth, which can in turn overcome inhibiting effects of low population size (Taylor and Hastings 2005).

Population establishment is further affected by frequency of immigration events (Drury et al. 2007), microsite limitations, and seed or pollen availability (Ehrlén and Eriksson 2000). These processes may interact with climate variability, which, together with differential environmental sensitivity of plant life-stages, can have major consequences for success or failure of new populations (Jackson et al. 2009).

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¹ E-mail: mlesser@uwyo.edu

Colonizing populations at expanding range margins provide ideal model systems for studying processes underlying population development (Higgins and Richardson 1999). However, real-time observational studies of plant demography are limited to plants with short life spans and low mean generation times (e.g., Levin and Clay 1984, Doak and Morris 2010). Establishment patterns of longer-lived species are confounded by the time spans (decades to centuries) over which colonization may occur (Brubaker 1986, Crawley 1990). Furthermore, even for species with short life spans, population development may proceed slowly, and effects of longer-term dynamics such as climate variability could be overlooked.

Paleoecological studies based on lake sediments or woodrat middens provide insights on long-term colonization dynamics (Huntley 1995, Jackson 1997), and also provide information on long-distance dispersal (Clark et al. 1998, Lyford et al. 2003). However, such studies typically have low temporal, spatial, and taxonomic precision, and are limited by the availability of suitable sites (Jackson and Overpeck 2000). They are generally effective at revealing broad patterns of expansion at millennial timescales, but seldom provide opportunity to infer population-level dynamics and the influence of climate variability at shorter timescales.

Dendroecology bridges the gap between the time spans and precision offered by real-time monitoring and paleoecology. With annual resolution and high spatial precision (Fritts and Swetnam 1989), tree-ring records can indicate population-level dynamics of long-lived tree species with annual to decadal resolution over periods spanning multiple centuries or even millennia (Lloyd and Graumlich 1997). In an ideal dendroecological study, original colonizing individuals should persist in the current population. Obviously, tree mortality followed by decomposition, burning, or harvesting will erase significant parts of the record. This problem can be minimized for recently established small, disjunct populations in semiarid regions. Recency of expansion maximizes the probability that colonizing individuals are still present. Every individual can be sampled from small disjunct populations. Finally, fuel-limited sites in a dry climate are likely to preserve snags and logs of dead individuals for centuries (Bunn et al. 2003, Gray et al. 2004).

Here, we present a dendroecological study of four populations of ponderosa pine (*Pinus ponderosa* Dougl. Ex. Laws) in the Bighorn Basin in north-central Wyoming. The populations are separated from continuous ponderosa pine forest by distances ranging from 15 to >100 km, and the relatively small size of each population (ranging from 82 to 927 trees) allowed sampling of every individual. All are on sparsely vegetated rocky uplands with low capacity for carrying surface fires. Woodrat midden records indicate that the nearest continuous populations of ponderosa pine, in the western Bighorn Mountains, were established <1500

years ago (Norris 2006), indicating that our study populations were established more recently.

Ponderosa pine is a long-lived conifer that occurs over a large expanse of western North America. Ponderosa pine produces winged seeds, but seeds are also often disseminated by birds and small mammals (Oliver and Ryker 1990). Masting occurs on average every eight years, and medium cone crops are produced every 2–5 years, but there is little synchronicity in seed production across the range. Finally, ponderosa pine is very poor at self-fertilization (Mitton 1992), which may constrain population growth in small populations.

Our study focuses on processes governing population establishment and development. We examine the roles of Allee effects, demographic stochasticity, climate variability, and other site-specific factors, over the course of 500 years of population development. We estimate long-term rates of population growth and the time spans required for populations to overcome Allee effects. Using independent regional climate records, we assess the influence of climate variability on tree recruitment and how climate may have interacted with population size at key junctures in population development. By comparing the four populations, we examine general patterns, similarities, and dissimilarities in terms of timing and rates of development.

METHODS

Field and laboratory analysis

Our study sites are in the southern Bighorn Basin, with one site near the southwestern slope of the Bighorn Mountains and the other three on the southeastern flanks of the Absaroka Mountains (Fig. 1). The semiarid Bighorn Basin, surrounded on all sides by mountain ranges, is vegetated primarily by desert shrubland and *Artemisia* steppe on the extensive fine-textured and alkaline soils. Scattered woodlands of *Juniperus scopulorum*, *J. osteosperma*, and *Pinus flexilis* occur on sandstone and limestone outcrops and escarpments (Knight 1994, Driese et al. 1997). Except for our study populations, no ponderosa pines have been recorded from the Basin (Fig. 1) (Little 1971, Rocky Mountain Herbarium Specimen Database 2011). At each of our sites, no ponderosa pine individuals could be found within 1 km of the outermost trees we located. The relatively small size of each population (Table 1) within these boundaries allowed us to sample every individual. (Detailed site information is given in Appendix A.)

