MECHANICAL THINNING EFFECTS ON HERBACEOUS SPECIES DISTRIBUTIONS AND INVASION PATHWAYS IN PONDEROSA PINE FORESTS OF BOULDER COUNTY, CO.

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August, 2008.

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ABSTRACT

A central objective of fire mitigation and forest restoration thinning treatments in ponderosa pine forests is to reinvigorate the native understory plant community. However, non-native plants often invade recently thinned areas, limiting the effectiveness of these treatments. We used a multifaceted sampling strategy to determine if mechanical thinning increases the susceptibility of forests to invasion and, if so, whether novel dispersal vectors or a more open canopy are responsible for the observed increases in invasive species. We measured understory vegetation in control unthinned forests and treated thinned forests and then compared the existing vegetation with plant species composition in the soil seedbank. Additionally, we searched trails and roads in control and treated forests for target invasive species of high management concern. Sampling occurred one to three growing seasons following treatment in ponderosa pine dominated forest at six open space properties in Boulder County (three managed by Boulder County POS, three by City of Boulder OSMP). There was no difference in the total or nonnative cover or species richness of understory plants between thinned and unthinned forests. Understory vegetation was strongly correlated with forest basal area regardless of management history, with lower basal areas supporting increased cover and species richness of both native and non-native plant species. The soil seedbank contained relatively few species compared with standing vegetation, but included some species that weren't present in the aboveground plant community. Two non-native species, mullein and cheatgrass, had a large number of seeds in the soil seedbank throughout the study area. Non-native species were more abundant and frequent on trails and roads in control unthinned forests than treated forests, but this trend was a consequence of the higher abundance of annual Bromus sp. in untreated forests. Individual species showed strong trends both negatively and positively associated with distance to roads and trails. While some non-native species of concern showed increasing abundance with increasing management intensity, non-native species invasion appears to be influenced more by forest structure than by management activities.

INTRODUCTION

Population growth in the Wildland-Urban Intermix (WUI) and large catastrophic megafires have intensified federal, state, local, and private land management efforts to prioritize fuels reduction treatments near human communities. While the WUI has expanded throughout Colorado forests over the past few decades, approximately 75 percent of communities at risk from wildfire in Colorado (a total of 1,274 communities) are characterized by or lie within one mile of ponderosa pine (*Pinus ponderosa*) dominated stands (CSFS, 2004). As the application of fire mitigation treatments increases, management effort and funding will likely be disproportionately directed towards these high priority areas in ponderosa pine dominated habitats.

Notwithstanding the escalating prioritization to reduce fuels around communities, accomplishing fuels mitigation and forest restoration has become increasingly difficult due to strict burning regulations and a dearth of markets for small diameter wood. In search of regional solutions, collaborative efforts such as the Front Range Fuels Treatment Partnership in Colorado have motivated managers and politicians to be forward thinking, encouraging forest restoration based on ecological principles. The effects of mechanical thinning treatments (Fettig *et al.*, 2006; Glitzenstein *et al.*, 2006; Wayman and North, 2007) have been well studied in some regions of the country. These studies have documented that thinning alters understory plant communities, in part by increasing the abundance of non-native species (Metlen *et al.*, 2004; Laughlin *et al.*, 2006). Merriam et al. (2006) found that fuel breaks in California significantly contributed to the spread of non-native species more than 50 meters beyond treatment boundaries. Transportation corridors such as roads and trails can contribute to the spread of non-native species by facilitating long range seed dispersal (Von der Lippe and Kowarik, 2007) and by creating favorable habitat for invasive species adjacent to roads (Potito and Beatty, 2005).

However, knowledge about understory responses to thinning and processes of exotic species invasions, including dispersal mechanisms of non-native species into thinned areas, are desperately lacking for Colorado (CFRI, 2005).

The goal of our research is to provide information that will allow managers to reduce the spread of non-native species in ponderosa pine forests along the Front Range of Colorado. Our first objective is to determine if forest thinning changes the abundance or richness of plant species in the understory and to what extent the practice contributes to the spread of exotic plant species. Our second objective is to separate the effects of novel dispersal vectors (mechanical equipment used in thinning and/or new dispersal corridors) from habitat changes brought by thinning on exotic species invasions into thinned areas.

We hypothesize that understory composition will change following thinning, and that non-native species will have increased levels of occurrence within thinning treatments due to the disturbances caused by management activities. We also hypothesize that, whether thinned or unthinned, areas adjacent to transportation corridors such as roads and trails will have more nonnative species than areas far from roads and trails.

METHODS

Study Site

Our study area was located in lower montane upland coniferous forests of Boulder County, Colorado. Six study sites were selected for sampling based on criteria of mechanical thinning completed between 2004 and 2006 and the opportunity to sample nearby unthinned forest with similar topography and forest composition. Three of the sites are managed by Boulder Open Space and Mountain Parks (Flagstaff Mountain Conservation Easement [FLG],

Lindsay Open Space [LIN], and Shannahan Ridge [SHA]), while three properties are managed by Boulder County Parks and Open Space (Bald Mountain Scenic Area [BLD], Betasso Preserve [BET], and Heil Valley Ranch [HVR]) (Figure 1). Most sites are strongly dominated (>95%) by ponderosa pine, with occasional individuals of Douglas-fir (*Pseudotsuga menziesii*) and Rocky Mountain juniper (Juniperus scopulorum). The FLG study site was dominated by ponderosa pine, but also contained significant amounts of Douglas fir and pockets of quaking aspen (*Populus tremuloides*). The understory flora in the lower montane ponderosa pine zone of the Front Range is generally sparse with patchy dominance of graminoids and occasional small shrubs (Peet, 1981). Dominant herbaceous species include the graminoids mountain multy (Muhlenbergia montana) and Carex sp., while small shrubs such as wax current (Ribes cereum) and delicious raspberry (Rubus deliciosus) are also frequent. Elevations of the study sites ranged from 1880 m to 2340 m and soils were generally a stony/gravelly sandy loam type (USDA, 2008b) (Table 1). Average minimum January temperature at the City of Boulder weather station (1672 m elevation) is -6.3° C, with average highs of 7.5° C. July is the warmest month with average maximum temperatures of 30.9° C and lows of 14.8° C. Average annual precipitation is 486 mm and the wettest months are April and May. Precipitation is relatively well distributed throughout the growing season from early spring through late fall (WRCC, 2008), with summer and fall precipitation dominated by short and often intense rain events.

Treatments and Data Collection

Stands at each study site were classified by treatment as either 1) control unthinned stands, or 2) treated thinned stands. Each of the six study sites was treated between 2004 and 2006. At each site, three plots were located in thinned areas, and three plots located in adjacent unthinned areas.

