

Season and severity of prescribed burn in ponderosa pine forests: Implications for understory native and exotic plants¹

Becky K. KERNS², Walter G. THIES & Christine G. NIWA, USDA Forest Service, Pacific Northwest Research Station, Corvallis Forestry Sciences Lab, 3200 SW Jefferson Way, Corvallis, Oregon 97331, USA, e-mail: bkerns@fs.fed.us

Abstract: We investigated herbaceous richness and cover in relation to fire season and severity, and other variables, five growing seasons following prescribed fires. Data were collected from six stands consisting of three randomly applied treatments: no burn, spring burn, and fall burn. Fall burns had significantly more exotic/native annual/biennial (an/bi) species and greater cover of these species (6.5% exotic; 1.7% native) compared to spring and unburned areas. These patterns are likely related to indirect fire effects associated with fire severity and resource availability, rather than direct fire effects due to burn timing. CART models indicated that high native and exotic an/bi richness and cover were associated with overstory gaps and higher fire severity areas, conditions common to fall burns. Exotics may be more successful at exploiting these environments. No treatment differences were found for native perennials. Location was important for explaining native perennial patterns, but richness and cover were also positively associated with lower fire severity, greater tree cover, and coarse woody debris. Expectations for increased native perennial plant diversity and abundance following prescribed fires may not necessarily be met and exotic species spread may compromise other ecosystem attributes. Restoration in these forests presents a challenge as prescribed fires interact with present environmental conditions that are very different from historical ones.

Keywords: *Bromus tectorum*, CART, exotic species, forest understory, ponderosa pine, prescribed fire.

Résumé : Nous avons examiné la richesse et la couverture en herbacées en relation avec la saison et la sévérité des feux, cinq saisons de croissance après des brûlages dirigés. Les données ont été récoltées dans six peuplements forestiers auxquels ont été appliqués au hasard trois traitements : pas de feu, un feu printanier et un feu automnal. Les feux d'automne comportaient significativement plus d'espèces exotiques et indigènes annuelles/bisannuelles (an/bi) et une plus grande couverture de celles-ci (6,5 % d'exotiques; 1,7 % d'indigènes) que les feux d'automne ou que les aires n'ayant pas été brûlées. Ces patrons sont probablement dus aux effets indirects associés à la sévérité du feu et à la disponibilité de la ressource plus qu'à l'effet direct du feu associé à la période de brûlage. Les modèles CART ont indiqués que la richesse et la couverture élevées des espèces exotiques et indigènes an/bi étaient associées à des trouées dans l'étage dominant et à des aires brûlées sévèrement, des conditions courantes à la suite d'un feu d'automne. Les espèces exotiques ont peut être plus de succès à exploiter ces environnements. Aucun effet du traitement n'a été trouvé pour les espèces indigènes pérennes. L'emplacement était important pour expliquer les patrons des espèces indigènes pérennes, mais la richesse et la couverture étaient également associées positivement avec des feux de faible sévérité, une plus grande couverture arborescente et des débris ligneux grossiers. Ainsi, les attentes d'une plus grande diversité et abondance de plantes indigènes pérennes à la suite de brûlages dirigés ne sont peut être pas remplies et la propagation d'espèces exotiques peut compromettre les autres attributs de l'écosystème. La restauration dans ces forêts représente donc un défi puisque les brûlages dirigés interagissent avec les conditions environnementales actuelles très différentes des conditions historiques.

Mots-clés : *Bromus tectorum*, brûlage dirigé, CART, espèces exotiques, pin ponderosa, sous-étage de la forêt.

Nomenclature: Hitchcock & Cronquist, 1973.

Introduction

Historic range of variability concepts and their application to natural disturbance management models and ecological restoration suggest that past conditions and processes provide context and guidance for managing ecological systems today (Mutch & Cook, 1996; Covington *et al.*, 1997; Fulé, Covington & Moore, 1997; Cissel, Swanson & Weisberg, 1999; Landres, Morgan & Swanson, 1999; Moore, Covington & Fulé, 1999; Franklin *et al.*, 2002). Fire has functioned historically as an important dis-

turbance agent and keystone process in forest ecosystems, and many consider the reintroduction of fire into western USA forests, particularly dry forest types, key for sustaining biodiversity and successful land management (Weaver, 1943; Cooper, 1960; Mutch & Cook, 1996; Covington *et al.*, 1997; Fulé, Covington & Moore, 1997; Covington, 2000; Fulé *et al.*, 2002; Wright & Agee, 2004). In dry forests dominated by ponderosa pine (*Pinus ponderosa*), present day stand structure and composition, accumulation of live and dead vegetative wildfire fuel and associated risk of severe fires, and insect and disease outbreaks are regarded as historically uncharacteristic and undesirable. These conditions are commonly attributed to decades of fire exclusion and suppression, timber harvesting, historical periods of overgrazing, and shifts in climate (Covington & Moore,

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²Author for correspondence. Present address: USDA Forest Service, Pacific Northwest Research Station, Western Wildland Environmental Threat Assessment Center, 3160 NE 3rd St., Princeville, Oregon 97754, USA.

1994; Savage, Brown & Feddema, 1996; Tiedemann, Klemmedson & Bull, 2000; Fulé *et al.*, 2002; Wright & Agee, 2004). Social and management goals for these forests, such as reducing the risk of severe wildfires and sustaining and promoting biodiversity, have prompted the use of prescribed fire to reduce fuels, lower stand densities, and alter stand composition. Prescribed fire simulates the frequent low-intensity surface fires considered characteristic of the historic environment of ponderosa pine forests throughout the interior west prior to non-indigenous settlement (Weaver, 1943; Cooper, 1960; Agee, 1993; Covington & Moore, 1994). While the ecological rationale and necessity for prescribed fire treatments are being discussed in the literature (Tiedemann, Klemmedson & Bull, 2000; Fulé *et al.*, 2002; Wright & Agee, 2004), land managers are continuing to use prescribed fire to reduce fuels and the risk of severe wildfires.

Increased native understory herbaceous diversity and abundance are common objectives for ecological restoration using prescribed fire treatments in ponderosa pine forests (Covington *et al.*, 1997). Understory communities contribute to virtually all of the plant biodiversity, regulate many processes (*e.g.*, conifer regeneration, soil retention, nutrient cycling), and provide critical wildlife habitat. The concept that native biodiversity is likely to benefit from restoration of natural conditions and processes is a central tenet of ecological restoration and ecological management frameworks (Grumbine, 1992; Kaufmann *et al.*, 1994; Fulé *et al.*, 2002). However, prescribed fires are now interacting with present and future environmental conditions that are very different from historical ones. Fire is being returned to landscapes where exotic plants are often present, native species may have tenuous or declining populations, native seed banks may be lacking, and tree densities and fuel loading are excessive (Keeley, Lubin & Fotheringham, 2003). Numerous studies have documented the introduction and spread of exotic invasive species after fire (D'Antonio, 2000 and citations within). Some exotic plants are relatively innocuous within their new ecosystems, but others can displace or hybridize with native species and alter ecosystem structure, fire regimes, and biogeochemical, geomorphological, and hydrological processes (Vitousek *et al.*, 1996; Walker & Smith, 1997; Evans *et al.*, 2001). These invasions can impact natural and agricultural systems and create serious ecological and economic problems. In forest ecosystems, exotic invasive species can also significantly inhibit conifer regeneration (Randall & Rejmánek, 1993). Exotic invasive species are significantly impacting forest and rangeland health and productivity in eastern Oregon and Washington (Harrod, 2001).