Each tree was georeferenced with sub-5 m precision using a handheld GPS unit. We collected two increment cores from every tree that lacked heart rot (Table 1). The first core was obtained as low to the ground as possible, given microsite topography (e.g., presence of boulders around tree base), and coring height above the current ground surface was recorded. The second core was taken, where possible, on the same side of the tree as the primary core, but 5–20 cm above the primary core to use in height-offset analysis.

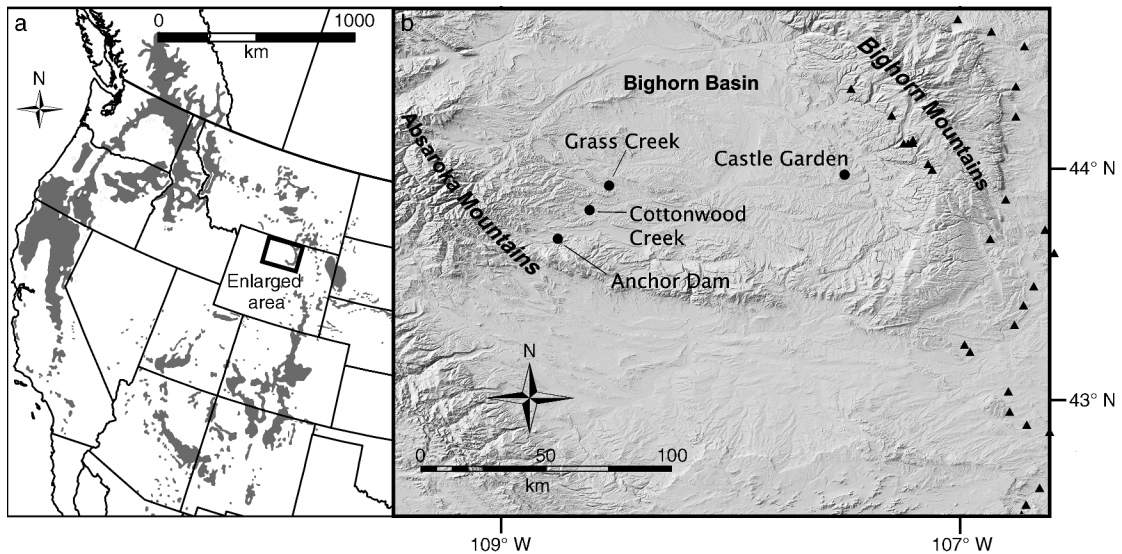


FIG. 1. (a) Map of the full distribution of ponderosa pine (gray shading) (U.S. Geological Survey 1999); box shows area of study sites in Wyoming, USA. (b) Enlarged map of study sites and surrounding area. Solid triangles designate ponderosa pine occurrence based on Rocky Mountain Herbarium Specimen Database records (2011). Study sites are shown with solid circles. Locations are overlaid on a hillshade surface.

Cores were mounted, sanded to >300 grit, digitally scanned at 1200 dots per inch, and dated using WinDENDRO (Regent Instruments 2008). We visually analyzed each core to corroborate ring boundaries identified by the WinDendro software. All cores were crossdated using standard visual cross-matching of ring patterns (Cook and Kairiukstis 1990), along with correlation analysis (Regent Instruments 2008) to ensure accurate dating. Chronology correlations within and between sites were high ($r = 0.40\text{--}0.97$). For cores where the pith was not obtained, we estimated the pith date using overlaid concentric circles (Brown and Cook 2006).

To correct for the difference between coring-height age and germination age (Romme and Knight 1981), we determined the age difference between the first and second increment cores for a subset of trees. We applied a regression model of age difference against height difference ($P < 0.001$, $r^2 = 0.93$) to tree ages (5 years per

10 cm of coring height above soil surface) to estimate individual recruitment dates (Appendix B).

Population growth analysis

Tree recruitment dates were binned into individual decades. We compared establishment patterns at each site to independent records of regional precipitation (Gray et al. 2004) and a global-temperature proxy (Stuiver et al. 1998), each spanning the last 1000 years. Relative population size was calculated as a ratio between the number of trees established within a given decade and the number of reproductively mature individuals already present in the population at the beginning of that time step (Morris and Doak 2002). Reproductively mature individuals were classified as all trees >10 years in age, based on reported values ranging from 7 to 16 years (Curtis and Lynch 1965).

