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## Effects of post-fire conditions on germination and seedling success of diffuse knapweed in northern Arizona

B.A.S. Wolfson<sup>a,b,\*</sup>, T.E. Kolb<sup>a</sup>, C.H. Sieg<sup>b</sup>, K.M. Clancy<sup>b</sup>

<sup>a</sup> Northern Arizona University, School of Forestry, Box 15018, Flagstaff, AZ 86011, USA

<sup>b</sup> USDA Forest Service Research and Development, Rocky Mountain Research Station, 2500 S. Pine Knoll Drive, Flagstaff, AZ 86001-6381, USA

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### Abstract

Introduction of exotic plant species is confounding treatments designed to reduce unnaturally high tree densities in ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests of the western United States. Also, the recent increase in large, stand-replacing wildfires may promote introduction and spread of species, such as diffuse knapweed (*Centaurea diffusa* Lam.), which may lead to reduced forage and land values and major ecosystem changes. We hypothesized that diffuse knapweed germination and seedling growth would respond positively to burned conditions in northern Arizona ponderosa pine forests. Our first field study was based on a May 2002 wildfire near Flagstaff, Arizona (Site I). For the field study at Site I, we buried diffuse knapweed seeds in sealed mesh packets in four forest floor conditions: severely burned, moderately burned, unburned bare soil and unburned. We removed packets monthly and measured percent germination. Germination under severely burned conditions at Site I (overall average 76%) was higher than in unburned conditions (59%) ( $P = 0.017$ ). Our second field study was based on a fuel reduction treatment with slash piles burned in February 2003 (Site II). Germination in seed packets was higher ( $P = 0.003$ ) in pile burn scars (67%) than in adjacent unburned locations (38%) at Site II. In fall 2002, we planted knapweed seeds in pots containing intact soil cores from Site I from unburned and severely burned conditions. We allowed competition to grow in half the pots, and removed competition in the other half. Diffuse knapweed biomass/pot was greater ( $P = 0.035$ ) in soil from the severely burned (2.6 g) compared to the unburned condition (0.6 g) from Site I. Knapweed biomass/pot also appeared greater when grown in soil from pile burn scars (3.3 g) compared with unburned locations (2.5 g) from Site II, although the difference was not significant ( $P = 0.317$ ). We conclude that severe wildfire or pile burning can promote germination and seedling growth of diffuse knapweed in northern Arizona pine forests. Moreover, diffuse knapweed may also threaten unburned forests, as average germination was 48% in unburned locations. Failure to consider exotic invasive species in fuel reduction and wildfire rehabilitation may result in trading one undesirable condition for another.

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**Keywords:** *Centaurea diffusa*; Wildfire; Slash pile burning; Seed viability; Invasive; Exotic; *Pinus ponderosa*

\* Corresponding author. Tel.: +1 928 556 2157;  
fax: +1 928 556 2130.

E-mail address: [bswolfson@fs.fed.us](mailto:bswolfson@fs.fed.us) (B.A.S. Wolfson).

## 1. Introduction

Diffuse knapweed (*Centaurea diffusa* (Lam.): Asteraceae) (USDA NRCS, 2004 is the source for all scientific nomenclature) is a designated noxious weed in 14 western states (USDA NRCS, 2004) and four Canadian provinces (Rice, 2004). Diffuse knapweed was likely introduced to North America in the late 1800s and is now widespread and problematic in many areas of the western United States and Canada (Watson and Renney, 1974; Roché and Roché, 1988, 1999; Sheley et al., 1998). Diffuse knapweed is a deeply taprooted, semelparous perennial, native to grassland steppes in the Mediterranean and parts of Asia (Watson and Renney, 1974; Nolan and Upadhyaya, 1988; Sheley et al., 1998; Roché and Roché, 1999). The invasion of grasslands and forest steppes by diffuse knapweed can reduce native species diversity (Roché and Roché, 1988; LeJeune and Seastedt, 2001) and forage for wildlife and livestock (Watson and Renney, 1974; Roché and Roché, 1988, 1999). Knapweed's spiny canopy reduces the availability of low growing forage species to animals (Watson and Renney, 1974). Heavy soil erosion can occur in areas where diffuse knapweed dominates the landscape (Roché and Roché, 1988; Sheley et al., 1997, 1998), and land values can decline upon infestation by knapweeds (Roché and Roché, 1988, 1999; Flores, 2002). An estimate of forage loss for 1988 in eastern Washington due to four knapweed species, including diffuse knapweed, was more than US\$ 3 million (Roché and Roché, 1988). It is important to understand the basic mechanisms for invasion of knapweeds and other exotic plants, such as disturbance, because their spread into new areas can be costly and damaging (Pimentel et al., 2000).