Prescribed fires are also frequently conducted in the spring, but most historic fires in the Pacific Northwest probably burned in the summer or fall (Agee, 1993; Heyerdahl, Brubaker & Agee, 2001; Wright & Agee, 2004). Air quality, weather, fuel loadings, fire control, outdoor recreation, and other factors often preclude summer burning options. Typical spring weather and fuel conditions generally allow fuel consumption and fire behaviour to be more easily controlled, but spring prescribed fires may not be preferable from an ecological viewpoint (Agee, 1993). Despite recent increases in scientific understanding of the role of distur-

bance and successional or recovery processes in ecosystems, investigations into how season of prescribed burn impacts flora in ponderosa pine forests are limited. Burn timing can directly impact plants by damaging or stimulating them at different developmental stages and indirectly by changing their environment (Platt, Evans & Davis, 1988; Copeland, Sluis & Howe, 2002). Both direct and indirect fire effects can favour or suppress competitors and alter vegetation patterns. Because species vary in the timing of peak sensitivity and response to burning, vegetation patterns in response to fire can also differ by season of burn (Platt, Evans & Davis, 1988; Kauffman & Martin, 1990; Sparks *et al.*, 1998). For example, spring burns may help control early-flowering cool season exotic annuals such as *Bromus* spp. (Whisenant & Uresk, 1990), but may kill seeds of native herbaceous perennials (Parker, 1987).

Our study examined patterns in understory herbaceous native and exotic species richness and foliar cover in relation to season and severity of prescribed fire, forest structure, substrate, and environmental heterogeneity, five growing seasons following prescribed fires in an eastern Oregon ponderosa pine forest. We investigated these patterns using different species groups based on life-history traits: exotic annuals/biennials (an/bi), native an/bi, native perennial forbs, and native perennial graminoids (Table I). We addressed the following questions: (1) For each species group, are there differences in richness and cover among the three burn treatments? (2) What factors (burn treatment, fire severity, overstory stand structure, substrate condition, and environmental heterogeneity) can be used to explain and predict richness and cover for each species group? (3) How do these results and their implications vary by species group and their associated life-history traits?

TABLE I. Plant life history group categories used for analysis and the most common species (> 15% occurrence on cover microplots) for each group.

Group	Species
Exotic annuals/biennials	<i>Bromus tectorum</i> , <i>Cirsium vulgare</i>
Native annuals/biennials	<i>Collinsia parviflora</i> , <i>Collomia grandiflora</i> , <i>Cryptantha torreyana</i> , <i>Epilobium</i> spp., <i>Gayophytum heterozygum</i> , <i>Microsteris gracilis</i> , <i>Montia perfoliata</i>
Native perennial forbs	<i>Antennaria microphylla</i> , <i>Achillea millefolium</i> , <i>Arnica cordifolia</i> , <i>Crepis acuminata</i> , <i>Erigeron corymbosus</i> , <i>Eriogonum heracleoides</i> , <i>Fragaria virginiana</i> , <i>Geranium viscosissimum</i> , <i>Hieracium albertinum</i> , <i>Kelloggia galioides</i> , <i>Lupinus caudatus</i> , <i>Microseris troximoides</i> , <i>Phacelia hastata</i> , <i>Phacelia heterophylla</i> , <i>Phlox longifolia</i> , <i>Senecio integerrimus</i> , <i>Silene menziesii</i> , <i>Thalictrum fendleri</i> , <i>Viola</i> spp.
Native perennial graminoids	<i>Agropyron spicatum</i> , <i>Bromus carinatus</i> , <i>Carex geyeri</i> , <i>Carex rossii</i> , <i>Elymus cinereus</i> , <i>Festuca idahoensis</i> , <i>Koeleria cristata</i> , <i>Melica fugax</i> , <i>Poa juncifolia</i> , <i>Poa nervosa</i> , <i>Poa sandbergii</i> , <i>Sitanion hystrix</i> , <i>Stipa occidentalis</i>

Note: Nomenclature and life history based on Hitchcock and Cronquist (1973) except for *Gayophytum heterozygum* (Lewis & Szwejkowski, 1964).

Methods

STUDY AREA AND EXPERIMENTAL DESIGN

The study area consisted of six stands of mixed-aged ponderosa pine located at the southern end of the Blue Mountains, Emigrant Creek Ranger District, Malheur National Forest, Oregon. Stands are at 1600-1700 m in elevation, with slopes ranging from 3% to 50%. Climate is characterized by a short growing season with annual precipitation averaging 430 mm (unpubl. data provided by the Emigrant Creek Ranger District). Summers are dry, and diurnal temperatures fluctuate widely, with hot days and cold nights. Winter temperatures are low, and snow can accumulate to considerable depths (Franklin & Dyrness, 1988). Snowmelt typically occurs May–June, and spring ephemeral annual and biennial plants emerge. Perennial grasses and forbs are in a period of rapid growth and expansion by mid-June and are dormant by mid- to late August. Mean annual precipitation in 2002 was approximately 50% below average (134 mm in 2002; 269 mm average) based on climate data from the nearest weather station (Drewsey, Oregon), which is approximately 600 m lower in elevation than the study area.

Four close proximity stands (stands 1-4) are located in the Driveway area in the southeastern part of the district at 43° 53' N, 118° 45' W. Soils are well to poorly drained gravelly loams and clay loams derived from basalt, andesite, tuffaceous interflow, altered tuffs, and breccia materials. Stands at Trout (stand 5) and Kidd Flat (stand 6) are located 18 km to the west at 43° 48' N, 118° 56' W and 43° 47' N, 118° 57' W, respectively. Soils at Trout are well to moderately well drained gravelly loams and clay loams derived from basalt, andesite, and tuffaceous interflow materials. Soils at Kidd Flat are well drained and gravelly loams derived from hard to very hard rhyolite. Ponderosa pine is the dominant overstory tree in the study area, but western juniper (*Juniperus occidentalis*) and mountain mahogany (*Cercocarpus ledifolius*) also occur. At the start of this study, trees in these stands were approximately 80-100 y old, with intermittent or frequent individuals of about 200 y old (unpubl. data from the Emigrant Creek Ranger District). Each stand received a consistent thinning prescription in 1994 or 1995, including areas we later delineated as controls. Stands were thinned from below, and no trees greater than 530 mm diameter at breast height were removed.