Relative population size was scaled to unity by dividing population size for each time step by the

TABLE 1. Coordinates, elevation, area, year of first establishment event (cal yr CE), and the total number of ponderosa pine trees present at each of the study populations in the Bighorn Basin, Wyoming, USA.

Population	Latitude	Longitude	Elevation (m)	Area (ha)	Year of first establishment	Total no. trees	No. aged trees	No. non-aged trees†	% of population aged
Castle Garden	43.96 N	107.52 W	1450–1550	94	1592	177	144	27	84
Grass Creek	43.88 N	108.63 W	1700–1900	136	1605	82	71	11	87
Cottonwood Creek	43.80 N	108.70 W	1700–1850	173	1531	927	835	92(17)	90
Anchor Dam	43.67 N	108.83 W	1950–2050	10	1655	143	128	13(6)	89

Note: The number of trees successfully aged, number of non-aged trees, and the percentage of the population successfully aged are also given.

† All non-aged trees were a result of heart rot. Numbers shown in parentheses indicate the number of non-aged trees that were dead as well as having heart rot.

population's cumulative total. Cumulative population size was then regressed against time using a logistic regression model. Logistic growth has a long history in population ecology (Kingsland 1991). While its use has been controversial (Law et al. 2003), and data rarely fit the model precisely (Hall 1988), it remains useful as a basis for determining processes affecting population growth. We use a logistic model as a null model for population growth. Deviations from the model indicate departures from the expected growth rate, and identify other processes affecting population growth. We use a simple logistic regression model, rather than the ecologically parameterized model (Pearl and Reed 1920), because we do not assume strict density dependence in our populations. Model goodness-of-fit was based on a χ^2 test of the difference between the null deviance and the residual deviance. The 95% confidence intervals (CI) were calculated for each population and used to assess deviations in population growth that departed significantly from the model expectations. Decades with significant departures from expected values were compared across populations to identify regional climatic patterns affecting population growth. Residuals were also used to assess lag times in the early periods of population growth.

RESULTS

Current population structure

The Castle Garden population comprises 177 individuals (144 were aged), with a maximum distance between individuals of 2.8 km (Table 1; Appendix A: Fig. A2). Median distance between trees was 795 m, and median distance to the nearest conspecific was 14 m (Appendix A: Fig. A2). No dead ponderosa pine trees were found at Castle Garden (Table 1).

The Grass Creek population is smaller, with 82 individuals (71 aged). Maximum distance between trees is >2 km, and median distance between trees is 722 m (Appendix A: Fig. A2). The median distance to the nearest tree is 26 m (Appendix A: Fig. A2). No dead trees were observed (Table 1).

The Cottonwood Creek population consists of 927 individuals (836 aged), with the most distant individuals >3 km apart (Appendix A: Fig. A2). Median distance between all trees was 570 m and median distance to the nearest neighbor was 8 m (Appendix A: Fig. A2). This site had 17 dead trees (Table 1), all of which appear to have died recently (within approximately 5–10 years). All had intact bark and most retained dead needles on their branches.

The Anchor Dam population comprises 143 trees (128 aged), with a maximum distance of 930 m between trees (Table 1; Appendix A: Fig. A2). Median distances between all trees, and median distance to the nearest tree, were 108 m and 7 m, respectively (Appendix A: Fig. A2). Seven dead ponderosa pines were observed; all appear to have died recently.

Patterns of establishment

The first establishment event at Castle Garden occurred in 1592 (Table 1, Fig. 2c), and was followed by intermittent establishment at low levels (about one tree per decade) for the next 140 years. The rate of establishment increased beginning in the 1740s, and continued to increase, with minor exceptions (e.g., 1801), for the next 160 years. Establishment per decade reached its peak in the 1880s. Establishment declined for several decades after the 1920s, but rose again to eight individuals in the 1960s (Fig. 2c; Appendix E: Table E1).

Grass Creek was first colonized in 1605 (Table 1, Fig. 2d). The second individual was established in the 1740s, and in the following decades the population reached its highest rate of establishment, with eight individuals recruited in the 1780s. Establishment rates were consistently low through the 19th and early 20th centuries (2–6 individuals per decade). In the mid-20th century establishment decreased to between zero and two individuals per decade (Fig. 2d, Appendix E: Table E1).

Cottonwood Creek is the oldest of the four populations (Table 1, Fig. 2e). Following initial colonization in 1531, recruitment continued at a low rate (1–3 trees per decade) for the next 100 years. Establishment rate increased to between four and nine trees per decade from 1640 to 1720, decreased during the 1730s and 1740s, increased again in the 1750s, and continued to increase until the end of the 19th century. At the highest point of population growth in the 1890s, more than 50 trees were established in a decade. The rate of establishment declined sharply in the early 20th century, and by the 1950s was <10 individuals per decade. Only one seedling has been established since 2001 (Fig. 2e; Appendix E: Table E1).

