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Recovery Status of a Sierra Nevada Forest Plant Community One-Half Century after Wildfire

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Abstract

Comparison of the burned and unburned portions of a Jeffrey pine stand in the eastern Sierra Nevada that was partially destroyed by a wildfire approximately a half century earlier served as the basis of an investigation intended to provide insight into the direction and pace of unaided recovery from such events in this and similar forest cover types. With Jeffrey pine the predominant species regardless of treatment, lodgepole pine was a secondary component of the overstory in both stand portions but a minor representation of white fir in the unburned portion was absent from the burned acreage. Commensurate with the large difference in age, tree dimensions, basal area, and biomass in the overstory of the burned stand portion were greatly exceeded by those of the overstory in the unburned portion. Tree seedlings and saplings were much more abundant in the burned acreage, with those of Jeffrey pine largely accounting for the disparity. Predominant among shrubs in the understory of the burned stand portion was snowbrush ceanothus with that in the unburned portion consisting of prostrate ceanothus, while among herbaceous species a small quantity of Sandberg bluegrass in the former contrasted against none in the latter. Fine and total fuel loading along with fuel bed depth on the burned substrate were greatly exceeded by those on the unburned substrate, while proportionally, less fine fuels but more of the coarsest ones were found on the former compared to the latter.

Keywords: Wildland fire; Forest succession; Natural regeneration; Understory vegetation; Wildland fuels; *Pinus jeffreyi*; *Pinus contorta*; *Abies concolor*

Introduction

Projections of a future escalation of wildfire activity in the forests of the western USA [1] essentially reflect the anticipated continuance of a trend encompassing heightened fire frequency, extent, and intensity that has been in place for a protracted period [2-6]. Attribution for this development, and that serving as rationale for the view that it represents a progression that will continue largely unabated for decades to come, rest upon a convergence of multiple causes including undesirable alterations of stand structure and composition, accumulations of fuels, proliferating ignition sources, and climate change [4,6-18]. Given the extreme and widespread nature of the disturbance inherent in most wildfires, it is probable that land managers will be forced to allocate the resources necessary for post-fire rehabilitation to sites deemed most critical, and to increasingly fewer of them as burned acreages accumulate. Consequently, it is imperative that they develop the capacity to distinguish sites where drastically debilitating post-fire conditions likely preclude vegetation recovery for the foreseeable future from those where natural succession unaided by cultural amendment will probably suffice in the reestablishment of a viable plant community within a reasonable time frame. In turn, this necessitates that the pace and direction of post-fire succession be determined for a wide variety of forest cover types subjected to wildfires producing a wide array of substrate conditions, which will ultimately provide some predictive capacity in the assessment of burned acreages regarding their recovery potential given varying levels of restorative treatment. Based on past observations, a frequent regulating factor, if not the most common one, in plant succession following wildfires in western USA forests as they undergo transition from a nearly or completely denuded landscape to one in which a tree cover prominently resides is colonization by shrub species with adaptive features permitting them to thrive under post-fire conditions [11,19,20].

The Study presented here concerns plant succession on an eastern Sierra Nevada site occupied by a yellow pine stand partially destroyed by wildfire in the distant past. Specifically examined was the status of the reestablishment of an overstory component, that of the understory community including natural regeneration and non-arborescent vegetation, and the extent to which recovery of the forest floor had progressed. Stand portions undamaged by the fire provided a basis of comparison for assessment of the degree of recovery extant in the burned portion.

Materials and Methods

Study site

The site upon which the study was conducted is located on the Truckee Ranger District of the Tahoe National Forest, specifically on the Sagehen Experimental Forest (39° 27′ 15″ N, 120° 12′ 30″ W). At an elevation of 1940 m, it consists of approximately 10 ha with a generally southern aspect and a slope varying from 15 to 25%. As measured by an on-site weather station, the long-term average annual precipitation is 85 cm consisting primarily of snowfall, and the mean annual temperature is 5.2°C. Soils are of the Jorge series, loamy skeletal, isotic, frigid Andic Haploxeralfs derived from andesite [21].

The forest stand occupying the study site was partially destroyed in late August of 1960 by the Donner Ridge Fire, a conflagration of human

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origin that burned approximately 17400 ha in total over approximately one week from ignition to containment. Located near the northern terminus of this wildfire, the subject stand ultimately sustained damage from a rapidly advancing flame wall in a mosaic pattern ranging from total destruction with exposed mineral substrate to completely untouched but also including a margin in the burned portion where a few scattered overstory constituents survived. In conducting this study, unimpacted acreage surrounding the burned stand portion provided the unburned control against which the recovery in the latter was compared. Data collection for this study, encompassing that related to the overstory, natural regeneration, understory vegetation, and downed and dead fuels, was completed a little over five decades after the wildfire.

