



The role of disturbance severity and canopy closure on standing crop of understory plant species in ponderosa pine stands in northern Arizona, USA

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ABSTRACT

Concerns about the long-term sustainability of overstocked dry conifer forests in western North America have provided impetus for treatments designed to enhance their productivity and native biodiversity. Dense forests are increasingly prone to large stand-replacing fires; yet, thinning and burning treatments, especially combined with other disturbances such as drought and grazing, may enhance populations of colonizing species, including a number of non-native species. Our study quantifies plant standing crop of major herbaceous species across contrasting stand structural types representing a range in disturbance severity in northern Arizona. The least disturbed unmanaged ponderosa pine stands had no non-native species, while non-native grasses constituted 7–11% of the understory plant standing crop in thinned and burned stands. Severely disturbed wildfire stands had a higher proportion of colonizing native species as well as non-native species than other structural types, and areas protected from grazing produced greater standing crop of native forbs compared to grazed unmanaged stands. Standing crop of understory plants in low basal area thinned and burned plots was similar to levels on wildfire plots, but was comprised of fewer non-native graminoids and native colonizing plants. Our results also indicate that size of canopy openings had a stronger influence on standing crop in low basal area plots, whereas tree density more strongly constrained understory plant standing crop in dense stands. These results imply that treatments resulting in clumped tree distribution and basal areas <math><10\text{ m}^2\text{ ha}^{-1}</math> will be more successful in restoring native understory plant biomass in dense stands. Multiple types and severity of disturbances, such as thinning, burning, grazing, and drought over short periods of time can create greater abundance of colonizing species. Spreading thinning and burning treatments over time may reduce the potential for non-native species colonization compared to immediately burning thinned stands.

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1. Introduction

Dry coniferous forest types in western North America have experienced fire exclusion and grazing by native and non-native ungulates. Resulting dense forests are prone to large-scale wildfires, insect outbreaks, and reduced understory production and biodiversity (Hessburg et al., 1999; Moore et al., 2006; Westerling et al., 2006). In an effort to restore structure and function to these forests, managers have introduced thinning and prescribed burning to create stands that are more productive and hopefully more resilient and resistant to disturbances (Millar et al., 2007). However, with the greater levels and types of disturbances,

efforts to enhance the sustainability of forests may have the unintended consequence of enhancing populations of non-native species (Hobbs and Huenneke, 1992; Keeley et al., 2003). But without such efforts, thick continuous forests are susceptible to stand-replacing wildfires that provide high levels of herbaceous production, but may also be invisable by colonizing non-native species (Hunter et al., 2006).

A number of studies have documented the absence of non-native plant species in undisturbed, high basal area stands (Griffis et al., 2001; Keeley et al., 2003; Wienk et al., 2004). Disturbances such as thinning and prescribed burning may enhance aboveground understory plant standing crop, but these activities may also encourage the establishment of a number of non-native species (Wienk et al., 2004; Moore et al., 2006). Especially severe disturbances, such as pile burning or stand-replacing wildfires, can create ideal habitat for non-native and native colonizing plant species (Crawford et al., 2001; Wolfson et al., 2005; Korb et al., 2005). Thus, land managers are faced with the difficult task of

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reducing tree densities and hopefully reducing fire spread potential without greatly enhancing populations of invasive, non-native plant species (Sieg et al., 2003).

The goal of reducing tree densities and enhancing native plant production in overly dense stands is sometimes confounded by other factors such as grazing (Huffman and Moore, 2004; Moore et al., 2006). Grazed rangelands usually have lower biomass production compared to ungrazed areas (Heitschmidt et al., 2005), and grazing may also enhance colonizing non-native species due to differences in animal preferences and plant tolerances to grazing (Stoddart et al., 1975). In blue oak savanna ecosystems in California, non-native plant cover and richness was higher in areas that were heavily grazed by cattle compared to ungrazed plots (Keeley et al., 2003). However, few studies have attempted to account for the influence of grazing on understory response in forest restoration projects.

A number of previous studies have quantified the relationship between basal area or tree density and understory plant standing crop, but most do not address the influence of variable tree arrangement. Linear and nonlinear models have been developed using basal area and percent overstory canopy cover to estimate understory plant standing crop in ponderosa pine ecosystems (Arnold, 1950; Uresk and Serverson, 1989; Mitchell and Bartling, 1991). These models show a nonlinear trend of decreasing understory plant standing crop in response to increasing tree basal area and percent canopy cover. In addition to these overstory attributes, variations in tree distribution resulting in the formation of large canopy gaps may influence understory development, especially of shade-intolerant species (Naumburg and DeWald, 1999), yet few studies have attempted to account for tree spacing or canopy gap size in predicting understory biomass.

In a previous paper, we documented significant differences in average aboveground plant production among stands varying in overstory structural types and management history (Sabo et al., 2008). In this paper, we explore how disturbance severity, based mostly on the proportion of the overstory removed, influences understory plant standing crop, and evaluate which overstory variables best predict aboveground understory standing crop. We hypothesized that: (1) the understory standing crop of native and non-native colonizing species would increase with increasing disturbance severity, with unmanaged stands representing the least severe disturbance and wildfires the most severely disturbed sites; and (2) overstory attributes that account for variable tree distribution and size of large canopy openings would be better predictors of standing crop than non-spatial measures such as tree basal area that do not include variations in tree distribution.

2. Methods

2.1. Study area

The research stands are located in close proximity to each other near Flagstaff, AZ, USA (35.12°N, 111.39°W) in the Coconino National Forest, at elevations ranging from 2160 to 2440 m. Most soils are basalt derived, and classified as either Typic Argiborolls or Mollic Eutroboralfs (Miller et al., 1995). Average annual precipitation is 57 cm, most of which is received as late summer rain and winter snow (Western Regional Climate Center, 2006). Precipitation in the years of study (1 October to 30 September) was 40.4 cm in 2003–2004 (hereafter referred to as 2004) and 83.9 cm in 2004–2005 (hereafter referred to as 2005).