The Anchor Dam population was initially colonized in 1655 (Table 1, Fig. 2f). Establishment rates were low in the century following initial colonization. However, rate of establishment began to increase in the late 1700s, persisting at levels of 2–6 individuals per decade until the 20th century. The highest rates of establishment were in the early 20th century, reaching 21 individuals in the 1950s. Establishment at Anchor Dam decreased drastically in the 1960s, and no individuals have been established since the 1970s (Fig. 2f; Appendix E: Table E1).

Population growth

Logistic regression of population growth against time was significant ($P < 0.001$) for each of the four populations (Table 2, Fig. 3a–d). The slopes of the regression models, (i.e., rates of natural increase or r) ranged from 0.0152 (Cottonwood Creek) to 0.0389 (Grass Creek). The proportional rate of increase (λ) between successive decades (Sibly and Hone 2002) ranged from 1.02 to 1.04 (Table 2). Following initial colonization of all four sites, growth was slow (Fig. 3a–

d). Although slow initial growth is inherent in logistic growth, the residuals for all four populations were negative during this time period (Fig. 3e–h), indicating that population growth was proceeding even more slowly than predicted by logistic growth.

All four populations show a leveling off and cessation of population growth in the late 20th century (Fig. 3a–d; Appendix A: Table A4), suggesting that a threshold was reached. However, this apparent threshold occurred at very different actual population sizes and densities in each of the study populations (Table 1), and suitable uncolonized microsites are extensive at each site.

Influence of climate

Regression analysis (Appendix C) showed no overall relationship between recruitment and precipitation ($R^2 < 0.1$). However, the mid-18th century increase in rate of establishment in all four populations coincides with a transition from a severe multidecadal drought to a prolonged wet period in the region (Fig. 2a). Furthermore, this transition coincides with the end of the coldest stage of the Little Ice Age and progressive warming from that point on (Fig. 2b) (Rind et al. 2004).

Residual plots from the logistic regression models of each population (Fig. 3 e–h) show significant residuals (i.e., decades that deviate significantly from the expected growth rate). If population growth was paced by regional climate, then decades with significant residuals should correspond across populations. However, residuals varied in timing between populations, suggesting that these deviations are site specific, unrelated to climate variation (Fig. 3 e–h). Additional analysis of between-population-growth trends are given in Appendix D.

DISCUSSION

Site colonization

During the last glacial maximum, ponderosa pine (var. *scopulorum*) was apparently restricted to scattered, isolated populations in southern Arizona and New Mexico and northern Mexico (Betancourt 1990). It migrated north into the Colorado Plateau during the late-glacial (Betancourt 1990, Weng and Jackson 1999). Its migration history in the Rocky Mountain region is less well known. Woodrat midden records show that ponderosa pine colonized the eastern slopes of the Bighorn Mountains around 3000 years ago, and the western Bighorns 1500 years ago, with some populations established <1000 years ago (Norris 2006).

Our four study sites have all been colonized since the 16th century (Table 1). The apparent time lag of 500–1000 years between establishment of the presumed source populations in the western Bighorns and initial colonization at our study sites is unsurprising. Several centuries may have elapsed before source populations were sufficiently large for seeds to disperse into the Bighorn Basin. The sheer dispersal distances between