Vegetation and forest floor measurements

For purposes of assessing the wildfire influences on the overstory, 12 circular 0.04 ha plots were established on the site for mensurational measurements of trees of pole size and larger, i.e., ≥ 10.2 cm DBH. Six of these plots were randomly located within the burned stand portion with the remaining six randomly situated along the periphery of the burned portion in locations where any remnant evidence of all possible fire impacts was absent. The measurements therein consisted of height, DBH, and live crown length, with each tree tallied by species. Subsequently, percent species representation within each plot was calculated while across species stem counts were summed by plot, height and live crown length were used to calculate live crown ratio, DBH values were used to derive their quadratic mean by plot according to the Curtis and Marshall [22] formula, basal area by plot was derived from plot stem counts and quadratic mean DBH using the Davis et al. [23] formula, and the total above-ground tree biomass within each plot was calculated using the formulas of Gholz et al. [24]. Ultimately, the stem count, basal area, and biomass for each plot were expanded to reflect equivalent 1.0 ha values. Included in the overstory inventory, but confined to the plots within the unburned stand portion, were additional measurements specific to selected site trees obtained for purposes of assessing site quality, stand age, radial growth, and fire history. One such tree in each of the pertinent plots was chosen from among representatives of the predominant species that were either of the dominant or codominant crown class. Coring of these trees (4.3 mm cores extracted 1.37 m above ground) permitted the determination of total age by counting the late wood rings from pith to phloem and adding 10, the latter an approximation of the average number of years required for Sierra Nevada conifers to reach sufficient size to produce their first countable ring at breast height [25], and ring counts confined to the outermost 2.54 cm of each core provided an indication of radial growth rate. Total age and height of the site trees were used to ascertain site index using the index curves of Meyer [26]. Examination of each core for evidence of fire scars provided an indication of whether the constituents of the unburned stand portion had ever incurred fire injury.

Seedling (≤ 1.37 m tall) and sapling (>1.37 m tall and ≤ 10.1 cm DBH) inventories encompassed counts by species within the two natural regeneration classes. Both inventories were performed using circular 54 m^2 plots established with the same centers as those for the 0.04 ha plots used in the overstory measurements. Ultimately, percent species representation segregated by regeneration class was calculated for each plot, total counts across species were determined for each plot by class, and the counts for each class both within and across species were expressed on a 1.0 ha basis.

The same 54 m^2 plots used in the seedling and sapling inventories were employed for grid mapping to scale of the understory species encountered on the site, which permitted expression of the prevalence of such species on a percent ground cover basis. In addition to the determination of the cover by individual species, those of shrubs in total and of herbs in total, along with all species in total, were calculated.

Downed and dead fuels were inventoried by individual timelag category [27] except for those designated as fine fuels, specifically the 1 hr and 10 hr categories, which were combined. For the 1+10 hr (≤ 2.5 cm diameter) fuels, duff, litter, and fine woody debris from three randomly located circular plots of 0.061 m^2 each within each of the 0.04 ha plots established for the overstory measurements were collected, dried to a constant weight, weighed, and the three weights were then averaged. For coarse fuels, specifically the 100 hr (>2.5 to ≤ 7.6 cm diameter) and 1000 hr (>7.6 cm diameter) categories, a single 4 m^2 and single 54 m^2 circular plot, respectively, was established with the same plot center as that of each of the 0.04 ha plots. Collection of the 100 hr fuels from the 4 m^2 plots permitted a dry weight determination by direct measurement as well. For 1000 hr fuels, however, lengths and the diameters at mid length were measured for use in the calculation of an estimate of volume according to the Huber formula [28]. Collection of 10 log sections from random locations outside the plots, measuring their dimensions, and then drying and weighing them provided a density constant for use in converting volume to dry weight by plot. Ultimately, all fuel weights were expanded to reflect equivalent 1.0 ha values, fine and coarse fuel weights were combined to determine total fuel loading, and the percentage of the total represented by each timelag category was calculated.

Statistical analyses

Data pertaining to each component of the study, specifically those derived from measurements of the overstory, natural regeneration, understory vegetation, and downed and dead fuels, were subjected to one-way analysis of variance (ANOVA) to test for the effect of the wildfire. Prior to analysis, the arcsine transformation was performed on all percentage data. Interpretively, fire effects were considered significant only when $p \leq 0.05$ according to the F test.