In 2004, we selected 13 stands: 3 unmanaged, 4 thinned, 3 thinned and burned, and 3 in severely burned areas of a wildfire (Table 1; Bailey et al., 2000). The stands, varying in size from 20 to 80 ha, represented a range of disturbance severity, where severity refers to the degree to which the physical environment is affected

(e.g., overstory removal, soil disturbance, proportion of bare ground). Unmanaged stands, on the low end of disturbance gradient, had not been thinned or burned for 30 years. Thinned, thinned and burned stands were commercially thinned between 1988 and 1995 using whole tree harvest. Non-merchantable trees were skidded to landings and burned off-site. Although over 30% of the basal area was removed in the harvesting (Griffis et al., 2001), thinned stands retained a continuous overstory cover and there was little evidence of soil disturbances from the timber harvest activities. Thinned and burned stands were prescribed burned between 1993 and 1999 by the United States Department of Agriculture (USDA) Forest Service. Fires were characteristic of low intensity fall underburns in this region, and resulted in <10% tree mortality (Griffis et al., 2001). Wildfire stands were in severely burned areas of the 1996 Hochderffer fire where >95% of the trees were killed and bare soil averaged >50% (Crawford et al., 2001). The Forest Service seeded 1.13 kg ha⁻¹ of seed on approximately 81 ha of steep slopes of the wildfire (Rory Steinke, USDA Forest Service, personal communication). The mostly native seed mixture included 50% western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Löve), 30% mountain brome (*Bromus marginatus* Nees ex Steud.), 10% blue flax (*Linum perenne* L.), and 10% “Regreen,” a sterile (non-native) wheat/wheatgrass hybrid.

In 1998, ten 20 m × 50 m plots were laid out on a 150–200-m grid in each of the 13 stands for 130 total plots (Bailey et al., 2000). We selected between two and six of these for our study from a larger pool of plots. The large majority of plots had basal area measurements similar to unmanaged plots; therefore, we chose a small subset that represented the low end of all basal area measurements from all plots. A total of 56 plots were established, of which 28 were fenced in the spring of 2004 to exclude livestock but not native ungulates (e.g., elk, *Cervus elaphus*, that are common in our study area), and were paired with 28 unfenced plots in the same stand that matched as closely as possible the tree basal area, soil type, time since treatment, and dominant understory species found in fenced plots. Livestock numbers were variable, as cattle and sheep were trailed through our stands throughout the growing season in addition to concentrated grazing beginning in early (2004) or mid-July (2005) with stocking rates ranging from 0.26 to 3.1 Animal Unit Months (AUMs; Michael Hannemann, USDA Forest Service, personal communication). We observed livestock (or fresh sign) in all stands. Estimates of native ungulate densities are not available, but elk use on the wildfire in our study area is high, based on another study that found significant impacts of elk browsing on aspen (Bailey and Whitham, 2002). In 2005, we added 12 additional unfenced plots in an attempt to capture plots with basal areas that fell between the range of high basal-area, unmanaged plots, and open wildfire sites (Table 1). These plots were established within two thinned and burned stands, and ranged in basal area from 2.4 to 13.1 m² ha⁻¹. We randomly selected the locations of the low basal area plots from a pool of 24 plots after first surveying the stands for potential sites.

2.2. Overstory

Overstory attributes measured or calculated included: diameter at breast height (dbh; 1.4 m), basal area, tree density, stand density index (SDI), overstory canopy cover, and open canopy ratio. Stand density index, developed by Reineke (1933), is based on trees per hectare, basal area, and average stand tree diameter (Moore and Deiter, 1992). Basal area and trees per hectare were calculated by tallying and measuring dbh of all trees >7.6 cm in each plot. Overstory canopy cover was measured at 1-m intervals using a GRS densitometer (Forestry Suppliers, Inc., Jackson, MS, USA) along two permanent 50-m transects. Percent canopy cover was estimated as the percentage of canopy hits in the 100 points. In addition, we

Table 1
Mean (and standard error) basal area, tree density, overstory canopy cover, stand density index, open canopy ratio, and tree diameter for each stand structural type for trees ≥ 7.6 cm.

Structural type	Basal area (m ² ha ⁻¹)	Tree density (trees ha ⁻¹)	Canopy cover (%)	Stand density index	Open canopy ratio ^a	Tree diameter (cm)	Sample size (n)
Unmanaged	43.8 (11.3)	1171 (256.9)	68.9 (3.9)	767.9 (76.2)	0.17 (0.05)	26.6 (1.2)	3
Thinned	17.4 (2.5)	271 (80.0)	52.9 (5.9)	317.4 (35.4)	0.31 (0.07)	30.0 (3.8)	4
Thinned and burned	13.8 (0.6)	193 (14.5)	40.7 (5.0)	252.2 (38.1)	0.37 (0.02)	28.9 (1.3)	3
Low basal area thinned and burned	7.8 (2.0)	81 (15.8)	25.7 (2.3)	128.0 (16.2)	0.60 (0.08)	33.5 (3.2)	2

^a Open canopy ratio is the longest run of no canopy hits divided by the total number of sampling locations along the transect line.

attempted to capture information on tree distribution in each plot by calculating an “open canopy ratio,” which we defined as the ratio of the longest consecutive non-canopy hits to the total number of sample locations.