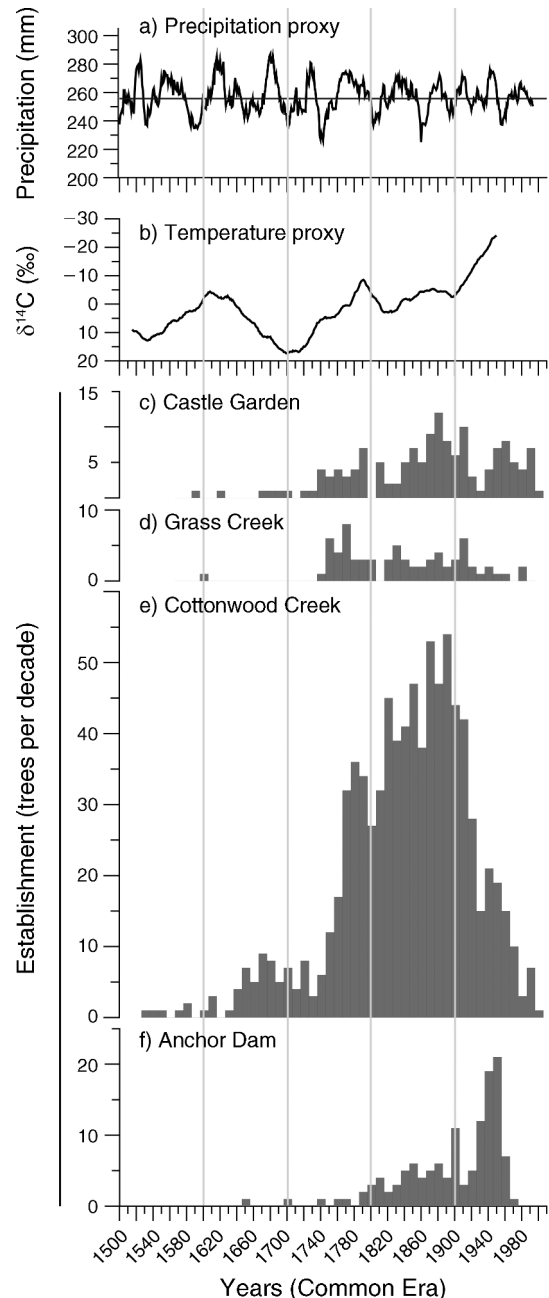


FIG. 2. (a) Precipitation reconstruction for Bighorn Basin. Precipitation values are calculated as a 10-year running average of annual values (taken from Gray et al. [2004]). The straight horizontal line is mean precipitation over the entire record (259 mm/yr). (b) The $\delta^{14}\text{C}$ levels, used as a proxy for global temperature (taken from Stuiver et al. [1998]). More negative values indicate higher temperatures (the y-axis has been inverted). The proxy precipitation and temperature values are reconstructions from tree-ring records. (c–f) Histograms of ponderosa pine establishment per decade at Castle Garden, Grass Creek, Cottonwood Creek, and Anchor Dam populations.

TABLE 2. Logistic regression coefficients, standard error, *z* score, and probability for logistic regression of scaled relative population size against time for the four ponderosa pine study populations.

Population and coefficient	Coefficient	SE	<i>z</i>	<i>P</i>
Castle Garden				
Intercept (β_0)	-30.9685	8.2368	-3.7600	0.0002
Growth rate (β_1)	0.01775 ($\lambda = 1.02$)	0.0047	3.7690	0.0002
Grass Creek				
Intercept (β_0)	-68.6738	24.5464	-2.7980	0.0052
Growth rate (β_1)	0.03886 ($\lambda = 1.04$)	0.0139	2.8000	0.0051
Cottonwood Creek				
Intercept (β_0)	-25.3891	6.3451	-4.0010	0.0001
Growth rate (β_1)	0.01516 ($\lambda = 1.02$)	0.0038	4.0220	0.0001
Anchor Dam				
Intercept (β_0)	-40.6852	11.8668	-3.4290	0.0006
Growth rate (β_1)	0.02253 ($\lambda = 1.02$)	0.0066	3.4300	0.0006

Notes: Population size is scaled as the ratio of number of establishments per number of reproductively mature individuals present in the population. The proportional rate of increase in the population between successive decades is λ . Probability in the last column is calculated as: $\Pr(Y = 1 | X = x) = [\exp(\beta_0 + \beta_1 x)] / [1 + \exp(\beta_0 + \beta_1 x)]$.

probable source populations and our study sites would have ensured that dispersal events occurred at low frequency and with low probability (Lyford et al. 2003).

Population development

All four populations show logistic-like growth (Fig. 3), the expected pattern for populations under density-dependent control (Pearl and Reed 1920, Sibly and Hone 2002). However, none of our four populations appears to be density limited today. Nearest-neighbor analysis (not shown) showed no density-related trend

through time, with trees recruiting at a wide range of distances from other trees throughout each population's history.

Population inferences from dendroecological records may be confounded by absence of formerly living trees. The recent establishment of the nearest source populations (western Bighorn Mountains) (Norris 2006), along with the absence of dead ponderosa pine at the sites, suggest that the colonizing individuals are still living. Dead wood persists for centuries in semiarid environments like the Bighorn Basin (Bunn et al. 2003, Gray et