The study was designed as a randomized complete block with each of the six stands considered a block. Prior to the prescribed fires, each stand was divided into three randomly assigned 7- to 25-ha experimental units (control - no burn, fall burn, and spring burn), yielding a total of 18 experimental units. There were no statistical differences in stand structure (tree density, size, height, basal area) among the experimental units prior to burning (Thies, Westlind & Loewen, 2005). Fall burns took place in late September and early October of 1997, and spring burns took place in mid-June of 1998. Weather conditions at the time of the burns were somewhat similar for the two seasons: temperature: fall from 17 to 21 °C, spring from 16 to 21 °C; relative humidity: fall from 26 to 35%, spring from 30 to 40%; wind speed: fall from 5 to 6 km·h⁻¹, spring from 3 to 11 km·h⁻¹. The ignition pattern was multiple-strip head fires using hand-carried

torches designed to control frontal intensity. Burns were planned to maintain a 60-cm flame length.

Within each experimental unit, six 0.20-ha circular plots were systematically established (except the control at Trout, which had five plots). Due to time constraints, only three plots in each experimental unit (determined randomly) were measured at one site at Driveway, yielding a total of 98 sampled plots. A 100-m buffer between plots and roads and fire lines was maintained most of the time. Because the study was originally established to examine the influence of treatments on black stain root disease and mortality in ponderosa pine, plots were rejected if they fell in areas with few or no ponderosa pine trees (*e.g.*, rock outcroppings, meadows, mountain mahogany stands) (Thies, Westlind & Loewen, 2005). Thus our results are only applicable to forested areas.

Stand and other data were collected prior to burn treatment, but understory vegetation data were not. In this respect, the present study is similar to a retrospective analysis. Although we compare burn treatment units to control areas, we realize that there could have been differences in understory vegetation among treatments prior to burning. However, treatments for this study were assigned randomly, thus it is less likely that treatment assignment coincided with a systematic *a priori* difference across all six replicate stands.

FIELD SAMPLING

To assess vegetation patterns in relation to direct measures of fire severity, we used post-fire data recorded in the summer of 1998 on each 0.20-ha plot. These data included plot values for percent ground blackened, average tree crown scorch height, proportion of trees with crown scorch, average and maximum tree bole scorch height, proportion of trees with bole scorch, and proportion of trees and proportion of basal area that were immediately killed by the fire (Thies, Westlind & Loewen, 2005; Thies *et al.*, in press). For each tree on the plot, average crown scorch height was recorded to the nearest 3.0 cm using a laser rangefinder with inclinometer. For each live tree on the plot, tree bole scorch height was recorded by measuring 4 quadrats, each ninety degrees apart, defined in relation to the slope. Immediate fire-caused mortality was assumed for all trees that had 100% crown scorch in 1998 and that did not regreen in 1999.

We collected understory vegetation data in the summer of 2002, five growing seasons after the prescribed fires using a series of nested plots. In each 0.20-ha circular plot, a concentric 0.03-ha circular subplot and eight 1-m² microplots were established. Two microplots were located 5 and 6 m from the circular plot center in each cardinal direction. Each microplot consisted of a gridded PVC square, and foliar plant cover was recorded by species to the nearest percent and other ground cover was also recorded (*e.g.*, bare soil, rock, litter, coarse woody debris). To increase consistency in ocular estimates of plant cover, the same person recorded cover in almost all the plots throughout the field season. Species that could not be identified due to herbivory, desiccation, immaturity, etc. were assigned to a genus or life-form group such as graminoid, forb, shrub, etc. Presence of all species was recorded in the 0.03-ha subplot, and cumula-

tive species (species not found in the 0.03-ha subplot) were recorded in the 0.20-ha plot. Each site was sampled as close to the vegetative phenological maximum as possible. All unknown species were collected off the plot and identified by Richard Halse, Oregon State University Botany and Plant Pathology Department. For several species, complete off-plot samples were not obtainable, and at the time of this writing, four forb species remain unidentified.

To assess species richness and cover patterns in relation to other potentially important variables, additional data were collected on each plot. O horizon depth was measured 7 m from the plot center in each cardinal direction. Overstory tree canopy cover was measured using a moosehorn densiometer at the plot centre, and 5 and 15 m from the centre in each cardinal direction (total of nine points for each plot). Ponderosa pine trees in the 0.20-ha plot were tallied and DBH (diameter at breast height, 1.4 m above mineral soil measured from the uphill side) was recorded. Slope and aspect were also recorded.

DATA ANALYSIS

To assess how vegetation patterns varied by life-history traits, four species group categories were analyzed (Table I). Except for presentation in the tables and figures, we will abbreviate these plant groups in the text as exotic an/bi, native an/bi, forbs, and graminoids. No winter annuals are present in this ecosystem, and no annual native grasses were found. Perennial exotics and legumes were not distinguished as separate groups because they were uncommon, as were warm season species (C_4). Cover data were generated for each plot by species group by combining the eight 1-m² microplots. For richness, species in each group category were summed using the presence data at two scales (0.03 and 0.20 ha). We chose to focus our analysis on species richness and cover, rather than diversity indices, because these metrics are straightforward, readily understood, easy to communicate to managers and policy makers, and do not obfuscate simple underlying units (McCune & Grace, 2002).

For forest structure and substrate variables, richness, and cover data, statistical tests were conducted using SAS 8.1 and the Proc Mixed ANOVA procedure (block was a random effect, dependant variables were fixed effects). Actual *P*-values are presented and we discuss significance using the following guidelines: significant: $P < 0.05$; marginally significant: $0.05 < P < 0.10$; and weakly significant $0.10 < P < 0.15$. If significant, Tukey's multiple comparison tests were conducted to examine pairwise differences. Count and cover variables were transformed to improve skewed distributions and heteroscedascity (square root and logit, respectively, Sabin & Stafford, 1990). For presentation of results throughout this text, including tables and figures, untransformed means are reported with associated standard errors of the mean.

We used classification and regression tree analysis (CART, Breiman *et al.*, 1984) to analyze relationships between burn treatments, burn severity, forest structure, substrate conditions, environmental heterogeneity, and native and exotic species richness and cover. CART models are basically decision trees and are both descriptive and

predictive. They are nonparametric and ideal for capturing relationships that make sense ecologically but are difficult to reconcile with conventional linear models; they are often preferred for modeling species richness and abundance (Franklin, 1998; De'Ath & Fabricius, 2000; McKenzie, Halpern & Nelson, 2000; Vayssières, Plant & Allen-Diaz, 2000; McCune & Grace, 2002; Kerns & Ohmann, 2004). CART modeling uses binary recursive partitioning based on reduction in deviance (sum of squares) to split the data into increasingly homogeneous groups. This method first fits an over large tree that is then "pruned" back using established procedures to remove branches that do not contribute significantly to the reduced deviance (Breiman *et al.*, 1984). The pruning process is conceptually similar to procedures for selecting the optimum model size for multiple regression (*e.g.*, stepwise).