Sampling occurred during July and August of 2007 in stands where treatments were one to three years old. At each site, plots were sampled in alternate treatments each day to ensure even sampling as conditions changed throughout the summer. All plots were located a minimum of 50 m from treatment boundaries to avoid transitional plant communities between treatments.

Vegetation was sampled using a nested-intensity sampling scheme, similar to the one described in Peet et al. (1998), but with ten 1 m² subplots located in a square plot 400 m² in size (Figure 2). Vascular plants were identified to the species level and ocular estimates of percent cover for each species were recorded in all 1 m² subplots. Additional species were recorded as present in the entire 400 m² plot. Naming conventions follow the PLANTS Database (USDA, 2008a). We define understory plants as all vascular plant species excluding trees. Therefore, all tree species (Douglas-fir, ponderosa pine, quaking aspen, and Rocky Mountain juniper) were excluded from understory analyses. Plants that were not identified to the species level were included in total cover estimates but excluded from all other analyses. In a few cases, similar species were easily confused when sampling occurred outside peak phenological development. In each case, data for similar plant species were combined and analyzed under one species name. All species were classified as either native or non-native to Colorado according to the PLANTS Database (USDA, 2008a).

Forest floor characteristics and environmental variables were also measured for each plot. In each 1 m² subplot, litter depth and duff depth were measured to the nearest $\frac{1}{2}$ cm. Litter was defined as fresh and partially decomposed organic forest debris located above the mineral soil (O_i and O_e horizons), while duff consisted of highly decomposed organic matter below the litter layer and above mineral soil (O_a horizon). Cover of forest floor substrate was estimated to the nearest percent (rock, mineral soil, woody plants [exposed roots, stems, and tree boles including fresh stumps], herb basal area [e.g. strongly tufted herbs], litter and duff, and coarse woody

debris >7.6 cm diameter). Environmental variables (slope, aspect, elevation), and digital photos were recorded within each 400 m² plot. Each plot was permanently marked on the Northwest corner with metal rebar and their location was recorded using a handheld GPS unit.

All trees greater than 15 cm tall within the 400 m² plot were tallied by size class based on diameter at breast height (DBH), including seedlings (> DBH), saplings (0 cm – 10 cm DBH), poles (10 cm – 20 cm DBH), and large trees (DBH > 20 cm). Fresh stumps were also tallied using the same size classes as live trees, although stump diameters were measured at ground level and not at DBH. Tree seedlings less than 15 cm tall (including germinants) were tallied in each 1 m² subplot. Canopy closure was measured using a spherical densitometer in the four cardinal directions at the center of each 400 m² plot and averaged. Basal area was measured from the center of each 400 m² plot using a glass prism with a basal area factor of 20 ft²/acre.

Soil cores were collected for seedbank analysis using a 6 cm diameter bulb planter at the corner of each 1 m² subplot. Soil samples were pooled for each plot in the field, mixed and stored in gallon Ziploc bags, then incubated in a freezer for 8 weeks. The samples were then divided into sub-samples weighing approximately 500g each. The sub-samples were spread in a thin layer, approximately 5 mm deep, on 250 x 500 cm flats filled with 2.5 cm of standard potting mix and incubated in a greenhouse for 5 months. The samples were hand watered twice a day for the first month of incubation. An automatic sprinkler system was then installed to provide consistent watering throughout the rest of the incubation period. Individual seedlings were tallied by species and discarded following identification. Seedlings that were not readily identifiable were transferred to individual pots until phonological development permitted identification. Due to time and space limitations in the greenhouse, we were not able to allow some species to reach full phonological development. As a result, we were not able to distinguish between field brome (*Bromus arvensis*) and cheatgrass (*B. tectorum*) in the seedbank

analysis. Therefore, the soil seedbank data includes individuals of both species analyzed under the name *Bromes*. Data for field brome and cheatgrass were also combined in the aboveground dataset to standardize comparisons between aboveground vegetation and the soil seedbank.

To examine the interactions of forest management and exotic species dispersal mechanisms, non-native understory plant species were sampled along trails and roads in ponderosa pine forests near the city of Boulder, Colorado. All trails and roads were sampled during July and August of 2007 in upland ponderosa pine forests between 1775 m and 2095 m elevation at five study sites: BET, HVR, LIN, SHA, and Enchanted Mesa (ENC), which is managed by Boulder Open Space and Mountain Parks. Trails were soft surface (e.g. dirt, sand or gravel) and ranged from narrow "social trails" created by public trampling to mechanically constructed trails with imported soft surface foundational materials. Roads sampled were also soft surface and ranged from temporary unimproved two-track paths used for transporting forestry equipment to established roads that are regularly graded with heavy machinery and/or augmented with soft surface foundational material. Trails and roads were used by hikers, horses, mountain bikers, and/or dogs, but motor vehicle use was restricted to open space staff and other permitted motor vehicles. We classified all paths that experienced some motorized vehicle use as roads, and those that were restricted to only non-motorized recreational use as trails. This classification allows us to distinguish the effects of recreational use from that of vehicle traffic and also serves as a relative measure of trail or road size.

A total of fifty one transects were established along roads and trails, including twenty six in control (unthinned) forests and twenty five in treated (thinned) areas. Transects were aligned perpendicular to the edge of each trail or road extending into the surrounding forest. Each transect was located a minimum of 100 m apart along a trail segment, with transect direction (left or right of the trail/road) chosen at random. For each sample transect, we searched a 4-m wide

by 25-m long belt transect (100 m² in area) for twenty two target non-native understory plant species of high management concern (Appendix B). The abundance of each target species was assessed by tallying the number of four square meters (comprising the width of the belt) with the species present at each meter distance from trail. For each species, abundance values were summarized by averaging within the following distance categories: zero to two meters, three to five meters, and every five meters thereafter through the length of the 25 meter transect. All trees greater than 15 cm tall within the 100 m² transect were tallied by species and size class based on DBH, including seedlings (> DBH), saplings (0 cm – 10 cm DBH), poles (10 cm – 20 cm DBH), and large trees (DBH > 20 cm). Basal area was estimated from the center of each transect using a glass prism with a basal area factor of 20 ft²/acre. Environmental variables (slope, aspect, elevation) were recorded from the center of each belt transect and transect location was marked using a handheld GPS unit.

Data Analysis

Statistical tests were carried out using SAS v9.1 (2003). Attributes were transformed when necessary to approximate assumptions of homoscedastic variance. A sqrt (X) transformation was applied to total understory vegetation cover and to tallies of ponderosa pines in seedling, sapling, and pole size classes. Significant differences for all tests were determined using $\alpha = 0.05$. Forest structure, forest floor characteristics, and abundance of ponderosa pine germinants were compared between treatments using a mixed effects ANOVA with treatment as a fixed factor and study site and treatment*site as a random factors.