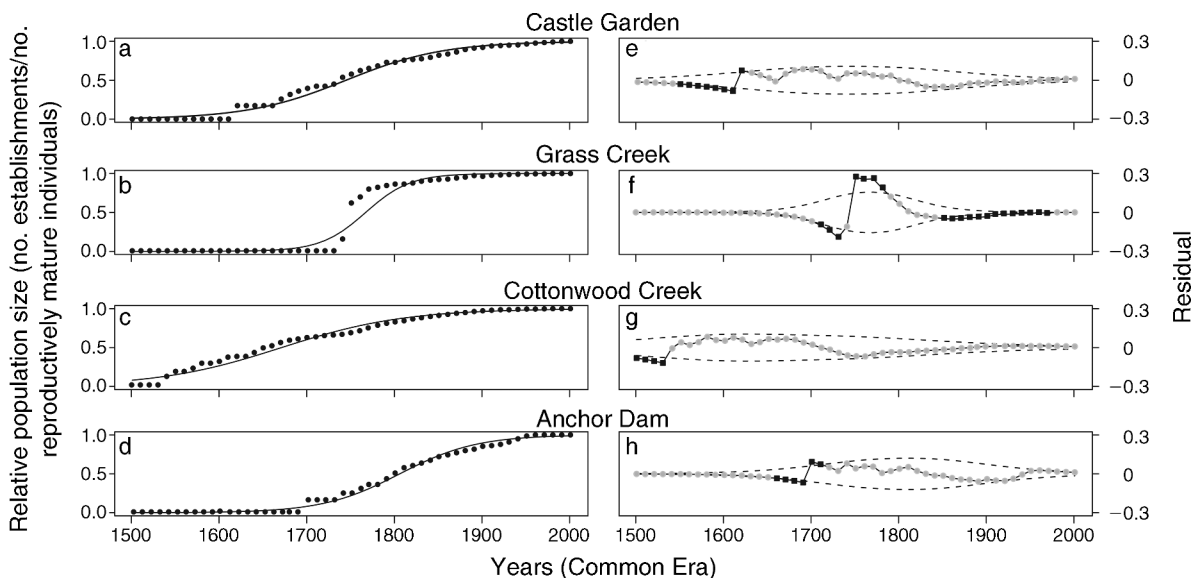


FIG. 3. (a–d) Scaled relative population size (calculated as a ratio of number of establishments per number of reproductively mature individuals present in the population) through time for four ponderosa pine populations. Solid circles represent observed data points. The solid line represents fitted values from the logistic regression model. (e–h) Residual plots from logistic regression models for each of four ponderosa pine populations. Dashed lines indicate the 95% CI of the fitted values from each model. Solid squares indicate residuals that fall outside of the 95% CI. Gray circles are nonsignificant residuals.

al. 2004), and all of our sites had snags and logs of dead limber pine and juniper. The scarcity and discontinuity of surface fuels at the sites, absence of surface or soil charcoal, and absence of fire-scarred trees of any species make it unlikely that fires have erased trees from the record. The presence of dead wood of other species indicates long-term persistence of downed-woody debris. Absence of dead adult ponderosa pines indicates that we have not missed significant establishment events in the populations that led to mature trees. We cannot exclude the possibility of past seedling or sapling mortality. Thus, our records provide minimum estimates of recruitment rates, insofar as they are based on documentation of successful long-term establishment (Harper 1977).

Population growth rates

Lambda (λ) is the proportional rate of population growth per time step (Sibly and Hone 2002). Our populations all had modeled growth rates >1 , but were often higher or lower than expected from simple logistic growth. Growth rates from temperate tree species are scarce, but the rates we observed ($\lambda = 1.02$ to 1.04) are similar to those estimated by Harcombe (1987) for 30 temperate tree species (0.88) and Lamar and McGraw (2005) for an eastern hemlock (*Tsuga canadensis* L.) population (1.23). However, our results show significant negative deviations from the expected model during early stages of population growth. One-time sampling, or studies encompassing short time periods, may miss significant departures from expected rates. This, in turn, may bias modeled expectations of species responses to climate change, and their migration capabilities (Caplat et al. 2008).

20th century decline in population growth

Declines in growth rate during the 20th century could be due to several factors. If density were responsible for the 20th century decline in growth rate, then distance between trees should reach a saturation point as available sites were maximally occupied. Although there appears to be no density limitation, suitable microsites might be saturated (Eriksson and Ehrlén 1992). Fine-scale differences in soil type or moisture availability could limit establishment over much of the population's spatial extent. Differences in microsite suitability, which may not be readily apparent to the observer, can lead to nonrandom or clumped distributions. Strong competitive effects create localized density-driven dynamics, while nearby microsites remain unoccupied. Thus, while overall population density appears low, and there appears to be no lack of suitable microsites, the population may actually be saturated (Harper 1977, Law et al. 2003). However, given that the median nearest distance between trees is >5 m at the four study sites (Appendix A: Fig. A2), we view this as highly unlikely for our populations.