For model development, we used 23 independent variables: burn treatment (control, spring, fall), stand (1-6), slope, aspect (transformed, Beers, Dress & Wensel, 1966), and all fire severity, forest structure, and substrate variables listed in Table II. The response variables modeled were richness (0.03 ha) and cover for our four species groups (Table I). Full models were developed using default settings in S-PLUS 2000 (stopping criteria = 0.01, minimum group size = 10, minimum split = 5), and final optimum model size was selected using ten-fold cross-validation (Clark & Pregibon, 1993). The optimum model size is equal to the number of final homogenous groups referred to as tree nodes. Because optimum model size suggested from cross-validation will vary for each run, we repeated this procedure 10 times and selected the mean value for our final model size. Response variables for CART models are not commonly transformed because relationship form is not an issue. However, greater weight will be given to data with higher variation, and variable transformation can improve model performance (De'Ath & Fabricius, 2000; Kerns & Ohmann, 2004). Thus, we ran our models on untransformed and transformed (square root and logit as described above) dependent variables and selected the models with the greatest explanatory power considering model size. Explanatory power for the models was assessed using PRD (proportional reduction in deviance), which is analogous to the multiple R^2 of regression.

Results

FIRE SEVERITY, FOREST STRUCTURE, AND SUBSTRATE

Fires conducted in the fall were more severe (Table II). The percent of trees with bole scorch and bole scorch height were marginally higher in the fall units. More trees also died immediately in the fall units, although this was only weakly significant. Results for forest structure and substrate also show significant post-burn differences among treatments. Five growing seasons after burning, fall units had less basal area compared to the control and marginally less basal area compared to spring burn units. A similar pattern was noted for stand density index. Fall units also had thinner O horizons, less coarse woody debris cover, and greater rock and bare soil cover. Evaluation of delayed ponderosa pine tree mortality indicated that significantly more trees died after

TABLE II. Fire severity (measured in 1998), forest structure and substrate conditions (both measured in 2002) in relation to treatments ($n = 6$).

	Treatment			<i>P</i>
	Control	Spring	Fall	
FIRE SEVERITY				
Ground blackened (%)	—	56.1 ± 8.86	58.1 ± 10.9	0.799
Crown scorch height (m)	—	2.7 ± 0.52	5.7 ± 1.80	0.152
Trees w/crown Scorch (%)	—	31.9 ± 6.71	53.3 ± 10.8	0.158
Bole scorch height (m)	—	0.64 ± 0.11	1.7 ± 0.49	0.077
Max bole scorch height (m)	—	1.9 ± 0.70	2.8 ± 0.81	0.293
Trees with bole scorch (%)	—	93.4 ± 2.09	98.5 ± 0.66	0.073
Tree mortality (%)	—	2.5 ± 0.88	7.8 ± 3.40	0.113
Tree mortality BA (%) ¹	—	2.3 ± 1.36	4.2 ± 1.90	0.152
FOREST STRUCTURE ²				
Basal area (m ² ·ha ⁻¹)	18.7 ± 0.41 A	18.1 ± 0.89 A	15.1 ± 1.31 B	0.044
DBH (cm)	30.8 ± 1.82	30.6 ± 1.11	31.9 ± 2.27	0.821
SD DBH (cm) ³	13.4 ± 1.21	14.1 ± 1.84	12.0 ± 1.61	0.375
Stand density index ⁴	63.2 ± 2.49A	61.5 ± 4.10AB	50.3 ± 5.69B	0.118
Canopy cover	35.4 ± 2.60	38.7 ± 2.20	34.4 ± 3.60	0.493
Density (trees·ha ⁻¹)	217 ± 17.62	215 ± 20.72	174 ± 27.23	0.292
SUBSTRATE				
Bare soil (%)	1.7 ± 0.55A	2.8 ± 1.04A	6.9 ± 2.86B	0.022
Coarse wood cover (%)	2.1 ± 0.29A	1.7 ± 0.55AB	0.70 ± 0.36B	0.108
Litter cover (%)	87.2 ± 1.37	86.3 ± 2.44	80.9 ± 5.07	0.357
O horizon depth (cm)	4.4 ± 0.39 A	3.5 ± 0.36 A	2.2 ± 0.23 B	0.002
Rock cover (%)	1.3 ± 0.55 A	2.9 ± 0.71 B	4.0 ± 1.31 B	0.012

Note: Data are means ± SE. *P* values are listed for ANOVA tests, and different letters denote statistically significant and marginally significant differences ($P < 0.10$, unless otherwise noted) for post hoc pairwise Tukey's tests.

¹Proportion of tree basal area that died after the fires.

²Except for canopy cover, stand structure variables are for ponderosa pine only. Small amounts of *Juniperus occidentalis* that occurred on the plots are not included.

³Standard deviation of DBH, a measure of variability in tree size distribution.

the fall fires. Results from related studies provide details for patterns and predictions relating to ponderosa pine tree mortality (Thies, Westlind & Loewen, 2005; Thies *et al.*, in press).

SPECIES RICHNESS AND COVER

Across the study area (98 plots), we encountered a total of 142 species plus four unknowns. Most of species were forbs (105), 15 were grasses, 12 were shrubs, five were trees, four were sedges, and one was a rush. Eighty-nine percent (126) of the species were native. We observed 16 exotic species in the study area, with 14 occurring on our study plots. The most common exotic was bull thistle (*Cirsium vulgare*), occurring on 47% of the 0.03-ha plots and 66% of the 0.20-ha plots. Downy cheatgrass (hereinafter cheatgrass, *Bromus tectorum*) occurred on 37% of the 0.03-ha plots and 54% of the 0.20-ha plots. Common dandelion (*Taraxacum officinale*) was found on 28.5% of the 0.03-ha plots and 51% of the 0.20-ha plots. Prickly lettuce (*Lactuca serriola*) occurred on 12% of the 0.03-ha plots and 20% of the 0.20-ha plots. All other exotics occurred on less than 10% of 0.20-ha plots. At the largest plot scale (0.20 ha), 95% of the plots contained at least one exotic species and most plots (75%) contained two or more. The five plots that were composed entirely of natives were either from control or spring units.

Cover microplots (1 m²) contained on average 5.4 ± 0.19 species (mean ± SE), 5.2 ± 0.18 native and 0.22 ± 0.04 exotic. Average cumulative species richness from the microplots (8 m²) was 16.1 ± 4.0, with a mean of 0.68 ± 0.9 for total exotic richness. The 0.03-ha plots contained 28.4 ±

0.99 species on average, 27 ± 0.94 native and 1.34 ± 0.21 exotic. The 0.20-ha plots contained 40.4 ± 1.3 species on average, 38.1 ± 1.1 native and 2.30 ± 0.22 exotic.

