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Abstract

Restoration of ponderosa pine ecosystems results in altered stand structure, potentially affecting microclimatic conditions and habitat quality for forest organisms. This research focuses on microclimatic changes resulting from forest and landscape structural alterations caused by restoration treatments in southwestern ponderosa pine forests. Three microclimate variableslight intensity, air temperature, and vapor pressure deficit (VPD)-were monitored over two field seasons. Differences in microclimate between the treated forest and the surrounding untreated forest were measured, and microclimatic gradients across the structural edge between these two forest types were quantified. Restoration treatments increased sunlight penetration to the forest floor but did not significantly impact ambient air temperature or VPD. Mean values for air temperature and VPD did not differ significantly between treatments, although temperature and vapor pressure deficit did exhibit a trend in the morning; both variables were higher at the structural edge and in the treated forest during morning hours. Significant edge gradients were detected for air temperature and VPD in the morning and evening, increasing from

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the structural edge into the untreated forest. Our results show that microclimatic effects of these restoration treatments are generally modest, but the changes are more prominent at specific locations and during certain times of day. Because even modest changes in microclimate have the potential to impact a range of key ecological processes, microclimatic effects should be considered when forest restoration treatments at the landscape scale are being planned and implemented.

Key words: ecological restoration, edge effects, landscape ecology, light intensity, microclimate, *Pinus ponderosa*, ponderosa pine, relative humidity, temperature, vapor pressure deficit.

Introduction

Present day *Pinus ponderosa* (ponderosa pine) forests in the southwestern United States support greater tree densities, lower tree growth rates, and reduced herbaceous understory production than did forest conditions that predominated during the past 200 years (Sutherland 1983; Covington & Moore 1994*b*; Covington et al. 1997). Overgrazing, logging, fire suppression, and periodic high recruitment of pine seedlings have resulted in a contemporary forest characterized by dense stands of small-diameter trees (Cooper 1960; Madany & West 1983; Savage et al. 1996). Ecological restoration treatments in ponderosa pine forests of northern Arizona are designed to recreate a forest structure that existed in the late 1800s prior to the interruption of natural disturbance regimes.

During the past five years, efforts have focused on thinning trees and reintroducing low-intensity, highfrequency fire regimes (Covington et al. 1997). These treatments create patches of relatively open forest within a matrix of denser, untreated forest dominated by smallerdiameter trees. These treatments, when applied at the landscape scale, create a shifting patchwork of treated and untreated forest, altering both forest and landscape structure. These patchy landscapes, generated systematically as restoration occurs site by site across large areas, are likely to influence ecological processes and species distributions, especially for organisms sensitive to patch size and edge effects (Quinn & Harrison 1988; Wiens et al. 1993).

Previous research on the ecological effects of ponderosa pine restoration has focused primarily on the response of older trees retained in the treatment areas. Restoration treatment has resulted in increased growth rates and vigor of older trees (Covington & Moore 1994*a*), while stimulating growth of the herbaceous understory (Covington et al. 1997). Belowground abiotic condi-

Microclimatic Changes Induced by Ecological Restoration of Ponderosa Pine Forests in Northern Arizona

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tions, such as elevated soil temperature and moisture, have been observed in treatments (Kaye et al. 1999), but aboveground microclimate has received scant attention. This study, focusing on aboveground microclimate changes resulting from both forest and landscape structural changes, is the first to examine microclimatic changes and gradients associated with ecological restoration in ponderosa pine forest.

A microclimate is the host of climatic variables unique to a specific location at a specific time (Geiger 1966; Oke 1996). It is an important factor influencing forest ecosystem structure and function (Wales 1967), affecting recruitment (Reifsnyder & Lull 1965; Tsubuki & Takizawa 1996) and growth (Kittredge 1948; Brothers 1993), and potentially influencing the fecundity of virtually all taxa (Meffe & Carroll 1994). For this research three aboveground microclimatic variables-light intensity, air temperature, and vapor presure deficit (VPD)-were chosen because of their importance to animal behavior, the subject of related research (Meyer & Sisk 2001). These variables can influence the dispersal of many flying insects (Johnson 1969), rates of larval development (Weiss et al. 1991), and foraging behavior of birds (Wachob 1996). Microclimate also affects plant growth by influencing physiological processes, including photosynthesis, seed germination, and mortality (Hungerford & Babbit 1987; Jones 1992).