To test for the effects of treatment on total understory vegetation cover, total species richness at the 1 m² and 400 m² scales, non-native species cover, and non-native species richness at the 1 m² and 400 m² scales, we performed a backwards stepwise model selection process using

a mixed effects ANOVA with treatment as a fixed factor, study site and treatment*site as random factors, and basal area, elevation, and slope as covariates.

To test for differences between treatments on the total number of understory plant species seedlings per 400 m² plot, species richness at the 400 m² scale, and the number of non-native seedlings at the 400 m² scale, we used a mixed effects ANOVA with treatment as a fixed factor and study site and treatment*site as random factors. We also tested for differences between treatments in the number of seedlings present per 400 m² plot for the two most frequent native and non-native species individually. The total number of seedlings per 400 m² plot and the tally of seedlings per plot for the individual species were sqrt(X) transformed to meet assumptions in the ANOVA model.

The degree to which exotic plant abundances increase along transportation corridors provides one estimate of how propagule pressure and habitat disturbance adjacent to trails and roads might contribute to invasions in treated areas. A regression model with distance to trail or road edge, trail type (trail or road), treatment (thinned or unthinned), and interaction terms of distance*treatment, distance*trail type, and treatment*trail type was run to determine which factors are correlated with observed species distributions. Analysis was conducted on total abundance of non-native species and abundance of each target species individually using backward stepwise model selection. For each species, explanatory variables that were not significant at $\alpha = 0.05$ were removed from the model until only significant variables remained.

RESULTS

Treatment Effects on Forest Structure

There were no significant differences between treatments in basal area, canopy cover, or total pine density, but control plots had higher numbers of sapling and pole sized trees (Table 2). Litter depth was higher in control areas than in treated areas (p = 0.041) and there was no difference in the cover of litter and duff between treatments (Table 2).

Understory Cover and Richness

A total of 125 understory plants were identified across all study sites, including 101 native and twenty four non-native species (Appendix A). Cover of understory vegetation was relatively low across all sites and averaged 5.7%. None of the understory variables we examined (total understory cover and richness at 1 m² and 400 m² scales, non-native species cover and richness at 1 m² and 400 m² scales) showed significant differences between treatments (Table 3). In contrast, basal area was correlated with all measures of understory cover and richness (p < 0.005; Figure 3). Elevation was not significantly correlated with any understory plant variables, but plots with gentle slopes had significantly higher total (p = 0.019) and non-native (p = 0.042) understory species richness at the 400 m² scale than did plots with steeper slopes. When study sites were considered individually, Heil Valley Ranch showed significant treatment effects, with increased understory cover, richness, non-native cover, and non-native richness in the thinned areas (Table 4).

There was a significant and very strong positive relationship at the 400 m^2 scale between species richness of native and non-native species throughout the study area (Figure 4).

Soil Seed Bank

A total of twenty four understory species were identified across all study sites in the soil seedbank, including seventeen native and seven non-native species (Appendix C). There were no differences between treatments in the total number of seedlings or species richness of the seedbank (Table 5). The species richness of non-native plants in the seedbank also did not differ between treatments. Bromes (field brome [*Bromus arvensis*] and cheatgrass [*Bromus tectorum*]) and mullein (*Verbascum thapsus*) were the most abundant and frequently occurring non-native species in the soil seedbank, with a total of 87 brome individuals recorded in 19 out of 36 plots, and 647 mullein plants, occurring in 75% of the plots. There was no difference between treatments in the average number of bromes or mullein seedlings per plot (Table 5).

Trails and Roads

Target non-native species were prevalent throughout the study area, with all but two transects (96%) containing at least one species. Contrary to our hypothesis, average abundance of all non-native target species was higher on control transects than on thinned transects (45.6% vs. 25.7% of square meters in transects supported at least one invasive species; p < 0.001). However, two annual bromes (field brome and cheatgrass) were more abundant than all other species and dominated these total abundance trends. When annual bromes were removed from the analysis, non-native species abundance was similar between both treatments (7.0% vs. 6.2%, p = 0.529). Total non-native species abundance was significantly higher on roads than on trails (p < 0.001 for both test including and test excluding annual bromes).

Nine target species were abundant enough to warrant analysis on an individual basis. Of these, three species, smooth brome (*Bromus inermis*), field brome, and prickly lettuce (*Lactuca serriola*), were more abundant near trail and road edges). Two species, Dalmatian toadflax (*Linaria dalmatica*) and nodding plumeless thistle (*Carduus nutans*), were more abundant with

increasing distance from trails and roads. Four species (cheatgrass, Canada thistle (*Cirsium arvense*), bull thistle (*Cirsium vulgare*), and mullein) did not have a significant linear relationship with distance to trails or roads. No species had a significant positive interaction between thinning and distance to trials or roads. However, three species (Canada thistle, bull thistle, and mullein) had a significant trail type*treatment interaction, with higher abundance on transects located on roads in thinned areas (Figure 5). Ten target species were not present on any transects: hardheads (*Acroptilon repens*), jointed goatgrass (*Aegilops cylindrical*), diffuse knapweed (*Centaurea diffusa*), leafy spurge (*Euphorbia esula*), myrtle spurge (*Euphorbia myrsinites*), orange hawkweed (*Hieracium aurantiacum*), butter and eggs (*Linaria vulgaris*), white sweetclover (*Melilotus albus*), yellow sweetclover (*Meliotus officinalis*), Mediterranean sage (*Salvia aethiopis*). Three additional species, tall oatgrass (*Arrhenatherum elatius*), crested wheatgrass (*Agropyron cristatum*), and spotted knapweed (*Centaurea stoebe*), occurred on only a few transects and were not analyzed individually.

DISCUSSION

Understory response to changes in forest structure

We found that disturbance caused by mechanical thinning did not have a significant effect on understory plant cover or species richness and did not favor non-native species. Rather, understory vegetation is correlated to forest basal area irrespective of whether or not the forest structure was actively managed. These results concur with the work of Mitchell and Bartling (1991), who found that understory vegetation productivity was strongly correlated with canopy cover in ponderosa pine forests along the Front Range of Colorado, while site factors of aspect and elevation were not correlated with understory productivity.

We failed to find an overall effect of thinning on understory cover and richness, likely because there were no differences in basal area or canopy cover between treatments at many of the sites we sampled. At most of our study sites, basal area was only marginally higher in the control sites relative to the thinned sites. This is most likely a consequence of management decisions such as selecting the densest forest stands to thin and/or stipulating removal of only small diameter trees.