2.3. Aboveground understory plant standing crop

Aboveground understory plant standing crop (hereafter referred to as understory standing crop) of understory species was estimated by clipping aboveground biomass in August of 2004 and 2005. Clipping locations were randomly selected along the 50-m transect line of the plot. Plant biomass was clipped to a height of 1.5 cm above the ground surface in 10, 0.25-m² circular frames placed in the 5-m buffer zone around the outside of each 20 m × 50 m plot (but within the grazing exclosures), to avoid disturbing vegetation within the plot. Clippings were sorted by species in the field, placed in paper bags, and then dried in an oven at 60 °C for 48 h and weighed (Wienk et al., 2004). New random numbers along the 50-m transect line were selected in the second year to avoid areas clipped the previous year.

2.4. Statistical analysis

We used split-plot (grazed, ungrazed), repeated measures (2004, 2005) analysis of variance (ANOVA), with $\alpha = 0.05$, to compare response variables among stand structural types and between years (SAS 9.1, 2002–2004). Assumptions of normally distributed data were tested using Shapiro–Wilks test and homogeneous variances were tested using Levene’s test (Neter et al., 1996). Data for all standing crop variables met the assumptions for normality ($p > 0.07$) and homogeneous variances ($p > 0.13$). If the interaction with structural type and year was significant, data from each year were analyzed separately, with a Bonferroni correction ($\alpha/2$). Further, if the interaction between structural type and grazing was significant within a given year, data from grazed and ungrazed plots were analyzed separately, with an additional Bonferroni correction to separate means from grazed and ungrazed stands ($\alpha/8$). When stand structural type main effects differed significantly, means were separated using Tukey’s honestly significant differences (HSD) test.

Understory response variables included total understory standing crop, plus standing crop of native forbs, non-native forbs, native graminoids, and non-native graminoids. Nativity and scientific nomenclature follows United States Department of Agriculture Natural Resource Conservation Service (USDA NRCS, 2007).

We used linear regression to evaluate the relationship of the dependent variable, total understory standing crop, with the independent variables: basal area, stand density, stand density index, canopy cover, and open canopy ratio. We linearized the nonlinear data by taking the natural log of the dependent variables. We did not add one to zero values. Normality of the residuals was evaluated using a Shapiro–Wilks test, which showed no significant deviation from normality. Data from wildfire stands were not used

in the regression analysis due to the large difference in standing crop compared to forested stands.

We ran separate ANOVA and regression analyses for low basal area thinned and burned stands that we added in 2005 using data collected from grazed plots in 2005. The separate analysis was used because there were no ungrazed pairs available for the low basal area thinned and burned plots, and we collected data only in 2005. We used one-way ANOVAs followed by Tukey’s HSD to separate means to quantify differences among stand structural types (unmanaged, thinned, thinned and burned, low basal area thinned and burned, and wildfire stands) for total understory standing crop and standing crop of groups of understory species (i.e., native and non-native graminoids, and native and non-native forbs). Linear regression analyses, including data from unmanaged, thinned, thinned and burned, and low basal area thinned and burned stand structural types, were used to evaluate the relationship of total understory standing crop with independent variables: basal area, stand density, stand density index, canopy cover, and open canopy ratio. Wildfire stands were not used in the regression analysis because of the large difference between standing crop of wildfire stands compared to forested stands.

3. Results

3.1. Influence of disturbance on plant community composition

Our results provided support for the hypothesis that the standing crop of native and non-native colonizing understory species would increase with increasing disturbance severity except for native graminoids which were similar across stand structural types. Native graminoids contributed the largest proportion to total standing crop in all forested stand structural types in both years (Fig. 1A), and total standing crop of native graminoid species did not differ significantly among stand structural types (Table 2). Major native graminoids in terms of standing crop on unmanaged, thinned, and thinned and burned stands were Arizona fescue (*Festuca arizonica* Vasey), squirreltail (*Elymus elymoides* (Raf.) Swezey), mountain muhly (*Muhlenbergia montana* (Nutt.) A.S. Hitchc.), and sedges (*Carex* spp.). In contrast, nearly half (110 kg ha⁻¹) of the total native graminoid standing crop on wildfire plots was comprised of the colonizing species, squirreltail and foxtail barley (*Hordeum jubatum* L.), followed by western wheatgrass.

Both total standing crop and composition of major native forbs varied with disturbance severity and were influenced by grazing. Native forbs constituted between 12% and 30% of the total standing crop across all stand structural types in 2004 and 2005 (Fig. 1A). Native forb standing crop was similar among stand structural types in grazed plots, but did differ among stand structural types in ungrazed plots (Table 2). Ungrazed plots in wildfire stands had significantly more native forb standing crop (246 kg ha⁻¹) than unmanaged stands (21 kg ha⁻¹). Showey goldeneye (*Heliomeris multiflora* Nutt.), Wheeler’s thistle (*Cirsium wheeleri* (Gray) Petrak), and goldenrod (*Solidago* spp.) dominated native forb standing crop in wildfire stands. Two forbs commonly found in ponderosa pine