Differences in species richness (0.03-ha scale) and cover in relation to burn treatment for the four species group categories are shown in Figure 1. For the exotic and native an/bi groups, significant differences in species richness in relation to treatment were found at both the 0.03- and 0.20-ha scales. At the 0.03-ha scale there were, on average, 1.8 ± 0.32 exotic an/bi and 4.6 ± 0.73 native an/bi species per plot in the fall burn units, significantly more species compared to both the control and spring units. At the 0.20-ha scale, both spring and fall units had more exotics compared to the control, with the fall units having more exotics than the spring ($P = 0.002$). For natives at this scale, fall units had more species only compared to the control units ($P = 0.01$). No significant differences due to treatment were found for forbs and graminoids (Figure 1; 0.20-ha scale: forbs, $P = 0.85$; graminoids, $P = 0.68$).

Total mean plant cover across the study area was 33.1 ± 2.4%, with 30.6 ± 2.3% native and 2.5 ± 0.80% exotic. We found a significant difference in plant cover in relation to treatment for both the exotic and the native an/bi groups (Figure 1). Mean exotic an/bi cover in fall burn units was 6.5 ± 3.9%, which was significantly greater compared to spring and control units. This pattern was largely driven by bull thistle and cheatgrass. Mean native an/bi cover in the fall burn units was 1.7 ± 0.72%, which was significantly greater compared to spring and control units. No significant differences due to treatment were found for forbs and graminoids (Figure 1).

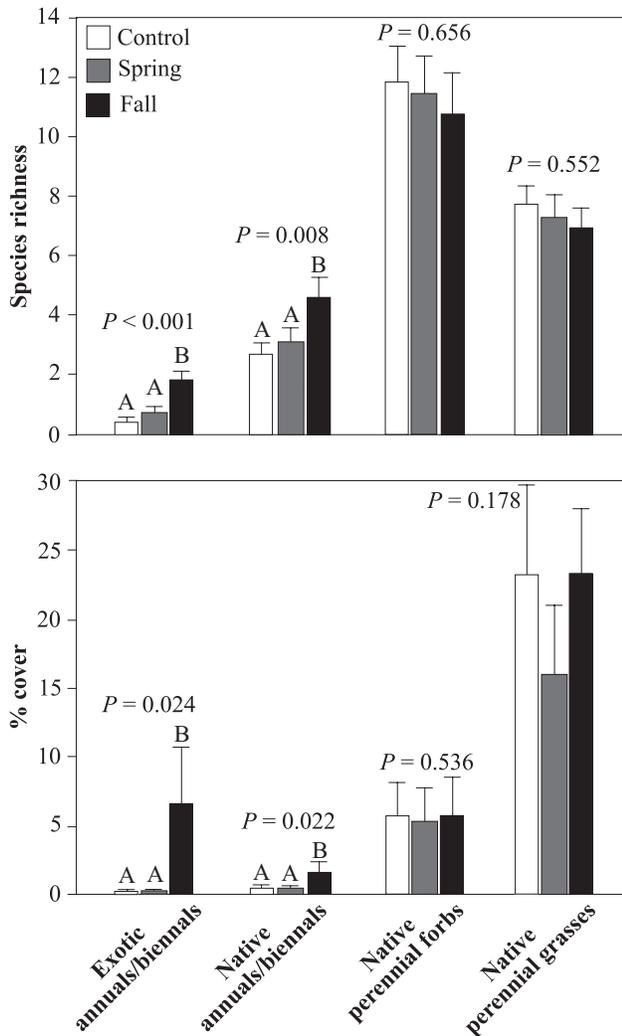


FIGURE 1. Richness (0.03 ha) and cover for each species group in relation to treatment ($n = 6$). Data are means \pm SE. P values are listed for overall ANOVA tests. Different uppercase letters denote statistically significant differences ($P < 0.05$) for *post hoc* pairwise Tukey's tests.

CART MODELS

CART model results are presented graphically and can be read as a flow chart (Figures 2-5). For each tree, the undivided data and the overall mean value are at the top and splits and final nodes are beneath. We present the untransformed model because transformed response variable models were similar in size but had reduced explanatory power.

The model for exotic an/bi richness explained 73% of the variability using five explanatory variables (Figure 2). The first split in the model is based on bole scorch height, and bole scorch height appears again on the left side of the tree. Looking at the right side of the tree the next split is based on tree canopy cover. The left and right sides of this split are strongly homogenous, and two terminal nodes are displayed. Important properties of a CART model are the hierarchical relationships between and among variables and comparison of terminal node values to each other and the overall mean value at the top. For example, this model shows that there is a positive relationship between exotic an/bi richness, bole scorch height, and canopy openness

(canopy cover, basal area) and a negative relationship with tree size variability. Predictor variables differed based on stand location. More species were found in areas where mean bole scorch height was higher and the canopy was more open. These conditions were only associated with six plots in the fall burns. In contrast, very few species were found in areas with lower bole scorch or in unburned areas (at three stands), and where variability in tree size was higher (standard deviation of DBH). These conditions were more common in the spring and control units.

For native an/bi richness, cross-validation suggested a much smaller tree with only two explanatory variables and three terminal nodes (Figure 2). Similar to the exotic richness model, the model shows a positive relationship between richness and bole scorch height and a negative relationship with tree size variability. More species were found in the burned areas where bole scorch height was higher, a condition much more common in the fall burns. The fewest species were found where bole scorch was lower or in unburned areas, and where tree size variability was high. These conditions were more common in the spring burn and control units.

The models for forb and graminoid richness shown in Figure 3 were very different from the an/bi models (Figure 2). The most important predictor (top split) was stand location, the relationship to fire severity (ground blackened) was negative, and cover of coarse woody debris and litter were important predictors. For forbs, species richness was high at one stand in association with coarse woody debris cover. For the other five stands, species richness was low if the percent of ground cover burned was high. If the percent of ground cover burned was less, low richness was also associated with high litter cover at two stands. For graminoids, species richness was high at one stand, and no other variables we measured were important predictors for this stand. For the other stands, graminoid richness was associated with percent ground blackened and stand location were also important.

Very high exotic an/bi cover was found in areas that had a low stand density index, but this condition only occurred for six plots in the fall burn unit (Figure 4). Exotic an/bi cover was also negatively associated with low fire severity or unburned conditions (low mortality). The model shows that the majority of the plots ($n = 87$) had low exotic annual/biennial cover. High native an/bi cover was found in areas where mean crown scorch height was also high, but this condition only occurred for eight plots in the fall burn units. Interestingly, in unburned areas and areas with lower crown scorch height and steeper slopes, native an/bi cover was positively associated with large trees.