To investigate possible linkages between variables, specifically ones based on the different components of the study, a series of simple linear regression models were computed that paired those variables considered to be plausibly related. The first subset of these models, hereafter denoted as the overstory subset, featured percent cover by individual understory species along with total shrub cover as the independent variables while overstory tree height, DBH, live crown length and ratio, basal area, stem count, total biomass, and the percent representation by individual species constituted the dependent variables. For the natural regeneration subset, the second of the series, both the independent and dependent variables identified above pertaining to the first subset, accompanied by downed and dead fuel loading by timelag category and in total along with the percentages of the total accounted for by the individual timelag categories, were designated the independent variables while seedling and sapling counts plus the total for each along with the percent representation by species within the seedling and sapling classes served as the dependent variables. Denoted hereafter as the forest floor fuels subset, the third of the three again combined the independent and dependent variables of the first subset to serve as independent variables with fuel loading by timelag category and in total along with the percentages accounted for by the individual categories designated the dependent variables. Concerning all three subsets, only individual understory species with at least 10% coverage in at least one of the two treatments were included when the independent variables involved understory vegetation, while specific to the second and third subsets, fuel bed depth constituted an additional independent and dependent variable, respectively, therein. In each of the subsets, regression models were considered significant only when p ≤ 0.05 according to the F test. All statistical analyses were performed using SAS (SAS Institute, Inc., Cary, NC).

Results

Overstory characteristics

Species represented among trees of pole size and larger in the burned stand portion were limited to two, specifically Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) and Sierra lodgepole pine (*Pinus contorta* var. *murrayana* [Grev. & Balf.] Engelm.), while these two plus California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.) resided in the unburned portion (Table 1). Nevertheless, Jeffrey pine was predominant in both portions, and it was only for white fir that ANOVA disclosed a significant fire treatment effect regarding any of the species in residence on the site.

As for tree size criteria, the total height, DBH, and live crown length of the overstory constituents in the burned stand portion were all significantly exceeded by those prevailing in the unburned portion, with the disparities amounting to 139%, 75%, and 61%, respectively. However, live crown ratio in the former surpassed that in the latter, although again with ANOVA distinguishing the treatment effect.

Of the density measures, a difference between treatments disclosed by ANOVA as significant in basal area, which was 333% greater in the unburned stand portion than that in its burned counterpart, contrasted somewhat against one in tree count, which although 51% greater in the former than the latter was not deemed significant. Largely representing a surrogate measure of overstory density for the purposes of this study, above-ground biomass was 407% greater in the absence of fire and with the two treatments statistically distinct.

Confined to the unburned stand portion, the site trees selected for measurement averaged 26.8 m in height with a mean total age of 91 years, indicating a site quality of SI_{100} 27.4 (index height in meters). Based on the year of the wildfire, the overstory occupying the burned portion, exclusive of the few stems that survived the conflagration, was approximately 50 years old at most, or 55% of the age of that in the unburned stand portion. Radial growth in the site trees of 6.8 annual rings in the outermost centimeter equates to recent diameter growth of approximately 2.9 mm yr^{-1}. None of the increment cores exhibited evidence of charring, indicating that the only fire to which the oldest trees occupying the site had been subjected was the Donner Ridge Fire.

Natural regeneration

Jeffrey pine, lodgepole pine, and white fir seedlings were found in both the burned and unburned stand portions, and while the former was predominant in both treatments, it was twice as abundant in the burned portion, a statistically significant disparity (Table 2). Largely reflecting the prevalence of Jeffrey pine where the fire burned, the total seedling count there also significantly exceeded that in the unburned portion, specifically by 71%. Nevertheless, proportional representation did not differ significantly between treatments for any of the seedling species.

A large number of Jeffrey pine saplings were also found in the burned acreage, and it was proportionally dominant there as well to such extent that not only its count and percentage but also the total number of saplings were significantly greater in the burned than in the unburned treatment, in large part simply reflecting a total absence of Jeffrey pine saplings in the latter (Table 2). Overall, the sapling count was 275% larger in the burned stand portion even though the only other species found there was white fir while some saplings of both lodgepole pine and white fir resided in the unburned acreage.

	Fire treatment		
Variable	**Burned**	**Unburned**	**P-value**
Jeffrey pine (%)	82.7	85.5	0.7011
Lodgepole pine (%)	17.3	7.7	0.2408
White fir (%)	0	6.8	0.0499
Total height (m)	8.7	20.8	<0.0001
DBH (cm)	25.3	44.3	0.0014
Live crown length (m)	5.1	8.2	0.0064
Live crown ratio (%)	58.6	39.4	0.0005
Basal area (m^2 ha^{-1})	13.5	58.5	0.0002
Tree count (stems ha^{-1})	275.9	416	0.1927
Biomass	53682	272043	0.0002

[1]Each mean is based on values from six plots (n=6).