Until recently, few studies have examined microclimate at edges between habitats. Microclimatic edge effects are important because they can potentially change the quality of the habitat within seemingly homogeneous habitat patches (Geiger 1966; Wales 1967; Ranney 1977; Kapos 1989; Williams-Linera 1990; Chen et al. 1993; Matlack 1993; Carmago & Kapos 1995; Chen et al. 1995; Jose et al. 1996; Sisk et al. 1997). Microclimatic gradients across forest edges have exhibited increased light intensity, higher air temperature, and lower VPD at or near forest edges, with these influences penetrating 100 m or more into the forest (Ranney 1977; Chen et al. 1995; Sisk et al. 1997). These influences are likely to be ecosystem-specific, and Chen et al. (1999) have cautioned that microclimatic effects caused by forest management may vary due to the unique influences of ecosystem structure, species composition, and characteristic landforms.

We investigated restoration treatment effects on microclimate and measured microclimatic edge effects that may have landscape-scale implications for restoration planning. We monitored light intensity, air temperature, and relative humidity (used in calculating VPD) at one meter above ground level. Our main objectives were to (1) quantify and compare microclimatic variables in restored and untreated forest, (2) compare microclimatic conditions at fixed points, prior to and following treatments, and (3) quantify microclimatic gradients across edges created by ponderosa pine forest restora-

tion. Although forest canopy removal will inevitably increase light penetration to the forest floor, it is not clear how forest restoration treatments affect shading, because thinning changes canopy structure, stem density, and shrub cover in complex ways. Because effects of restoration treatments on microclimate are indirect and complex, direct empirical measurements offer the best approach for addressing the impacts of restoration treatments on understory microclimatic conditions. We observed the extent to which light intensity would increase in response to the removal of overstory biomass and the extent to which air temperature and VPD would respond to increased penetration of sunlight into the forest understory. Based on changes in shading related to tree density, we expected to document gradual, monotonic gradients for all three microclimatic variables across the abrupt edges between treated and untreated forest.

Methods

Study Sites

This research was conducted in northern Arizona at the Mt. Trumbull Resource Conservation Area and the Flagstaff Urban Wildland Interface (FUWI) restoration sites. Mt. Trumbull is located in Grand Canyon-Parashant National Monument, approximately 96 km southwest of Fredonia, Arizona, and at an elevation of approximately 2,000 m (lat 36°24'N, long 112°19'W). FUWI is located 10 km northwest of Flagstaff, Arizona, at approximately 2,100 m elevation (lat 35°22'N, long 111°44'W). Summers in northern Arizona are characterized by warm, dry conditions in June and early July, followed by monsoonal rain from mid-July through September. Mean annual precipitation in the Flagstaff vicinity is 573 mm, with half the precipitation falling as snow and half during summer rains (Schubert 1974; Savage et al. 1996). Mean annual summer air temperature is 17.4°C at FUWI, with approximately 162 clear days per year (Western Regional Climate Center 2000). Climatic data were unavailable for Mt. Trumbull, but conditions there are similar to Flagstaff.

Forest Structure and Treatments

Both study sites are characterized by ponderosa pine forest composed of large, presettlement pines established prior to Euro-American settlement around 1870, surrounded by small postsettlement pines established after the initiation of grazing and fire suppression in the early twentieth century (Covington et al. 1994). At Mt. Trumbull presettlement trees constituted about 14.4% of the trees per hectare, and postsettlement trees constituted about 85.6%, prior to treatment (Waltz 1998). At FUWI, 5.3% of the trees per hectare prior to treatment existed prior to Euroamerican settlement, and 94.7% were postsettlement (W. W. Covington, unpublished data). At all study sites, the first stage of restoration treatment, involving the thinning of small-diameter trees, occurred during 1998. All presettlement-era trees were retained, and selected postsettlement trees were retained as replacements for cut or dead presettlement-era trees identified in historical reconstructions (Covington et al. 1997). All other postsettlement trees were cut, and burning treatments in 2000 and 2001 have completed restoration treatments. Our microclimate measurements were taken prior to burning to avoid recording the transitory effects of surface fires. Thus, our results reflect changes in forest structure, not burning. At Mt. Trumbull we monitored microclimate at two treatment areas in 1998 and one in 1999 and 2000, ranging in size from 25 to 400 ha. At FUWI we worked in four treatment areas, each 12 to 14 ha.