Again, CART models for perennial forb and graminoid cover were very different than the an/bi cover models, and the first split is based on stand location (Figure 5). For forbs, the model shows low cover at four stands (1-4) and high cover at another (6). No other variables were important predictors for these stands. For stand 5, the model shows a positive relationship between forb cover and tree canopy cover. For graminoids, the model shows that four stands

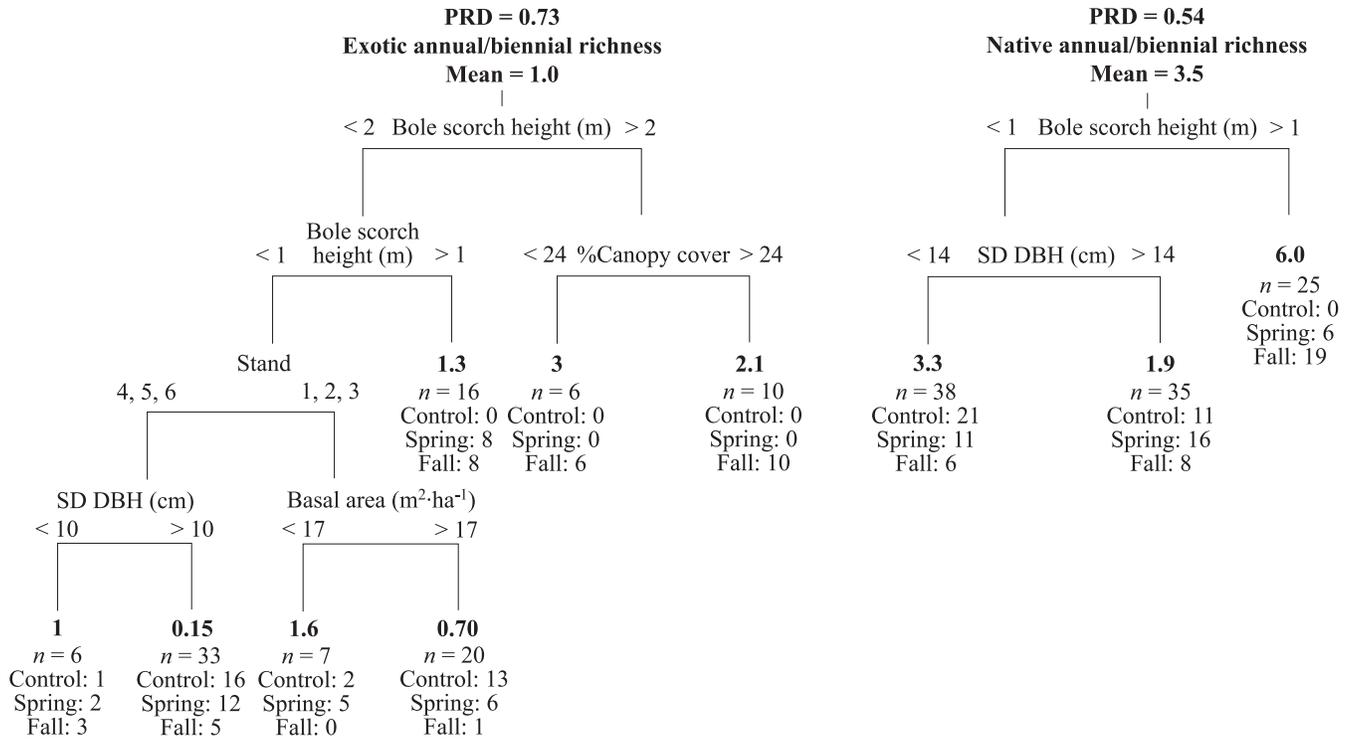


FIGURE 2. CART model results for exotic and native annual/biennial richness ($n = 98$). PRD refers to proportional reduction in deviance, which is analogous to the multiple R^2 of regression. Terminal nodes are denoted by mean values in bold, the number of plots in each group, and distribution by treatment. Detail for variable codes are in Table II.

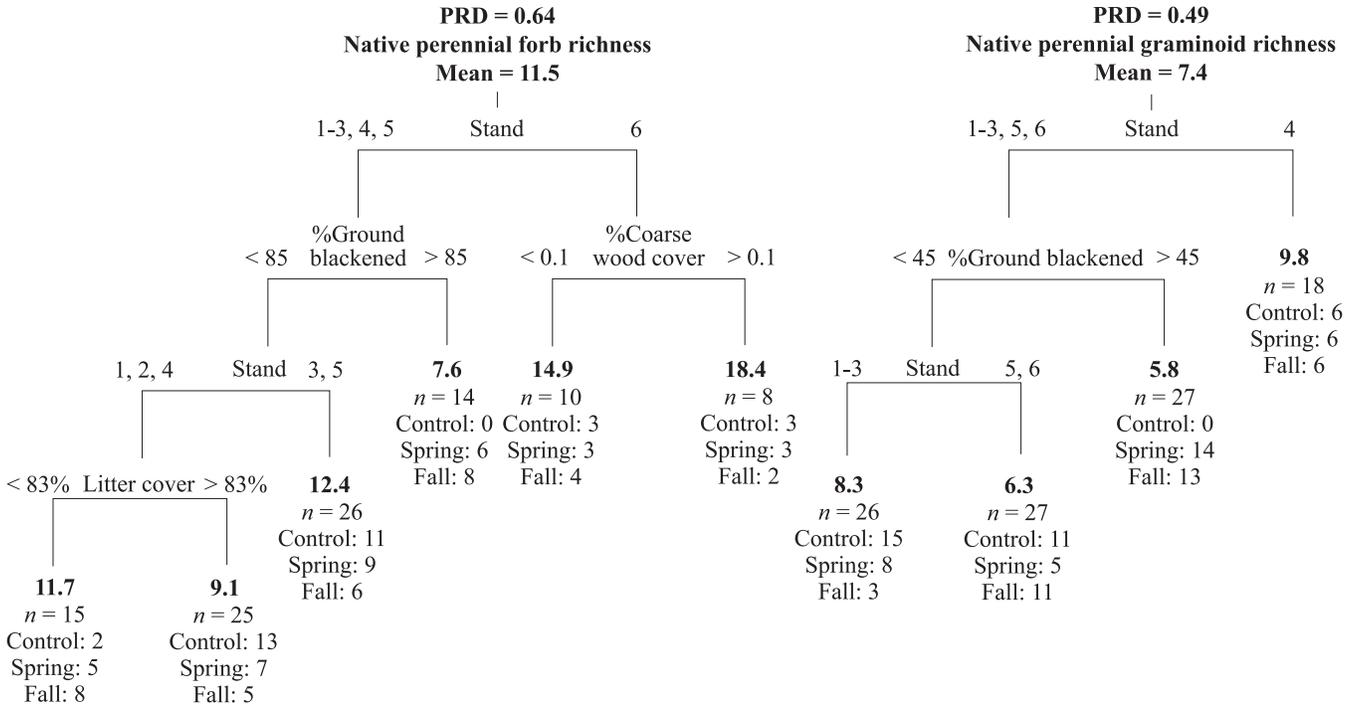


FIGURE 3. CART model results for native perennial forb and graminoid richness. See Figure 2 legend for details.

(1-3, 5) have low cover and no other variables were important predictors. For the other two stands, the model shows that high graminoid cover was associated with areas where fire severity was very low (low mortality) or the area was unburned and litter cover was lower.