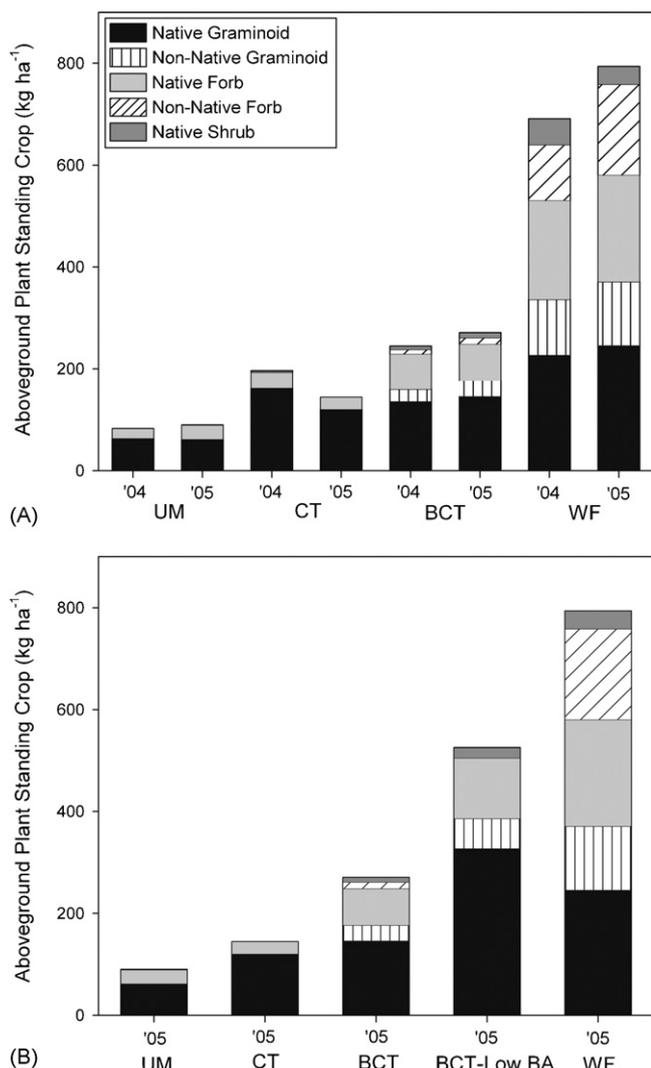


Fig. 1. Mean (grazed and ungrazed) understory standing crop by species groups across stand structural types (A) during 2004 and 2005; (B) in grazed only plots in 2005 among stand structural types including low basal area thinned and burned plots. Abbreviations: unmanaged (UM), commercially thinned (CT), thinned and burned (BCT), low basal area thinned and burned (BCT-low BA), and wildfire (WF).

stands in this region, Silvery lupine (*Lupinus argenteus* Pursh) and Douglas' knotweed (*Polygonum douglasii* Greene) were among the few forbs in unmanaged stands.

In support of our hypothesis, standing crop of both non-native graminoids and forbs increased with increasing disturbance severity. In both sampling years, unmanaged and thinned stands were nearly devoid of non-native graminoid species, but non-native graminoids accounted for 7–11% of the total standing crop on thinned and burned stands, and 16% on wildfire stands (Fig. 1A). The non-native graminoid standing crop was significantly different among stand structural types (Table 2). Wildfire stands had significantly more non-native graminoid standing crop than thinned stands. Non-native graminoids were mostly absent with only trace amounts found in unmanaged (0 kg ha^{-1}) and thinned stands (0.04 kg ha^{-1}), but constituted an average of 125 kg ha^{-1} on wildfire sites. Cheatgrass (*Bromus tectorum* L.) was the dominant non-native graminoid in wildfire stands and represented 61 kg ha^{-1} of the non-native graminoid standing crop. In addition, crested wheatgrass (*Agropyron cristatum* L. Gaertn.), intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey), Kentucky blue-

Table 2

Results of analysis of variance for structural type effects on standing crop of major species groups. For variables with significant interactions ($\alpha = 0.05$), main effects are not given. In these cases, data from each individual year or grazed and ungrazed plots were analyzed separately, with Bonferroni adjustments to maintain the overall significance level.

Response variable	P-value	α
Native graminoid standing crop		
Structural type	0.371	0.05
Year	0.679	
Grazing	0.100	
Structural type * year	0.072	
Structural type * grazing	0.488	
Native forb standing crop		
Structural type	– ^a	0.05
Year	0.552	
Grazing	–	
Structural type * year	0.878	
Structural type * grazing	0.011	
Grazed [structural type effect] ^b	0.052	0.025
Ungrazed [structural type effect]	0.018	
Non-native graminoid standing crop		
Structural type	0.042	0.05
Year	0.379	
Grazing	0.296	
Structural type * year	0.732	
Structural type * grazing	0.500	
Non-native forb standing crop		
Structural type	–	0.05
Year	–	
Grazing	0.618	
Structural type * grazing	0.875	
Structural type * year	<0.001	
2004 [structural type effect]	0.023	0.025
2005 [structural type effect]	<0.001	

^a Indicates an interaction between main effects.

^b Indicates how the interaction was analyzed.

grass (*Poa pratensis* L.), and smooth brome (*Bromus inermis* Leyss.) were other non-native graminoid species in wildfire stands. Increasing disturbance severity also influenced the standing crop of non-native forb species, but due to the significant interaction between structural type and year (Table 2), we analyzed each year's data separately. In both 2004 and 2005, non-native forb standing crop differed among stand structural types (Table 2), with the highest levels occurring on wildfire stands. Non-native forbs were not detected on unmanaged, thinned, and thinned and burned stands in 2004, but constituted 7% of the total standing crop on wildfire stands (Fig. 1A). In 2005, 22% of total standing crop on wildfire stands was contributed by non-native forbs. This pronounced difference in non-native forb standing crop in 2005 on wildfire sites was largely attributed to common mullein (*Verbascum thapsus* L.), which in 2004 averaged 27 kg ha^{-1} and increased to an average of 140 kg ha^{-1} in 2005. In addition to common mullein, other non-native forbs, in decreasing standing crop, were: Dalmatian toadflax (*Linaria dalmatica* (L.) P. Mill.), yellow salsify (*Tragopogon dubius* Scop.), Russian thistle (*Salsola kali* L.), prickly lettuce (*Lactuca serriola* L.), common dandelion (*Taraxacum officinale* G.H. Weber ex Wiggers), lambsquarters (*Chenopodium album* L. var. album), and bull thistle (*Cirsium vulgare* (Savi) Ten.).

