Postfire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*

V.H. Bonnet, A.W. Schoettle, and W.D. Shepperd

Abstract: Regeneration of ponderosa pine after fire depends on the patterns of seed availability and the environmental conditions that define safe sites for seedling establishment. A transect approach was applied in 2002 to determine the spatial distribution of regeneration from unburned to burned areas within the landscape impacted by the Jasper Fire of 2000 in the Black Hills of South Dakota (USA). Canopy conditions alone, reflecting seed availability, at the stand level were not correlated with regeneration success. However, canopy conditions in combination with ground conditions explained patterns of regeneration success at the plot level (2 m × 6 m scale), and ground conditions explained these patterns at the quadrat level (0.2 m × 0.2 m scale). Only at the finer level of the quadrat could environmental factors explain seedling survival. Safe sites were characterized, in part, by the presence of scorched needle litter on blackened mineral soil. Areas with high understory cover restricted regeneration in the undisturbed forest and reduced seedling survival in the burned areas. The description of environmental conditions that favor and discourage ponderosa pine regeneration success will improve our understanding of how environmental heterogeneity within burned areas will contribute to the future forested landscape.

Résumé : La régénération du pin ponderosa après un feu dépend de la disponibilité des semences et des conditions environnementales qui déterminent les microsites réceptifs à l'établissement de semis. Une approche par inventaire linéaire a été appliquée en 2002 pour caractériser la distribution spatiale de la régénération dans des stations brûlées et non brûlées faisant partie du territoire touché par le feu Jasper qui a eu lieu en 2000 dans les Black Hills du Dakota du sud (É.-U). Seules, les caractéristiques du couvert dominant, qui reflètent la disponibilité des semences à l'échelle du peuplement, n'ont pas été corrélées au succès de la régénération. Cependant, les caractéristiques du couvert dominant jumelées aux conditions du sol ont expliqué les patrons de régénération retrouvés à l'échelle de la placette (2 m × 6 m) et les conditions du sol ont expliqué ces patrons à l'échelle de la micro-placette (0,2 m × 0,2 m). Les facteurs environnementaux ne peuvent expliquer la survie des semis qu'à une échelle plus fine que celle des micro-placettes. Les microsites réceptifs étaient en partie caractérisés par la présence d'une litière composée d'aiguilles légèrement brûlées déposées sur le sol minéral noirci. Un sous-étage abondant a diminué la régénération dans les forêts non brûlées et le taux de survie des semis dans les stations brûlées. La description des conditions environnementales qui favorisent ou défavorisent la régénération du pin ponderosa améliorera notre compréhension de la façon dont l'hétérogénéité environnementale des territoires brûlés contribuera au développement du paysage forestier.

[Traduit par la Rédaction]

Introduction

The spatial distribution of trees results from the combination of factors controlling seed availability, seed germination, seedling growth, and seedling survival (Greene et al. 1999; Dovciak et al. 2003). In homogeneous environments, seedling distribution is expected to be highly correlated to factors controlling seed availability. For species with wind-dispersed seeds in homogeneous environments, the seedling distribution would follow the seed dispersal curve that decreases and flattens almost exponentially with the distance from seed sources (McCaughey et al. 1986; Clark et al. 1999). In contrast, in heterogeneous environments, environmental conditions are expected to contribute an important role in seedling distribution. In these environments, seed availability and seedling distribution are not necessarily spatially correlated (Houle 1998).

Large-scale disturbances such as wildfire (Turner et al. 1998) and small-scale disturbances such as lightning, tree falls, and diseases (Lundquist 1995; Kneeshaw and Bergeron 1998) contribute to forest ecosystem structure and functioning. These disturbances create macro- and micro-environmental

Received 15 April 2004. Accepted 13 September 2004. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 3 February 2005.

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 doi: 10.1139/X04-157

heterogeneity (Rice 1993; Turner et al. 1994) that affects population and community spatial distributions (Dooley and Bowers 1998; Plotnick and Gardner 2002; Hutchings et al. 2003). Microenvironments are particularly important for tree seedling establishment in harsh environments (Cornett et al. 1997; Moir et al. 1999; Germino and Smith 2000). Habitats suitable for seed germination and seedling establishment, called "safe sites" by Harper et al. (1961), are created by processes at the macro- and micro-scales. Understanding at multiple spatial scales the complexity of factors controlling tree regeneration and distribution constitutes one of the fundamental goals of forest ecology.

The effects of wildfire on landscapes vary depending on fire regime (type of fire, intensity, season, frequency, duration) and on the community burned. Although burned areas provide a general increase in soil nutrients such as mineralizable nitrogen (Norton and Firestone 1996; Choromanska and DeLuca 2001) and provide opened habitats with less competition, they are not uniform and present a variety of postfire environments (Segura et al. 1998; Laterra and Solbrig 2001). Because of its propensity to benefit from mineral-soil seedbeds (Harrington and Kelsey 1979) and open habitats, *Pinus ponderosa* Dougl. ex Laws. (ponderosa pine) has long been considered a species well adapted to fire (Vlamis et al. 1955; Weaver 1967, 1974). However, less attention has been focused on how heterogeneity of postfire environments influences ponderosa pine regeneration, especially during the early stages of seedling establishment.

The objective of this study was to examine the effects of postfire environmental conditions on ponderosa pine regeneration. The spatial distribution of the occurrence and survival of ponderosa pine seedlings after fire was analyzed and correlated with measured postfire environmental conditions. These relationships were explored at two different spatial scales in the field: (1) at the plot level (2 m × 6 m plots along transects) to assess the spatial relationship of successful regeneration across a mosaic of conditions generated by a large fire and (2) at the quadrat level (0.2 m × 0.2 m quadrats) to characterize the influence of environmental conditions immediately around each seedling on regeneration success.