Table 1: Species composition and mensurational characteristics of a Sierra Nevada conifer stand as influenced by wildfire[1].

		Fire treatment		
Regeneration class	**Species**	**Burned**	**Unburned**	**P-value**
Seedling (# ha^{-1})	Jeffrey pine	247.1	123.6	0.0468
	Lodgepole pine	30.9	30.9	0.9998
	White fir	92.7	61.8	0.6867
	Total seedling	370.7	216.3	0.0438
Seedling (%)	Jeffrey pine	66.7	57.1	0.8593
	Lodgepole pine	8.3	14.3	0.7746
	White fir	25	28.6	0.9448
Sapling (# ha^{-1})	Jeffrey pine	432.4	0	0.0471
	Lodgepole pine	0	30.9	0.3409
	White fir	30.9	92.7	0.2596
	Total sapling	463.3	123.6	0.0497
Sapling (%)	Jeffrey pine	93.3	0	0.0422
	Lodgepole pine	0	25	0.2856
	White fir	6.7	75	0.1345

[1]Each mean is based on values from six or fewer plots (n≤6) depending on the presence of regeneration of the pertinent class within individual plots.

Table 2: Quantities and species composition of seedlings and saplings in the understory of a Sierra Nevada conifer stand as Influenced by wildfire[1].

Ground cover

Shrub species residing in the burned stand portion consisted of snowbrush ceanothus (*Ceanothus velutinus* Douglas ex Hook.), prostrate ceanothus (*Ceanothus prostratus* Benth.), green leaf manzanita (*Arctostaphylos patula* Greene), Utah serviceberry (*Amelanchier utahensis* Koehne), bitter cherry (*Prunus emarginata* [Douglas ex Hook.] D. Dietr.), wax currant (*Ribes cereum* Douglas), creeping snowberry (*Symphoricarpos mollis* Nutt.), yellow rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.), and antelope bitterbrush (*Purshia tridentata* [Pursh] DC.), and with the exception of the latter each of these were found in the unburned portion also, but an additional species occurring there that was not present in the burned acreage was bush chinquapin (*Chrysolepis sempervirens* [Kellogg] Hjelmqvist). By a substantial margin, the most prevalent species where the fire had burned was the snowbrush ceanothus, and its coverage there not only entailed well over one-third of the acreage but constituted two-thirds of its total shrub cover (Table 3). It was also significantly more prevalent in the burned than the unburned treatment with the difference amounting to 855%. The most common shrub species in the unburned stand portion was the prostrate ceanothus, and here again a significant

		Fire treatment		
Plant form	Species	Burned	Unburned	P-value
Shrub (%)	Snowbrush ceanothus	39.17	4.1	0.0376
	Prostrate ceanothus	5.08	28.43	0.0048
	Green leaf manzanita	12.28	5.07	0.2292
	Utah serviceberry	0.49	0.64	0.687
	Bitter cherry	0.35	0.08	0.2323
	Wax currant	0.09	0.21	0.5389
	Creeping snowberry	0.13	0.17	0.8808
	Yellow rabbitbrush	0.19	0.07	0.404
	Antelope bitterbrush	0.92	0	0.1032
	Bush chinquapin	0	0.21	0.3409
	Total shrub	58.7	38.98	0.1581
Herb (%)	Bottlebrush squirreltail	0.01	0.01	0.8727
	Sandberg bluegrass	0.05	0	0.0252
	Woolly mule-ears	0.03	0.04	0.7556
	Rose thistle	0.01	0.03	0.2924
	Holboell's rockcress	0	0.01	0.3409
	Total herb	0.1	0.09	0.8153
	Total ground cover	58.8	39.07	0.1576

[1]Each mean is based on values from six plots (n=6).

Table 3: Ground cover of shrub and herbaceous species in the understory of a Sierra Nevada conifer stand as influenced by wildfire[1].

disparity between treatments was revealed with coverage 460% greater in the unburned than the burned acreage. The only other shrub with a substantial presence on the site was green leaf manzanita, which although numerically was more abundant in the burned portion, the two treatments were not statistically distinct regarding its prevalence. Total shrub cover was greater overall in the burned acreage as well, but again this was a numerical distinction only.