To argue that forest management does not have an effect on understory vegetation would be misleading, since the tree harvesting that results in reduced basal area should correspond to increased cover and species richness of understory plants. The relationship between the understory plant community and basal area is encouraging for restoration efforts that are aimed at invigorating understory vegetation. Other studies in ponderosa pine forests have found little or no increase in understory vegetation soon after thinning (Metlen *et al.*, 2004; Wienk *et al.*, 2004), but our data suggest that even one year post thinning there is a significant response to major reductions in basal area. For example, the HVR study site had the largest difference in basal area between treatments out of all our study sites, and only one year after treatment this site also had the largest difference in understory species cover and richness between control and thinned treatments. This suggests that the understory plant community in ponderosa pine forests of Boulder County can respond rapidly to mechanically manipulated changes in forest structure if significant numbers of standing trees are removed from the forest.

Importantly, we did not find elevated cover or numbers of non-native species in thinned areas compared with unthinned. In other parts of the western U.S., thinning treatments and fuel breaks have been found to exacerbate invasion by non-native understory plants (Dodson and Fiedler, 2006; Merriam *et al.*, 2006). Rather than favoring non-native over native species, disturbances caused by forest thinning in ponderosa pine forests along the Front Range of

Colorado appear to increase native and non-native understory plants relatively equally. In a ponderosa pine forest near Deckers, Colorado, Fornwalt *et al.* (2003) also found no difference in the amount of non-native species between managed and unmanaged watersheds. Other studies have found similar correlations between native and non-native species richness on the landscape (e.g. Stohlgren *et al.*, 1999), with increases in non-native species not only in heavily disturbed areas, but also in habitats high in native plant diversity.

When management objectives include increasing native understory vegetation productivity, significant reductions in tree basal area are suggested. Managers might consult Figure 3 as a rough guideline for expected understory plant responses at corresponding basal areas, keeping in mind that understory responses will likely vary widely among sites. However, we caution that as total understory vegetation cover and richness increases, proportional increases in non-native species should also be expected.

Soil Seed Bank

The dearth of native understory species in the soil seedbank suggests either that most native plants are likely colonizing sites through dispersal from nearby populations and are not omnipresent in the soil seedbank, or that our methods failed to detect a subset of species which were actually present in the soil. Our methods favored species that do not require special cues to germinate, such as fire, animal digestion, or other unique processes, and as a result some viable native seeds in our samples might not have germinated. However, cold scarification followed by seedling emergence has been shown to yield the most species when comparing several common seedbank analysis techniques (Gross, 1990). In addition, soil cores were collected from a relatively small area compared to the aboveground vegetation sampling and we almost certainly did not sample intensively enough to collect seeds of rare species or even make definitive

statements about many common species. Our results should be viewed as a minimum estimate of the viable seedbank in ponderosa pine forests of Boulder County, and we emphasize results of observed species in the seedbank (such as mullein) rather than drawing conclusions from the absence of species in the seedbank.

While we found no differences between thinned and control areas in the abundance of above-ground mullein or mullein seedbank, viable mullein seeds were present in the seedbank in twice as many plots as compared with live plants observed in the aboveground vegetation. An individual mullein plant can produce upwards of 35,000 seeds (Lortie and Aarssen, 2000), which remain viable in the seedbank for up to 100 years (Kivilaan and Bandurski, 1981). Mullein's frequency in the seedbank throughout all study sites suggests that establishment from the seedbank is perhaps an important factor contributing to the continued propagation of this species.

Trails and Roads

If roads and trails act as dispersal pathways for non-native species, and an invasion is in its early stages, we would expect to see a negative relationship between distance to road/trail and species abundance. Smooth brome, field brome, and prickly lettuce fit this pattern. These species are found most often adjacent to trails and roads, either because the roadside provides favorable habitat for invasion (high light, disturbance), or because of propagule pressure and dispersal of seeds by road/trail users. Our data do not allow us to differentiate these mechanisms, warranting future investigation focused on dispersal of these three species. We were surprised that dalmation toadflax and nodding plumeless thistle were more abundant away from roads and trails, and we speculate that these species may, in fact, be well-dispersed, with the observed pattern a consequence of aggressive weed management activities along the roadside. The species that showed no relationship to distance to road/ trail (cheatgrass, Canada

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thistle, bull thistle, and mullein) are likely in later stages of invasion and are no longer restricted to transportation corridors.

Overall, trails and roads did not appear to serve as corridors for non-native plant dispersal into thinned areas more readily than into unthinned areas. However, thinning increased the abundance of many non-native species, and three species in particular had their greatest abundance on roads in thinned areas. Forest managers should be extra vigilant for Canada thistle, bull thistle, and mullein on roadways entering thinned areas. Canada thistle, in particular, appears to be highly correlated with actively thinned forests and possibly transported into thinned areas via roads. Canada thistle was absent from all control areas throughout our study and it was only found by thinned roadsides in our transportation corridor survey. Other studies in Colorado substantiate these trends. A survey of thinning treatments throughout Colorado found that Canada thistle was present in several thinned stands, but absent from uncut forests (Mike Battaglia, USFS Rocky Mountain Research Station, personal communication, May 2008). Wolk and Rocca (2008) also found that Canada thistle was only present in thinned treatments in a detailed study at the HVR. We suspect that dispersal of Canada thistle is being enhanced by seed transport on road corridors, and the open canopy in thinned areas provides suitable habitat for this species to establish.

Putting it all together: invasion pathways in ponderosa pine forests

It appears that thinning *per se* (i.e., transporting mechanical equipment into the forest and, possibly, disturbing the forest floor) does not lead to an increased invasion potential in ponderosa pine forests along the Colorado Front Range. In contrast, basal area reduction-typically a desired outcome when thinning treatments are implemented--will lead to increased cover and richness of non-native species, but this occurs in proportion to increases in native understory cover and richness. Managers working with the City of Boulder and Boulder County Open Space agencies are apparently doing a good job at mitigating invasive species transport into thinned forests during management operations.

With a few exceptions, the non-native species that occurred in our field plots are already well dispersed within our study area and, therefore, not specifically associated with transportation corridors. Cheatgrass and mullein were ubiquitous above ground and in the seedbank in both treatments, and showed no relationship with distance-to-road/trail. That both of these species were more abundant along roads in thinned areas (compared to control areas or along trails) might at first appear contradictory. However, we suspect that these species are found everywhere, and that they especially flourish in disturbed areas with an open canopy. In contrast, Canada thistle is found only in thinned areas and along roadsides, suggesting that this species may be dispersed by mechanical equipment and thrive in disturbed habitat. Smooth brome, field brome, and prickly lettuce, which were found more often close to roads and trails than away from them, may also be transported by novel dispersal vectors (people, vehicles) and be at an early stage of invasion.

Acknowledgements

We would like to thank Amanda Brennen, John Shannon, and Hannah Varani for their hard work and diligence collecting data in the field. Danita Dickinson, Bryan Brown, and Nick Krick assisted in the greenhouse for the soil seedbank study. Staff at both City of Boulder and Boulder County Open Space agencies were very helpful throughout this project, particularly Chris Wanner and Chad Julian. This project was funded by grants from the City of Boulder

Open Space and Mountain Parks, Boulder County Parks and Open Space, and Colorado State

University.