Materials and methods

Study area

The study area is located in the south-central Black Hills of South Dakota on the western section of the limestone plateau in Black Hills National Forest. The elevation varies from 1800 to 2200 m. The climate is continental, with an average annual precipitation of approximately 400 mm (Driscoll et al. 2000), predominantly occurring from April to July. Mean annual temperature is 9.0 °C, with a July mean of 17.2 °C and a January mean of 2.1 °C (Shepperd and Battaglia 2002). The Palmer Drought Severity Index (Palmer 1965) is 0.44 on average, with driest values in June and July. The vegetation in the Black Hills is mainly *Pinus ponderosa* forests, with *Populus tremuloides*, *Quercus macrocarpa,* and *Picea glauca* groves.

The Jasper Fire occurred in August and September 2000, burning 34 000 ha dominated by ponderosa pine forests. Within the burned-area perimeter, it created a mosaic of burned and unburned patches, with different severities of canopy- and ground-burn conditions. Field studies were conducted during the summer of 2002 within the Jasper fire area. January through August 2002 was drier than the average respective periods between 1895 and 2001. July 2002 was drier than 70% of those years (Palmer Drought Severity Index data collected from the Rapid City Weather Service, South Dakota).

Experimental design

To quantify the natural distributions of seedlings, seedling survival, and environmental variables in the mosaic of burn conditions created by the Jasper fire, 20 transects crossing 10 severely burned patches of different sizes (two transects per burned patch) were sampled. Transects in small, burned patches were installed perpendicular to and crossing the middle of the longest side of the patch to minimize the influence of sideways seed sources. Transects began 36 m within the unburned area (–36 m) and extended to the center of the burned patches (distance depended on the size of the burned patch). Tree crowns in the unburned areas were intact and cone bearing; understory vegetation in these areas was at least 75% unburned. The unburned–burned interface corresponded to 0 m on the transects; it was positioned so that no seed sources were present within the burned patch. Total transect length varied from 66 to 288 m.

Rectangular plots, measuring 2 m × 6 m, were installed at 6-m intervals along each transect, with the longest side of each plot perpendicular to the transect line. A total of 423 plots were installed along the transects in the study area.

Quadrats, measuring 0.2 m × 0.2 m, were sampled around each ponderosa pine seedling within each of the 2 m × 6 m plots along the transects to examine the influence of environmental factors on seedling occurrence at the microscale (N = 378). In addition, microenvironmental conditions at the quadrat scale within the plots were characterized with five 0.2 m × 0.2 m quadrats randomly located within every third plot (–36, –18, 0, 18 m, etc.). A total of 685 random quadrats were measured. None of the randomly located quadrats contained ponderosa pine seedlings. A comparison of the environmental conditions immediately around seedlings ("occupied" quadrats) with the conditions in the randomly located quadrats ("empty" quadrats) in the same plots will reveal whether the seedlings are located preferentially in particular conditions or randomly dispersed within the plots.

Stand-scale characterization of the forest canopy was achieved with 18 m × 18 m plots around every third 2 m × 6 m plot (–36, –18, 0, 18 m, etc.) along the transects.

Data collection

Plot scale (2 m × 6 m)

Newly germinated ponderosa pine seedlings were counted in June and July 2002. Seedling density is expressed as the number of seedlings per hectare. Surviving seedlings in September were counted in each plot along the transects.

Ground cover within each 2 m × 6 m plot was measured using estimated percentages of unburned soil surface (USoil), unburned needle litter on unburned soil surface (ULitt), scorched needle litter on burned (i.e., blackened) mineral soil (SLitt), exposed burned mineral soil (BSoil), burned needle litter on burned mineral soil (BLitt), Cryptogam (i.e., bryophytes in this study) (CRY), rock (>5 cm diameter) (RCK), gravel (<5 cm diameter) (GRV), coarse woody debris (CWD), and the total cover of understory vegetation (UndVeg) (Table 1). The total cover of these variables equaled 100% of the ground cover seen from above, excluding the overstory canopy.

Vegetation covers were classified into five strata based on plant height (0–10 cm, 10–50 cm, 50–200 cm, 2–10 m, and > 10 m tall). Percent cover and burn status were recorded for each stratum. The “burned” or “unburned” status of the trees was established in relation to the percentage of the foliar canopy consumed in the fire (>50% or <50%, respectively). In addition to vegetation strata, total understory plus overstory vegetation cover (TCov) was also recorded. Because of overlapping strata, the total cover of these different strata could be greater than 100%. All trees greater than 3 m tall and with greater than 7 cm DBH were counted (TreeDen), and their diameter and height were measured for each plot. The basal area (BArea) per plot was calculated by summing the basal area of each tree in the plot.

For each plot, we also measured plant species richness (Richn), slope (SLP), aspect (ASP), and in June and July 2002, volumetric soil moisture (SoilM) for the top 12 cm of soil and soil temperature (SoilT) at 10 cm depth. A type T thermocouple (Omega, Stamford, Connecticut) was used to measure soil temperature, and time domain reflectometry (Hydrosense, Campbell Scientific, Logan, Utah) was used to measure soil volumetric water content.

Quadrat scale (0.2 m × 0.2 m)

Ground cover conditions in each of the occupied and random (empty) 0.2 m × 0.2 m quadrats were recorded according to the classification used at the plot level (Table 1).

Stand scale (18 m × 18 m)

Forest canopy conditions were assessed by estimating the percentage of the foliated crown of each tree that was consumed by the fire. Five categories of fire severity were distinguished: unburned, 10%–40% burned, 40%–60% burned, 60%–90% burned, and totally burned crown. Trees were also categorized by height (greater than or less than 10 m) and DBH (greater than or less than 20 cm).