3.2. Low basal area thinned and burned plots

Total understory standing crop in low basal area plots (518 kg ha^{-1}) was greater than in unmanaged, thinned, and thinned and burned stand structural types and similar to wildfire stands ($p < 0.001$). Native graminoids constituted 62% of the total standing crop in low basal area thinned and burned plots (Fig. 1B);

Arizona fescue and mountain muhly were the dominant species. Native forbs constituted 23% of the total standing crop in low basal area thinned and burned plots. Non-native graminoids constituted 11% of the total understory standing crop on low basal area thinned and burned plots (Fig. 1B), and did not differ ($p = 0.290$) from standing crop of non-native graminoids on other grazed stand structural types in 2005. Kentucky bluegrass constituted the majority of the majority non-native graminoid standing crop in low basal area plots. Silvery lupine, trailing fleabane (*Erigeron flagellaris* Gray), small-leaf pussytoes (*Antennaria parvifolia* Nutt.), American vetch (*Vicia americana* Muhl. ex Willd), and groundcover milkvetch (*Astragalus humistratus* Gray) dominated the native forb species standing crop in low basal area plots. Non-native forbs constituted 3% of the total standing crop on low basal area thinned and burned plots, compared to 26% on wildfire stands. Standing crop of non-native forbs (20 kg ha^{-1}) on low basal area thinned and burned plots did not differ from standing crop on wildfire stands (146 kg ha^{-1}), but non-native forb standing crop on these two stand types was greater ($p = 0.043$) than standing crop on unmanaged and thinned stands. Dalmatian toadflax and common mullein dominated non-native forb standing crop in low basal area thinned and burned stands. Non-native forb standing crop on wildfire stands was dominated by common mullein.

3.3. Overstory attributes as predictors of total aboveground understory plant standing crop

Regression analyses indicated that most overstory attributes were useful for predicting standing crop in forested stands. These metrics explained between 30% and 90% of the variation in standing crop, with relatively higher r^2 values in the wet year (2005) and on ungrazed plots compared to in the dry year and on grazed plots (Table 3). Tree density (trees ha^{-1}) was the best predictor of understory standing crop on grazed plots in the dry year, but either overstory canopy cover (ungrazed plots in the dry year) or open canopy ratio (grazed and ungrazed plots in the wet year) explained the greatest amount of variation otherwise (Table 3).

Regressions of 2005 understory standing crop in low basal area thinned and burned plots and other grazed non-wildfire plots indicated that overstory canopy cover ($r^2 = 0.68$; $p < 0.001$; $\log(y) = 6.82 - 0.04x$) was the best predictor of standing crop. Standing crop was also significantly correlated with basal area ($r^2 = 0.63$; $p < 0.001$; $\log(y) = 6.03 - 0.04x$), open canopy ratio ($r^2 = 0.65$; $p = 0.002$), tree density ($r^2 = 0.53$; $p = 0.009$; $\log(y) = 5.76 - 0.002x$), and SDI ($r^2 = 0.54$; $p = 0.006$; $\log(y) = 5.76 - 0.002x$).

Table 3

Relationship between mean understory standing crop in grazed and ungrazed plots (kg ha^{-1}) and basal area, tree density, stand density index (SDI), canopy cover, and open canopy ratio across the three stand structural types (unmanaged, commercially thinned, and thinned and burned, $n = 44$) and within each year.

	2004				2005			
	Grazed		Ungrazed		Grazed		Ungrazed	
	r^2	P-value	r^2	P-value	r^2	P-value	r^2	P-value
Basal area ($\text{m}^2 \text{ha}^{-1}$)	0.28	0.063	0.60	0.002	0.40	0.021	0.65	<0.001
	$\log(y) = 5.58 - 0.020x$		$\log(y) = 6.18 - 0.052x$		$y = 428.76 - 7.07x$		$y = 659.10 - 19.30x$	
SDI	0.36	0.03	0.55	0.004	0.62	0.001	0.82	<0.001
	$\log(y) = 5.65 - 0.001x$		$\log(y) = 6.08 - 0.002x$		$\log(y) = 5.93 - 0.002x$		$\log(y) = 6.46 - 0.003x$	
Canopy cover (%)	0.49	0.008	0.64	0.001	0.76	<0.001	0.80	<0.001
	$y = 420.51 - 4.18x$		$\log(y) = 6.47 - 0.027x$		$y = 609.63 - 7.65x$		$\log(y) = 6.88 - 0.035x$	
Open canopy ratio ^a	0.43	0.015	0.60	0.002	0.85	<0.001	0.92	<0.001
	$y = 80.20 + 354.71x$		$y = -15.38 + 743.50x$		$y = -51.78 + 733.84x$		$y = -62.28 + 922.94x$	
Tree density (trees ha^{-1})	0.66	<0.001	0.30	0.05	0.59	0.002	0.28	0.063
	$\log(y) = 5.85 - 0.002x$		$\log(y) = 5.67 - 0.001x$		$\log(y) = 5.95 - 0.002x$		$y = 461.10 - 0.255x$	

^a Open canopy ratio is the longest number of no canopy hits divided by the total number of points along the transect line.

4. Discussion

4.1. Influence of disturbance on plant community composition

As we predicted, unmanaged stands were characterized by high tree density, low disturbance, and few colonizing plant species—either native or non-native. Light commercial thinning, with or without prescribed burning, did not significantly enhance the proportion of colonizers. This is in agreement with other studies that have shown that when overall tree density remains high, minimal disturbances such as light thinning that removes few trees or low-severity prescribed burning have little impact on plant community production or composition (Uresk and Severson, 1998; Wienk et al., 2004; Keeley et al., 2003). Also in line with our predictions, the most severely disturbed wildfire site supported the greatest standing crop of native and non-native colonizing species. Native graminoids and forbs constituted the majority of standing crop on the wildfire, although species composition differed from other stand structural types. In contrast to the native bunchgrasses that dominated unmanaged, thinned, and thinned and burned stands, native species on the wildfire sites included colonizing species such as squirreltail (Naumburg and DeWald, 1999; Laughlin et al., 2004) and foxtail barley (Badger and Ungar, 1991), plus a native species seeded after the wildfire, western wheatgrass. The native bunchgrasses, mountain muhly and Arizona fescue, can be slow to expand into disturbed areas (Vose and White, 1991; Naumburg and DeWald, 1999; Laughlin et al., 2004). The impacts on species composition we observed on wildfires sites may be evident for decades, especially in the face of droughts and continued grazing (Bataineh et al., 2006).