With shrubs accounting for nearly all of the ground cover in both stand portions, herbs were sparsely represented, with only bottlebrush squirrel tail (*Elymus elymoides* [Raf.] Swezey), woolly mule-ears (*Wyethia mollis* A. Gray), and rose thistle (*Cirsium andersonii* [A. Gray] Petr.) residing in either treatment while Sandberg bluegrass (*Poa secunda* J. Presl) and Holboell's rockcress (*Arabis holboellii* Hornem.) were exclusive to the burned and unburned treatments, respectively. Of these, only for the bluegrass was a significant difference between treatments detected, which reflected in part its confinement to the burned acreage but also its constituting one-half of the total herb coverage there (Table 3). Nevertheless, total herb cover was nearly identical in the two stand portions.

Forest floor fuels

With regard to downed and dead fuel dry weights, 1+10 hr timelag loading was significantly greater, by 253%, in the unburned than the burned stand portion, while the disparities between treatments in the 100 hr and 1000-hr categories were non-significant (Table 4). Although fine fuels were disproportionally represented in total fuel weights regardless of treatment, with the 1+10 hr categories constituting two-thirds of the total in the burned stand portion and nearly all of it in the unburned portion, the disparity was statistically distinct, and a total loading that was 161% greater in the latter than the former was as well. Despite the lack of significance between treatments in 1000 hr loading, its proportional representation in the burned treatment was significantly greater than that in the unburned acreage. As for fuel bed depth, such in the unburned stand portion that exceeded the depth in the burned portion by 359% was an especially apparent, and statistically significant, distinction between treatments.

Linkages between variables

The overstory subset of the simple linear regression series generated 11 significant models, with both positive and negative correlations prevailing therein (Table 5). Specifically, overstory height, DBH, live crown length, basal area, and biomass were all negatively related to snowbrush ceanothus cover but positively related to that of prostrate ceanothus. Additionally, the live crown ratio within the overstory was negatively correlated with the latter. For the significant models in the overstory subset in its entirety, the variation in the dependent variables explained by that in the independent variables ranged from 35% to 75%, with the two models divulging associations of basal area and biomass with prostrate ceanothus of particular strength.

For the natural regeneration subset, only five models proved to be significant, and all of them featured positive correlations (Table 5). These disclosed correlations between the Jeffrey pine seedling count and percentage and the percentage of this species in the overstory, one between the white fir seedling percentage and the percent representation of this species in the overstory, another between the white fir seedling count and green leaf manzanita cover, and lastly, one between the Jeffrey pine sapling percentage and snowbrush ceanothus cover. Ranging from more than 35% to more than 75% with regards to the variation in the dependent component explained by that in the independent counterpart, the model divulging an association between the percentages of Jeffrey pine among seedlings and overstory constituents was the strongest within this subset by a substantial margin.

Easily the largest of the three regarding significant models, the forest floor fuels subset produced 24 of them, with most disclosing positive relationships (Table 5). Specifically, 1+10 hr and total weights plus fuel bed depth were positively related to overstory height, DBH, basal area, and biomass along with prostrate ceanothus cover, total weight and fuel depth were positively related to live crown length, and 1000-hr fuel percentage was positively related to live crown ratio and green leaf manzanita cover. Negative correlations entailed pairings of 1+10 hr weight and percentage, total weight, and fuel depth with live crown ratio plus another coupling the 1+10 hr percentage with green leaf manzanita. The two strongest models computed in the study were in this subset, specifically the ones disclosing relationships between fuel depth and overstory height and biomass, each of which explained more than 80% of the variation in the dependent components, while other models of notable strength included those divulging associations of 1+10 hr weight with live crown ratio and biomass along with the two coupling fuel depth with live crown ratio and basal area, which accounted for at least 70% of such variation. An additional indication of the overall strength of this subset is that only four its many significant models explained less than 50% of the variation in the dependent components.

	Fire treatment		
Fuel	Burned	Unburned	P-value
1+10 hr (kg ha^{-1})	27841	98403.8	0.0015
100 hr (kg ha^{-1})	1597.2	2326.6	0.5947
1000 hr (kg ha^{-1})	12305	8145	0.5041
Total fuel (kg ha^{-1})	41743.2	108875.4	0.0035
1+10 hr (%)	66.7	90.4	0.049
100 hr (%)	3.8	2.1	0.4052
1000 hr (%)	29.5	7.5	0.0492
Fuel depth (cm)	3.2	14.7	<0.0001

[1]Each mean is based on values from six plots (n=6).

Table 4: Downed and dead fuel loading by time lag category and in total in a Sierra Nevada conifer stand as influenced by wildfire[1].