Greenhouse study

To complement the field study, a greenhouse experiment was conducted to test the influence of scorched litter on top of burned mineral soil on soil temperature and moisture. Ten 13 cm × 13 cm × 15 cm pots were filled with burned mineral soil collected from the field site; the surface of half the pots was left bare, while the others were covered with scorched needles. All pots were insulated from side heat sources by 2.5 cm thick polystyrene boards. The soils were brought to field capacity (day 1), and water was withheld for 4 weeks. During the drying period, soil temperature 1 cm below the soil surface was measured continuously (Tidbit logger, Onset Corp, Bourne, Massachusetts) and soil moisture in the top 12 cm of soil (Hydrosense, Campbell Scientific, Logan, Utah) was recorded every other day in each pot.

Data analyses

Statistical methods

Standard regressions were created using SPSS (SPSS Inc., Chicago, Illinois) and Statistica (StatSoft France 1997).

Partial least squares (PLS) regression analysis was used to test the influence of environmental variables on regeneration success. This technique, first developed by Wold (1966), combines features from principal component analysis and multiple regression. Unlike ordinary least squares (OLS) regression, the PLS regression does not assume that the explanatory variables are independent of each other. The goal of PLS regressions is to describe the common structure of an explanatory (or predictor) variable matrix X and a dependent variable matrix Y, using principal components of X that are also relevant for Y. The components are first calculated to explain as much as possible of the covariance between X and Y. Then, regressions are performed using as many components as are significant; the significance of components is tested by permutation tests. The prediction of Y by the predictor variables X_i is optimal for the number of significant components. If only one component is significant, a PLS regression is equivalent to a regression on the first coordinate of a co-inertia analysis. The PLS regressions were performed using ADE-4 (Thioulouse et al. 1997).

Dissimilarity analyses were performed according to Dyer (1978). The multiresponse permutation procedure based on Euclidian distance was performed according to Mielke and Berry (2001).

Plot scale (2 m × 6 m)

Nineteen of 20 transects were used for the analyses. The 20th transect was excluded from the data analyses and interpretations because of the low representativeness of two plots along this transect that contained more than 48 000 seedlings/ha (55 times the average seedling density in any other plot) yet represented together only 0.5% of the total number of plots sampled (Fig. 1). The two plots were located at the unburned–burned edge and were likely a result of a high seed producing tree in close proximity. Data collected along the 20th transect displayed the same spatial and environmental patterns that related to seedling distribution as data collected on other transects. However, inclusion of these data would produce unrealistic quantitative results that would mask the variability in conditions and seedling density along the other transects.

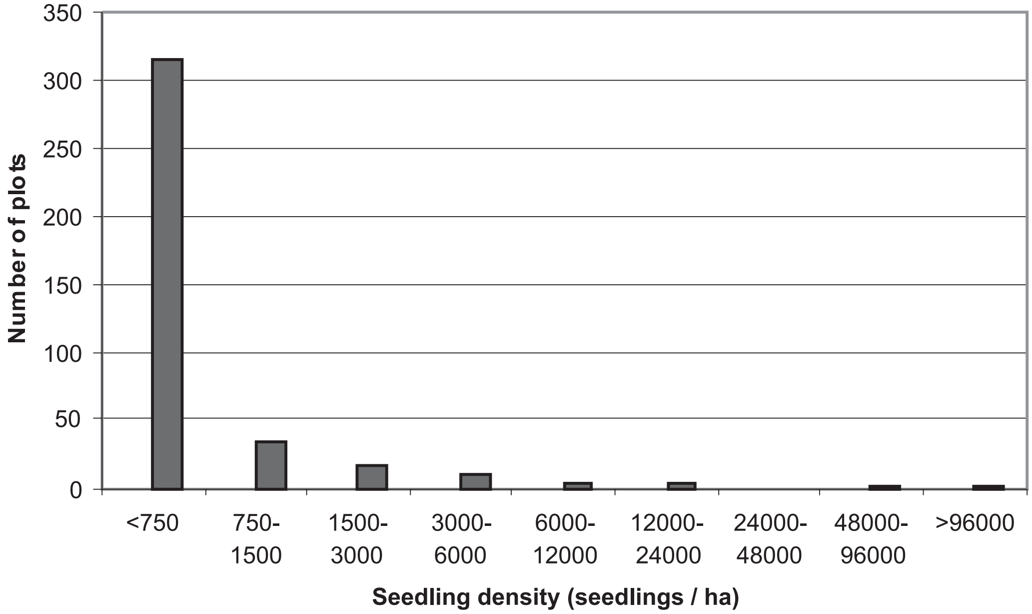
Plots within transects were found to be relatively uncorrelated (serial r = 0.19) (Proc Mixed, SAS Institute Inc., Cary, North Carolina). A total of 382 plots along the 19 transects located from –36 to 102 m from the unburned edge were used in the analyses. Plots in the burned patches located farther than 102 m from the unburned edge (41 plots) were only used as observations because of low sample size.

The similarity of transects within patches and the similarity of transects between patches were calculated using a percent similarity index based on two variables: seedling density and the calculated variable relative germination success (see definition below) per plot. When dissimilarity analyses (Dyer 1978) were used, the similarity values were not significantly different after 10 000 permutations (P = 0.270 when using seedling density and P = 0.120 when using relative germination success), suggesting that transects were equally dissimi-

Table 1. Definitions and ecological significance for each of the 28 variables measured along transects. Plots refer to the 2 m × 6 m scale and the quadrats are 0.2 m × 0.2 m scale.

