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Modeling high-severity fire, drought and climate change impacts on ponderosa pine regeneration

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ABSTRACT

We describe a model to investigate the effects of high-severity fire and drought on ponderosa pine regeneration using a water balance approach. Based on literature reviews and an analysis of annual and monthly correlations against tree regeneration, climate envelopes are constructed to simulate conditions during the flowering, seed production, germination phase, seedling growth in the season following germination, and seedling growth in the 2 years following germination. The model was tested against observed regeneration at five sites in the Southwest that experienced high-severity fires during a drought from ca. 1945 to 1956. For validation purposes single fire events, as occurred at each field site, were simulated by altering maximum and minimum temperatures and runoff conditions in declining stages of severity for 7 years. To evaluate long term fire and climate impacts four sensitivity tests were conducted on climate records from 1914 through 2009: (1) a climate control with no modifications to temperature and precipitation inputs; (2) a permanently burned condition simulation; (3) a simulation where climate conditions were altered based on IPCC future climate change projections and; (4) a simulation with both climate change and fire modifications. Results show that annual data correlate poorly with ponderosa pine regeneration compared to monthly correlations. On average the model correctly predicts regeneration outcomes 62% of the time at the field sites. The sensitivity tests suggest that regeneration rates are reduced by 43% in post high-severity fire environments because of changed conditions during germination and post-germination establishment phases. Future climate projections result in mixed outcomes across the 5 sites and an average reduction of regeneration rates by 8%. Ponderosa pine forests on the dry end of the climate envelope are predicted to experience severe reduction in regeneration.

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1. Introduction

Ponderosa pine forests in the southwestern U.S. appear to be slow to recover after high-severity fire, and may even be replaced by alternative vegetation types for some period of time (Savage and Mast, 2005; Savage et al., under review). In this paper we develop a model to test the influence of high-severity fire, drought and potential future climate change on ponderosa pine regeneration, and explore possible explanations for the simulated changes. Our model differs from others that assess forest dynamics by using daily rather than annual climate data to analyze specific developmental phases and aggregate outcomes of these phases in the regeneration process of ponderosa pine trees.

High-severity fire and drought can affect regeneration of ponderosa pine trees in three ways: (1) physical changes to climate variables, such as radiation, temperature and water availability (Savage et al., 1996; Moody and Martin, 2001; Humphries and Bourgeron, 2003; Zhang and Cregg, 2005; Fajardo et al., 2006; Rehfeldt et al., 2006; Vankat, 2011) or soil factors such as texture (Puhlick et al., 2012); (2) biogeochemical changes, such as changes to nutrient levels and soil chemistry (e.g. Hart et al., 2005; Gundale et al., 2005; Lezberg et al., 2008); (3) and ecological changes, such as those related to competition, seed availability and predation (e.g. Bailey and Covington, 2002; Keyes and Maguire, 2007; Keyes et al., 2007; Haire and McGarigal, 2010). We investigate how ponderosa pine trees respond to the combined stressors of high-severity fire and drought with an emphasis on the impacts of changes in physical variables. We then examine how the interaction of high-severity fire impacts combine with regional climate change may affect ponderosa pine regeneration.

High-severity fires alter microclimate conditions over burned areas (e.g. Neuenschwander and Wright, 1984; Oakley and Blanken, 2004; Monteith and Unsworth, 2008; Montes-Helu et al., 2009; Fontaine et al., 2010; Ma et al., 2010). Ash and bare soil affect

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surface albedo immediately after fire, resulting in increased absorption of solar radiation and higher surface temperatures. Removal of vegetation leads to reduced surface roughness resulting in altered temperature and wind profiles, as well as reduced trapping of terrestrial longwave radiation, leading to lower nighttime temperatures. Reduced vegetation also increases runoff and soil erosion, thereby reducing soil moisture and nutrient availability.

Global scale climate forcing is projected to affect conditions in the southwestern U.S. significantly, altering base moisture and temperature conditions (MacDonald, 2010; Seager and Vecchi, 2010; Williams et al., 2010). In concert with micro-climate change brought on by high-severity fire events, global climate change would likely further affect future forest recovery. In this paper, we explore the potential influence of climate change on ponderosa pine regeneration, but not on fire regime characteristics (e.g. Moritz et al., 2012). Using a water balance methodology similar to the model in Savage et al. (1996), we determine the variables that correlate most closely with ponderosa pine regeneration, and develop climate envelopes to simulate several phases of regeneration. We validate the model against observed regeneration data from 5 high-severity fire sites in New Mexico (Savage et al., under review). To assess the interactions of local fire impacts and potential future global climate conditions, we run simulations to evaluate the effects of high-severity fires on ponderosa pine regeneration under prevailing climate conditions, under future climate projections, and under future climate projections with fire impacts. Unlike many previous studies on ponderosa pine regeneration, we evaluate sub-annual climate impacts on different phases of the regeneration cycle, and we apply our model to multiple sites to test its validity at a regional scale. Our goal is to understand how climate changes at local and global scales interact to affect future ponderosa forest regeneration in the U.S. Southwest.

2. Methods

We use the concept of a climate envelope (e.g. Gates, 1980) to assess the capacity of ponderosa pine trees to regenerate after high-severity fires under drought conditions. We recognize that there are weaknesses in the climate envelope approach (Pearson and Dawson, 2003; Heikkinen et al., 2006; Hijmans and Graham, 2006; Beale and Lennon, 2012; Evans, 2012), but we use it to explore a process-based analysis of potential impacts of biophysical changes on regeneration rates. Savage et al. (1996) presented a water balance based climate envelope approach to test various hypotheses proposed by Maguire (1956) for ponderosa pine regeneration success at the Gus Pearson Natural Area in northern Arizona. They tested 11 climate factors that influence tree regeneration, and concluded that both rare seasonal and inter-annual climatic factors, and a unique set of circumstances associated with anthropogenic disturbances played a role in shaping a ponderosa pine germination pulse early in the 20th century. This paper aims to extend the Savage et al. (1996) model to a regional scale and to convert the relative water balance measures (i.e. climate anomalies measured in deviation measures) used in the Pearson study to absolute metrics that apply on a regional scale. We also test the premises of the Savage et al. (1996) water balance model by investigating the correlation between annual and monthly water balance variables with observed regeneration at high severity fire sites in New Mexico (NM).

2.1. Study sites

We document establishment of ponderosa pine trees over the decades after high-severity fires that burned during the drought of ca. 1945–1958 (Savage et al., under review). Tree-ring counts are used to document the years in which tree germination occurred (Stokes and Smiley, 1968); sites were sampled in 2002/2003 and 2008/2009. For best estimate of age, trees were cored diagonally at the tree base toward the point of germination. Cores ages were double-checked by crossdating in an independent dendrochronology lab (Savage et al., under review). We do not age seedlings and saplings, hence 1990 was selected as a cut-off date for the analysis period to ensure that there was no under-sampling of trees in regeneration estimates.

2.2. Water balance methodology

To create a set of variables for assessing the impacts of climate and post-fire conditions on ponderosa pine regeneration, we use a water balance methodology to assess thermal and moisture conditions at each site. Microsoft Excel software is used to develop a model using basic water balance methodologies (Thornthwaite, 1948; Mather, 1978; Willmott et al., 1985; Savage et al., 1996; Feddema, 2005). The model partitions overland runoff from precipitation using the Soil Conservation Service (SCS, 1972; Mather, 1978) overland runoff model. The SCS methodology requires estimates of SCS curve numbers to calculate the proportion of precipitation that becomes overland runoff. Runoff conditions vary by land cover type and with 5 day antecedent rainfall conditions, where dry conditions allow for more infiltration and reduced overland runoff (lower curve number) and progressively wetter conditions leading to saturated soils and more runoff (higher curve numbers). Standard curve numbers (CN) used are 60/78/90 for CN1/CN2/CN3 (SCS, 1972; Mather, 1978) to represent conditions in unburned locations. These numbers can be changed upward or downward to simulate burn or other landcover conditions. From infiltrated precipitation and temperature, estimates of potential evapotranspiration (PET), snow accumulation and snowmelt (as implemented in Willmott et al., 1985), soil moisture conditions, actual evapotranspiration (AET), moisture surplus and deficit conditions are estimated on a daily basis. Key variables are aggregated by month and by year.

2.3. Data sources

To implement the water balance model, daily precipitation (P), minimum temperature (Tn) and maximum temperature (Tx) observations are needed for each study site. Long term trends in regeneration are assessed by selecting a minimum of 90 years of record for each site. Simulations are run for the entire period of record, but for validation purposes we evaluate the records from the year of the high-severity fire at each site through 1990. Long-term climate records are available from the Cooperative Observer Program (COOP), managed by the National Weather Service (http://www.nws.noaa.gov/om/coop/). The closest COOP stations may have incomplete or short-term records, whereas long-term stations may be sufficiently distant from a site that they may not represent actual conditions. For several of the sites, there are nearby stations with very limited data (only precipitation in some cases, or very short periods of observations in others). We used these stations to develop monthly adjustments relative to more distant, longer station records near each site (Table 1).