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	Betasso	Preserve	Bald M	Iountain	Flagstaff	Mountain	Heil Val	ley Ranch	Lindsay O	pen Space	Shannaha	an Ridge
	Control	Thinned	Control	Thinned	Control	Thinned	Control	Thinned	Control	Thinned	Control	Thinned
Elevation (m)	1928	1945	2120	2092	2331	2343	2103	2099	1933	1932	1878	1889
Aspect (0 – 360)	233	208	192	185	19	295	87	74	80	51	82	72
Slope (degree)	24.0	16.0	22.0	15.3	21.3	11.3	13.3	9.7	5.7	7.7	12.7	9.0
Soil Type*	JrF	JrF	JrF	JrF	FcF	FcF	PrF	PrF	NdD and 47	NdD and 47	GrF and 1 plot NdD	GrF
Basal Area (ft ² /acre)	166.7	146.7	213.3	220.0	126.7	120.0	293.3	36.7	180.0	66.7	153.3	140.0
Canopy Cover (%)	63.7	61.3	85.3	80.4	43.0	53.6	52.6	18.2	75.7	34.3	60.5	65.3
Litter Depth (cm)	2.1	1.7	2.2	1.3	1.9	1.6	1.7	1.3	2.1	1.5	2.4	1.9
Duff Depth (cm)	0.3	0.1	1.5	0.3	0.5	0.6	0.4	0.1	1.1	1.0	1.1	0.6
Litter and Duff Cover (%)	93.6	81.6	97	92.9	97.1	97.7	95.6	95.3	97.4	97.2	96.6	94.4
Mineral Soil Cover (%)	3.1	13.6	0.6	1.5	0.4	0.3	0.7	2.7	0.0	0.0	0.0	1.3
Ponderosa Pine												
Seedlings (< DBH)	0.7	0.0	2.3	3.7	4.7	2.0	17.3	0.0	0.7	0.3	0.0	4.3
Saplings (0 - 10 cm)	6.7	0.0	15.0	7.0	5.7	0.0	38.3	0.0	6.0	0.3	2.3	0.7
Poles (10 - 20 cm)	6.3	2.3	20.0	17.3	7.3	1.3	35.7	0.0	10.7	0.3	4.7	0.3
Large Trees (> 20 cm)	12.0	11.0	21.7	17.7	2.7	4.3	15.3	3.3	15.7	5.0	11.7	18.0
Stumps (0 - 10 cm)	0.0	13.7	0.0	13.3	0.0	20.0	0.0	18.3	0.0	0.3	0.0	2.3
Stumps (10 - 20 cm)	0.0	12.7	0.0	7.7	0.0	11.0	0.0	9.3	0.0	2.3	0.0	3.0
Stumps (> 20 cm)	0.0	8.3	0.0	0.0	0.7	7.3	0.0	2.3	0.0	9.7	0.0	4.0

Table 1. Site characteristics and forest structure for the six Boulder County properties selected for understory and seed bank sampling.

*Soil Type Descriptions:

47 — Flatirons. Very stony sandy loam.

 $\mbox{FcF}-\mbox{Fern Cliff-Allens Park-Rock}$ outcrop complex. Stony sandy loam

GrF — Goldvale-Rock outcrop complex. Stony coarse sandy loam.

JrF — Juget-Rock outcrop complex. Very gravelly sandy loam

NdD — Nederland. Very cobbly sandy loam.

PrF - Pinata-Rock outcrop complex. Very stony loamy fine sand

	Control	Thinned	p - value
Basal Area (ft ² /acre)	189	122	0.118
Canopy Cover (%)	63.5	52.2	0.254
Ponderosa Pine (#/400 m ²)	43.9	16.6	0.108
Seedlings	4.3	1.8	0.486
Saplings	12.3	1.3	0.026
Poles	14.1	3.6	0.049
Large Trees	13.2	9.9	0.310
Litter Depth (cm)	2.1	1.5	0.041
Litter and Duff Cover (%)	96.2	93.2	0.178

Table 2. Forest structure and ground cover measurements associated with forest understory plots, averaged across all six study sites. P-values are the probabilities that there is no treatment effect in a mixed-effects ANOVA model that accounts for site (random factor) and treatment.

	Control	Thinned	p value
Understory Cover (%)			
Total	4.7	6.7	0.419
Non-native	0.6	1.0	0.490
Understory Species Richness			
Total (1 m ²)	4.7	6.3	0.293
Non-native (1 m ²)	0.8	1.3	0.526
Total (400 m ²)	33.0	35.8	0.585
Non-native (400 m ²)	5.5	6.4	0.712

Table 3. Understory plant cover and species richness by treatment, averaged across all six study sites. P-values are the probabilities that there is no treatment effect in a mixed-effects ANOVA model that accounts for site (random factor) and treatment, but no other covariates.

Table 4. Understory plant cover and species richness by treatment, separated by study site. Notice that the largest effects on understory cover and richness are observed at Heil Valley Ranch, the site with the largest basal area difference between control and treated stands.

	Betasso	Preserve	Bald N	<u>Iountain</u>	<u>Flagstaff</u>	<u>Mountain</u>	<u>Heil Val</u>	ley Ranch	Lindsay C	Dpen Space	<u>Shannah</u>	an Ridge
	Control	Thinned	Control	Thinned	Control	Thinned	Control	Thinned	Control	Thinned	Control	Thinned
Understory Cover (%)												
Total	2.9	2.6	1.8	1.2	9.0	9.6	1.5	15.5	7.8	9.4	4.2	2.9
Non-native Species	0.5	0.2	0.4	0.2	0.7	0.4	0.5	2.6	1.3	1.8	0.6	0.0
Species Richness												
Total (1 m ²)	3.4	3.0	3.9	3.5	6.8	7.6	5.4	7.2	8.4	10.4	4.4	2.2
Non-native (1 m ²)	0.7	0.4	0.6	0.3	0.8	0.6	0.6	2.8	2.0	2.7	1.0	0.0
Total (400 m ²)	28.9	31.2	29.3	28.7	35.9	34.7	25.3	44.4	47.4	51.2	34.6	21.4
Non-native (400 m ²)	3.7	4.9	5.4	1.5	6.1	5.4	2.0	11.8	10.8	12.0	6.3	1.6

	Control	Thinned	p value
All Seedlings (#/400 m ²)	69.2	75.0	0.962
Species Richness (400 m ²)	5.3	5.0	0.778
Non-native Richness (400 m ²)	1.9	1.8	0.814
Brome Seedlings (#/400 m ²)	3.1	1.8	0.694
Mullein Seedlings (#/400 m ²)	8.9	27.0	0.711

Table 5. Treatment effects on plants germinating from the seedbank. P-values are the probabilities that there is no treatment effect in a mixed-effects ANOVA model that accounts for site (random factor) and treatment.