Variable label	Level measured	Variable definition	Ecological significance
Ground covers			
USoil	Plot; quadrat	Bare unburned soil surface	Indicates low burn or unburned severity on the ground, potentially less nutrients than in burn
ULitt	Plot; quadrat	Unburned compacted litter on top of unburned soil surface	Indicates unburned conditions and potential reduction of seedling emergence by shading and physical obstruction
SLitt	Plot; quadrat	Scorched litter on top of burned mineral soil (scorched needles that fell on burned soil after fire)	Indicates high burn severity on the ground and moderate in the canopy, potential protection for seeds; may also prevent strong soil erosion
BSoil	Plot; quadrat	Bare burned mineral soil	Indicates high fire severity on the ground
BLitt	Plot; quadrat	Burned litter (needles or leaves are burned but not totally consumed)	Indicates high fire severity on the ground
CRY	Plot; quadrat	Cryptogams = bryophytes	Indicates moisture in upper layers of the soil; may constitute a protection for seeds
RCK	Plot; quadrat	Rock (>5 cm diameter)	Linked to stress tolerance of species
GRV	Plot; quadrat	Gravel (rock < 5 cm diameter)	Linked to stress tolerance of species
CWD	Plot; quadrat	Coarse woody debris (burned or unburned)	Can change soil moisture and temperature by shading; constitutes a protection against predation or an obstruction to seedling emergence; change nutrient levels through wood decomposition
UndVeg	Plot; quadrat	Total cover of understory vegetation	Indicates competition pressure
Vegetation covers			
E	Plot	Vegetation <10 cm high	Herbaceous species or small woody species
D	Plot	Vegetation 10–50 cm high	Tall herbaceous or woody species
C	Plot	Unburned vegetation 50–100 cm high	Indication of unburned area or very prolific postfire species
BShr	Plot	Burned shrubs 50–100 cm tall (stems are still visible and not totally consumed)	Indicates passage of fire and potentiality for sprouting processes after fire
UTr < 10	Plot	Unburned trees <10 m tall (at least 50% of needles are not consumed)	Seed sources, shade producers
BTr < 10	Plot	Burned trees <10 m (more than 50% of the needles are totally consumed)	Burned trees (no longer seed source)
UTr > 10	Plot	Unburned trees >10 m tall (at least 50% of needles are not consumed)	Seed sources, shade producers
BTr > 10	Plot	Burned trees >10 m (more than 50% of the needles are totally consumed)	Burned trees (no longer seed source)
TCov	Plot	Total cover of vegetation	Indicates competition pressure
Others			
TreeDen	Plot	Tree density	Indicates shading and potential competition
MeanDm	Plot	Average DBH per tree in a plot	Affects seed production, related to fire resistance
MeanHg	Plot	Average height of trees in a plot	Affects seed dispersal, related to fire resistance
BArea	Plot	Basal area (surface occupied by trees per surface area)	Indicates competition intensity, particularly when trees are unburned
Richn	Plot	Floristic richness (number of species per surface unit)	Index of floristic diversity; can be related to competition pressure
SoilM	Plot	Soil moisture in the upper 12 cm of soil	Influence seed germination and seedling survival
SoilT	Plot	Soil temperature at 10 cm below ground level	Influence seed germination and seedling survival
SLP	Plot	Slope	Influences seedling establishment through erosion processes; also linked to micro-climatic conditions (sunshine, temperature, frost, water regime)
ASP	Plot	Aspect (1, north; 2, northeast or northwest; 3, east or west; 4, southeast or southwest; 5, south)	Related to microclimatic conditions (sunshine, temperature, frost, water regime)

Fig. 1. Distribution of sampled plots by seedling density class for all 20 transects.



lar within and between patches. Consequently, the transects were considered as independent within a patch and were used individually for statistical analyses.

The distribution of ponderosa pine seedlings along transects was analyzed using nonlinear regressions. Relationships were tested between average seedling density in June 2002 and distance from the unburned areas.

To separate the effect of environmental conditions from seed availability on the observed seedling distribution along the transects, a new variable was calculated for each plot from modeled seed availability estimates and measured seedling densities. This variable, called relative germination success (rel. germ. success), was calculated for each plot:

$$\text{rel. germ. success} = \frac{\text{measured seedling density}}{\text{modeled seed availability}} \times 100$$

Because the modeled seed availability does not accurately predict the exact number of seeds distributed to each plot during the study, it was used only to correct for predictable differential seed inputs along the transects. Seed availability for each plot was modeled using the seed dispersal curve for ponderosa pine from McCaughey et al. (1986) and data on average seed production for this species in the Black Hills from Rumble and Anderson (1996). The seed dispersal equation used was

$$[1] \qquad y = 86800\ \mathrm{e}^{-0.026x}$$

where y is the seed availability and x is the distance, in metres, from the seed source. To estimate the theoretical seed availability on each of the 423 plots, eq. 1 was applied assuming that there were two main seed sources for each plot from the two seed sources in closest proximity (i.e., opposite sides of the burned patch). For each plot, the seed availability was calculated to be

$$[2] \qquad Y = yA + yB = 86800\ \mathrm{e}^{-0.026xA} + 86800\ \mathrm{e}^{-0.026xB}$$

where xA and xB were the distances to the first and to the second seed sources, and yA and yB were the number of seeds coming from the first and from the second seed sources. Two assumptions were made: (1) secondary dispersal of seed on the ground was minor, as shown for ponderosa pine by Vander Wall and Joyner (1997), and (2) predation was uniform throughout the study area, as suggested from an independent study with caged and uncaged plots (Bonnet and Schoettle unpublished data). Relative germination success standardizes the data to reduce the influence of predictable seed availability on seedling density, within the stated assumptions. In addition to analyzing measured seedling densities, the calculated variable of relative germination success was also analyzed.

To test the influence of plot-level environmental variables on seedling presence in June, a PLS regression was performed between the 28 quantitative environmental variables per plot (Table 1) as explanatory variables and the relative germination success as the dependent variable.