To create a daily record, missing data at the long-term station data are filled in as follows. For temperature, if no more than 3 consecutive days are missing, the missing day Tn and Tx are linearly interpolated from the last and first observations bracketing the missing days. If more than 3 consecutive days are recorded as missing, the average daily Tn or Tx for that day is estimated from the entire long term station record and inserted for that day. For days of missing precipitation, the average daily precipitation value for the entire period of record is inserted for the day. This is

Table 1
COOP weather stations used to simulate weather conditions at each field site, short term stations used to make adjustments to calibrate the long term station inputs, and estimated mean annual temperature and mean total precipitation at each site.

Field site	Long term station	Nearby station for calibration	Mean annual temperature (°C)	Mean total precipitation (mm)
Archuleta Mesa	Dulce, NM		6.8	448
Cebollita	Jemez Springs, NM		10.81	429
Ocate	Cimarron, NM	Ocate, NM	8.5	438
Allen Canyon	Cloudcroft, NM	Mayhill, NM	13.6	345
Circle Cross	Cloudcroft, NM	Mayhill, NM	13.6	345

typically a very low value, but in cases where whole months are missing, this method results in an average monthly precipitation or temperature value. This methodology allows the water balance model to simulate representative conditions during periods when a station has extensive missing data. Relatively few years of these records have significant missing data, and, if the missing values occur during months not critical to assessing development conditions, this approach will have little impact on the analysis. There is one exception to the data filling algorithm, and that is a missing observation on July 9, 1961 in Jemez Springs. The missing observation is a notable gap in an otherwise wet period evidenced by observations at nearby Los Alamos. The 6 day total precipitation (July 6–11) at Los Alamos was 39.12 mm, and to reach a similar 6 day total of 37.44 mm at Jemez Springs we substituted 25 mm for the missing observation. The variable terrain and resulting variable precipitation regimes in the region preclude better results using other extrapolation methods (El-Sadek et al., 2011).

Some long-term weather stations are too distant from the study sites to use the data directly as input to the model. To create final daily weather input time series, the long-term station data are adjusted based on the differences between the monthly temperature values at the long-term station and a short-term station closer to the site. For precipitation, the observed monthly percentage difference is used. In most cases these differences are relatively small, but in a few cases these monthly adjustments make adjustments by a factor of 2 (e.g. Cloudcroft and Mayhill, and Cimarron and Ocate).

Information about soil water holding capacity is also required by the model. Our information is based on empirical data collected from our sampling plots (Savage et al., under review) and USGS soil survey map information for each site. Based on observed soil conditions and soil survey data, simulations use an average 75 mm water holding capacity for all sites.

2.4. Determination of climate envelopes

As part of this study we want to test the climate envelope assumptions made for each regeneration phases as used in Savage et al. (1996). To test whether these climate envelopes are valid, we correlate annual and monthly water balance variables against successful regeneration at each of the study sites. From these correlations we assess whether modifications are needed for the climate envelopes, or whether additional criteria are needed.

We extend the work by Savage et al. (1996) by adjusting and extending the multiple climate conditions for each regeneration phase. As suggested by Beale and Lennon (2012), we incorporate a measure of uncertainty, or relative success, with scores between 0 and 5, where 0 represents conditions that are deemed unfavorable or detrimental, 3 represents average conditions, and 5 represents very favorable conditions needed for a particular phase of development. Threshold values for each climate-related factor within each phase of development are listed in Table 2 and are based on values used by Savage et al. (1996); observations from Pearson (1924, 1930, 1942), Korstian (1924), Maguire (1956), Daubenmire (1960), Schubert (1970), Despland and Houle (1997), Fajardo et al. (2006), League and Veblen (2006) and Heidmann (2008); and from the correlation results of this study. We intend this methodology to apply to the region, but the climate envelopes are sensitive to the quality of the weather observations at each local site. By scaling the likelihood of success from 0 to 5 it is possible to allow that there is a range of possible outcomes within a site. For example,

Table 2
Climate conditions associated with specific development stages of Ponderosa Pine. GDD = growing degree days, AET = actual evapotranspiration, PET = potential evapotranspiration, Tn = minimum temperature, SM = soil moisture, WHC = water holding capacity.

Development stage	Time relative to germination	Climate variable	Condition 1 Min value	Condition 2 Min value	Condition 3 Min value	Condition 4 Min value	Condition 5 Min value
Flowering phase	3 Years prior	June GDD	375 °C	400 °C	425 °C	450 °C	475 °C
	3 Years prior	June Tn	−5 °C	−4 °C	−3 °C	−2 °C	−1 °C
	3 Years prior	Sep–Oct GDD	575 °C	600 °C	625 °C	655 °C	675 °C
	2 Years prior	Jun–Jul GDD	900 °C	930 °C	960 °C	990 °C	1020 °C
Cone development phase	2 Years prior	Aug–Oct AET/PET	0.65	0.70	0.75	0.80	0.85
	2 Years prior	Aug–Oct GDD	1070 °C	1100 °C	1130 °C	1160 °C	1190 °C
	Year prior	Jul AET/PET	0.55	0.6	0.65	0.7	0.75
	Year prior	Sep–Nov GDD	640 °C	670 °C	700 °C	730 °C	760 °C
	Germ year	May GDD	225 °C	250 °C	275 °C	300 °C	325 °C
Germination phase	Germ year	5 day Tn	−6 °C	−5 °C	−4 °C	−3 °C	−2 °C
	Germ year	5 day GDD	55 °C	65 °C	75 °C	85 °C	95 °C
	Germ year	5 day rain + melt	15 mm	20 mm	25 mm	30 mm	35 mm
	Germ year	SM	87.5% WHC	90.0% WHC	92.5% WHC	95.0% WHC	97.5% WHC
Seedling phase	Germ year	Tmn	−6.5 °C	−5.25 °C	−4 °C	−2.75 °C	−1.5 °C
	Germ year	Daily AET	0.7 mm	0.85 mm	1.0 mm	1.15 mm	1.3 mm
Post germination phase	Germ year	Nov soil moisture	40% WHC	55% WHC	70% WHC	85% WHC	100% WHC
	Year following	May 15–Sep 15 Min daily AET	0.3 mm	0.4 mm	0.5 mm	0.6 mm	0.7 mm
	2 Years following	May 15–Sept 15 Min daily AET	0.2 mm	0.3 mm	0.4 mm	0.5 mm	0.6 mm

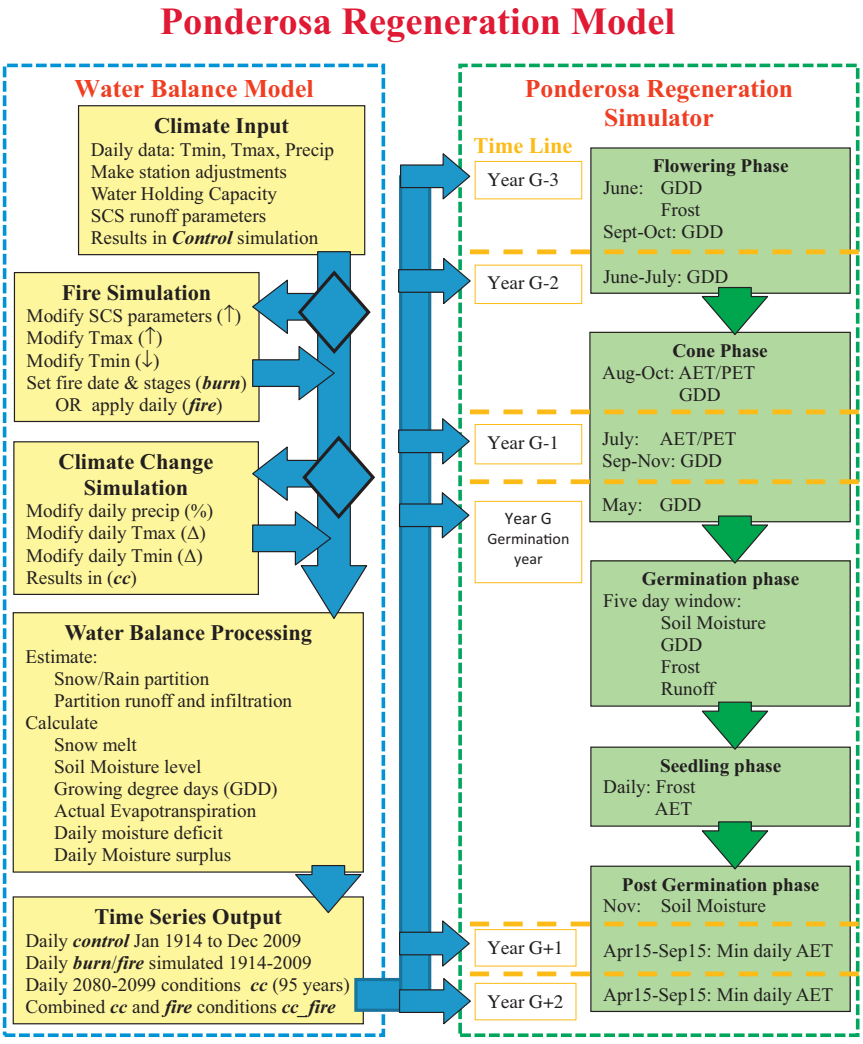


Fig. 1. Schematic representation of the ponderosa pine regeneration model, including the water balance model including modules to simulate fire and climate change conditions. The ponderosa regeneration simulator shows the stages of regeneration simulated, the variables used to simulate the stage, and a timeline relative to germination date for the event.