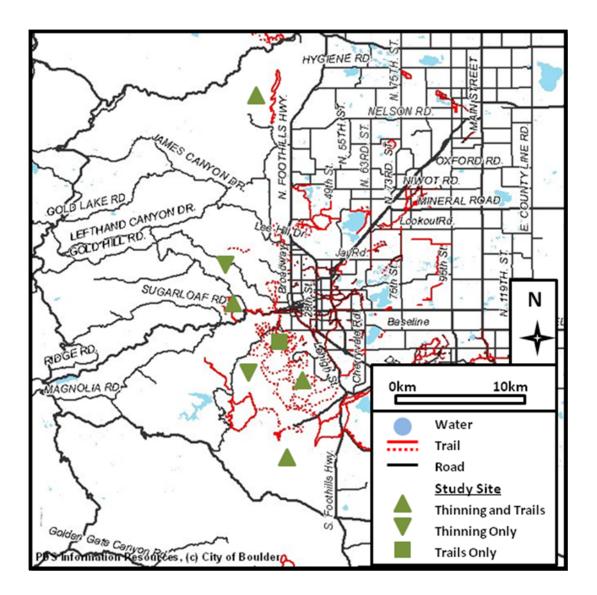


Figure 1. Study area in Boulder County, Colorado. Six open space properties were selected for researching the effects of thinning on understory vegetation (green triangles); five properties were used for transportation corridor study (square and upwards pointing triangles).

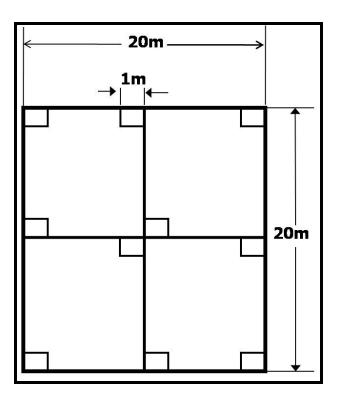


Figure 2. Schematic diagram of plot layout. Understory cover was estimated in each of the ten 1 m x 1 m quadrats. Canopy variables were assessed at the plot scale, and all species present in the 400 m² plot were recorded. Ten soil cores, taken adjacent to each quadrat, were pooled at the plot scale.

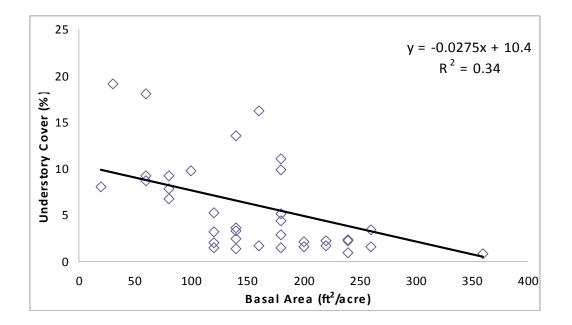


Figure 3. Linear regression showing the relationship between tree basal area and average understory plant cover. Treatment (thinning vs control) did not influence understory plant cover.

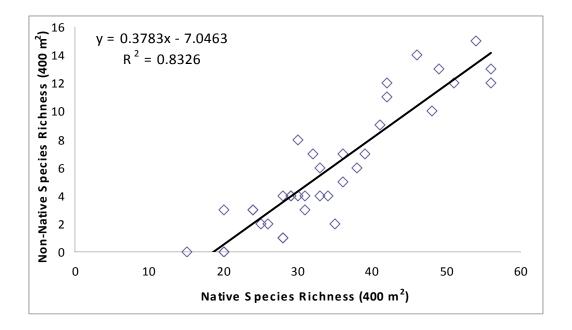


Figure 4. Linear regression demonstrating that non-native species richness is predictable based on native species richness. Data summarized at the plot scale; plots from all six study sites are included.

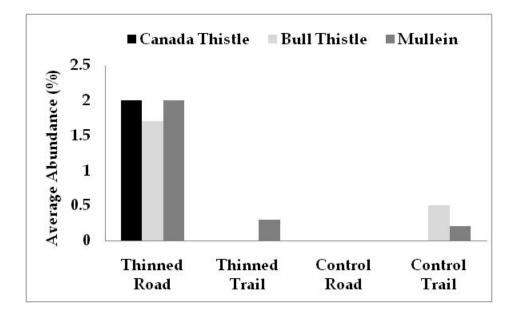


Figure 5. Abundances (average % of square meters containing species/transect) for three species: Canada thistle (*Cirsium arvense*), bull thistle (*Cirsium vulgare*), and mullein (*Verbascum thapsus*).

Appendix A. Plant species present in the aboveground vegetation plots at the six study sites in Boulder County, Colorado. Nomenclature and US Nativity follows U.S. Department of Agriculture Natural Resources Conservation Service Plants Database (http://plants.usda.gov/).

Species Name	Common Name	Family	Longevity	US Nativity
Acer glabrum	Rocky Mountain maple	Aceraceae	Perennial	Native
Achillea millefolium	common yarrow	Asteraceae	Perennial	Native
Achnatherum nelsonii	Columbia needlegrass	Poaceae	Perennial	Native
Achnatherum robustum	sleepygrass	Poaceae	Perennial	Native
Allium cernuum	nodding onion	Liliaceae	Perennial	Native
Alyssum alyssoides	pale madwort	Brassicaceae	Annual, Biennial	Introduced
Ambrosia psilostachya	Cuman ragweed	Asteraceae	Annual, Perennial	Native
Anaphalis margaritacea	western pearly everlasting	Asteraceae	Perennial	Native
Andropogon gerardii	big bluestem	Poaceae	Perennial	Native
Angelica ampla	giant angelica	Apiaceae	Perennial	Native
Antennaria parvifolia	small-leaf pussytoes	Asteraceae	Perennial	Native
Arabis drummondii	Drummond's rockcress	Brassicaceae	Biennial, Perennial	Native
Arabis glabra	tower rockcress	Brassicaceae	Annual, Biennial, Perennial	Native
Arctostaphylos uva-ursi	kinnikinnick	Ericaceae	Perennial	Native
Arenaria fendleri var. fendleri	Fendler's sandwort	Caryophyllaceae	Perennial	Native
Arnica fulgens	foothill arnica	Asteraceae	Perennial	Native
Artemisia filifolia	sand sagebrush	Asteraceae	Perennial	Native
Artemisia frigida	prairie sagewort	Asteraceae	Perennial	Native
Artemisia ludoviciana	white sagebrush	Asteraceae	Perennial	Native
Bouteloua curtipendula	sideoats grama	Poaceae	Perennial	Native
Bouteloua gracilis	blue grama	Poaceae	Perennial	Native
Bromus arvensis	field brome	Poaceae	Annual	Introduced
Bromus briziformis	rattlesnake brome	Poaceae	Annual	Introduced
Bromus inermis	smooth brome	Poaceae	Perennial	Introduced
Bromus porteri	Porter brome	Poaceae	Perennial	Native
Bromus tectorum	cheatgrass	Poaceae	Annual	Introduced
Buglossoides arvensis	corn gromwell	Boraginaceae	Annual	Introduced
Calochortus gunnisonii	Gunnison's mariposa lily	Liliaceae	Perennial	Native
Camelina microcarpa	littlepod false flax	Brassicaceae	Annual, Biennial	Introduced
Campanula rotundifolia	bluebell bellflower	Campanulaceae	Perennial	Native
Carduus nutans	nodding plumeless thistle	Asteraceae	Biennial	Introduced
Carex geophila	White Mountain sedge	Cyperaceae	Perennial	Native
Ceanothus fendleri	Fendler's ceanothus	Rhamnaceae	Perennial	Native
Ceanothus herbaceus	Jersey tea	Rhamnaceae	Perennial	Native
Ceanothus velutinus	snowbrush ceanothus	Rhamnaceae	Perennial	Native