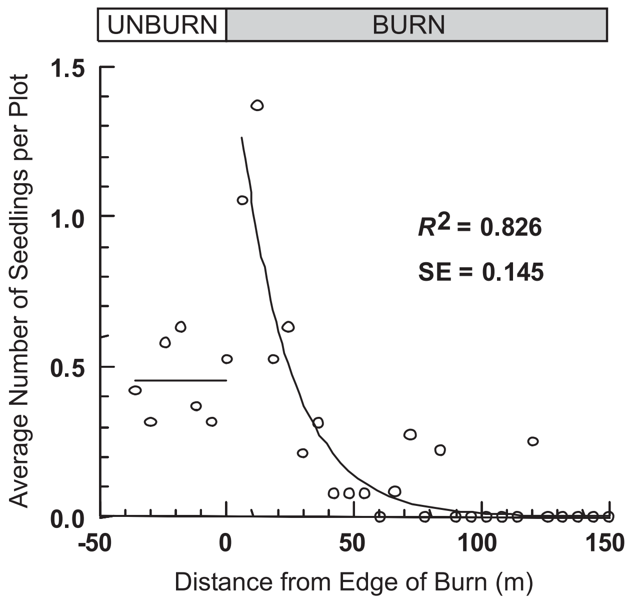
To determine the conditions favorable for seedling survival, a second PLS regression was performed between the percentage of surviving seedlings per plot and the 28 environmental conditions (Table 1), on the subset of 80 plots where seedlings were present in June and July.

Quadrat scale (0.2 m × 0.2 m)

To detect whether seedlings were preferentially located in specific microenvironments, microconditions in quadrats containing seedlings in June were compared with microconditions in random quadrats within the same 2 m × 6 m plots using a multiresponse permutation procedure based on Euclidian distance for unreplicated randomized block designs (Mielke and Berry 2001). Seedling versus random quadrat was the grouping variable, and the categorical blocking variable was the different distances along transects (–36, –18, 0, 18, 36, 54, 72 m).

Multiresponse permutation procedure based on Euclidian distance for one-variable designs (Mielke and Berry 2001)

Fig. 2. Mean number of seedlings per 2 m × 6 m plot in June 2002 as a function of distance from the edge of the forest with unburned crowns. Each point is the mean of plots at that position for the 19 transects.



was applied to compare microconditions where seedlings survived (82 quadrats) with microconditions where seedlings died (296 quadrats). The grouping variable was surviving seedling versus dead seedlings.

Stand scale (18 m × 18 m)

To test the influence of stand-level environmental variables on seedling presence in the 2 m × 6 m plots, a third PLS regression was performed between the relative germination success in June and the overstory stand canopy characteristics using the set of 18 m × 18 m plots and the tree categories recorded inside these plots.

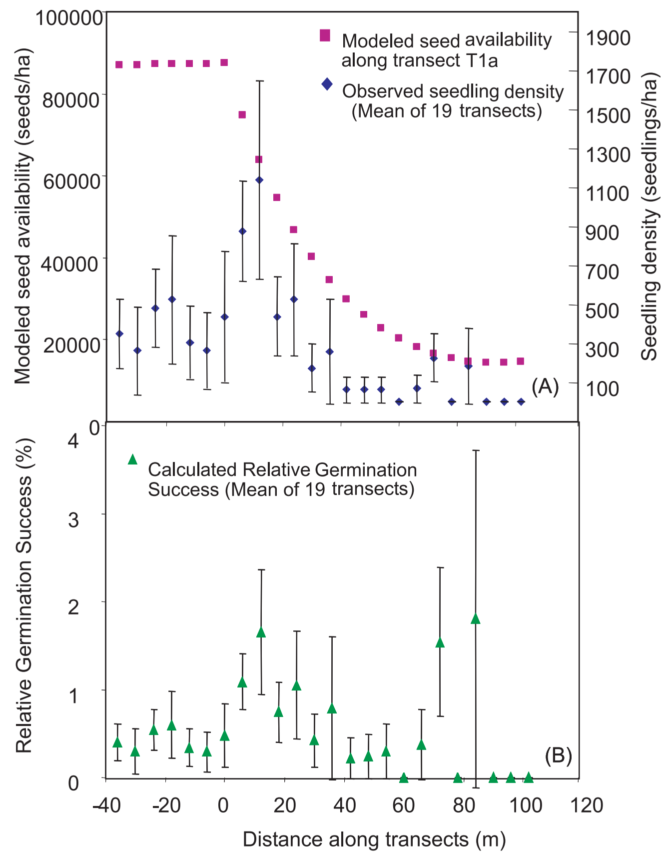
Results

Seedling distribution and relative germination success at the plot level along transects

Ponderosa pine seedlings were irregularly distributed along transects that traverse the mosaic of burned and unburned areas within the perimeter of the Jasper Fire. Consistent with past studies, greater seedling densities were found in the burned compared with the unburned areas. The average seedling density was correlated with the distance along the total length of the transects (piecewise regression, r^2 = 0.826, Fig. 2). The distribution of seedlings was flat within the unburned canopy areas (0.451 seedlings/plot = 376 seedlings/ha). Seedling density increased at the edge of the burned patches, with peaks at 6 and 12 m, and decreased exponentially toward the center of the burned patch ($y = 1.706\ e^{-0.0502X}$). Seedlings were still present at 72, 84, and 120 m from the edge. Seedlings were observed up to 180 m from an edge.

If the seedling establishment success was only related to seed availability, the pattern of seedling establishment along transects would follow the theoretical pattern of seed dispersal. The differences observed between the pattern of modeled seed availability and the pattern of observed seedling occurrence (Fig. 3A) can be interpreted to reflect variations in relative seed germination success attributable to variations in environmental conditions (Fig. 3B). Greater regeneration success was observed inside the burned patch near the unburned edge and at isolated locations within the burned patch than in unburned areas, which is different from what would be expected from seed availability alone.

Fig. 3. Spatial distributions of observed seedling density, modeled seed availability, and the calculated variable relative germination success. (A) Observed seedling density (±SE) and an example of the modeled seed availability along one transect (T1a) for each plot receiving seeds from the two opposite sources along transects (see text) and (B) Calculated Relative Germination Success in relation to distance along transects.