climate may be unsuitable due to low temperatures, but germination may still be possible in warm microclimates, resulting in patches of regeneration (Cooper, 1961; Mast et al., 1999; Boyden et al., 2005).

To better represent the impacts of climate factors on ponderosa pine regeneration, the conditions in Table 2 are used to develop measures of success for several phases of regeneration (Fig. 1). The phases represented include: (1) success of cone production, (2) likelihood of germination, (3) seedling establishment in the year of germination, and (4) potential seedling mortality in the 2 years after germination. First, cone production success is based on determining how successful the flowering and cone production phases are in the years prior to germination. A flowering phase (*flower*) score is determined by summing the success scores associated with the 4 climate factors used to assess the success of the flowering phase (Table 2: flowering phase with a maximum possible value of 20). After the flowering phase, other climate factors determine whether flowers are likely to develop into significant cone production. A *cone* score is created from the relative success scores of the 5 climate factors that influence successful cone production in the post-flowering phase (Table 2, cone development phase; with a maximum value of 25).

Second, the likelihood of germination (*germ*) score is based on 4 climate conditions representing immediate and long-term moisture and thermal conditions (Table 2; germination phase). A *germ* score is based on the sum of the relative scores associated with each climate condition divided by the maximum possible score (20). Third, seedling establishment in the year of germination (*seedling*) scores are based on the number of consecutive days (*sDays*) when minimal actual evapotranspiration and Tn conditions (Pearson, 1924) are met following the germination event (Table 2). The *seedling* score is ratio adjusted relative to a 38-day standard period (based on a sensitivity analysis) to provide a relative score comparable to the other scores. Fourth, potential seedling mortality in the 2 years after germination is calculated based on soil moisture conditions on November 30th (*Nov*(*St*)) of the germination year (maximum 5), and minimum daily actual evapotranspiration scores during the summer of the year following the germination event (*Yr* + 1)*AE* (maximum 5) and the second year following germination (*Yr* + 2)*AE* (maximum 5).

An overall regeneration score (*regen*) is created by combining cone, germination, seedling and post germination scores as follows:

$$Regen = \frac{(flower/20 + cone/25)}{2} * \frac{germ}{20} * \frac{sDays}{38} * \frac{(Nov(St)/5 + (Yr+1)AE/5 + (Yr+2)AE/10)}{3} \quad (1)$$

A score greater the zero indicates the potential for regeneration. This formulation considers additive conditions related to the cone production phase and post-germination phase (with year 2 carrying half the weight of the fall and year 1 conditions), and the multiplicative relationship between each of these phases and the germination and seedling phases in order to ensure that each phase wields equivalent influence on the outcome. Higher scores are indicative of more favorable conditions overall, although there are instances where high scores in several phases may mask the low likelihood of germination. It is useful, therefore, to consider the individual components separately from the *regen* score in any analysis. The dimensionless scores are then compared to the observed regeneration values at each site.

2.5. Simulations

To assess the influence of high-severity fire and climate change on regeneration, we first run our ponderosa pine regeneration model in a control run to simulate normal conditions, i.e. without any modification to any of the input variables (Fig. 1). To simulate high-severity fire conditions we alter the model to simulate changed surface conditions, and to simulate climate change conditions, we alter the climate input variables (Fig. 1). Assumptions for each of these simulations are described below.

2.5.1. Control simulations

Simulations using water balance values derived from the estimated daily temperature and precipitation records for each site from 1914 to 2009 are considered the ***control*** simulation. This simulation assumes that the forest sites and their associated weather stations did not experience fire events or any microclimate modifications as a result of fire events.

2.5.2. Simulating high-severity fire conditions

To better understand the impacts of high-severity fire on tree regeneration, the daily temperature and runoff conditions for the sites are altered to simulate post-burn microclimate modifications (Oke, 1992; Jones, 1992; Monteith and Unsworth, 2008). In the first year following a fire, soils will be significantly darker due to carbon on the surface, and denuded soils will be exposed to more direct solar radiation during the day and to greater longwave radiation losses at night. In addition, the loss of the canopy and ground vegetation results in much greater runoff potential during high-intensity rainfall events. To simulate these conditions, daily maximum temperatures are elevated by 4 °C, while daily minimum temperatures are lowered by 2 °C. These are conservative values, based on observations from Neuenschwander and Wright (1984), Ewing and Engle (1988), Oakley and Blanken (2004), Fontaine et al. (2010) and Ma et al. (2010). To simulate runoff conditions, the CN values are increased to 86/94/98 for CN1/CN2/CN3 (based on SCS, 1972; Mather, 1978). To determine the statistical effects of high-severity fires on regeneration, this simulation applies these conditions to every day in the record, i.e., as if the site was experiencing severe burn conditions from 1914 through 2009. This simulation is called the ***fire*** simulation. While it is completely unrealistic to assume that severe fires occur annually, this simulation, in comparison to the control simulation, provides a statistical assessment of how fire suppresses regeneration.

2.5.3. Simulating historical fire events

To simulate actual observed conditions at a site, the historical single fire events as recorded from observations are simulated (***burn*** simulation). To simulate that the site is experiencing severe burn conditions for about a year right after the actual burn takes place, fire conditions described for the ***fire*** simulation are applied for 400 days following August 1st of the year in which a high-intensity fire occurred at a site. To simulate a gradual return to more normal runoff and temperature conditions, a second stage of fire effects is simulated with less severe conditions compared to the first phase. These less severe fire impacts are simulated with a Tx increase of 2 °C, a Tn decrease of 1 °C and CN numbers of 71/86/94 for 1200 days following the last day of the intense fire simulation. Finally, following stage 2, a third stage lasting 2400 days, implements a Tx increase of 1.0 °C, a Tn decrease of 0.5 °C, and CN numbers of 64/81/92. This simulation assumes that post-burn conditions are gradually eased after the fire, and that blackened soils are gradually covered by vegetation. For all other periods during the 1914–2009 simulation period control conditions are assumed at the sites. For validation purposes predicted ***burn*** outcomes are compared with empirical observations of regeneration following high-severity fires.

2.5.4. Simulating future climate change projections

To simulate the potential impacts of climate change (***cc*** simulation), we use the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report projections for the region (Christensen et al., 2007) which suggest the 50 percentile multi-model ensemble projection for the region, and the 2080–2100 period, to be 3.23, 3.33, 3.77 and 3.27 °C warmer, and −0.67%, −1.22%, −4.33% and +2.00% wetter respectively for winter (DJF), spring (MAM), summer (JJA) and fall (SON). To simulate impacts of these potential changes, the seasonal changes are applied to all the daily temperature and precipitation values for the entire period of record from 1914 to 2009. This methodology only captures changes in the mean state of the climate and does not account for any projected changes in climate variability. By comparing these ***cc*** results to the control conditions we can assess the projected impact of climate changes on regeneration rates.

2.5.5. Simulating future climate change projections combined with fire conditions

A final simulation combines the fire and projected climate change simulations (***cc-fire***) by applying both the climate change (***cc***) conditions to the daily input temperature and precipitation data, and applying fire (***fire***) conditions to each day for the entire simulation from 1914 through 2009.

2.6. Statistical analyses

The validation component of the results compares the ***burn*** simulation to empirical observations, covering the period studied by Savage et al. (under review) from the year following the high-severity fire at each site through 1990. The model is tested to evaluate how well it predicts observed outcomes and to assess correlations between *regen* scores and observed tree regeneration dates. The model rates the relative success of regeneration on an annual basis which can then be compared to observed regeneration each year.