Instrumentation

We used two types of microclimate monitoring systems in this research. Hobo dataloggers (Spectrum Technologies, Plainsfield, IL), with integrated light intensity, air temperature, and relative humidity sensors, were used to monitor diurnal changes in microclimate at multiple locations over two summers in 1998 and 1999. In 1999, we used a Campbell 10× micrologger (Campbell Scientific Inc., Logan, UT) combined with a Li-Cor quantum sensor (Li-190SA, Li-Cor, Inc., Lincoln, NE) and a temperature and relative humidity probe (CS500-L, Campbell Scientific Inc., Logan, UT) to monitor microclimatic gradients and to cross-reference readings from the simpler Hobo units. Air temperature and relative humidity sensors were shielded from the sun using standard radiation shields (Spectrum Technologies, Plainsfield, IL). In the field, Hobo light intensity sensors were shielded from moisture by clear plexiglass cases (Spectrum Technologies, Plainsfield, IL). Between the 1998 and 1999 field seasons, the Hobo light intensity sensors were modified to eliminate obstructions from the datalogger case. Both Hobo and Campbell sensors were calibrated by the manufacturers prior to purchase. The Hobo air temperature sensors were recalibrated in our lab prior to the 1999 field season.

The two types of light intensity sensors differ in how they measure insolation. The Hobo sensors measure radiant flux density between 400 and 1,100 nm, whereas the quantum sensor measures photon flux density between 400 and 700 nm (photosynthetically active radiation). In all cases, these two technologies produced similar results regarding relative values among points and trends along forest structural gradients. No novel insight was derived from separate comparison of results from the different sensors. To simplify presentation of the results and permit consistent units of measure, we calibrated the modified Hobo sensors against the quantum sensor in full sun and converted the Hobo readings to standard units (W/m^2) using conversion equations provided by Li-Cor (Li-Cor, Inc., Lincoln, NE; details available from authors).

Study Design and Data Analysis

The Effect of Restoration Treatments on Microclimate. For the purpose of examining restoration treatment effects on microclimate, we analyzed data collected 100 m from the edge in the treated forest, at the edge, and 100 m from the edge in the untreated forest. Transects were established perpendicular to the edge, and microclimate was monitored one meter above ground level during clear days from July through September. Edge points for each transect were selected randomly; points near atypical landscape features (i.e., canopy gaps in untreated forest or exceptionally steep topography) were discarded prior to establishing transects. In 1998 Hobo dataloggers recorded air temperature and relative humidity every five minutes for one 24-hour period at six transects centered on the forest edge. Using the Campbell micrologger during the 1999 field season, we monitored light intensity, in addition to temperature and relative humidity, one meter above ground level on eight pairs of transects with eastand west-facing edges (16 total). These data were collected as instantaneous measurements along all transects, between 1000 and 1400 hours over three clear days at the end of September 1999; equipment limitations prevented us from collecting microclimate data over 24-hour periods with the Campbell micrologger. Relative humidity values were used to calculate VPD using equations from Lowe (1977).

The 1999 air temperature and VPD data were analyzed for three time periods-morning (0630 to 0730 hr), midday (1000 and 1400 hr), and evening (1630 to 1730 hr)-using a repeated measures analysis of variance (ANOVA), with effects for treatment and time period. These time periods were chosen to examine microclimate at midday and during transitions between daylight and night, when variables changed rapidly and pronounced differences were expected between treatments. The data collected with the Campbell micrologger in 1999 were analyzed for treatment effects during midday using a three-way ANOVA, with treatment and edge orientation as factors, and transect pairs as a blocking variable. When ANOVA results were significant for treatment, Tukey's honestly significant difference test was used to determine relationships between microclimatic conditions in the treatment, at the edge, and in the untreated forest. Due to modifications in sampling methods between seasons, data from each field season were analyzed separately. For these data, assumptions were met for homogeneity of variances and normality.

Comparison of Pre- and Post-Restoration Microclimatic Conditions at Fixed Points. Hobo dataloggers were used to examine microclimatic conditions in 1999 before restoration treatments and during the 2000 field season in the same locations after the treatments had occurred. Light intensity, air temperature, and VPD were recorded every minute for one 24-hour period, at one meter above ground level. We analyzed data from clear days during the last two weeks of June 1999, prior to implementation of restoration treatments. Fifteen transects were placed in areas where restoration treatments were planned at the Mt. Trumbull site. The transects contained three sampling points, one 100 m from the edge in the treatment, one at the edge, and one 100 m from the edge in the untreated forest. Due to implementation delays, restoration treatments occurred at only seven of these transects. Posttreatment microclimatic data were monitored along the same transect points on clear days one year later, in June 2000, when location of the sun was equivalent to that during pretreatment data collection.

Relative values of light intensity, air temperature, and VPD were used to examine pre- and post-treatment effects. To account for interannual macroclimatic differences at each transect, treatment and edge microclimatic conditions for pre- and post-treatments were normalized to conditions in the untreated forest location for each transect (for example, $X_{\text{treated}} - X_{\text{untreated}} = X_{\text{relative}}$, for any variable X). Three times of day, morning (0630 to 0730 hr), midday (1000 to 1400 hr), and evening (1630 to 1730 hr), were examined using a split-plot repeated measures ANOVA with two factors, pre-/post-treatment and time period nested within pre-/post-treatment. The nested factor allowed us to examine the between-subject variability (Sokal & Rohlf 1981).