In contrast to the nominal standing crop of non-native plants in the forested stand structural types, the nearly complete elimination of trees on severely burned areas of the wildfire enhanced both non-native forbs and non-native grasses compared to high density forested stands. We attributed the suite of non-native forbs found on the wildfire to a combination of available propagules and the severity of the fire, as well as the high amount of post-fire precipitation. Some species, such as yellow salsify and common dandelion, are ubiquitous in this region and were likely present before the fire. Other forbs, including Dalmatian toadflax and common mullein, are enhanced by especially severe disturbances that remove the overstory and increase bare ground (Ffolliott et al., 1977; Gross and Werner, 1978; Dodge et al., 2008). Common mullein is usually short-lived following disturbances, but seeds readily germinate following adequate moisture, as occurred in 2005 in our study and on Moore et al.'s (2006) restoration plots.

This supports previous work that indicates that precipitation patterns, in addition to fire severity and availability of propagules, influence the degree to which non-native species dominate following fires (Keeley et al., 2005; Hunter et al., 2006; Kerns et al., 2006).

The non-native grasses on the wildfire sites also reflect available propagules, which for some species were the result of intentional seeding. We did not detect the non-native wheat hybrid in the wildfire seed on our plots. However, four perennial grasses commonly included in seed mixes in this region (Doran, 1951; Rich, 1962; Fowler et al., 2008) were contributors to non-native grass standing crop on wildfire sites: smooth brome, intermediate wheatgrass, crested wheatgrass, and Kentucky bluegrass. Intentionally seeded species were contributors to the post-fire plant community composition in other studies (Hunter et al., 2006; Kuenzi et al., 2008), and such practices may unintentionally introduce other species such as cheatgrass (Keeley et al., 2006). Cheatgrass was the dominant non-native grass on our wildfire sites, constituting nearly 8% of the total standing crop. Whether it eventually disappears, as was observed following a wildfire in California (Countryman and Cornelius, 1957), or dramatically expands, as noted by Floyd et al. (2006) following wildfires in Mesa Verde National Park, remains to be seen. Given the risk of accidentally introducing species such as cheatgrass, the need for seeding projects should be carefully assessed.

Our analyses that included data from the low basal area thinned and burned plots added in 2005 indicated that these plots had similar standing crop to wildfire sites, but were dominated by late successional bunchgrasses and fewer colonizing native species. However, these low basal area plots also had a greater standing crop of non-native forbs compared to unmanaged and thinned stands. The same two forbs that dominated on the wildfire also constituted the majority of the non-native forb standing crop on the low basal area plots. Thus, treatments designed to enhance understory standing crop in areas with high non-native propagule availability may also inadvertently enhance populations of some invasive non-native species (Wienk et al., 2004).

4.2. Overstory attributes as predictors of total aboveground understory plant standing crop

Previous studies have documented the interaction between overstory attributes and understory standing crop by primarily using measures of tree density. We hypothesized that overstory metrics based on the size of the largest canopy openings would be better predictors of understory standing crop compared to measures such as tree density. Support for our hypothesis was found to some degree, especially in the wet year, in ungrazed plots and in low basal area plots. However, most metrics we tested were significant predictors of understory standing crop, and tree density (trees ha⁻¹) explained the highest percentage of variation in standing crop in the dry year. Stand density index, which incorporates tree density, basal area, and quadratic mean tree diameter, has also been found to be a useful predictor of standing crop (Moore and Deiter, 1992).

Our study was dominated by high basal area plots with little standing crop, which limited our ability to assess the value of overstory attributes across a number of plots with low enough basal area to support a range in standing crop responses. The addition of the low basal area thinned and burned plots quantified the importance of attaining basal areas below the threshold in order to observe an understory response in ponderosa pine stands. Basal areas below 10 m² ha⁻¹ were needed to increase standing crop, which was similar to Uresk

and Severson's (1989) results. In contrast to our hypothesis, our results suggest that in high basal area stands, which are too dense to support a small understory standing crop, tree distribution does not matter. However, in low basal area stands, overstory cover and open canopy ratio explained the greatest amount of variation in standing crop. Therefore, we suggest that the significant response of standing crop in low basal area stands is attributed, in part, to tree spatial pattern.

4.3. Conclusion and management implications

Our results indicate that in high basal area stands, understory is largely constrained by tree density and less so by the distribution of trees. In contrast, treeless areas burned 8–9 years previously in a wildfire have higher standing crop, as well as a higher proportion of native colonizing and non-native species. Based on our data collected in 2005 in low basal area stands, tree distribution has a greater influence on standing crop than tree density; thinning to <10 m² ha⁻¹ results in standing crop levels similar to those on treeless wildfire plots, but consisting of mostly native late successional plants and fewer non-native species. If the goal is to restore open ponderosa pine forests with a predominantly native plant understory, land managers should consider thinning to basal areas <10 m² ha⁻¹ and clumping leave trees to enhance the size of resulting canopy openings (Covington et al., 1997; Laughlin et al., 2006).