Influence of quantitative environmental variables at the plot level on relative germination success and seedling survival

The PLS regression performed between relative germination success and the 28 variables (Table 1) gave a significant first component (P = 0.020; Table 2). This component corresponds to a gradient of environmental conditions defined on the positive side by the abundance of scorched litter on burned mineral soil and on the negative side by high understory cover (Table 2). Relative germination success was highly positively correlated with scorched litter on burned mineral soil (r = 0.136), high cryptogam cover (r = 0.070), and high cover of tall trees with greater than 50% of their crowns burned (r = 0.040). Relative germination success was negatively correlated with understory plant cover (r = –0.061),

Table 2. Partial least squares (PLS) regression coefficients (first component) of 28 environmental variables on relative germination success per 2 m × 6 m plot along the transects.

Variables	$r < 0$	$r > 0$
UndVeg	–0.060 556	
E	–0.059 986	
BSoil	–0.040 192	
TCov	–0.038 834	
GRV	–0.037 738	
Richn	–0.034 348	
ULitt	–0.032 090	
BLitt	–0.027 166	
SoilT	–0.022 704	
SLP	–0.013 045	
C	–0.010 097	
USoil	–0.009 769	
CWD	–0.003 165	
TreeDen	–0.001 856	
UTr < 10	–0.001 275	
D		0.003 926
RCK		0.005 312
SoilM		0.006 532
BShr		0.006 965
UTr > 10		0.009 727
ASP		0.018 929
BArea		0.019 729
MeanDm		0.021 273
MeanHg		0.027 438
BTr < 10		0.030 945
BTr > 10		0.039 301
CRY		0.069 736
SLitt		0.136 370

Note: See Table 1 for definitions of variable acronyms.

cover of plants shorter than 10 cm high (r = –0.060), and exposed burned mineral soil (r = –0.040). It was also negatively correlated with total understory plus overstory cover, gravel, high floristic richness, and unburned litter on unburned soil.

The PLS regression performed between relative germination success and overstory stand characteristics had no significant component (P = 0.330), which indicates that the status of the canopy as classified (height, diameter, and percentage of canopy burned at the 18 m × 18 m spatial scale) had no influence on relative germination success. This confirms that predictable seed sources and dispersal were not primordial factors in explaining the spatial pattern of relative germination success.

Finally, the PLS regression performed between the percentage of seedlings that survived until September and the 28 environmental variables within the plots where seedlings occurred was not significant (P = 0.590). This indicates that environmental conditions at the 2 m × 6 m plot scale do not explain seedling survival.

Influence of microenvironmental conditions on seedling distribution

All along the transects, the average microenvironmental conditions immediately around seedlings were significantly different from the microenvironmental conditions within random quadrats located in the same 2 m × 6 m plots (P = 0.016). Therefore, within a 2 m × 6 m plot, where seed availability would be expected to be uniform, seedlings were present in distinct microenvironments and absent from others. At all distances along the transects (Table 3), seedlings were predominantly located in microconditions characterized by high percentage of scorched litter on top of burned mineral soil. Microenvironmental conditions within the random quadrats varied with the distance along transects (Table 3) and, as expected, were characterized by a high percentage of unburned characteristics at the beginning of the transects, and a high percentage of burned soil and burned litter at the end of the transects. The distances 0 and 18 m were characterized by a high percentage of scorched litter on burned mineral soil and were also areas where relative germination success was high (Fig. 3B).

Influence of microenvironmental conditions on seedling survival

At the quadrat scale (0.2 m × 0.2 m), in contrast with the plot scale (2 m × 6 m), environmental conditions influenced seedling survival. The microenvironmental conditions around surviving seedlings were significantly dissimilar from the microenvironmental conditions around seedlings that died (P < 0.001). Quadrats where seedlings survived had a lower percentage of vegetation cover than quadrats where seedlings died (5.3% vs. 11.1%, respectively) (Table 4).

Effects of scorched litter on soil temperature and soil moisture

Scorched needles on the surface of burned mineral soil, which are conditions most favorable for seedling occurrence, reduced soil temperature variation during the day. While the mean soil temperature was very similar with or without scorched needles (16.9 and 16.7 °C, respectively), the variations in soil temperature were attenuated by scorched needles compared with the bare soil (Fig. 4A). The presence of scorched needles on the soil surface also affected soil drying (Fig. 4B). For burned mineral soil not covered by scorched needles, the soils dropped below the saturation threshold of 40% volumetric soil water content (VWC) after 7 days of water-withholding compared with twice as long (14 days) for the soils covered with scorched needles.

Discussion

The aim of this study was to identify environmental conditions contributing to the distribution of successful regeneration of ponderosa pine after a fire. The distribution of ponderosa pine seedlings throughout the unburned and burned areas was explained not only by the location of seed sources but also by the distribution of macro- and micro-environmental conditions within the burn perimeter. The highest seedling densities were found within the burned patches near the edges of the unburned forest canopy and densities decreased with increasing distance away from the edge both into the unburned forest and into the burned patch. As expected in response to the influence of seed sources, seedling density exponentially decreased from the edge toward the center of burned patches. The high number of seedlings close to the

Table 3. Average percent ground cover (SE) for random (empty) and seedling-occupied quadrats (0.2 m × 0.2 m) at each of seven distances along the transects.