Discussion

The most evident understory vegetation pattern in relation to treatment, five growing seasons after prescribed fires, was that areas burned in the fall were characterized by

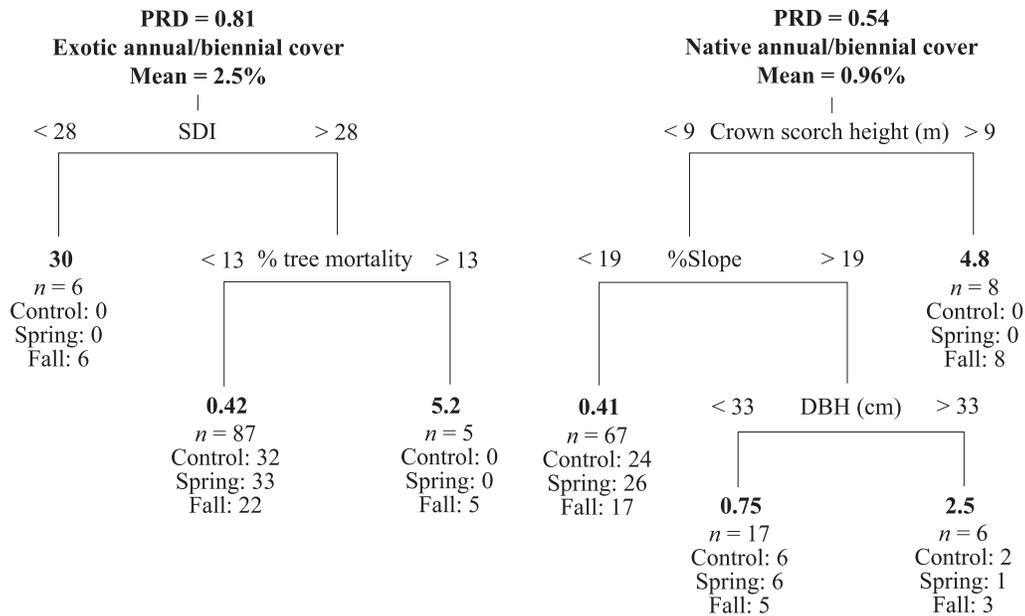


FIGURE 4. CART model results for exotic and native annual/biennial cover. See Figure 2 legend for details.

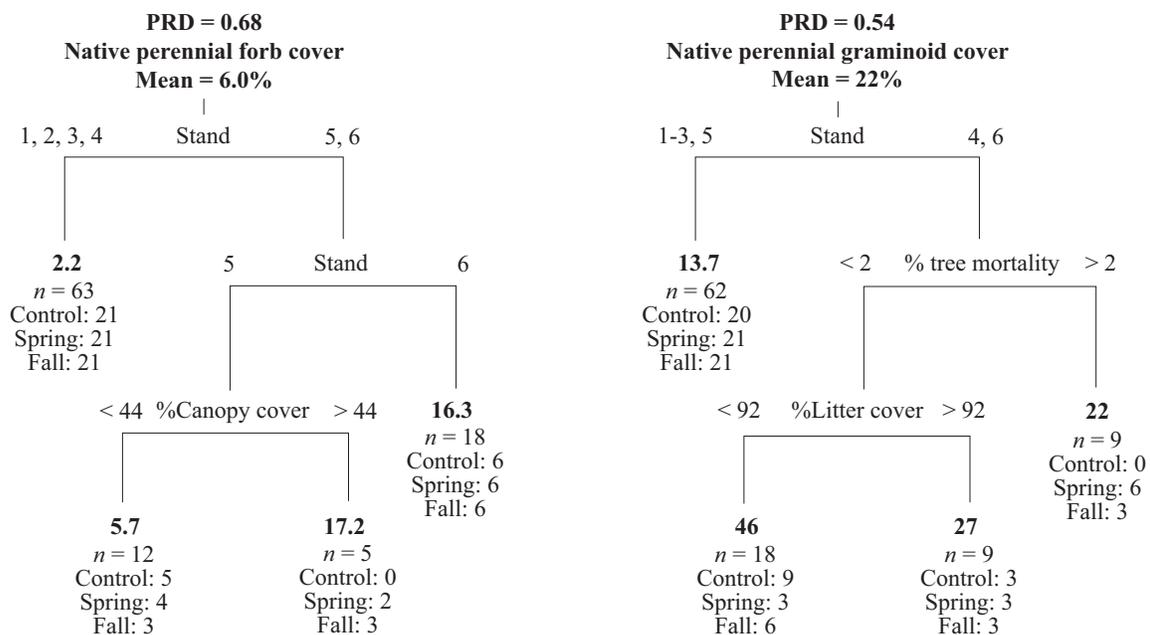


FIGURE 5. CART model results for native perennial forb and graminoid cover. See Figure 2 legend for details.

significantly more, and greater cover of, annual and biennial exotics and natives compared to spring and control areas. These results could be explained by (1) direct burn timing effects related to physiological, phenological, and morphological differences in plants, (2) indirect fire effects related to burn conditions, fire severity, environmental alteration, and changes in resource availability, (3) prior seed bank and seed source conditions, and/or (4) differences in operational activities associated with different burn seasons (e.g., seed sources on people and equipment). We have no way to assess this last possibility. Because treatments were randomly applied, it is unlikely that prior conditions (possibility 3) would have systematically coincided in such a significant manner. Decoupling the first two possibilities mentioned,

both associated with seasonal burning (direct and indirect fire effects), is problematic because season of burn greatly influences fire behaviour due to weather and fuel conditions. However, results from our study provide some important insights. We did not directly measure plant growth status at the time of the burns, but most of the annual and biennial species in this ecosystem are spring ephemerals. Thus, it is possible that spring burning could cause more direct damage to these species compared to fall burning. However, our spring burns were conducted very late because fuels needed to dry adequately.

It is more likely that indirect fire effects related to environmental changes and changes in resource availability were largely responsible for the understory vegetation pat-

terns observed rather than direct fire effects related to burn timing. Model results indicated that high exotic and native annual and biennial richness and cover were associated with overstory gaps and high fire severity areas that occurred more commonly in fall burns, although only a small number of plots were characterized by these conditions. The fall burns were significantly more severe compared to spring burns, and five growing seasons after the fires the fall burn areas had less basal area compared to the control and spring groups, thinner O horizons, less coarse woody debris cover, and greater substrate exposure. Disturbances such as fire alter resource availability by opening forest canopies, reducing above- and belowground competition, exposing mineral soil, and providing new habitat. Native and exotic annuals and biennials are well adapted to exploit these resources. Fluctuation in resource availability, coinciding with available propagules, is a key factor for understanding the invasibility of an environment and influx of both native and exotic increaser species associated with early secondary succession following disturbance (Halpern, 1989; Davis, Grime & Thompson, 2000). Others have also emphasized the importance of fire severity for explaining plant population dynamics, tree growth, and mortality rather than direct fire effects related to burn timing and plant growth status (Glitzenstein, Platt & Streng, 1995; Thies *et al.*, in press).