Previous studies have suggested that the low level of native plant cover in high density stands puts these sites at risk to non-native plant invasion following severe wildfires (Harrod, 2001). Hunter et al. (2006) provided some evidence in support of this hypothesis; fire severity was the best predictor of cover of non-native species on three wildfires, but low native species cover was also a significant predictor of high non-native cover. Therefore, there is merit to considering a strategy for restoring historic structural aspects and processes in dense ponderosa pine stands that involve delaying prescribed burning after thinning until understory vegetation is well-established (Laughlin et al., 2008). Moore et al. (2006) found understory standing crop in restoration treatments that were thinned and burned was lower than in thinned treatments four years after the treatments. Thinning promotes increased graminoid standing crop due to increased light and resource availability; however, it has also been documented that prescribed fire can initially decrease graminoid standing crop (Vose and White, 1991; Naumburg and DeWald, 1999). Allowing understory plants to respond to thinning treatments by increasing belowground carbon storage that would allow plants to respond after prescribed fire (Hart et al., 2005) would likely reduce the dominance of non-native plant species compared to burning immediately after thinning in the absence of a well-developed graminoid community. Adapting an incremental approach to restoration activities for ecosystems that are well outside the historic range of variability may be helpful if the goal is to create resilient ecosystems that can respond to future changes in environmental conditions (Millar et al., 2007).