		Distance along transects (m)						
Ground cover	Quadrat type	–36	–18	0	18	36	54	72
SLitt	Occupied	53.3 (5.3)	57.2 (2.0)	48.4 (4.2)	55.9 (8.8)	49.8 (6.2)	83.0 (—)	36.7 (14.5)
SLitt	Empty	16.4 (2.5)	23.9 (2.8)	16.9 (2.7)	48.9 (2.9)	20.5 (2.7)	19.6 (2.8)	17.4 (2.9)
UndVeg	Occupied	3.1 (1.1)	10.3 (1.0)	6.8 (1.2)	10.5 (4.8)	1.2 (1.0)	2.0 (—)	6.7 (2.2)
UndVeg	Empty	22.4 (2.2)	17.9 (1.9)	23.6 (2.6)	14.7 (1.8)	16.1 (2.1)	17.0 (2.6)	14.9 (2.3)
BSoil	Occupied	13.8 (4.1)	15.0 (1.4)	15.1 (3.7)	19.8 (9.9)	43.0 (4.9)	5.0 (—)	23.3 (4.4)
BSoil	Empty	8.7 (1.9)	10.2 (1.9)	5.4 (1.4)	9.6 (1.5)	29.5 (3.0)	36.3 (3.7)	44.8 (3.7)
USoil	Occupied	0.6 (0.4)	0.0 (0)	2.7 (0.8)	0.0 (0)	0.0 (0)	0.0 (—)	0.0 (0)
USoil	Empty	4.3 (0.8)	2.2 (0.6)	2.3 (0.6)	0.1 (0.1)	0.8 (0.3)	1.2 (0.7)	0.0 (0)
CRY	Occupied	4.4 (2.9)	1.0 (0.3)	2.5 (0.7)	1.8 (1.0)	0.0 (0)	0.0 (—)	0.0 (0)
CRY	Empty	0.4 (0.2)	0.7 (0.3)	0.5 (0.2)	0.4 (0.2)	0.9 (0.5)	0.3 (0.2)	0.0 (0)
BLitt	Occupied	7.8 (3.3)	11.8 (1.2)	10.1 (1.4)	4.7 (1.3)	6.0 (1.0)	5.0 (—)	28.3 (15.9)
BLitt	Empty	2.9 (0.7)	4.0 (0.9)	3.1 (0.8)	6.6 (1.2)	11.7 (1.8)	14.6 (2.3)	10.4 (1.7)
ULitt	Occupied	1.3 (1.0)	0.0 (0)	2.1 (1.5)	0.0 (0)	0.0 (0)	0.0 (—)	0.0 (0)
ULitt	Empty	33.0 (3.0)	29.1 (3.2)	37.3 (3.3)	6.0 (1.9)	10.3 (2.4)	0.7 (0.4)	0.0 (0)
CWD	Occupied	12.6 (2.3)	4.7 (0.5)	11.6 (2.3)	6.3 (2.3)	0.0 (0)	5.0 (—)	5.0 (2.9)
CWD	Empty	9.0 (1.0)	9.5 (1.1)	8.5 (1.1)	8.5 (1.1)	6.3 (0.7)	5.5 (1.0)	8.3 (1.9)
RCK	Occupied	1.1 (0.6)	0.0 (0)	0.6 (0.2)	0.0 (0)	0.0 (0)	0.0 (—)	0.0 (0)
RCK	Empty	1.5 (0.6)	2.0 (0.6)	1.4 (0.5)	4.4 (0.6)	1.6 (0.7)	0.7 (0.4)	1.8 (0.8)
GRV	Occupied	2.1 (1.8)	0.0 (0)	0.3 (0.2)	1.0 (0.5)	0.0 (0)	0.0 (—)	0.0 (0)
GRV	Empty	1.4 (0.5)	0.5 (0.2)	1.1 (0.3)	0.8 (0.2)	2.1 (0.5)	4.2 (1.2)	2.4 (0.5)
Sample size	Occupied	8	86	18	10	5	1	3
Sample size	Empty	115	110	110	110	95	80	65

Note: See Table 1 for definitions of variable acronyms.

Table 4. Average percent ground cover (SE) for quadrats (0.2 m × 0.2 m) containing seedlings that died (N = 296) and for quadrats containing seedlings that were still alive (N = 82) at the end of their first growing season.

	Ground cover									
Seedling status	SLitt	UndVeg	BSoil	USoil	CRY	BLitt	ULitt	CWD	RCK	GRV
Dead	52.6 (1.1)	11.1 (0.6)	14.0 (0.9)	0.2 (0.2)	1.4 (0.2)	12.5 (0.7)	0.8 (0.4)	6.8 (0.4)	0.3 (0.1)	0.3 (0.1)
Surviving	55.1 (2.4)	5.3 (0.6)	13.4 (1.6)	0.6 (0.4)	1.8 (0.4)	9.2 (1.2)	0.9 (0.7)	10.3 (0.9)	2.1 (0.6)	1.5 (0.4)

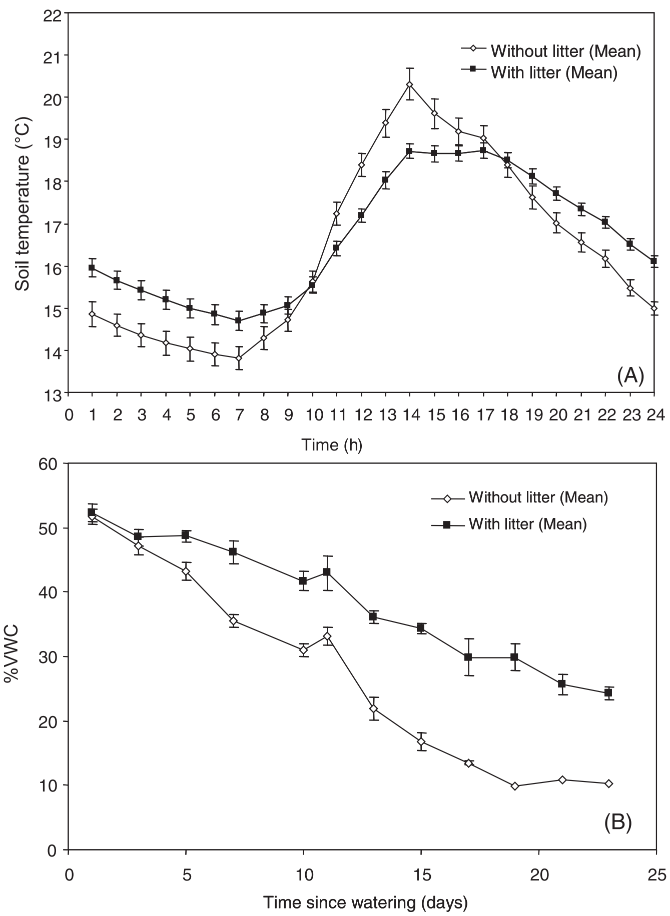
Note: See Table 1 for definitions of ground-cover acronyms.

unburned canopy edge but inside the burned patches was explained by the coincidence of both high seed availability and environmental conditions conducive to seedling-establishment success.