Other factors potentially underlying the recent growth rate decline include livestock grazing, and/or changing climate. Overgrazing in ponderosa pine woodlands typically leads to increases in ponderosa pine seedlings due to the indirect effects of limiting herbaceous competition (Rummell 1951, Madany and West 1983, Covington et al. 1997, Allen et al. 2002), and actual grazing on pine seedlings is reported as low (Pfister et al. 1998). However, livestock will eat pine seedlings when other food sources are scarce (Pfister et al. 1998), which may have occurred at our study sites, where grass and herbaceous cover is sparse.

Climate variation over the last century may have created unfavorable conditions for ponderosa pine establishment in the Bighorn Basin. Increasing temperature over the past century (Rosenzweig et al. 2007) may have pushed our sites beyond the tolerance of seedlings to survive, while remaining within the tolerance range of adults to persist (Jackson et al. 2009). Furthermore, slight changes in weather patterns may have pronounced effects on recruitment success. Summer precipitation in the Bighorn Basin is primarily delivered through localized convective thunderstorms (Gray et al. 2004). While the overall amount of precipitation has not changed much over the past century (Wyoming State Climate Office 2011), slight differences in the position and timing of thunderstorms could have a significant effect on seedling survival.

Controls on initial stages of population growth

The slow initial growth observed at all our sites may be attributable to the lag in initial growth inherent in most founder populations undergoing exponential growth, owing to density dependence at low population size (Crooks and Soulé 1999). Our data indicate that this lag was more pronounced than expected under normal exponential growth, suggesting involvement of other factors.

Genetic maladaptation caused by founder effects and genetic bottlenecks can induce lags in population growth (Ellstrand and Elam 1993, Crooks and Soulé 1999). Ongoing analyses will clarify the extent to which genetic variability influenced population growth. Here we discuss potential influences of climate variability (Crooks and Soulé 1999, Jackson et al. 2009) and Allee effects on population expansion (Taylor and Hastings 2005).

Climate effects.—Many studies in western North America show strong dependence of tree population growth on climate variability (Swetnam et al. 1999, Boyden et al. 2005, Brown and Wu 2005, Norman and Taylor 2005, Brown 2006, League and Veblen 2006, Jackson et al. 2009). However, this dependence is likely restricted to sites that are climatically marginal. Our results suggest that climate is an important factor at our study sites, but only at specific instances in time. Specifically, climate appears to have influenced population growth in the mid-18th century, when the pulse in

establishment at all four populations followed a transition from dry to wet conditions in the precipitation record. The mid-18th century also coincides with the end of the Little Ice Age and an overall warming in global temperature (Fig. 2) (Beniston et al. 1997, Luckman 2000), although the climatic manifestations of Little Ice Age termination in the Bighorn Basin remain unclear.

The mid-18th century pulse in establishment events in our four populations coincides with similar establishment pulses in ponderosa pine across the northeastern portion of its range (Brown 2006), suggesting that regional climate change had a broad influence on population structure. Brown (2006) postulates a long-term interaction between surface fires and favorable climate, in the form of extended wet periods, during the mid-18th century to explain a ponderosa pine establishment pulse across the Black Hills of northeastern Wyoming and southwestern South Dakota. High precipitation is not only favorable for ponderosa pine establishment (Pearson 1950), but can limit the severity and frequency of surface fires, allowing more seedlings to mature (Brown and Wu 2005). Thus, the prolonged mid-18th century wet period documented in the Bighorn Basin (Gray et al. 2004), and the Great Plains (Brown 2006), may have been ideal for ponderosa pine establishment across the region. The role of fire was probably minimal at the Bighorn Basin sites, given the low amounts and discontinuity of fuels.

Although climate change contributed to the mid-18th century growth pulse, its role over the entire history of the Bighorn Basin populations remains unclear. Establishment pulses did not accompany wet periods in the tree-ring record for most of the record. In fact, following the mid-18th century, establishment occurred during both dry and wet periods (Fig. 2). Furthermore, the lack of synchronous deviations among sites from the modeled growth curves suggests absence of a climatic driver for population growth (Fig. 3e–f). Before the mid-18th century, population density at each site may have been too low to take advantage of favorable establishment conditions, owing to normal density dependence, Allee effects, or both. The mid-18th century establishment pulse may have increased population density to the point where recruitment success in any given decade was no longer limited by either favorable climate or Allee effects.

The similar patterns observed when population growth for each site was standardized to the year of initiation (Appendix D: Fig. D1) provides further evidence that climate variation did not control recruitment success. The coherent patterns suggest that population growth is constrained within a trajectory based on density and the number of individuals contributing to growth. If climate were the primary driver of population growth, then the populations should be asynchronous on a standardized timescale.