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References

- Arnold, J.F., 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. *J. For.* 48, 118–126.
- Badger, K.S., Ungar, I.A., 1991. Life history and population dynamics of *Hordeum jubatum* along a soil salinity gradient. *Can. J. Bot.* 69, 384–393.
- Bailey, J.D., Wagner, M.R., Smith, J., 2000. Stand treatment impacts on forest health (STIFH): structural responses associated with silvicultural treatments. In: van Riper, C. (Ed.), Proceedings of the Fifth Biennial Conference of Research on the Colorado Plateau, Flagstaff, AZ, pp. 25–27.
- Bailey, J.K., Whitham, T.G., 2002. Interactions among fire, aspen, and elk affect insect diversity: reversal of a community response. *Ecology* 86, 1701–1712.
- Bataineh, A.L., Oswald, B.P., Bataineh, M.M., Williams, H.M., Coble, D.W., 2006. Changes in understory vegetation of a ponderosa pine forest in northern Arizona 30 years after a wildfire. *For. Ecol. Manage.* 235, 282–294.
- Countryman, C.M., Cornelius, D.R., 1957. Some effects of fire on a perennial range type. *J. Range Manage.* 10, 39–41.
- Covington, W.W., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S., Wagner, M.R., 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. *J. For.* 95, 23–29.
- Crawford, J.A., Wahren, C.H., Kyle, S., Moir, W.H., 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *J. Veg. Sci.* 12, 261–268.
- Dodge, R.S., Fulé, P.Z., Sieg, C.H., 2008. Dalmatian toadflax (*Linaria dalmatica*) response to wildfire in a southwestern USA forest. *Ecoscience* 15, 213–222.
- Doran, C.W., 1951. Reseeding trials in a sagebrush–pinyon–juniper area in western Colorado. USDA Forest Service, Rocky Mt. For. Range Exp. Station, Res. Note No. 9. Ft. Collins, CO.
- Ffolliott, P.F., Clary, W.P., Larson, F.R., 1977. Effects of a prescribed fire in an Arizona ponderosa pine forest. USDA For. Serv. Res. Note RM-336, Rocky Mountain Research Station, Fort Collins, CO.
- Floyd, M.L., Hanna, D., Romme, W.H., Crews, T.E., 2006. Predicting and mitigating weed invasions to restore natural post-fire succession in Mesa Verde National Park, Colorado, USA. *Int. J. Wildl. Fire* 15, 247–259.
- Fowler, J.F., Sieg, C.H., Dickson, B.G., Saab, V., 2008. Roadside and adjacent ponderosa pine forest exotic plant species diversity: a pre-/post-prescribed fire comparison in northern Arizona. *Range Ecol. Manage.* 61, 284–293.
- Griffis, K.L., Crawford, J.A., Wagner, M.R., Moir, W.H., 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. *For. Ecol. Manage.* 146, 239–245.
- Gross, K.L., Werner, P.A., 1978. The biology of Canadian weeds: *Verbascum thapsus* and *V. blattaria*. *Can. J. Plant Sci.* 58, 410–413.
- Harrod, R.J., 2001. The effect of invasive and noxious plants on land management in eastern Oregon and Washington. *Northwest Sci.* 75, 85–90.
- Hart, S.C., DeLuca, T.H., Newman, G.S., MacKenzie, M.D., Boyle, S.L., 2005. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *For. Ecol. Manage.* 220, 166–184.
- Heitschmidt, R.K., Klement, K.D., Haferkamp, M.R., 2005. Interactive effects of drought and grazing on Northern Great Plains rangelands. *Range Ecol. Manage.* 58, 11–19.
- Hessburg, P.F., Smith, B.G., Salter, R.B., 1999. Detecting change in forest spatial patterns from reference conditions. *Ecol. Appl.* 9, 1232–1252.
- Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. *Cons. Biol.* 6, 324–337.
- Huffman, D.W., Moore, M.M., 2004. Responses of *Fendler ceanothus* to overstory thinning, prescribed fire, and drought in an Arizona ponderosa pine forest. *For. Ecol. Manage.* 198, 105–115.
- Hunter, M.E., Omi, P.N., Martinson, E.J., Chong, G.W., 2006. Establishment of non-native plant species after wildfire: effects of fuel treatments, abiotic and biotic factors, and post-fire grass seeding treatments. *Int. J. Wildl. Fire* 15, 271–281.
- Keeley, J.E., Lubin, D., Fotheringham, C.J., 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecol. Appl.* 13, 1355–1374.
- Keeley, J.E., Baer-Keeley, M., Fotheringham, C.J., 2005. Alien plant dynamics following fire in Mediterranean-climate California shrublands. *Ecol. Appl.* 15, 2109–2125.
- Keeley, J.E., Allen, C.D., Betancourt, J., Chong, G.W., Fotheringham, C.J., 2006. A 21st century perspective on postfire seeding. *J. For.* 104, 1–2.
- Kerns, B.K., Thies, W.G., Niwa, C.G., 2006. Season and severity of prescribed burn in ponderosa pine forests: implications for understory native and exotic plants. *Ecoscience* 13, 44–55.
- Korb, J.E., Springer, J.D., Powers, S.R., Moore, M.M., 2005. Soil seed banks in *Pinus ponderosa* forests in Arizona: clues to site history and restoration potential. *Appl. Veg. Sci.* 8, 103–112.
- Kuenzi, A.M., Fulé, P.Z., Sieg, C.H., 2008. Effects of fire severity and prefire stand treatment on plant community recovery after a large wildfire. *For. Ecol. Manage.* 255, 855–865.
- Laughlin, D.C., Bakker, J.D., Stoddard, M.T., Daniels, M.L., Springer, J.D., Gildar, C.N., Green, A.M., Covington, W.W., 2004. Toward reference conditions: wildfire effects on flora in an old-growth ponderosa pine forest. *For. Ecol. Manage.* 199, 137–152.
- Laughlin, D.C., Moore, M.M., Bakker, J.D., Casey, C.A., Springer, J.D., Fulé, P.Z., Covington, W.W., 2006. Assessing targets for the restoration of herbaceous vegetation in ponderosa pine forests. *Rest. Ecol.* 14, 548–560.
- Laughlin, D.C., Bakker, J.D., Daniels, M.L., Moore, M.M., Casey, C.A., Springer, J.D., 2008. Restoring plant species diversity and community composition in a ponderosa pine–bunch grass ecosystem. *Plant Ecol.* 197, 139–151.
- Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecol. Appl.* 17, 2145–2151.
- Miller, G., Amos, N., Boness, P., Reyher, D., Robertson, G., Scalzone, K., Steinke, R., Subirge, T., 1995. Terrestrial Ecosystem Survey of the Coconino National Forest. USDA For. Serv., Southwestern Region, Albuquerque, NM, 405p.
- Mitchell, J.E., Bartling, P.N.S., 1991. Comparison of linear and nonlinear overstory–understory models for ponderosa pine. *For. Ecol. Manage.* 42, 195–204.
- Moore, M.M., Deiter, D.A., 1992. Stand density index as a predictor of forage production in northern Arizona pine forests. *J. Range Manage.* 45, 267–271.
- Moore, M.M., Casey, C.A., Bakker, J.D., Springer, J.D., Fulé, P.Z., Covington, W.W., Laughlin, D.C., 2006. Herbaceous vegetation responses (1992–2004) to restoration treatments in a ponderosa pine forest. *Rangeland Ecol. Manage.* 59, 135–144.
- Naumburg, E., DeWald, L.E., 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presence and abundance. *For. Ecol. Manage.* 124, 205–215.
- Neter, J., Kutner, M.H., Nachtsheim, C.J., Wasserman, W., 1996. Applied Linear Statistical Models, fourth edition. McGraw-Hill, San Francisco, CA, United States, 1408p.
- Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* 46, 627–638.
- Rich, L.R., 1962. Erosion and sediment movement following a wildfire in a ponderosa pine forest of central Arizona. USDA Forest Service, Rocky Mt. For. Range Exp. Station, Res. Note No. 76. Ft. Collins, CO.
- Sabo, K.E., Hart, S.C., Hull, C., Bailey, J.D., 2008. Tradeoffs in overstory and understory aboveground net primary productivity in southwestern ponderosa pine stands. *For. Sci.* 54, 408–416.
- SAS, 2002–2004. SAS 9.0 for Windows. SAS, Chicago, IL.
- Sieg, C.H., Phillips, B.G., Moser, L.P., 2003. Exotic invasive plants. In: Friederici, P. (Ed.), Ecological Restoration of Southwestern Ponderosa Pine Forests. Island Press, Washington, USA, pp. 251–267.
- Stoddard, L.A., Smith, A.D., Box, T.W., 1975. Range Management, third edition. McGraw-Hill Series in Forest Resources, New York, United States.
- Uresk, D.W., Severson, K.E., 1989. Understory–overstory relationships in ponderosa pine forests, Black Hills, South Dakota. *J. Range Manage.* 42, 203–208.
- Uresk, D.W., Severson, K.E., 1998. Response of understory species to changes in ponderosa pine stocking levels in the Black Hills. *Great Basin Nat.* 58, 312–327.
- United States Department of Agriculture, Natural Resource Conservation Service., 2007. The PLANTS database. National Plant Data Center, Baton Rouge, LA. <<http://plants.usda.gov>> (07.07.2007).
- Vose, J.M., White, A.S., 1991. Biomass response mechanisms of understory species the first year after prescribed burning in an Arizona ponderosa-pine community. *For. Ecol. Manage.* 40, 175–187.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313, 940–943.
- Western Regional Climate Center., 2006. <<http://www.wrcc.dri.edu>>.
- Wienk, C.L., Sieg, C.H., McPherson, G.R., 2004. Evaluating the role of cutting treatments, fire and soil seed banks in an experimental framework in ponderosa pine forests of the Black Hills, South Dakota. *For. Ecol. Manage.* 192, 375–393.
- Wolfson, B.A.S., Kolb, T.E., Sieg, C.H., Clancy, K.M., 2005. Effects of post-fire conditions on germination and seedling success of diffuse knapweed in northern Arizona. *For. Ecol. Manage.* 216, 342–358.