Ground conditions contributed to patterns of seedling occurrence at macro- and micro-scales, while seedling survival was only explained by micro ground conditions. Variables that favored the presence of ponderosa pine seedlings, within the Jasper fire, were strongly related to the abundance of scorched needles on top of burned mineral soil, characteristic of edge areas. Trees producing scorched needles may also have been an unpredicted source of seeds. However, the quadrat data reveal that seedlings were not randomly located within the plots even in the vicinity of scorched trees. If seed availability is assumed to be uniform within a 2 m × 6 m plot, microconditions on the ground must be responsible for seedlings being present in distinct microenvironments and absent from others. Therefore, the spatial pattern of micro safe sites contributes to the pattern of seedling success.

Scorched needles that have fallen onto blackened mineral soil, after a fire, serve as a mulch to mitigate subsurface soil temperature extremes that affect seed and seedling viability (Viro 1974; Amacher et al. 2001). In addition, the presence of scorched needles on the soil surface increases soil moisture retention. This is especially important within burned soils, where the clay particles tend to be leached out towards lower soil layers (Giovannini 1997; Bonnet et al. 2002) consequently reducing soil water-holding capacity. Because ger-

Fig. 4. Effect of scorched litter on the surface of burned soil on soil temperature and moisture during a period of soil drying. (A) Time course of soil temperature (±SE) at 1 cm depth in burned soil with or without scorched litter on top (N = 10 per



mination of ponderosa pine seeds is substantially reduced by low soil moisture (Oliver and Ryker 1990) and 2002 was an exceptionally dry summer in the Black Hills, the preference for a seedbed characterized by scorched litter on burned soil was particularly significant in this study. The presence of litter on the surface of the burned soil surface may also have provided mechanical protection for seeds by restricting secondary movement.

The abundance of mosses, lichens, and trees with burned crowns was also highly correlated with seedling occurrence, whereas high herbaceous and total vegetation covers negatively affected seedling incidence at the plot level (2 m × 6 m). Evans and Johansen (1999) demonstrated the enhancement of seed germination and seedling survivorship through mechanical protection by microbiotic crusts. The protection of seeds by lichen crusts is particularly effective in extreme systems such as xeric (Houle and Phillips 1989) or high-elevation habitats (Moir et al. 1999). These crusts are very sensitive to fire (Houle and Phillips 1989), and their survival in micropatches contributes to the regeneration success of ponderosa pine.

The favorable effects of abundant trees with burned crowns at the plot level on seedling incidence may be related to intermediate shade conditions provided by the standing tree skeletons. (The trees with burned crowns may also provide the source of scorched litter to cover the blackened burned soil to generate suitable ground conditions for seedling establishment.) Oliver and Ryker (1990) support the idea that ponderosa pine seedlings need intermediate shade conditions for good establishment. The combined effects of abundant burned trees and scorched litter on the ground were predictive of seedling occurrence at the plot level. However, at the stand scale (18 m × 18 m) the condition of the canopy did not, by itself, explain the relative germination success for ponderosa pine.

Finally, relative germination success suffered in areas with high herbaceous cover and floristic richness at plot and quadrat levels. While obvious in the unburned areas, apparent plant competition affected regeneration in the burned patches as well. Though floristic richness was usually low within burned patches, covers of ruderal species sporadically reached up to 75% (as for *Lactuca serriola*) in these patches.

The survival of seedlings was explained at the microscale by low competition pressure. Competition between ponderosa pine seedlings and herbaceous species is an important factor affecting seedling establishment (Elliott and White 1987). Within the conditions favorable for seedling occurrence, micropatches with high vegetation covers were correlated with high seedling mortality. Hutchings et al. (2003) demonstrated that population and community structure resulting from plant interaction and competition are highly influenced by patterns of nutrient supply, and that soil heterogeneity is therefore a major component in explaining plant distribution. Microenvironments characterized by abundant scorched litter and low vegetation cover are "safe sites" for ponderosa pine seedlings.

This study demonstrates that ponderosa pine regeneration is most successful in specific macro- and micro-environmental conditions. Within burned patches, the spatial pattern of regeneration appears to reflect seed availability; however, upon closer inspection, it was shown that this pattern is a result of both the distributions of predictable seed availability and safe sites. Canopy condition alone, reflecting seed availability, at the stand level was not well correlated with regeneration success. However, canopy condition in combination with ground conditions explained patterns of regeneration at the plot level (2 m × 6 m) and quadrat level (0.2 m × 0.2 m). Only at the finer level of the quadrat could the environmental factors explain seedling survival. Areas with high competitive pressure restricted regeneration in the undisturbed forest and reduced seedling survival in the burned areas. Safe sites were characterized, in part, by the presence of scorched needle litter on blackened mineral soil and low vegetation cover. The description of environmental conditions that favor and discourage ponderosa pine regeneration will improve our understanding of how heterogeneity of environments within burned areas contributes to the heterogeneity of the future forested landscape.

Acknowledgements

We are grateful to Rudy King for help with nonlinear regression, Carrie Berger for help in the field, and Mike Battaglia for reviewing an earlier version of this manuscript. We thank

Christopher Carcaillet and the Associate Editor and reviewers for their helpful comments. This work was financially supported by National Fire Plan funds awarded to the Black Hills National Forest and transferred to the Rocky Mountain Research Station as part of the Jasper Fire Monitoring Project.

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