Microclimatic Gradients at the Forest Structural Edge. So that microclimatic gradients across forest structural edges could be examined, additional data collection points were added to the established transects discussed in the treatment effects section above. In 1998 we monitored microclimate at one meter above ground level at points 0, 10, 25, 50, and 100 m from the edge in both treated and untreated forest, for a total of nine sampling points along each transect. Gradients for air temperature and VPD in 1998 were analyzed for three time periods, morning (0630 to 0730 hr), midday (1000 to 1400 hr), and evening (1630 to 1730 hr). During the 1998 field season, we discovered that the placement of the sensor on the Hobo light intensity dataloggers obstructed some of the incoming solar radiation, precluding insightful analysis and necessitating the modifications discussed above. In 1999 at the FUWI site, we focused on sampling the effects of edge orientation, centering data collection more closely around the edge with sampling points at 0, 5, 10,

25, 50, 75, and 100 m into each forest type, for a total of 13 sampling points per transect. During this field season we collected midday edge-gradient data for light intensity, air temperature, and VPD with the Campbell micrologger.

For the purpose of edge-gradient analyses, transects were divided into two sections, one from the edge into the untreated forest and another from the edge into the treatment area. For each transect portion, linear regression was used to determine the best fit to the relationship between microclimatic values and distance from the edge. A significant microclimatic gradient was defined as a gradient where the mean of the slopes from each regression equation differed significantly from zero (t test). In cases of nonnormality, the Wilcoxen signed rank test was used. Finally, to examine the nature of the light intensity response across the edges, we calculated the frequencies at which different values were measured along each of the 16 edge transects. We compared the frequencies of observed values in six light intensity classes to a uniform distribution (chi-square test) to test the null hypothesis that midday insolation values were evenly distributed between the maximum and minimum values observed. All statistical analyses were performed using the statistical package JMP IN (version 3.2.1, SAS Institute Inc., Cary, NC) with $p \le 0.05$ deemed sufficient to reject the null hypothesis that microclimate was independent of distance from the edge.

Results

The Effect of Restoration Treatment on Microclimate

To determine changes in microclimate induced by the restoration treatments, we analyzed data from the 1998 and 1999 field seasons collected at the edge and at points 100 m from the edge, in both the treated and untreated forest. In 1998 air temperature and VPD were examined for treatment effects during three time periods, morning, midday, and evening. Although trends were evident, especially during morning periods, the differences between the treated, edge, and untreated forest were not statistically significant in an analysis of variance that included all time periods (temperature, p = 0.08; VPD, p = 0.48; Fig. 1). In the morning, air temperature and VPD exhibited strong trends; on average, both were higher in the treated forest and near the edge than in untreated forest, but similar trends were not observed during midday or evening (Fig. 1). Morning air temperature was about 15% higher (3.3°C) in the restoration treatment compared to the control forest, while morning VPD was about 47% higher (0.6 kPa). A significant diurnal effect was present throughout the day for



Figure 1. The effect of restoration treatment on (a) air temperature (°C) and (b) vapor pressure deficit (VPD, kPa) for untreated forest, edge, and restoration treatment areas at the Mt. Trumbull site during morning, midday, and evening, 1998 field season. Treatment effects were not significant for either variable, although morning hours exhibited a strong trend for both variables (temperature, p = 0.08; VPD, p = 0.48, n = 6for both).

both variables (temperature, p < 0.001; VPD, p < 0.01). The interaction terms of temperature and time period and VPD and time period were not significant (temperature, p = 0.58; VPD, p = 0.16).

Light intensity, monitored only during midday during the 1999 field season, was the only variable to exhibit statistically significant differences due to restoration treatments. On average light intensity was 2.3 times higher in the treatment area and 1.5 times higher near the edge than in the untreated sites during midday (p = 0.0005; Fig. 2). When compared to light intensity in the untreated forest, this amounted to a 200 W/m^2 increase in the treated forest and a 130 W/m² increase near the structural edge. Light intensity in the treatment area and near the edge was significantly higher than in the untreated forest (Tukey's HSD, p < 0.05). Midday air temperature and VPD, collected in 1999 with the Campbell micrologger, did not exhibit significant differences between the treatment, edge, and untreated forest (temperature p = 0.86; VPD, p = 0.94; Fig. 2).