All other simulations (***control***, ***fire***, ***cc*** and ***cc-fire***) are used as sensitivity tests to assess the impacts of fire and climate change projections on the ponderosa pine regeneration processes and the long term response of these forests. The simulations analyze statistical changes in the climate record over the 95-year period from 1914 (the first year where all stations have complete data) to 2009. Future simulations (***cc*** and ***cc-fire***) are presented on the same time scale as the historical simulation, but represent climate projections 80 years into the future. We not only assess change in *regen* scores, but consider trends in the component scores for each development phase separately. To better assess long-term trends, we use 5- and 19-year moving averages to assess temporal changes over the duration of the record and between simulations.

Table 3
Annual water balance variables correlated against tree establishment dates by site. Only correlations greater than 0.20 are reported, correlations significant at the 0.05 significance level are indicated in bold type.

Water balance variable	Ocate	Cebollita	Allen Canyon	Circle Cross	Archuleta Mesa
T mean				−0.23	
Precipitation				0.22	0.29
Mean snow depth	−0.25			0.26	−0.22
Snow melt	−0.24				
Growing degree days (GDD)				−0.22	
Freezing degree days (FDD)				0.25	−0.22
Potential evapotranspiration			−0.21	−0.23	
Actual evapotranspiration		0.25		0.23	0.30
Mean soil moisture storage		0.22		**0.33**	**0.35**
Moisture deficit				−0.29	−0.30
Moisture surplus			0.21		
Total runoff	−0.21				
Moisture index (Im)				0.24	**0.32**
Maximum monthly Im	−0.31			0.29	
Minimum monthly Im		**0.46**		0.2	
Moisture index range	−0.28			0.24	
AE/PE ratio		0.19		0.26	**0.31**

3. Results

3.1. Evaluation of climate envelope assumptions based on annual and monthly correlations

When comparing all the water balance variables against regeneration events, 5 annual water balance variables showed significant correlations at the 5% significance level (Table 3). Significant factors were a correlation for *minimum monthly moisture index* values at Cebollita ($r = 0.46$), *mean soil moisture* conditions ($r = 0.33$) at Circle Cross and *mean soil moisture* conditions ($r = 0.35$), *annual moisture index* ($r = 0.32$) and *AE/PE ratio* ($r = 0.31$) at Archuleta Mesa. The same correlation for Cebollita using either Jemez Springs climate data or Los Alamos climate data resulted in very similar correlation outcomes. At these 3 sites there are additional correlations that suggest that moisture is critical to regeneration success. While no significant correlations (at the 5% confidence level) were found at Allen Canyon and Ocate, the correlation trends at these sites did differ from the other 3 sites. At Allen Canyon the highest correlations were with *potential evapotranspiration* ($r = -0.21$), *surplus moisture* ($r = 0.21$) and *growing degree days* ($r = -0.16$). Highest correlations in Ocate were *maximum monthly moisture index* value ($r = -0.31$), *moisture index range* ($r = -0.28$), *snowmelt* ($r = -0.25$) and *runoff* ($r = -0.21$).

Compared to annual correlations, monthly correlations at the 5% confidence level are significantly higher and more frequent. Significant correlations vary from $r = -0.61$ (September Tn at Ocate) to $r = 0.72$ (February Snow melt at Circle Cross). Rather than report all the values, we aggregate the number of significant energy (Table 4) and moisture (Table 5) related correlations for each month, and highlighted those that are consistent across multiple sites. In general, there are few strong correlations between energy related variables (Table 4, aggregating monthly average correlations for mean temperature, Tn, Tx, GDD, FDD and PET). Only low May energy variables showed correlations across three sites (Ocate, Allen Canyon and Circle Cross) in the second year following germination, suggesting that lower temperatures result in less desiccation and seedling mortality. Similarly, low temperatures (Tn) in June of the germination year also correlate with higher regeneration rates at Allen Canyon and Circle Cross. In contrast, maximum temperature (Tx) for the same month correlates positively with regeneration success in Ocate, perhaps indicating that this site occupies a colder space in the climate envelope (Table 1). For moisture related variables (Table 5, aggregating monthly precipitation, maximum snow storage, snow melt, AE, soil moisture storage at the end of the month, moisture deficit, moisture surplus, recharge, runoff, estimated streamflow, moisture index and AE/PE ratio), most correlations are positive, indicating that wetter conditions favor regeneration.

Table 4
Number of significant monthly energy correlations (6 variables tested) at the 0.05 significance level for observations from 2 years prior to 2 years past seedling establishment dates at 5 sites. Italic indicates regeneration is correlated with cooling, bold indicates correlation is related to warmer conditions. Numbers in parentheses indicate the number of stations where the indicated trend occurs; if none, then only one station showed these correlations.

	Year −2	Year −1	Year 0	Year +1	Year +2
Jan	3	*5* (2)	3	0	4
Feb	0	1	1	0	**3** (2)
Mar	2	0	1	0	3
Apr	0	0	1	0	5
May	1	3	4	4	*9* (3)
Jun	0	2	*6* (3)	1	3
Jul	0	4	1	0	2
Aug	7	3	1	2	0
Sep	0	3	0	1	0
Oct	3	3	4	1	1
Nov	0	0	0	1	0
Dec	2	0	4	2	5

Monthly correlations show strong regional agreement with wet conditions in the year prior to germination in January (snow depth in Cebollita, Ocate and melt and several surplus indicators in Circle Cross) and May (negative correlation with deficit in Circle Cross, positive correlations with AE in Archuleta Mesa and several high surplus indicators), and over a number of months in fall (with Ocate

Table 5
Number of significant monthly moisture correlations (12 variables tested) at the 0.05 significance level for observations from 2 years prior to 2 years past seedling establishment dates at 5 sites. Italic indicates regeneration is correlated with drying, bold indicates correlation is related to wetter conditions. Numbers in parentheses indicate the number of stations where the indicated trend occurs; if none, then only one station showed these correlations.

	Year −2	Year −1	Year 0	Year +1	Year +2
Jan	**9**(2)	**5**(3)	*3*(2)	**5**(2)	3
Feb	7	4	**3**(2)	6	1
Mar	4	2	2	3	2
Apr	1	0	2	2	2
May	0	**6**(3)	**7**(2)	5	1
Jun	5	**5**(2)	**5**(2)	0	0
Jul	**7**(2)	4	0	0	0
Aug	7	0	0	4	1
Sep	3	**6**(2)	**18**(3)	0	0
Oct	2	**10**(2)	**6**(2)	0	0
Nov	2	**4**(2)	**2**(2)	0	4
Dec	**3**(2)	1	**6**(2)	*4*(2)	**2**(2)

Table 6
Percent of years where non-regeneration and generation events are correctly predicted from the year following the fire event to 1990 (% correct). Percent of observed germination events that are correctly predicted (% germination), and correlation statistics based on annual observations of *regen* scores and tree measured tree densities. For reference average annual temperature and precipitation estimates are given for each site.

Location	% correct	% germination	Correlation of *regen* and tree density	Mean annual temperature (C)	Total annual precipitation (mm)
Ocate	67.65	76.67	0.23	8.51	438
Cebollita	53.33	64.71	0.01	10.81	429
Allen Canyon	58.97	60.00	−0.11	13.61	345
Circle Cross	59.46	70.00	0.17	13.61	345
Archuleta Mesa	69.23	50.00	0.06	6.80	448
Average	61.73	64.27	0.07	10.67	401

the exception over the 3 month period). In addition, monthly correlations are high for wet conditions in the September following germination (negative correlations with deficit and several positive correlations with moisture indices at Cebollita, Circle Cross and Archuleta Mesa). The strong September correlations following germination are followed by multiple correlations in late fall and early winter for all sites except Allen Canyon. Savage et al. (1996) do not have a climate envelope related to wet fall conditions of the germination year. These results suggest moisture in the fall of the germination year is an important variable to successful ponderosa pine regeneration. Hence November soil moisture conditions are included as a climate envelope condition for the post-germination phases of ponderosa pine regeneration model.

3.2. Model validation

The ***burn*** simulation correctly models observed germination conditions (both non-regeneration and regeneration events) 62% of the time across all sites (Table 6), with a highest accuracy of 69% at Archuleta Mesa and a low of 53% at Cebollita. When evaluating whether observed germination is matched by the ***burn*** simulation, the average success rate is 64% with a high of 77% at Ocate and lows of 50% at Archuleta Mesa. Correlations between observed tree densities and *regen* scores in the ***burn*** simulations range from a low of −0.11 at Allen Canyon and to a high of 0.23 at Ocate (none significant at the 5% confidence level), suggesting that the magnitude of the *regen* scores correlates poorly with tree densities in the decades post establishment.