Independent variable	Dependent variable	Correlation	Model F-test p-value	Model r^2
Overstory subset:				
Snowbrush ceanothus cover	Height	Negative	0.0219	0.4237
Snowbrush ceanothus cover	DBH	Negative	0.012	0.4838
Snowbrush ceanothus cover	Live crown length	Negative	0.0232	0.4176
Snowbrush ceanothus cover	Basal area	Negative	0.0307	0.3873
Snowbrush ceanothus cover	Biomass	Negative	0.0203	0.4314
Prostrate ceanothus cover	Height	Positive	0.004	0.5804
Prostrate ceanothus cover	DBH	Positive	0.0104	0.4979
Prostrate ceanothus cover	Live crown length	Positive	0.0415	0.3533
Prostrate ceanothus cover	Live crown ratio	Negative	0.0023	0.6209
Prostrate ceanothus cover	Basal area	Positive	0.0003	0.7385
Prostrate ceanothus cover	Biomass	Positive	0.0002	0.7538
Natural regeneration subset:				
Jeffrey pine percentage	Jeffrey pine seedling count	Positive	0.0378	0.364
Jeffrey pine percentage	Jeffrey pine seedling percentage	Positive	0.0022	0.7604
White fir percentage	White fir seedling percentage	Positive	0.0407	0.4159
Green leaf manzanita cover	White fir seedling count	Positive	0.0356	0.3709
Snowbrush ceanothus cover	Jeffrey pine sapling percentage	Positive	0.0415	0.5356
Forest floor fuels subset:				
Height	1+10 hr fuel weight	Positive	0.004	0.5791
Height	Total fuel weight	Positive	0.0042	0.5754
Height	Fuel depth	Positive	<0.0001	0.8334
DBH	1+10 hr fuel weight	Positive	0.0339	0.3761
DBH	Total fuel weight	Positive	0.0313	0.3852
DBH	Fuel depth	Positive	0.001	0.6772
Live crown length	Total fuel weight	Positive	0.0408	0.3552
Live crown length	Fuel depth	Positive	0.0067	0.5371
Live crown ratio	1+10 hr fuel weight	Negative	0.0003	0.7396
Live crown ratio	Total fuel weight	Negative	0.0021	0.6275
Live crown ratio	1+10 hr fuel percentage	Negative	0.0082	0.5189
Live crown ratio	1000 hr fuel percentage	Positive	0.0314	0.3846
Live crown ratio	Fuel depth	Negative	0.0003	0.7519
Basal area	1+10 hr fuel weight	Positive	0.0007	0.6976
Basal area	Total fuel weight	Positive	0.0016	0.6483
Basal area	Fuel depth	Positive	0.0002	0.7702
Biomass	1+10 hr fuel weight	Positive	0.0007	0.7011
Biomass	Total fuel weight	Positive	0.0014	0.6584
Biomass	Fuel depth	Positive	<0.0001	0.8186
Prostrate ceanothus cover	1+10 hr fuel weight	Positive	0.0034	0.5932
Prostrate ceanothus cover	Total fuel weight	Positive	0.0044	0.5717
Prostrate ceanothus cover	Fuel depth	Positive	0.0012	0.6679
Green leaf manzanita cover	1+10 hr fuel percentage	Negative	0.0105	0.497
Green leaf manzanita cover	1000 hr fuel percentage	Positive	0.0069	0.5343

[1]Models are based on 12 or fewer observations ($n \leq 12$) depending on the number of plots from which the pertinent values could be derived.

Table 5: Significant simple linear regression models relating selected variables quantified in a Sierra Nevada conifer stand subjected to wildfire[1].