Disturbances, such as fire or fuel reduction treatments, may play a role in the invasion success of diffuse knapweed because of changes in resource availability. Disturbance to forests across the western U.S. is increasing due to wildfire, as well as thinning and prescribed burning projects aimed at fuel reduction (Covington and Moore, 1994; Allen et al., 2002). Fuel reduction treatments to reduce the risk of wildfire in and around urban areas of the western U.S. are currently a priority in the wildland urban interface (WUI) (Farnsworth and Summerfelt, 2002; Marzluff and Bradley, 2003). The WUI, by definition, is close to

urban populations, therefore, thinning and removal of resulting slash are often necessary before managers can safely reintroduce fire to the landscape (Farnsworth and Summerfelt, 2002). Although fire frequency and intensity may have varied, there is little debate that many forest types in the western U.S. coevolved with fire, including southwestern ponderosa pine forests (Weaver, 1951; Cooper, 1960; Covington and Moore, 1994; Pyne et al., 1996). Local land managers currently recommend pile burning on site for slash disposal (Farnsworth and Summerfelt, 2002) as do management agencies in other areas where diffuse knapweed or other exotic plants are problematic (Hann et al., 2004). Pile burning may create highly disturbed microsites that are excellent habitat for exotic plants (Korb et al., 2004).

Diffuse knapweed populations in northern Arizona currently exist primarily along roadsides and other disturbed areas (EnviroSystems Management, 2001). Roads can often contribute to the spread of exotic weeds (Gelbard and Belnap, 2003). Some of the largest populations of diffuse knapweed exist close to the WUI (EnviroSystems Management, 2001), and because knapweed is wind-dispersed, similar to tumbleweeds, invasion into the WUI may occur easily. Because of knapweed's affinity for disturbed areas and its exponential expansion in the northwestern U.S. (Roché and Roché, 1988), there is a concern that it will expand similarly in the southwestern U.S. (Sieg et al., 2003).

Performance and impacts of diffuse knapweed are likely to vary among ecosystems. For example, diffuse knapweed has a stronger negative effect on plant competitors native to North America than on competitors native to its original range in Eurasia (Callaway and Aschehoug, 2000). This may be due to a combination of factors, including its ability to more effectively compete for resources and potential tolerance of Eurasian plants to its allelopathic properties (Callaway and Aschehoug, 2000). Neither diffuse nor spotted knapweed (*C. biebersteinii* DC) competes as well with their native counterparts as they do with North American plants (Sheley et al., 1998; Callaway and Aschehoug, 2000). Therefore, performance and impacts of diffuse knapweed in the southwestern U.S. may be different than in Eurasia, and other regions of North America.

Our study is the first to directly address the capability of diffuse knapweed to germinate and grow

under post-fire conditions in forests, and it is the first study of knapweed in Arizona. We examined whether diffuse knapweed can germinate and establish in burned and unburned ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests around Flagstaff, Arizona using field studies and experiments repeated over 2 years. We planted contained diffuse knapweed seeds in the field under a variety of burned and unburned conditions to evaluate whether disturbance by wildfire, slash pile burning and removal of litter influence seed germination. In a separate experiment, we compared seedling survival and growth of diffuse knapweed in soils from forest stands exposed to different levels of wildfire and pile burning. Our results provide insight on the potential for establishment of diffuse knapweed in fire-disturbed and non-disturbed forested sites.

## 2. Methods

### 2.1. Field seed germination study

We conducted field studies over 2 years (beginning in 2002 and 2003) at two sites near Flagstaff in northern Arizona. Diffuse knapweed was not present at either site prior to the study. Consequently, we studied seed germination at the field sites using contained seed packets to prevent knapweed introduction.

Site I was near Hart Prairie, on the Coconino National Forest (elevation of 2560 m) approximately 24 km north of Flagstaff (UTM coordinates: 12S, 432,273E and 3,909,632N). Annual average precipitation at the nearby Fort Valley weather station, is 56.3 cm and is distributed bimodally, with the majority occurring between January and March as snow and in July and August as rain (Western Regional Climate Center, 2004). During our study period from mid-October 2002 to mid-October 2003, precipitation totalled approximately 52.9 cm as recorded by a nearby weather station (RMRS, 2005). Long-term average monthly minimum and maximum temperatures for the warmest and coldest months are as follows: July 7.2° and 26.8 °C and January –12.3° and 5.2 °C (Western Regional Climate Center, 2004). Site I was dominated by ponderosa pine. The dominant understory species was Arizona

fescue (*Festuca arizonica* Vasey); other species included squirreltail (*Elymus elymoides* (Raf.) Swezey), cinquefoil (*Potentilla* sp.), silvery lupine (*Lupinus argenteus* Pursh) and thistle (*Cirsium* sp.). Soils at Site I are derived from basalt (Miller et al., 1995).