We detected no significant prescribed fire treatment effects for native perennial forb and graminoid richness and cover. Native perennials may not respond strongly to a single entry prescribed fire (Busse, Simon & Riegel, 2000), or in the case of our study, those effects may not still be present after five growing seasons. Or native forbs and graminoids may persist and maintain consistent cover under a broad range of conditions. Assessment of other studies suggests that there are no consistent responses in native perennial herbaceous plant richness, diversity, or abundance following fires in ponderosa pine forests, but these studies differ considerably in field and analytical methodology, treatment type, and post-fire measurement periods (Harris & Covington, 1983; Armour, Bunting & Neuenschwander, 1984; Covington *et al.*, 1997; Busse, Simon & Riegel, 2000; Griffis *et al.*, 2001; Fulé *et al.*, 2002; Metlen, 2002; Gildar, Fulé & Covington, 2004). Climatic variability can also overwhelm treatment response (Fulé *et al.*, 2002), and the year we collected our data was dry (precipitation 50% below average). Many studies are also limited by constraints on sample and plot size for collection of understory plant data, which can greatly influence the ability to detect change (Korb, Covington & Fulé, 2003). In our study, pretreatment data could have improved our ability to detect change, as location was the most important CART model predictor for both richness and cover for forbs and graminoids. This suggests that different outcomes can be expected at local scales depending on site location, propagule supply and dispersal processes, site conditions, land-use history, and interactive and hierarchical effects.

For each life history group we analyzed using CART, different explanatory variables reflecting species life history traits and disturbance interactions were important for explaining richness and cover; these variables have been well described based on ecological principles (*e.g.*, resource

availability, competition, succession). As discussed above, annual and biennial richness and cover were associated with higher fire severity areas and overstory gaps. Outside of the strong relationship to location, native perennial forbs and graminoids were associated with areas that were unburned or only lightly disturbed by the fires or where key structural components (tree cover, coarse woody debris) were present. However, our models also suggest that low severity fires may benefit native perennials by reducing litter cover.

Our data suggest that ecological controls over the invasion and spread of native and exotic annuals and biennials were somewhat similar, a phenomenon discussed and documented by others (Stohlgren *et al.*, 1999; Levine, 2000; Keeley, Lubin & Fotheringham, 2003; Stohlgren, Barnett & Kartesz, 2003). Many studies have documented exotic invasive species spread after fires, particularly in association with either widespread or local high severity burn conditions (Crawford *et al.*, 2001; Keeley, Lubin & Fotheringham, 2003; Korb, Johnson & Covington, 2004). In our study area, exotic species comprised only 6% of the flora in terms of richness and about 8% of the mean understory total cover and still represent a small percentage of the forest ecosystem, but they can pose a problem as source populations for establishment and spread further into the interior forest. Moreover, our data indicate that exotics such as cheatgrass and bull thistle may be more successful at capturing resources for growth within early successional habitats. Mean native annual and biennial richness was more than three times greater than exotic richness, but mean exotic annual and biennial cover was more than twice the native cover. Differences in species traits and ecological interactions could also potentially lead to dominance by exotic species. For example, lack of herbivores may increase their invasive and persistence capabilities (Carpenter & Cappuccino, 2005), and unlike many native annual and biennial species, exotics may be temporally persistent. Some speculate that exotic species with large ecosystem impacts are those that have no functional analog in the native community (Chapin *et al.*, 1996; Mack and D'Antonio, 1998). Cheatgrass has few functional native analogs (*e.g.*, annual grasses) in many ponderosa pine communities, which are characterized by perennial graminoids, forbs, and shrubs. In the study area there is a native thistle (gray-green thistle, *Cirsium canovirens*), but it is longer-lived and uncommon, suggesting that it functions differently than bull thistle.

Management implications and conclusion

Expectations for increased native perennial plant diversity and abundance following prescribed fires may not necessarily be met, and prescribed fires can create conditions conducive to the introduction or spread of exotic weed species into forest ecosystems. Higher severity prescribed burns, commonly associated with fall burning in our study, create localized gaps favourable for the spread of short-lived exotic and native species. Exotics may be more successful at capturing resources for growth and exploiting these environments.

Invasion of western forests by exotics may be particularly problematic as fire is reintroduced into areas adjacent

to seed sources. Areas burned by prescribed fires (*e.g.*, wild and urban interface, roaded and high use areas) may be more vulnerable to such invasions compared to large wildfires because they can be well positioned for exotic species invasion and spread (Turner *et al.*, 1997; Keeley, Lubin & Fotheringham, 2003). Management activities associated with pre-fire stand and fuel manipulations also introduce source seeds ready to opportunistically colonize treated areas. Small populations of well-known invaders (*e.g.*, cheatgrass) that establish after prescribed fire treatments may be ignored or viewed as hopeless problems. However, small populations can be important seed sources for slow regional spread. Expanded concepts of control and eradication could provide a basis for halting spread and improving control (D'Antonio *et al.*, 2004).

Cheatgrass is of particular concern to managers when prescribed fire is used. Cheatgrass is widely distributed in North America (USDA & NRCS, 2004), is abundant and dominant in western steppe communities (Mack 1981), and has invaded and become dominant in several locations throughout eastern Oregon and Washington (Quigley & Arbelbide, 1997). Our study and others (Zouhar, 2003) suggest that reintroduction of fire in forests, particularly fall burning, can provide conditions conducive to the invasion, spread, and dominance of cheatgrass. Highly competitive traits enhance this species' ability to exploit soil resources after fire and to increase its status in the community (Melgoza, Nowak & Tausch, 1990; Melgoza & Nowak, 1991), and dominance may be persistent (Zouhar, 2003). Pierson, Mack, and Black (1990) pointed out that the spread of cheatgrass into western forests had been restricted because of a variety of factors, one of which is its inability to acclimate photosynthetically to shade. Thus, densely stocked stands that develop following long-term exclusion of fire may inhibit invasion of exotic species (Keeley, Lubin & Fotheringham, 2003).

There are risks associated with not taking action to reduce fuels and severe wildfire and disease outbreaks, but there are also risks associated with fuel reduction activities such as prescribed fire (*e.g.*, fuel reduction *versus* exotic species invasion or spread). A systematic assessment of these risks can give managers a better understanding of the potential tradeoffs associated with prescribed fire treatments (GAO, 2004). There are also activities that can mitigate undesirable consequences. Equipment washing during all operational phases can reduce the chance of exotic species introduction and their rate of dispersal. Post fire native seeding and soil amendments can help increase the rate of native plant establishment and discourage invasion of exotics (Korb, Johnson & Covington, 2004). If invasive annual exotics such as cheatgrass are present, low severity spring burning will probably not exacerbate populations as much as fall or higher severity burning. However, spring burning may adversely impact some native species (Zouhar, 2003). Our results do not necessarily suggest this, but we did not analyze species-specific responses. Reintroducing fire into these dramatically altered ecosystems in a manner that will not exacerbate existing resource problems or create new problems can present significant challenges for resource managers.

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