Pre- and Post-Restoration Microclimatic Conditions at Fixed Points

In 1999 we collected microclimate data in locations slated for restoration treatments the following year. When we compared microclimate collected at these fixed points in 1999, before the restoration treatment, to data collected in 2000, after treatment, the only variable to exhibit significant differences (p = 0.04; Fig. 3) was light intensity. On average, the difference between the treated and untreated forest was 47 W/m² higher after restoration and 15 W/m² higher at the edge after restoration. Air temperature and VPD were not significantly different after restoration treatment (temperature, p =0.25; VPD, p = 0.21) or near the edge (temperature, p =0.95; VPD, p = 0.93; Fig. 3). For these data, we did not observe significant time-of-day effects following restoration for any of the variables in the treated area (light intensity, p = 0.36; temperature, p = 0.13; VPD, p =0.10) or near the edge (light intensity, p = 0.18; temperature, p = 0.63; VPD, p = 0.48).

Microclimatic Gradients at the Forest Structural Edge

Air temperature and VPD exhibited significant edge gradients at certain times of day, but differences in light intensity were abrupt, rather than gradual. Significant microclimate gradients were observed from the edge into the untreated forest for air temperature and VPD in the morning and evening (Fig. 4). Data collected in 1998 showed that morning air temperature was about 12% lower (2.3°C, p = 0.02) and morning VPD was 40% lower in the untreated forest than at the edge (0.4 kPa, p = 0.009; Fig. 4). On average, evening air temperature was 1% lower (0.1°C, p = 0.003) and VPD 3% lower in the untreated forest (0.1



Figure 2. The response of (a) light intensity (W/m^2) , (b) air temperature (°C), and (c) vapor pressure deficit (VPD, kPa) for the untreated forest, the edge, and the restoration treatment areas at the Flagstaff Urban Wildland Interface (FUWI) site during midday (1000 to 1400 hr), 1999 field season. *P*-values correspond to treatment effects for each of the three variables (n = 16).

kPa, p = 0.006; Fig. 4). During midday, no edge gradient was observed for either variable from the edge into the untreated forest (temperature, p = 0.59; VPD, p = 0.42; Fig. 4).



Figure 3. A comparison of pre- and post-treatment (a) light intensity (W/m²), (b) air temperature (°C), and (c) vapor pressure deficit (VPD, kPa) during morning, midday, and evening at sampling points in the restoration treatment (left) and near the edge (right), in June 1999 and 2000. Data were normalized to the value in the untreated forest to eliminate differences due to interannual variation. Time of day was not a significant factor explaining differences (n = 7).

In 1998 neither temperature nor VPD showed significant edge gradients from the edge into the restoration treatment at any time of day. Air temperature was highly variable throughout the day, yet showed a strong morning trend that approached statistical significance (morning, p = 0.06; midday, p = 0.84; evening, p = 0.22). Trends in VPD were similar over the course of the day, and no gradient was detected from the edge into the treatment (morning, p = 0.63; midday, p = 0.50; evening, p = 0.12).

Using data collected during midday in 1999, we were able to stratify transects for edge orientation. This did not help identify midday edge gradients from either the edge into the untreated forest or the edge into the treated forest. At both east- and west-facing edges, midday air temperature decreased slightly within 10 m of the edge, remaining 0.5% lower (0.1°C) into the dense control forest (east-facing edge, p = 0.11; west-facing edge, p = 0.14). Air temperature increased 0.5% (0.1°C), from the edge into the treatment but was also not signif-



Edge into the untreated forest

Morning

p=0.02 26

a) Air temperature

2.0p=0.009

b) Vapor pressure deficit

Midday

Figure 4. Edge gradients in (a) air temperature (°C) and (b) vapor pressure deficit (VPD, kPa) for three times of day, morning (top), midday (middle), and evening (bottom), from the edge into the untreated forest at the Mt. Trumbull study site, 1998 field season. Bars represent standard errors for transects (n = 6).



icant for east- and west-facing edges (east-facing edge, p = 0.20; west-facing edge, p = 0.84). VPD was 1% lower (0.02 kPa) lower in the control forest for both edge orientations (east-facing edge, p = 0.74; west-facing edge, p =0.71) and 1% higher (0.02 kPa) into the treatment area (east-facing edge, p = 0.74; west-facing edge, p = 0.30). Midday light intensity edge gradients were also not significant, nor did they exhibit any clear patterns, at either east- or west-facing edges from the edge into the untreated forest (east-facing edge, p = 0.39; west-facing edge, p = 0.71) or into the treated forest (east-facing edge, p = 0.96; west-facing edge, p = 0.55).