Discussion

With a little more than a half century elapsed since the wildfire that constituted the basis for this study, the comprehensive inventory of the vegetation and forest floor conducted on either side of the interface between the burned and unburned acreages illuminated clear disparities between them but also some emerging commonalities. Regarding the overstory vegetation, the dominant stand constituent for the site in its entirety was Jeffrey pine, the most common yellow pine on the eastern slopes of the Sierra Nevada [29] and one well adapted to the growing environment extant there [30], plus it also features seed dispersal conducive to establishment well removed from the parent tree following disturbance [31,32] which likely contributed to its successful colonization of the burned acreage within the decade after the fire. The other overstory species prevailing on both the burned and unburned substrates was lodgepole pine, another native yellow pine that is notable for its prolific seeding [33], and it is probable that an abundance of sunlight and exposed mineral soil in the aftermath of the fire favored the occupancy of each of these pines where it had burned given their shade intolerance [34] and affinity for mineral seed beds [30,33]. The sole constituent of the overstory in the unburned stand portion not present as such in the burned portion was white fir, which is likely the climax species for this site or at least a component of the climax community [30], but younger stems among those of seed-bearing age are somewhat erratic producers of seed that is often of uncertain viability and seedling establishment is more dependable in partial shade [35]. A perplexing aspect of the absence of any white fir of pole size or larger in the burned acreage is that of the three conifers found on the site, it is the one renowned for the capacity to become established under a dense shrub cover, best exemplified here by the prevalence of snowbrush ceanothus on the burned acreage at the time of inventory, yet eventually emerge to form a tree stand [35,36] whereas Jeffrey and lodgepole pine are no more than minimally able to do so [31,33], which suggests that the two pines may have been well established there before the shrub community was as prominent as it later became. That the basic dimensions of height, DBH, and live crown length of overstory constituents would be significantly larger in the unburned than the burned stand portion was inevitable given the disparity in the average tree age involved as were the greater basal area and above-ground biomass, while the lower live crown ratio in the unburned portion likely reflected the self-pruning capacity of the predominant Jeffrey pine when its crown is subjected to lateral competition [37]. With the exception of the latter, each of these mensurational variables was negatively correlated with snowbrush ceanothus cover in significant regression models, but it is probable that these simply reflect the abundance of this shrub on the burned acreage where trees were younger and therefor smaller far more than they do the general tendency for shrub understories to depress overstory growth in western USA forests [20].

The suitability of burned substrates for natural Jeffrey pine regeneration [38-40] was readily apparent in the significantly greater quantities of seedlings of this species found on that here compared to the unburned acreage, and was further demonstrated by the total confinement of all Jeffrey pine saplings to the burned acreage, with the latter likely a manifestation of the limited ability of this species to persist in the shade of an overstory [31] such as that in the undisturbed stand portion. Nevertheless, irrespective of treatment, most seedlings were Jeffrey pine, and two regression models demonstrated the role of seed source abundance among overstory constituents in this outcome, but another featuring a positive correlation between the percentage of total saplings accounted for by this species and snowbrush ceanothus cover was probably little more than a reflection of the prevalence of this shrub where the fire had burned, which coincidentally was where all Jeffrey pine saplings resided. A general paucity of lodgepole pine seedlings and saplings, including none of the latter in the burned stand portion, may in part simply demonstrate the maladaptation of this species to low light environments, which exceeds even that of Jeffrey pine [34]. Conversely, the ability of both seedlings and saplings of white fir to persist in the shade of either shrub or tree canopies [41] is probably the factor to which a greater overall prevalence of both than of those of lodgepole pine can be attributed, including in the burned acreage where there was no representation of this species in the overstory. Nevertheless, a significant regression model revealing a positive correlation between percentages of white fir among seedlings and overstory constituents again conveyed the importance of seed source availability to natural regeneration, and another revealed such a relationship between the fir seedling count and green leaf manzanita cover, both of which were numerically greater on the burned substrate, but neither the counts nor representation percentages of either white fir seedlings or saplings differed significantly between treatments.

Of the wide array of species represented in the shrub component of the understory, totaling ten in all, only two differed significantly between treatments in their coverage and only one other besides these had any more than a minimal presence on the site. Of the two for which statistical distinctions between treatments prevailed, snowbrush ceanothus was more prevalent by a substantial margin on the burned substrate while prostrate ceanothus was much more abundant on the unburned one. Both of these species are common associates of Jeffrey pine-dominated stands on eastern Sierran sites [29]. Other similarities are that both are actinorhizal N fixing species plus they each produce seed banks from which germinants can emerge after protracted storage and they feature extensive root systems from which new shoots can originate following injury to above-ground tissues, with the latter two factors of particular importance to rapid colonization of disturbed substrates [20,42]. Among dissimilarities are their growth forms, with that of prostrate ceanothus essentially a low mat barely extending above ground level [42,43] and therefore lacking the stature to deprive trees larger than young seedlings of sunlight, and in fact this species has been suspected of creating microsite characteristics that promote natural regeneration of some conifers [20,38,44]. In contrast, the relatively elevated and dense canopy of snowbrush ceanothus permits it to shade forest regeneration of even smaller sapling size so completely that its colonization of disturbed sites, including burned ones, can preclude development of tree stands for decades [20]. However, such was not the case here, at least not completely, as the tree overstory found on the burned acreage was sufficiently developed at the time of inventory to prompt the aforementioned assumption that the establishment of the Jeffrey and lodgepole pine of pole size and larger residing there preceded the proliferation of this shrub. This may have also been true regarding green leaf manzanita, a species with a capacity to retard forest regeneration similar to that of snowbrush [20] and which was numerically more abundant in the burned stand portion. The herbaceous component of the understory was exceedingly sparse on this site, which is common in present day Jeffrey pine forests but constitutes a pronounced divergence in composition from their understory communities prior to the last century [15]. Nevertheless, only five species were in residence between the two stand portions, none with more than marginal representation in either. The only one of the five for which a significant disparity in coverage existed between treatments was Sandberg bluegrass. To large extent, this was a reflection of its occurrence in the burned acreage, which albeit very limited was nevertheless greater than that of any other herbaceous species in either treatment, juxtaposed against its total absence in the unburned acreage. Reductions in overstory density and duff thickness are two ecological drivers likely to prove stimulatory to this species [45], both of which were accomplished by the wildfire here.