When comparing annual simulated and observed regeneration across all sites from the fire year through 1990, the ***burn*** simulation predicts an average of 20.4 seedling germinations over the average 38.8 years analyzed per site compared to 15.8 observed germinations on average per site for the same period (Table 7; Fig. 2). The model under-predicts germinations compared to observed germinations at Ocate (27 vs 30) and over-predicts germinations compared to observed germinations at Allen Canyon (18 vs 10) and Circle Cross (19 vs 10) and at Cebollita (26 vs 17), while simulated and observed events are correctly matched at Archuleta Mesa (12 events).

To evaluate the effectiveness of average germination events it is possible to compare observed tree densities at each site to the magnitude of the simulated *regen* scores, indicative of greater germination potential for a higher scoring event. On average, Ocate has the highest regeneration densities, at 13.88 trees/ha and the highest average *regen* score per simulated event (0.83) of any site (Table 6). Current observed regeneration densities show little difference across the other sites with values ranging from 4.33 to 6.38 trees/ha. Similarly, simulated *regen* scores are likewise very similar (0.37–0.55) for sites (Allen Canyon, Circle Cross and Archuleta Mesa). Cebollita stands out with relatively low observed regeneration densities at 4.7 trees/ha, while its *regen* score is ranked second at 0.55, in part because of one exceptionally high *regen* score in 1985.

The match of observed vs. ***burn*** simulation scores varies from site to site. Ocate had few years without successful observed regeneration (Fig. 2), with a peak in establishment in the early 1970s, a tapering off, but a secondary minor peak in the mid-1980s. Both these peaks are captured to some extent by the simulation. The simulation shows a third peak 5 years post-fire, not evident in the observed data. Compared to Ocate all the other sites have much lower simulated and observed regeneration. At Cebollita there is only one observed germination in the first 15 years following the fire, although the model predicts 5 low *regen* score events during this period (Fig. 2). After this period the model suggests 2 more active periods from 1965 to 1973 and post-1985, the latter matched by observed regeneration in most years. Neither Allen Canyon nor Circle Cross, with similar simulation results based on Cloudcroft data, exhibit observed regeneration until 1970, which, with the exception of 3 simulated germinations within 4 years of the fire, is matched by the simulations. Post-1970 both observed and simulated germination become more frequent, with peak periods around 1980 in Allen Canyon and post-1985 in Circle Cross. As suggested earlier local factors appear to play an important role that result in simulations matching well with observed germination at Circle Cross, but less so in Allen Canyon. Archuleta Mesa has very few observed germinations through 1970, although there are 3 low scoring simulated events over that period (Fig. 1) while the 1980s show sustained regeneration, which is matched by simulations half the time.

Table 7
Number of years of record for the observed and simulated validation periods from the year following the fire events through 1990; observed frequency of regeneration events and the average observed tree densities per event at each study cite; and the simulated successful regeneration events and their scores for the validation (***burn***) simulations at each site.

Location	Years of record	Observed		*Burn* simulation	
		Events	Trees/ha	*Events*	*Regen score*
Ocate	34	30	13.88	27	0.83
Cebollita	45	17	4.70	26	0.55
Allen Canyon	39	10	5.33	18	0.38
Circle Cross	37	10	4.33	19	0.37
Archuleta Mesa	39	12	6.38	12	0.37
Average	38.8	15.8	6.92	20.4	0.50

3.3. Sensitivity analyses

3.3.1. Fire simulation

In general, the results of the ***fire*** simulation, where fire conditions are simulated every year to compare the impacts of fire to simulations where there is never a fire (***control***) or climate change (***cc***), suggest that successful germination outcomes are significantly affected by fire-induced microclimate conditions. Simulated germinations are reduced on average over the 95 year period from 51.25 in the ***control*** simulation to 29.25 (43%

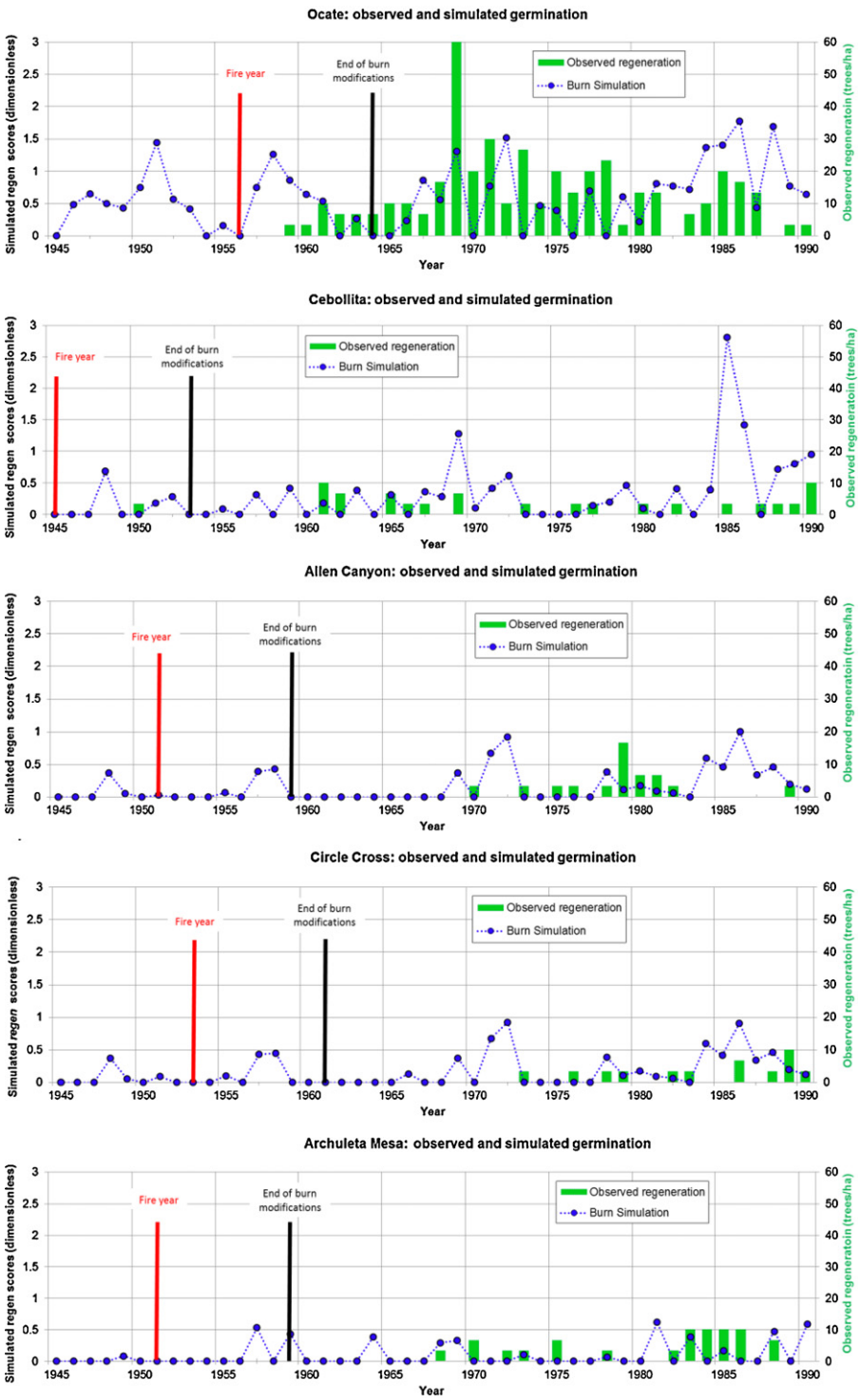


Fig. 2. Comparison of annual observed germination (Savage et al., under review) against the control and burn simulations during the validation period. Allen Canyon and Circle Cross use the same simulation results.

reduction) in the ***fire*** simulation (Table 8). ***Fire*** simulated *regen* scores are less than half (0.15) compared to ***control*** simulations results (0.33), a reduction of 55%; suggesting that fire conditions have a strong influence on the effective outcome of individual regeneration events. This reduction is primarily due to less success in the germination phase, illustrated by a reduction in average *germ* scores from 60 to 36. Increased frost conditions associated with the lower minimum temperatures and lower soil moisture conditions in the fire simulation both result in less favorable germination conditions on average and also reduce the number of times that minimal germination conditions are met in the ***fire*** simulation. *Regen* scores are also reduced because of lower scores in post-germination moisture conditions ~15% reductions in each (*Oct*(*St*), (*Yr* + 1)*AE* and (*Yr* + 2)*AE*; Table 8); a result from greater water loss to runoff and less moisture retention in the soils due to the fire condition. Pre-germination *flower* and *cone* conditions show little change, as would be expected because they are less dependent on moisture variables and dictated more by growing degree day

Table 8
Comparative sub-component and *regen* scores for the ***control***, ***fire***, climate change (***cc***) and combined climate change and fire (***cc-fire***) simulations. Scores are expressed as percentages of perfect scores, except ***sDays*** which are in number of days. See methods section for explanation of variables. AC & CC = Allen Canyon and Circle Cross.