Across all transects, light intensity values showed great spatial and temporal variability, with very low and very high values occurring more commonly than would be expected by chance alone ($\chi^2 = 121$, p < 1210.001; Fig. 5)

Discussion

Ecological restoration in ponderosa pine forest increased sunlight penetration to the forest floor but did not significantly impact ambient air temperature or VPD. Typically forested areas that are more open, such as ponde-



Figure 5. Frequency of light intensity values measured during midday along sixteen 200-m transects established perpendicular to the edge between treated and untreated ponderosa pine forest. Thirteen points were sampled along each transect in September 1999, six in the more open, treated forest (striped bars), six in the dense, untreated forest (black), and one point at the edge between the two forest types (gray). The frequency of observed light intensity values differed significantly from an even distribution (p <0.001, n = 96 for treated and untreated forest, 16 for edge).

rosa pine after thinning treatments, are sunnier, warmer, and drier than areas under denser forest canopy (Geiger 1966; Wales 1967). At our study sites, 60 to 90% of the trees were removed through thinning, but only solar radiation increased significantly in the treatment areas, and even this change was modest. Early studies by Pearson (1931) reported similar results for air temperature in stands of ponderosa pine forest and open areas adjacent to these stands in Arizona and New Mexico. Kittredge (1948) noted that, of many forest types, thinning in ponderosa pine forests had the least effect on air temperature and relative humidity.

Our findings, however, contrast those from a more recent study in old-growth Douglas fir forest. During clear days in summer, Chen et al. (1993) found higher air temperature and lower relative humidity near edges between Douglas fir forest and clearcuts, with intermediate conditions in clearcuts. We observed that morning air temperature and VPD at the structural edge were more similar to values in the treated area but that edge microclimate was intermediate between the treated and untreated forest. Light intensity showed a similar pattern during midday.

When detected, microclimatic gradients were gradual across the structural edge between treated and untreated forest. Air temperature and VPD dropped gradually over a distance of 100 m from the edge into the untreated forest during the morning and evening. No microclimatic edge gradient was observed during midday. We did not detect significant effects due to edge orientation, but equipment limitations permitted only midday data collection at paired east- and west-facing transects. Results from a related experiment indicate that edge orientation can exert strong influence on

morning air temperature and VPD (Meyer & Sisk 2001). Our gradient results are qualitatively similar to findings from other ecosystems, although the magnitude of the response appears to be considerably lower in ponderosa pine forest. Several studies have shown that air temperature and VPD decreased in the tropics from the edge into tropical forest, with little change detected after the initial 20 m (Kapos 1989; Williams-Linera 1990). Air temperature gradients in old-growth Douglas fir forests, however, have been shown to penetrate up to 180 m from the edge into the forest during the day (Chen et al. 1995). We found the most prominent gradients in the morning, with changes of 2.3°C and 0.4 kPa over 100 meters. In the evening, the magnitudes of change were lower: 0.1°C and 0.1 kPa over 100 m. In fact, these evening values were equivalent to gradients observed during midday, but the midday readings were much more variable. We did not observe microclimatic gradients from the edge into the restoration treatment; conditions at the edge were equivalent to those in the center of the treatment area for all time periods. Our results indicate that restoration treatments exert an influence up to 100 m into the dense, untreated forest but that the forest exerts little influence on the microclimate of treated areas.

In southwestern ponderosa pine forests, air temperature and VPD appear to be less influenced by restoration treatments than is light intensity. This unexpected decoupling of microclimatic variables may be due to boundarylayer mixing of air across the edge between treated and untreated forest. Wind movement in open meadows is similar to that near the forest floor in stands of ponderosa pine (Arthur 1969), which is probably due to the simple canopy structure (i.e., a single semi-open canopy layer) of ponderosa pine forest and the relatively dry climate of northern Arizona. In comparison, most oldgrowth forests of the Pacific Northwest and tropical regions develop closed canopies and multilayered stand structures, resulting in a distinct forest microclimate and much greater contrasts to thinned and cleared areas (Williams-Linera 1990; Chen et al. 1995).

Further examination of the response of light intensity, compared with temperature and VPD, provides insight into how restoration treatments affect microclimatic conditions in ponderosa pine forests. Light intensity was higher in treated areas than in untreated areas, and the values changed abruptly at edges between the two forest types. Ambient air temperature and VPD were similar at midday in treated and untreated forest stands but showed modest, decreasing gradients from the treated areas to adjacent untreated stands in the morning and evening. These patterns may result from the nature of light intensity, shading, and insolation near the forest floor. We categorized midday light intensity data from 1999 based on magnitude, as illustrated in Figure 5. Light readings, when graphed by frequency and magnitude, followed a bimodal distribution within both forest types, exhibiting fewer intermediate values of light intensity (Fig. 5). These fewer intermediate values suggest that overstory structure in this system creates a light environment that fluctuates between "high" (direct sun) and "low" (shade). Treated areas are not necessarily receiving more intense light, but they are in direct sun more often than untreated areas. This contrasts with many other forested ecosystems, where incident light filters through several vegetative layers, resulting in a more continuous gradient in light intensity near the forest floor (Kapos 1989; Chen et al. 1995).