Even after a half century, the impact of the wildfire on this site was profound regarding the forest floor, with downed and dead loading of fine fuels still drastically reduced in the burned stand portion, and because the 1+10 hr timelag categories were preponderant regardless of treatment, by extension total loading and fuel bed depth were significantly diminished in the burned acreage compared to that unburned also. Obvious contributing factors include a fire intensity that was sufficient to consume most, if not all, forest floor materials in its path, especially those fine enough to readily ignite, and an aftermath during which very gradual development of a forest cover resulted in a likewise gradual replenishment of litter and duff that had not yet nearly equaled the amounts that had accumulated over a much longer time span in the unburned acreage. Numerous regression models reported here bear witness to the second of these factors, including ones featuring positive correlations that coupled, in various combinations, 1+10 hr loading, total fuels, and fuel bed depth with overstory tree height, DBH, live crown length, basal area, and biomass, thus reflecting the influences of more advanced stand development, plus others that negatively related 1+10 hr fuel weight and percentage, total loading, and bed depth to live crown ratio, which demonstrate the effects of the self-pruning induced by higher tree density on surface deposits of needles and twigs. Wildfire impacts on downed and dead fuel loading in western USA forests have received little attention, but the lone study conducted in the eastern Sierra Nevada documented an exceedingly pronounced combustion of fine fuels [40], suggesting that such a response may now be commonplace with the high intensity conflagrations afflicting the forest stands extant there. Somewhat in contrast to the fine fuels, those of the 1000-hr category were numerically more abundant in the burned than the unburned stand portion, which had the ancillary effect of significantly increasing their percentage of total loading while reducing the fine fuel percentage in the former compared to the latter. Generally, 1000-hr loading in unmanaged, second-growth eastern Sierran Jeffrey pine stands is considerably lower [46] than in those with heavy white fir representation [16,47], and it is probable that their abnormally high prevalence in the burned acreage here, which approximated that in fir-dominated stands more closely than in ones of pure pine, is largely a consequence of the retention of coarse debris remnants of the trees killed in the fire. Of the remaining significant regression models concerned with downed and dead fuels, it is conceivable that the ones positively relating fine and total fuel weights along with fuel depth to prostrate ceanothus cover embodied some degree of causation given the prevalence of this shrub, which can achieve high densities in the mats it forms [20], in the unburned acreage where these fuel measures were highest, but less apparent is such for those positively correlating 1000-hr fuel percentage with live crown ratio and green leaf manzanita cover and one negatively correlating the 1+10 hr percentage with the latter, which seem to simply reflect coincidental spatial associations.

In summary, the partial destruction of an eastern Sierran Jeffrey pine stand by wildfire permitted comparisons between the burned and unburned portions of overstory development, that of the understory community including natural regeneration and the shrub and herbaceous components, and the forest floor in order to assess the degree of recovery in the affected acreage approximately a half century later. Although similar in composition with Jeffrey pine the predominant overstory species throughout accompanied by lodgepole pine as a secondary component in both the burned and unburned acreages, a small contingent of white fir in the latter contrasted against none in the former. Being considerably younger, overstory constituents on the burned substrate were considerably smaller as well with a basal area and above-ground biomass largely commensurate with tree dimensions. Jeffrey pine seedlings were more numerous in the burned stand portion and saplings of this species resided there exclusively. Snowbrush ceanothus was the predominant shrub in the burned acreage while prostrate ceanothus was in that left unburned, with Sandberg bluegrass among the more prevalent herbaceous species but confined solely to the former. Fine and total fuel loads along with fuel bed depth on the burned substrate were greatly exceeded by those on the unburned substrate, with fine fuels proportionally less and 1000 hr fuels proportionally more of the total loading on the former than the latter. This investigation serves to provide land managers with some predictive capacity regarding the direction and pace of unaided forest recovery following wildfire in Jeffrey pine and similar dry site forest types.

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