Location	*flower*	*cone*	*germ*	*sDays*	*Nov(St)*	*(Yr+1)AE*	*(Yr+2)AE*	*regen*	*# events*
Control *simulation*									
Ocate	95.10	70.83	77.03	74.54	31.67	54.53	67.23	0.66	72
Cebollita	98.59	63.71	65.57	56.55	40.83	27.79	39.79	0.33	58
AC & CC	99.90	61.54	56.46	46.95	16.25	22.32	33.19	0.19	43
Archuleta Mesa	74.58	52.33	42.19	31.52	52.92	30.95	42.98	0.15	32
Average	92.04	62.10	60.31	52.39	35.42	33.89	45.80	0.33	51.25
Fire *simulation*									
Ocate	96.82	68.46	53.65	46.14	25.63	48.84	61.28	0.33	49
Cebollita	98.44	61.17	40.36	29.67	32.71	22.95	34.68	0.13	34
AC & CC	99.79	60.58	25.21	21.78	8.96	15.16	25.32	0.07	18
Archuleta Mesa	77.55	58.92	24.27	16.43	47.92	27.16	38.51	0.06	16
Average	93.15	62.28	35.87	28.50	28.80	28.53	39.95	0.15	29.25
Climate change *(**cc**) simulation*									
Ocate	99.95	68.83	75.52	72.98	27.29	43.79	55.32	0.55	68
Cebollita	99.17	61.67	66.15	53.36	36.46	14.95	24.68	0.24	54
AC & CC	100.00	60.25	44.53	32.45	11.25	7.58	14.68	0.06	27
Archuleta Mesa	98.85	61.46	44.22	37.28	49.58	19.37	30.21	0.19	41
Average	99.49	63.05	57.60	49.02	31.15	21.42	31.22	0.26	47.50
Climate change and fire *(**cc-fire**) simulation*									
Ocate	99.84	64.33	44.64	39.38	18.96	34.95	46.81	0.23	39
Cebollita	99.11	60.42	40.42	29.92	27.29	9.89	18.09	0.10	30
AC & CC	100.00	60.08	13.07	10.39	5.00	4.00	9.57	0.01	7
Archuleta Mesa	95.00	60.54	31.30	24.92	42.08	14.11	24.26	0.09	27
Average	98.49	61.34	32.36	26.15	23.33	15.74	24.68	0.11	25.75

and temperature conditions. Warm dry sites, Allen Canyon and Circle Cross (Table 8), are more adversely affected (especially with respect to *germ* scores), in part because *germ* and *regen* scores are already low, and even slight degradations in moisture conditions result in unmet threshold values for successful germination.

3.3.2. Climate change simulation

The climate change (***cc***) simulation over 95 years shows a slight decrease in average total germinations (47.5) compared to the ***control*** simulation (51.25). However, this average change masks highly divergent simulation results across the sites. Successful germinations over the simulation period are predicted to decline by 16 events at Allen Canyon and Circle Cross, to decrease slightly at Ocate and Cebollita (4) and to increase by 9 events at Archuleta Mesa. Average *regen* scores decrease from 0.33 to 0.26, but at Allen Canyon and Circle Cross, they are reduced from 0.19 to 0.06. The primary reason for this decline is the much drier average conditions in the years following germination, leading to increased seedling mortality. In the year following germination, scores are particularly low (7.58 compared to 22.32 in ***control***) at these 2 sites under climate change conditions. In contrast, in Archuleta Mesa germination (*germ*; from 42 to 44) and seedling conditions (*sDays*: from 32 to 37 days) improve for this relatively cold location (Table 1). In conclusion, overall climate change conditions had relatively little impact on germination and seedling survival conditions in most locations (except Allen Canyon and Circle Cross), but post-germination conditions decline in all locations. This suggests that regeneration will respond very differently at the different boundaries of the ponderosa forest climate envelope. Under climate change the dry end of the forest climate envelope will experience a significant decline in regeneration, while at the cold and wet end of the forest climate envelope regeneration is likely to improve with climate change.

3.3.3. Climate change and fire simulation

In the simulation of combined future climate conditions and fire (***cc-fire***) there are 25.75 germinations on average at all sites, compared with 51.25 in the ***control*** (Table 8) over the 95 year period of simulation. *Regen* scores aggregated across sites fall from an average of 0.33 in the ***control*** to 0.11 in ***cc-fire***. As in the ***fire*** simulations, seedling germination and survival conditions are strongly reduced relative to ***control*** (especially at Allen Canyon and Circle Cross). At the same time, conditions in the years following germination are worst of all the simulations, combining the negative effects observed in the ***fire*** and ***cc*** simulations.

3.3.4. Time series analysis

The sensitivity simulations show several important temporal trends. The 5-year moving average simulations from 1914 to 2009 (Fig. 3) show that the regeneration cycle is highly cyclical on this relatively short timescale, with all sites showing regeneration episodes on the order of 10–12 years. However, these cycles are repressed in several sites during the extensive drought period of the mid-20th century. These patterns are consistent with other observations (Milne et al., 2003) and clearly illustrate that the high-severity fires occurred during a drought period, and that the drought appears to have had a significant impact on the regeneration at Cebollita, Allen Canyon, Circle Cross and Archuleta Mesa. Ocate was least affected by the drought; the simulation predicts more vigorous regeneration early in the 20th century and during the 1980s and 1990s, a pattern which is less true at the other sites. However, the simulated regeneration remains strong throughout the record while observed regeneration tapers off through time, possible related to earlier generations preventing later generations from establishing.

Long-term trends are more pronounced in the 19-year moving average graphs, making the differing responses to each sensitivity test more apparent (Fig. 3). All sites show a strong response to fires, with a clear reduction in average *regen* scores associated with both fire simulations (***fire*** and ***cc-fire***) compared to comparable climate simulations (***control*** and ***cc***). The extensive mid-20th-century drought has a strong influence on all simulations but Ocate. The effect of the climate change simulation varies significantly by site,