Although the microclimatic effects due to restoration treatments and the magnitude of the gradients observed across edges were smaller than those found in other forest ecosystems, our findings are still likely to be biologically relevant. Increased light intensity is almost certainly driving observed increases in soil temperature following restoration (Covington et al. 1997; Kaye et al. 1999). Increased insolation, combined with higher soil temperature and moisture, could increase tree vigor and forest productivity (Kittredge 1948) and benefit pine regeneration in the treated areas by increasing germination and photosynthetic rates (Jones 1992). An increase of even 1°C, roughly what we observed in this study during midday, can lead to earlier germination and a longer growing season (Jones 1993).

For some animals, the modest microclimatic changes induced by ponderosa pine restoration treatments could indirectly affect food resources and survival rates. Mobile organisms that are sensitive to forest microclimate, particularly butterflies and other volant, diurnal arthropods, may respond directly to altered light regimes, such as those we observed in the treated forest (Heinrich 1981). Indeed, the behavior, dispersal, and distribution of butterflies have been shown to respond to such microclimatic changes in patchy landscapes (Clench 1966; Tsuji et al. 1986). In these ponderosa pine forests, Meyer and Sisk (2001) have shown the flight behavior of two common butterfly species to be directly affected by the increased light levels and higher air temperature associated with restoration treatments.

Given increasing concerns about the dense and overstocked conditions of pine forests throughout the intermountain West, restoration treatments, as well as other thinning prescriptions designed to reduce the likelihood of catastrophic crown fires, are likely to be implemented over increasingly larger areas. Our research shows that the microclimatic effects of such treatments are relatively modest when compared to the effects of similar treatments in more structurally complex forest ecosystems. However, differences in microclimate between treated and untreated ponderosa pine forest stands were magnified at certain times of day (morning and evening) and in certain locations (untreated forest near the edge). Because even modest changes in light intensity, air temperature, and moisture availability are likely to have meaningful effects on seedling recruitment and productivity, as well as on the distribution and abundance of arthropods, forest managers should address the implications of changing microclimates when they are planning and implementing landscape-scale restoration treatments.

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LITERATURE CITED

- Arthur, J. P. J. 1969. Environmental measurements in a natural park and in surrounding ponderosa pine stands. Northern Arizona University, Flagstaff.
- Brothers, T. S. 1993. Fragmentation and edge effects in central Indiana old-growth forests. Natural Areas Journal **13:**268–274.
- Carmago, J. L. C., and V. Kapos. 1995. Complex edge effects on

soil moisture and microclimate in central Amazonian forest. Journal of Tropical Ecology **11:**205–221.