Species Name	Common Name	Family	Longevity	US Nativity
Cerastium arvense	field chickweed	Caryophyllaceae	Perennial	Native
Chenopodium album	lambsquarters	Chenopodiaceae	Annual	Introduced
Chenopodium leptophyllum	narrowleaf goosefoot	Chenopodiaceae	Annual	Native
Cirsium arvense	Canada thistle	Asteraceae	Perennial	Introduced
Cirsium vulgare	bull thistle	Asteraceae	Biennial	Introduced
Collinsia parviflora	maiden blue eyed Mary	Scrophulariaceae	Annual	Native
Convolvulus arvensis	field bindweed	Convolvulaceae	Perennial	Introduced
Conyza canadensis	Canadian horseweed	Asteraceae	Annual, Biennial	Native
Corallorhiza	coralroot	Orchidaceae	Perennial	Native
Cynoglossum officinale	gypsyflower	Boraginaceae	Biennial	Introduced
Cystopteris fragilis	brittle bladderfern	Dryopteridaceae	Perennial	Native
Danthonia spicata	poverty oatgrass	Poaceae	Perennial	Native
Dianthus armeria	Deptford pink	Caryophyllaceae	Annual, Biennial	Introduced
Elymus albicans	Montana wheatgrass	Poaceae	Perennial	Native
Elymus elymoides	squirreltail	Poaceae	Perennial	Native
Erigeron elatior	tall fleabane	Asteraceae	Perennial	Native
Erigeron vetensis	early bluetop fleabane	Asteraceae	Perennial	Native
Eriogonum flavum	alpine golden buckwheat	Polygonaceae	Perennial	Native
Eriogonum umbellatum	sulphur-flower buckwheat	Polygonaceae	Perennial	Native
Erysimum inconspicuum	shy wallflower	Brassicaceae	Biennial, Perennial	Native
Festuca saximontana	Rocky Mountain fescue	Poaceae	Perennial	Native
Fragaria virginiana	Virginia strawberry	Rosaceae	Perennial	Native
Gaillardia aristata	common gaillardia	Asteraceae	Perennial	Native
Galium aparine	stickywilly	Rubiaceae	Annual	Native
Gentiana affinis	pleated gentian	Gentianaceae	Perennial	Native
Geranium caespitosum	pineywoods geranium	Geraniaceae	Perennial	Native
Grindelia squarrosa	curlycup gumweed	Asteraceae	Annual, Biennial, Perennial	Native
Harbouria trachypleura	whiskbroom parsley	Apiaceae	Perennial	Native
Hesperostipa comata	needle and thread	Poaceae	Perennial	Native
Heterotheca villosa	hairy false goldenaster	Asteraceae	Perennial	Native
Juniperus communis	common juniper	Cupressaceae	Perennial	Native
Juniperus scopulorum	Rocky Mountain juniper	Cupressaceae	Perennial	Native
Koeleria macrantha	prairie Junegrass	Poaceae	Perennial	Native
Lactuca serriola	prickly lettuce	Asteraceae	Annual, Biennial	Introduced
Leucopoa kingii	spike fescue	Poaceae	Perennial	Native
Liatris punctata	dotted blazing star	Asteraceae	Perennial	Native
Linaria dalmatica	Dalmatian toadflax	Scrophulariaceae	Perennial	Introduced

Species Name	Common Name	Family	Longevity	US Nativity
Lupinus argenteus	silvery lupine	Fabaceae	Perennial	Native
Luzula parviflora	smallflowered woodrush	Juncaceae	Perennial	Native
Mahonia repens	creeping barberry	Berberidaceae	Perennial	Native
Mertensia lanceolata	prairie bluebells	Boraginaceae	Perennial	Native
Microseris nutans	nodding microceris	Asteraceae	Perennial	Native
Microsteris gracilis	slender phlox	Polemoniaceae	Annual	Native
Mirabilis hirsuta	hairy four o'clock	Nyctaginaceae	Perennial	Native
Monarda pectinata	pony beebalm	Lamiaceae	Annual	Native
Muhlenbergia filiformis	pullup muhly	Poaceae	Annual	Native
Muhlenbergia minutissima	annual muhly	Poaceae	Annual	Native
Muhlenbergia montana	mountain muhly	Poaceae	Perennial	Native
Muhlenbergia richardsonis	mat muhly	Poaceae	Perennial	Native
Opuntia fragilis	brittle pricklypear	Cactaceae	Perennial	Native
Packera cana	woolly groundsel	Asteraceae	Perennial	Native
Packera fendleri	Fendler's ragwort	Asteraceae	Perennial	Native
Pascopyrum smithii	western wheatgrass	Poaceae	Perennial	Native
Pediocactus simpsonii	Simpson hedgehog cactus	Cactaceae	Perennial	Native
Penstemon virens	Front Range beardtongue	Scrophulariaceae	Perennial	Native
Phacelia heterophylla	varileaf phacelia	Hydrophyllaceae	Biennial, Perennial	Native
Phemeranthus parviflorus	sunbright	Portulacaceae	Perennial	Native
Phleum pratense	timothy	Poaceae	Perennial	Introduced
Pinus ponderosa	ponderosa pine	Pinaceae	Perennial	Native
Poa compressa	Canada bluegrass	Poaceae	Perennial	Introduced
Poa fendleriana	muttongrass	Poaceae	Perennial	Native
Poa pratensis	Kentucky bluegrass	Poaceae	Perennial	Introduced
Polemonium brandegeei	Brandegee's Jacob's- ladder	Polemoniaceae	Perennial	Native
Polygonum douglasii	Douglas' knotweed	Polygonaceae	Annual	Native
Populus tremuloides	quaking aspen	Salicaceae	Perennial	Native
Potentilla fissa	bigflower cinquefoil	Rosaceae	Perennial	Native
Potentilla hippiana	woolly cinquefoil	Rosaceae	Perennial	Native
Prunus virginiana	chokecherry	Rosaceae	Perennial	Native
Pseudotsuga menziesii	Douglas-fir	Pinaceae	Perennial	Native
Psoralidium tenuiflorum	slimflower scurfpea	Fabaceae	Perennial	Native
Pulsatilla patens	eastern pasqueflower	Ranunculaceae	Perennial	Native
Ranunculus ranunculinus	tadpole buttercup	Ranunculaceae	Perennial	Native
Rhus trilobata	skunkbush sumac	Anacardiaceae	Perennial	Native
Ribes cereum	wax currant	Grossulariaceae	Perennial	Native
Rosa woodsii	Woods' rose	Rosaceae	Perennial	Native
Rubus deliciosus	delicious raspberry	Rosaceae	Perennial	Native
Rubus idaeus	American red raspberry	Rosaceae	Perennial	Native