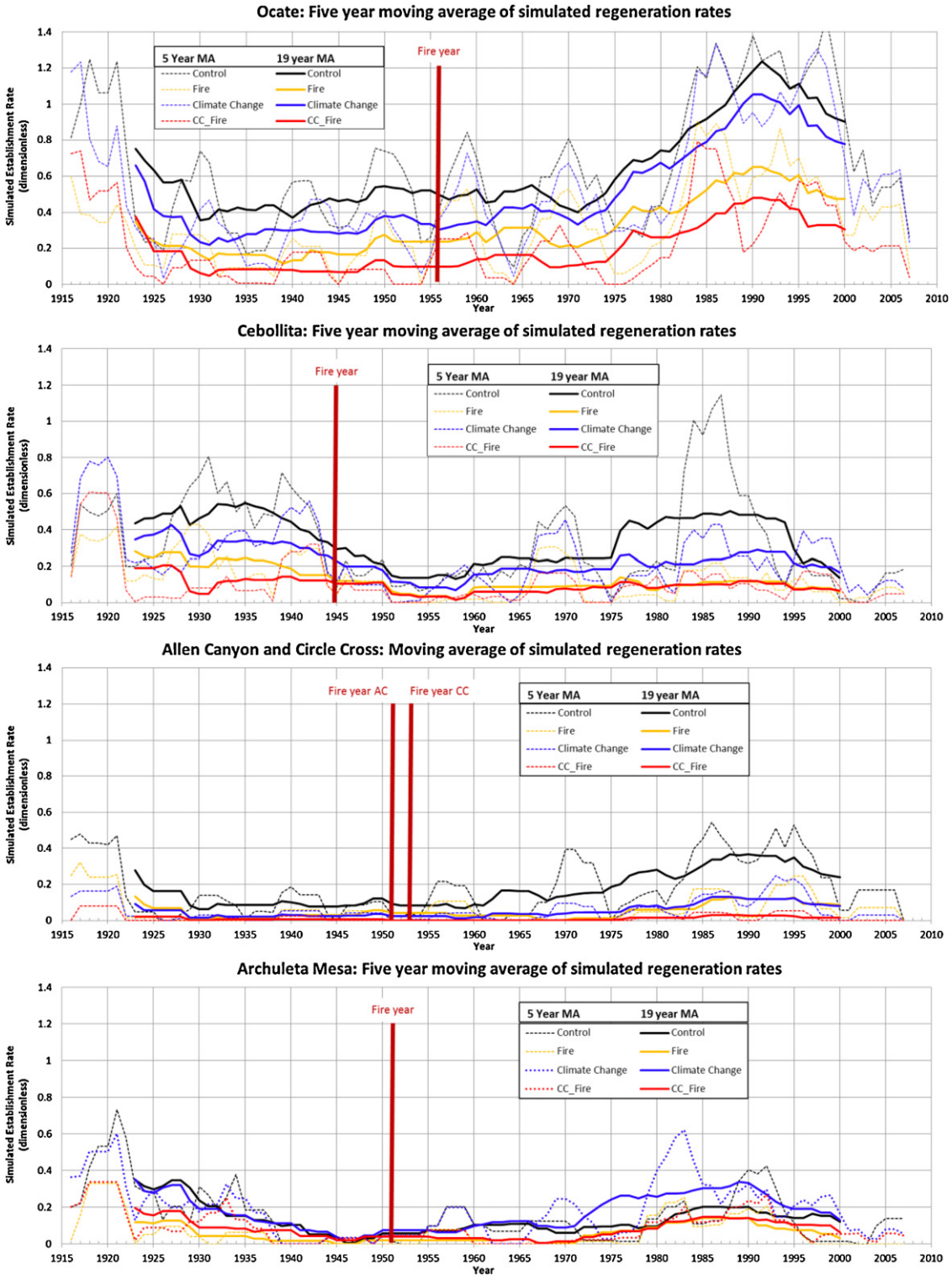


Fig. 3. Comparison of 5 and 19 year moving average scores for the ***control*** (no weather modifications), the fire modified simulation (***fire***), the Climate Change simulation (***cc***) and combined climate change and fire simulations (***cc-fire***). Dates for the ***cc*** and ***cc-fire*** represent conditions 100 years into the future.

as exemplified by reduced *regen* scores at Allen Canyon and Circle Cross for the ***cc*** simulation, but improving *regen* scores at Archuleta Mesa, a relatively cold site (Table 8). These more general trends suggest that the regeneration response is variable within the overall ponderosa pine forest climate envelope and that the drier parts of the climate envelope will experience a reduced regeneration response due to drying. The wetter and colder ends of the forest climate envelope will likely experience increased regeneration because more favorable temperature conditions, without associated water stress, will improve germination success and seedling growth. In the middle of the forest climate envelope, locations show variable regeneration impacts with climate change reducing

regeneration outcomes during local dry periods and potentially increasing regeneration rates during locally wet periods (i.e., the crossing lines in Ocate and Cebollita in Fig. 3).

4. Discussion

From our correlation analysis it is apparent that in addition to the climatic factors identified in Savage et al. (1996), fall moisture conditions during the germination year have a major influence on ponderosa pine regeneration events. Our revised model suggests that high-severity fire reduce germination because the fire induced microclimate changes result in increased numbers of killing frost days and increased mortality of seedlings post-germination because these same microclimate conditions result in reduced water availability to seedlings in the summer and fall following germination. In addition, the model shows that impacts of climate change may differ across the forest climate envelope, with forests on the dry end of the climate envelope likely experiencing severe reduction in regeneration events while forests on the wet and cold end of the climate envelope potentially experiencing benefits from warmer climate conditions (reduced killing frosts etc.) that lead to increased regeneration at these locations.

Specific results from the water balance variable correlations show that monthly statistics (Tables 4 and 5) perform better than annual statistics (Table 3). For annual statistics, 5 variables showed significant correlations with germination at 3 sites. Three of these correlations are for similar variables (mean soil moisture storage, moisture index and AE/PE ratio) at Archuleta Mesa. Mean soil moisture storage at Circle Cross and the minimum annual moisture index at Cebollita are the other 2 significant correlations. The sign of these correlations suggest that moisture content either at a specific time of year (minimum moisture index) or over the entire year (moisture index, mean soil moisture) are the critical reasons for the correlations at these 3 sites. Although not significant at the 5% confidence level, at Ocate there are many weak negative correlations with overall moisture conditions, suggesting that thermal factors are more important to regeneration success at this colder site. The outcome of this analysis is that correlations against a small set of annual climate statistics are unlikely to capture the full complexity of the relationship between climate factors and ponderosa pine regeneration. Hence mean annual climate statistics appear to be poor indicators of tree regeneration.

In contrast, monthly statistics (Tables 4 and 5) correlate far better with ponderosa pine regeneration, and suggest that in particular, conditions in specific times of year are critical to successful regeneration. For the sites used in this study, the temperature variables are less important in determining successful germination outcomes. For example, an observed correlation between low temperatures in June following germination and germination success is likely a reflection that cool conditions that reduce drying of seedlings, perhaps related to cloudiness and other meteorological factors affecting temperatures. These results also suggest that seasonal high temperatures in years prior to germination, while perhaps important to seed production (Maguire, 1956; Savage et al., 1996) and subsequent germination, may not be critical to regeneration outcomes. Warmer conditions could result in lower soil moisture and increased moisture stress during the seedling phases. It is also apparent that the monthly temperature related observations miss some critical factors that determine regeneration success. There does not appear to be a strong correlation between monthly temperature variables and killing frost events (perhaps these events are masked in the monthly averages) that are known to be critical to regeneration success (Maguire, 1956).

Monthly correlations are much stronger for moisture related variables. We found a number of expected relationships (Pearson, 1942; Maguire, 1956; Savage et al., 1996; Stein and Kimberling, 2003), such as wet conditions in the spring and fall of the year prior to germination, perhaps reflecting abundant seed production and thereby possible higher seedling densities during regeneration (Maguire, 1956). High moisture conditions in the fall prior to germination is highly correlated to germination success and is likely indicative of adequate soil moisture in the year of germination. The strongest monthly correlations with regeneration success are wetter conditions in the fall of the germination year. Moist conditions at this time could translate into seedling resilience in the first winter season, related to hardening for the winter season.

Our correlation results suggest that targeting shorter timescales with specific climate envelopes for each phase of development should result in a much better model for assessing how changes in climate conditions affect ponderosa pine regeneration and forest recovery, as compared to regression based models using monthly or annual observations. These monthly and annual observations typically mask such short term climate impacts as are associated with frost kill events and the narrow climate windows associated with germination.

The model is reasonably successful in simulating regeneration across all sites with successful simulation of germination varying from 53% at Cebollita to 69% at Archuleta Mesa (Table 6). There are a number of possible explanations as to why the simulations do not match observations more closely. Significant variation could be caused by different microclimates within each site. Also, the extrapolation of climate data to each site introduces potentially large errors in estimating local weather conditions. An important climate event may be missed when using daily values due to poor data quality or extrapolation error of daily precipitation data. This issue is best illustrated in the contrast of observed germination trends in Allen Canyon and Circle Cross. The model simulation for both of these sites uses the same source climate information, Cloudcroft data calibrated with short term Mayhill data; Cloudcroft is at a higher elevation and has different relief compared to the 2 sites. Therefore, the only difference in modeled generation outcomes are during the 7 years following the fire dates at each site, 1951 and 1953 respectively (see Fig. 2 for details). Hence modeled outcomes are almost identical for the 2 locations. However, observed conditions are quite different at the 2 locations, with 10 observed regeneration events in Allen Canyon and 10 at Circle Cross, with only 6 (60%) overlapping events. This suggests that local factors such as slope, aspect and chance convective rainfall events play a role in regeneration outcomes, and that extrapolated climate data may miss some of these important events, thus reducing the effective simulation of these events when there are no nearby climate data. Tree-ring dating limitations also may introduce uncertainty into the resolution of germination dates. Another final shortcoming of the methodology is that we only applied one set of fire modifications to all sites. Additional ecological data, such as whether high albedo grass cover has established, may result in a different post-fire microclimate signal than is simulated by our assumptions (see post fire temperature responses in Montes-Helu et al., 2009). It is possible that recovery of shrubs and grasses may change the microclimate in a way that our simulation does not capture.

Results from our sensitivity tests do provide a potential explanation for the lack of tree regeneration immediately following high-severity fires. Simulated changes to temperature and runoff result in a simulated decrease of germination events by 43% (Table 8), indicating that there are likely significant fire-induced microclimate effects that suppress regeneration. The more extreme temperatures on denuded and blackened surfaces present harsher conditions for germination, particularly by decreasing night time temperatures, which can fall below freezing and inhibit germination or kill seedlings. In addition to affecting germination rates, high-severity fire-induced conditions also dry out soils in the

post-germination phase, reducing water availability for seedling establishment. This can occur immediately following germination and in the years following, reducing seedling survival. This is illustrated by the difference in the number of seedlings cohorts predicted to survive past 45 days, 56.75, over the 95 years of the ***control*** simulation, compared to only 30.75 cohorts in the ***fire*** simulation. Similarly, the average number of seedling cohorts predicted to survive past 100 days is 18.25 over the 95 year period in the ***control*** simulation compared to 8.75 in the ***fire*** simulation.