- Chen, J., J. F. Franklin, and T. A. Spies. 1993. Contrasting microclimates among clearcut, edge, and interior old-growth Douglas fir forest. Agricultural and Forest Meteorology 63:219–237.
- Chen, J., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. Ecological Applications **5:**74–86.
- Chen, J., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosofske, G. D. Mroz, B. L. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. Bio-Science 49:288–297.
- Clench, H. K. 1966. Behavioral thermoregulation in butterflies. Ecology **47**:1021–1034.
- Cooper, C. F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecological Monographs **30**:129–164.
- Covington, W. W., R. L. Everett, R. Steele, L. L. Irwin, T. A. Daer, and A. N. D. Auclair. 1994. Historical and anticipated changes in forest ecosystems of the inland west of the United States. Journal of Sustainable Forestry 2:13–63.
- Covington, W. W., P. Z. Fulé, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. Journal of Forestry 95:23–29.
- Covington, W. W., and M. M. Moore. 1994a. Postsettlement changes in natural fire regimes and forest structure: ecological restoration of pre-settlement ponderosa pine forests. Journal of Sustainable Forestry **2**:153–181.
- Covington, W. W., and M. M. Moore. 1994b. Southwestern ponderosa forest structure. Journal of Forestry **92:**39–47.
- Geiger, R. 1966. The climate near the ground. Harvard University Press, Cambridge, Massachusetts.
- Heinrich, B. 1981. Ecological and evolutionary perspectives. Pages 235–302 in B. Heinrich, editor. Insect thermoregulation. John Wiley and Sons, New York.
- Hungerford, R. D., and R. E. Babbit. 1987. Overstory removal and residue treatments affect soil surface, air, and soil temperatures: implications for seedling survival. USDA Forest Service Intermountain Research Station, Ogden, Utah.
- Johnson, C. G. 1969. Migration and dispersal of flying insects. Methuen, London.
- Jones, H. 1992. Plants and microclimate: a quantitative approach to environmental plant physiology. Cambridge University Press, New York.
- Jones, M. B. 1993. Plant microclimate. Pages 47–64 in D. O. Hall, J. M. O. Scurlock, H. R. Bolhar-Nordenkampf, R. C. Leegood, and S. P. Long, editors. Photosynthesis and production in a changing environment. Chapman Hall, New York.
- Jose, S., A. R. Gillespie, S. J. George, and B. M. Kumar. 1996. Vegetation responses along edge-to-interior gradients in a high altitude tropical forest to peninsular India. Forest Ecology and Management 87:51–62.
- Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. Journal of Forest Ecology 5:173–185.
- Kaye, J. P., S. C. Hart, R. C. Cobb, and J. Stone. 1999. Water and nutrient outflow following the ecological restoration of a ponderosa pine–bunchgrass ecosystem. Restoration Ecology 7:252–261.
- Kittredge, J. 1948. Forest influences. McGraw-Hill Book Company, Inc., New York.
- Lowe, P. R. 1977. An approximating polynomial for the computation of saturation vapor pressure. Journal of Applied Meteorology 16:100–103.

- Madany, M. H., and N. E. West. 1983. Livestock grazing—fire regime interactions within montane forests of Zion National Park. Ecology 64:661–667.
- Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation 66:185–194.
- Meffe, G. K., and C. R. Carroll. 1994. Principles of conservation biology. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Meyer, C. L., and T. D. Sisk. 2001. Butterfly response to microclimatic conditions following ponderosa pine restoration. Restoration Ecology 9:453–461.
- Oke, T. R. 1996. Boundary climate layers. Routledge, New York.
- Pearson, G. A. 1931. Forest types in the southwest as determined by climate and soil. United States Department of Agriculture, Washington, D.C.
- Quinn, J. F., and S. P. Harrison. 1988. Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. Oecologia **75**:132–140.
- Ranney, J. W. 1977. Forest island edges: their structure, development, and importance to regional forest ecosystem dynamics. Environmental Sciences Division, Publication No. 1069. Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- Reifsnyder, W. E., and H. W. Lull. 1965. Radiant energy in relation to forests. United States Department of Agriculture, Washington, D.C.
- Savage, M., P. M. Brown, and J. Feddema. 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. Ecoscience 3:310–318.
- Schubert, G. H. 1974. Silviculture of southwestern ponderosa pine: the status of our knowledge. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
- Sisk, T. D., N. M. Haddad, and P. R. Ehrlich. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. Ecological Applications 7:1170–1180.
- Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Company, New York.
- Sutherland, E. K. 1983. The effects of fire exclusion on growth in mature ponderosa pine in northern Arizona. University of Arizona, Tucson.
- Tsubuki, T., and T. Takizawa. 1996. Flight activities of *Colias erate* (Lepidoptera, Pieridae) in high and low altitudes. Transcontinental Lepidopteran Society of Japan **47**:17–28.
- Tsuji, J. C., J. G. Kingsolver, and W. B. Watt. 1986. Thermal physiological ecology of *Colias* butterflies in flight. Oecologia 69: 161–170.
- Wachob, D. G. 1996. The effect of thermal microclimate on foraging site selection by wintering Mountain Chickadees. Condor 98:114–122.
- Wales, B. A. 1967. Climate, microclimate, and vegetation relationships on north and south forest boundaries. The William L. Hutcheson Memorial Forest Bulletin 2:1–60.
- Waltz, A. 1998. Mt. Trumbull Ecosystem Restoration Project: annual report. Northern Arizona University, Flagstaff.
- Weiss, S. B., P. M. Rich, D. D. Murphy, W. H. Calvert, and P. R. Ehrlich. 1991. Forest canopy structure at overwintering Monarch butterfly sites: measurements with hemispherical photography. Conservation Biology 5:165–175.
- Western Regional Climate Center. 2000. Western U.S. climate historical summaries. Western Regional Climate Center, http://www.wrcc.dri.edu/climsum.html.
- Wiens, J. A., N. C. Stenseth, B. van Horne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos 66:369–380.
- Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. Journal of Ecology 78:356–373.