Species Name	Common Name	Family	Longevity	US Nativity
Rumex salicifolius var. mexicanus	Mexican dock	Polygonaceae	Perennial	Native
Scutellaria brittonii	Britton's skullcap	Lamiaceae	Perennial	Native
Sedum lanceolatum	spearleaf stonecrop	Crassulaceae	Perennial	Native
Silene antirrhina	sleepy silene	Caryophyllaceae	Annual	Native
Solidago nana	baby goldenrod	Asteraceae	Perennial	Native
Solidago simplex	Mt. Albert goldenrod	Asteraceae	Perennial	Native
Sonchus arvensis	field sowthistle	Asteraceae	Perennial	Introduced
Sonchus asper	spiny sowthistle	Asteraceae	Annual	Introduced
Symphoricarpos albus	common snowberry	Caprifoliaceae	Perennial	Native
Symphyotrichum porteri	smooth white aster	Asteraceae	Perennial	Native
Taraxacum officinale	common dandelion	Asteraceae	Perennial	Introduced
Toxicodendron rydbergii	western poison ivy	Anacardiaceae	Perennial	Native
Tragopogon dubius	yellow salsify	Asteraceae	Annual, Biennial	Introduced
Triodanis perfoliata	clasping Venus' looking- glass	Campanulaceae	Annual	Native
Verbascum thapsus	common mullein	Scrophulariaceae	Biennial	Introduced
Vulpia octoflora	sixweeks fescue	Poaceae	Annual	Native
Yucca glauca	soapweed yucca	Agavaceae	Perennial	Native

Species Name	Common Name	Family	Longevity
Acroptilon repens	hardheads	Asteraceae	Perennial
Aegilops cylindrica	jointed goatgrass	Poaceae	Annual
Agropyron cristatum	crested wheatgrass	Poaceae	Perennial
Arrhenatherum elatius	tall oatgrass	Poaceae	Perennial
Bromus arvensis	field brome	Poaceae	Annual
Bromus inermis	smooth brome	Poaceae	Perennial
Bromus tectorum	cheatgrass	Poaceae	Annual
Carduus nutans	nodding plumeless thistle	Asteraceae	Biennial
Centaurea diffusa	diffuse knapweed	Asteraceae	Annual, Perennial
Centaurea stoebe	spotted knapweed	Asteraceae	Biennial, Perennial
Cirsium arvense	Canada thistle	Asteraceae	Perennial
Cirsium vulgare	bull thistle	Asteraceae	Biennial
Euphorbia esula	leafy spurge	Euphorbiaceae	Perennial
Euphorbia myrsinites	myrtle spurge	Euphorbiaceae	Biennial, Perennial
Hieracium aurantiacum	orange hawkweed	Asteraceae	Perennial
Lactuca serriola	prickly lettuce	Asteraceae	Annual, Biennial
Linaria dalmatica	Dalmatian toadflax	Scrophulariaceae	Perennial
Linaria vulgaris	butter and eggs	Scrophulariaceae	Perennial
Melilotus albus	white sweetclover	Fabaceae	Annual, Biennial, Perennial
Melilotus officinalis	yellow sweetclover	Fabaceae	Annual, Biennial, Perennial
Salvia aethiopis	Mediterranean sage	Lamiaceae	Biennial
Verbascum thapsus	common mullein	Scrophulariaceae	Biennial

Appendix B. Twenty two introduced (non-native to US) species of management concern selected as target species for the trail and road surveys.

Species Name	Common Name	Family	Longevity	US Nativity
Achillea millefolium	common yarrow	Asteraceae	Perennial	Native
Agrostis scabra	rough bentgrass	Poaceae	Perennial	Native
Ambrosia psilostachya	Cuman ragweed	Asteraceae	Annual, Perennial	Native
Anaphalis margaritacea	western pearly everlasting	Asteraceae	Perennial	Native
Androsace septentrionalis	pygmyflower rockjasmine	Primulaceae	Annual, Perennial	Native
Arabis drummondii	Drummond's rockcress	Brassicaceae	Biennial, Perennial	Native
Arabis hirsuta	hairy rockcress	Brassicaceae	Annual, Biennial, Perennial	Native
Artemisia frigida	prairie sagewort	Asteraceae	Perennial	Native
Artemisia tridentata	big sagebrush	Asteraceae	Perennial	Native
Bromus tectorum	cheatgrass	Poaceae	Annual	Introduced
Campanula rotundifolia	bluebell bellflower	Campanulaceae	Perennial	Native
Capsella bursa-pastoris	shepherd's purse	Brassicaceae	Annual	Introduced
Carduus nutans	nodding plumeless thistle	Asteraceae	Biennial	Introduced
Cerastium arvense	field chickweed	Caryophyllaceae	Perennial	Native
Collinsia parviflora	maiden blue eyed Mary	Scrophulariaceae	Annual	Native
Danthonia spicata	poverty oatgrass	Poaceae	Perennial	Native
Draba reptans	Carolina draba	Brassicaceae	Annual	Native
Fragaria virginiana	Virginia strawberry	Rosaceae	Perennial	Native
Hypericum perforatum	common St. Johnswort	Clusiaceae	Perennial	Introduced
Pinus ponderosa var. scopulorum	ponderosa pine	Pinaceae	Perennial	Native
Poa compressa	Canada bluegrass	Poaceae	Perennial	Introduced
Schizachyrium scoparium	little bluestem	Poaceae	Perennial	Native
Thlaspi arvense	field pennycress	Brassicaceae	Annual	Introduced
Verbascum thapsus	common mullein	Scrophulariaceae	Biennial	Introduced
Viola bicolor	field pansy	Violaceae	Annual	Native

Appendix C. Species found germinating in the soil seed bank.