Sensitivity tests to assess the potential impact of future climate change show a mix of outcomes. Some sites, Cebollita (slight) and Archuleta Mesa (strong) show improvement in outcomes and *regen* scores suggest an enhanced potential for regeneration under the selected climate change scenario. The all site average number of days that are suitable for germination in ***cc*** decreases from 781 to 706, and 54.75 (15.25) germinations reach the 45- (100-) day thresholds compared to 56.75 (18.25) days in the ***control*** simulation. However, Allen Canyon and Circle Cross have strongly reduced *regen* scores under warming climate conditions primarily due to projected drier conditions in summer following the year of germination, leading to seedling mortality from desiccation. The complexity of the interactions are illustrated by results from Cebollita, where the number of days with suitable germination conditions increases from 778 to 791 between the ***control*** and ***cc*** simulations resulting in 95 to 106 seedling cohorts respectively over the 95 year period. Post germination 68 ***control*** and 70 ***cc*** cohorts survive through 45 days, but by 100 days 15 cohorts survive in the ***control*** compared to 13 for the climate ***cc*** simulation. Thus the overall likelihood of establishment is higher in the ***control*** simulation, but not all aspects of the regeneration process are negatively affected by the projected climate change conditions.

The climate change simulation also suggests that the regeneration response will be different during drought periods than in moist periods. At several sites, responses in *regen* scores to simulated climate change conditions were weak during drought periods, but much stronger during relatively moist periods. Different sites, and different time periods at sites, show both negative and positive responses to climate change simulations. These results suggest that the impacts of climate change will likely vary significantly depending on which developmental phase is affected, where a site is located within the ponderosa forest climate envelope, and whether the base climate is wet or dry.

The combined interactions of fire and climate change are similar to the conditions expected due to fire alone especially with respect to germination. However, with an extension of the warm season, impacts from frost-thaw cycles during the shoulder seasons, and summers desiccation all tend to generally produce less favorable regeneration conditions post germination (except in Archuleta Mesa). This is partially offset by wetter winter and therefore spring soil moisture conditions. These offsetting signals lead to site dependent responses, with the fire response muted by climate change in Archuleta Mesa while climate change greatly exacerbate fire impacts at Allen Canyon and Circle Cross.

Overall, our results indicate that based on the water balance variable correlations, monthly statistics perform much better than annual statistics as correlates, suggesting that simulation of specific climate parameters at appropriate time scales is critical to developing better models for predicting forest dynamics under a variety of disturbances. This conclusion is further supported by model results that show that the impacts of climate change and fire on ponderosa regeneration are complex, and simulations need to account for the impacts of local, regional and global scale climate impacts on the various phases of the regeneration process. In sum, the overall impacts will depend on the accumulated impacts of climate forcing on each phase of the regeneration cycle. In addition, if any one of the phases is particularly affected (e.g. the *germ* phase), that impact may take precedence over the others, in essence representing the weakest link in a chain of impacts.

To build a better model of ponderosa pine regeneration in the face of high-severity fire, drought, and climate change, there is a need for better site-specific climate and microclimate observations as well as better empirical data on ecological factors such as competition, improved data sets will be needed: climate records, regeneration records, and burn-site microclimate conditions (e.g. Hayes and Robeson, 2011).

5. Conclusion

Our results suggest that in addition to the climate factors used in Savage et al. (1996), fall moisture conditions during the germination year are an additional critical climate control on regeneration success of ponderosa pine forests. While the lack of site specific climate data make it difficult to develop precise climatic envelopes for all phases on ponderosa pine regeneration, our model does perform sufficiently well to provide insight into how fire and future climate interactions might affect forest outcomes.

Our model suggests that high-severity fires have negative impacts on microclimate conditions that affect ponderosa pine regeneration. Burn sites tend to have higher diurnal temperature variability, leading to lower daily minimum temperature and frost conditions later in spring and earlier in fall. At the same time, altered soil conditions increase runoff and higher daytime temperatures lead to higher evapotranspiration conditions, resulting in decreased soil moisture necessary for germination and seedling development. The combined effect of lower minimum temperatures later in spring, combined with drier soil conditions earlier in summer appear to combine to reduce germination. The impacts of these combined effects vary by site and during different periods in the historical climate record. Locations that are near the cold edge of the climate envelope will be more affected by the temperature changes, while places on the dry edge of the forest climate envelope will be more affected by the drying during the seedling phase of regeneration. Similarly, during extensive drought conditions simulations show all locations experience suppressed regeneration, but especially those locations at the dry end of the climate envelope (Allen Canyon, Circle Cross and Archuleta Mesa) show almost no regeneration. An evaluation of individual phases of regeneration shows that this comes about because of a reduction in favorable germination conditions due to general low soil moisture availability during the germination phase, reduced survival of seedling in the summer and fall of the germination year, and reduced survival in the years following germination due to general drier conditions. The drought appears to have less impact on the flowering and seed development phases of the regeneration cycle.

Climate change simulations suggest that projected drier summer conditions may lead to reduced regeneration at 2 of the 5 study sites, increased regeneration at 2 sites, and little change in regeneration in the remaining site. Drier sites are projected to decrease regeneration, especially due to increased drought in the years following germination, key to seedling establishment. At wetter sites, warmer temperatures may lead to earlier germination dates and increased survival because the earlier germination dates allow for better seedling maturation before fall, and in the climate change scenario falls are expected to get wetter, helping sustain seedlings that survive into the monsoon and fall seasons. The climate change response is very much dependent on the location of the site with respect to the climate envelope of the forest. Regeneration will be reduced on the dry end of the envelope, and enhanced on the wet end of the envelope. Coincidently, the wet end typically is at higher elevation in the southwestern US, which also means that global warming will enhance germination conditions because of reduced killing frost episodes. However, because these are high

elevation sites, it is typically difficult for the forest to expand into new areas because there are few places to move to. At the same time the dry fringes of the forest are likely to see tree losses and reduced regeneration resulting in an overall shrinking of forest area.

The simulation of climate change combined with high-severity fire generally follows the severe reduction in regeneration also associated with the simulated impacts of fire during the historical period. However, closer evaluation shows that here also there is a complex set of interactions. For example during particularly wet phases of the Cebollita site (e.g. 1915–1920) fire appears to have less impact on the future climate change simulation (***cc-fire***) regeneration compared to its impact in the historical fire simulation (***fire***). This suggests that the enhanced temperatures and the temporary wet phase in the climate overcome many of the fire impacts on regeneration. Similar situations are evident in Archuleta Mesa. However, there are also examples where fire in combination with future climate change projections result in net impact that is more detrimental to regeneration (e.g. the last half decade in Ocate). This effect is even more pronounced during the 1985–1995 period in Allen Canyon and Circle Cross in large part because the climate change conditions significantly degrade regeneration conditions and then the fire conditions add to that reduction. As with the other results, the overall impact is very much dependent on which phase of regeneration is impacted and how the impacts for each phase interact to produce an overall regeneration rate.

Many climate envelope studies that evaluate the impacts of climate change use annual statistics and consider the total distribution of a species. Our work suggests that it is important to consider the climate envelopes for specific life cycle phases, and that each phase can be impacted quite differently and different phases can show opposite responses to the same climate forcing. In some cases one phase of the process can be the limiting factor that determines a final outcome. In addition, where a site is located in the climate envelope of a system can determine the observed response to a climate forcing. Our observations and fire impact simulations suggest that fire has a significant impact on ponderosa pine regeneration rates, typically reducing regeneration frequency by half. This is in large part because of extended freezing conditions in spring and drying of soils due to increased runoff and evapotranspiration rates in denuded landscapes. From our study the effects of climate change are projected to lead to more favorable regeneration conditions in cool wet portions of the ponderosa pine climate envelope and lead to reduced regeneration on the dry and warm portions of the climate envelope, potentially forcing a shift in the forest distribution. The combined effects of fire and climate change also lead to a general reduction on regeneration, although this is not true for all locations, and time periods. During wet periods, under future climate simulations a few sites are less impacted by fire conditions compared to drier periods at the same site. Drought conditions typically exacerbate the impacts of both fire and climate change impacts.

Climate factors play an important role in the frequency and success rates of ponderosa pine regeneration. Fire typically suppresses regeneration rates, while climate change has different impacts on regeneration rates depending on the location of a site within the ponderosa pine climate envelope. This work also suggests that regeneration is not a function of simple annually aggregated climate statistics, but rather is dependent on specific short term climate factors (e.g. frost and overall moisture conditions) that affect different phases on the regeneration process. To understand potential future climate impacts it is important to consider future fire and climate impacts on all phases of the regeneration cycle, and to recognize which phases are most sensitive to specific climate forcings.

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