Savage et al. (1996) presented evidence that climate was responsible for a 1919 recruitment pulse in northern

Arizona. Warm and wet springs were needed in conjunction with above-average precipitation distributed throughout the year (Savage et al. 1996). However, another study of ponderosa pine in northern Arizona showed no correlation between establishment patterns and regional climate (White 1985). White (1985) noted that precipitation reconstructions obtained from mature trees may not represent moisture during critical growth periods for seedlings. Juvenile trees often have different environmental tolerances and requirements than adult trees (Jackson et al. 2009), and therefore a good year for adults may still be a bad year for juveniles. Conversely, years that appear dry in the reconstruction may nonetheless have provided moisture at critical periods for seedling establishment and survival (Pearson 1950). We used tree-ring records of limber pine and Douglas-fir as a proxy for annual precipitation (Gray et al. 2004), which may not capture the summer precipitation that is essential for ponderosa pine recruitment. If summer precipitation has remained or fluctuated above the threshold for juvenile success since the mid-18th century, then overall annual precipitation, as recorded in the tree ring record, may be inconsequential to establishment.

Allee effects.—Allee effects emerge when reproductive success is reduced in small populations (Stephens et al. 1999). For anemophilous trees, the probability that a receptive ovule will be fertilized by windborne pollen may be very low at low population densities, particularly for obligate outcrossing species. Ponderosa pine is almost completely outcrossed, with very low selfing rates (Mitton 1992), and hence seed production may be severely limited at low population densities (Farris and Mitton 1984). Seed availability limits tree establishment and population expansion (Eriksson and Ehrlén 1992, Ehrlén and Eriksson 2000).

Taylor and Hastings (2005) observe that Allee effects can substantially alter range-margin populations in their initial stages, often driving them to extinction. However, demographic stochasticity at early stages of population establishment can override Allee effects. In particular, stochastic immigration events can increase the probability of population success and compensate for Allee effects (Taylor and Hastings 2005, Drake and Lodge 2006). In our study, the Grass Creek population experienced a 13-decade delay in expansion after establishment of the first individual ca. 1610 CE. The most parsimonious explanation for this gap is that there were simply no successful seed dispersal and establishment events during this time, and hence there was no opportunity for the single tree present at the site to reproduce, due to its inability to self-fertilize. Once the second individual at Grass Creek reached maturity, there was a rapid response in population growth (Fig. 2d). The Grass Creek population presents the most striking evidence for Allee effects. However, the low establishment rates during the early phases of colonization in all of the populations coupled with the negative residuals from the modeled growth rate suggest Allee

effects were operating in all of the populations. We postulate that Allee effects in these populations were strong enough that without multiple immigration events, none of the populations would ever have grown beyond the initial founder(s). This can be tested via genetic analysis of the populations, which we are doing at this time.

CONCLUSIONS

We document colonization and population expansion for four ponderosa pine populations over the course of 500 years. Initial growth rates were slower than expected, and deviations from the logistic model occurred throughout each population's history. Our study shows that a combination of Allee effects, demographic stochasticity, and climate variability all play substantial roles in the initial development of populations. In each of our populations, initially strong Allee effects were eventually surmounted by stochastic establishment events that increased reproductive success. Favorable climate conditions in conjunction with population size appear to have facilitated rapid population expansion in the mid-18th century.

The development of new populations is contingent on many interacting processes. To fully understand population development, the relative roles and interactions among life-history traits (e.g., dispersal capability, Allee effects), population-level processes (e.g., microsite limitations, seed availability), and regional processes (e.g., climate variability and change) must all be considered. Findings from this study have potentially strong implications for predicted species migration patterns and distributional shifts over the coming century. Many studies predict large-scale shifts in species distributions, yet do so based solely on climatic forcings (Dormann 2006, Caplat et al. 2008). Our study empirically demonstrates the importance of considering other ecologically relevant factors, in conjunction with climate, when considering the rate at which species may migrate and colonize new territory.

Further studies are required to determine if these results are applicable to ponderosa pine expansion across its range, and to the expansion and development of other long-lived tree species populations. Identifying general patterns within and among species in population colonization and expansion is fundamentally important to population ecology and conservation efforts.

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SUPPLEMENTAL MATERIAL

Appendix A

Site description (*Ecological Archives* E093-093-A1).

Appendix B

Age–height offset analysis (*Ecological Archives* E093-093-A2).

Appendix C

Establishment–precipitation regressions (*Ecological Archives* E093-093-A3).

Appendix D

Among-population-growth comparison (*Ecological Archives* E093-093-A4).

Appendix E

Establishment and cumulative growth data (*Ecological Archives* E093-093-A5).