Site I burned during a May 2002 wildfire, the Hart Fire. The fire was approximately 20 ha in size and resulted in varying degrees of burn severity. We selected the Hart Fire for our research from several fires that occurred in northern Arizona in 2002, because of its burn variability within a small area, and also due to its accessibility.

Site II was in the Northern Arizona University (NAU) Centennial Forest, approximately 3 km southwest of Flagstaff, Arizona (UTM coordinates: 12S, 432,749E and 3,890,486N). The approximate elevation is 2300 m. Annual average precipitation at the nearby Flagstaff weather station is 53.9 cm with the same bimodal distribution as described for Site I (Western Regional Climate Center, 2004). During our study period from mid-October 2003 to mid-October 2004 precipitation totalled approximately 44.7 cm (Western Regional Climate Center, 2004). Average monthly minimum and maximum temperatures for the warmest and coldest months are as follows: July 10.2° and 27.7 °C and January –8.9° and 5.9 °C (Western Regional Climate Center, 2004). This area is dominated by ponderosa pine with a minor component of Gambel oak (*Quercus gambelii* Nutt.). The primary understory species were squirreltail and Arizona fescue with lesser amounts of Fendler's ceanothus (*Ceanothus fendleri* Gray), milkvetch (*Astragalus* spp.), phlox (*Phlox* sp.) and stemless Townsend daisy (*Townsendia exscapa* (Richards.) Porter). Soils at Site II are primarily basalt derived (Miller et al., 1995).

In February 2003, the Arizona State Land Department burned slash piles at Site II resulting from a thinning in fall 2002 that reduced tree density. Pile burn scars were approximately 1.2–1.5 m in diameter. Most fuel was consumed by fire in the center of the piles, although some woody debris remained unconsumed at the edges. We selected this site primarily because of the timing of pile burning and accessibility to the site. Site II is typical of stands treated for fuel reduction within the Flagstaff WUI.

We collected seeds from three diffuse knapweed populations in the city of Flagstaff, Arizona in fall

2002 and again in fall 2003. Collection involved clipping seed heads (about 30 per plant) from approximately 20 plants per population and harvesting mature seeds. We tested a random sample of 5% of these seeds for viability in a growth chamber (Model 1-35L, Percival Scientific Inc., Perry, Iowa) on a 14-h light:10-h dark cycle at a temperature of 25/10 °C (day/night) for 21 days ( $n = 10$  Petri dishes  $\times$  20 seeds each) (Doucet and Cavers, 1996). We tested viability of both loose seeds and seeds in packets in Petri dishes. We initially hydrated the seeds with 3 ml of water, and then rehydrated every 2–3 days as necessary. We considered as viable all seeds that germinated under growth chamber conditions within 21 days (Doucet and Cavers, 1996).

We used enclosed seed packets to study knapweed seed germination to avoid introducing knapweed to our field sites. We created the seed packets using plastic photographic slide mounts (with an opening of 28 mm  $\times$  28 mm) and plankton netting following a method developed by Rasmussen and Whigham (1993) for orchid seed studies (Fig. 1). This method allows seed interaction with soil, mycorrhizae and microorganisms as large as nematodes, and flow of nutrients and water (Rasmussen and Whigham, 1993), but does not allow seed escape. Each seed packet contained 20 seeds and we did not select for seed viability.

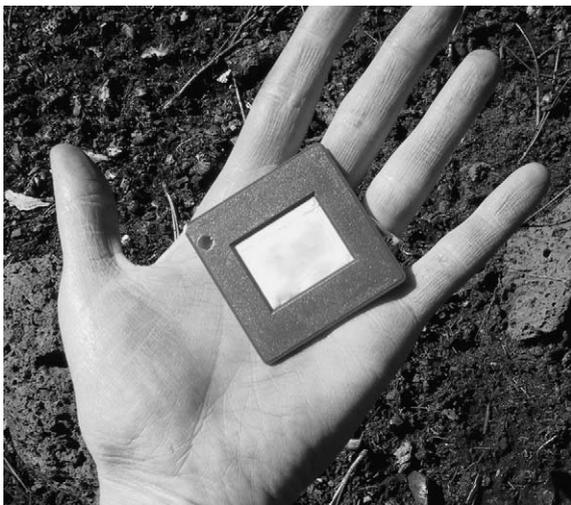


Fig. 1. Packet used to contain diffuse knapweed seeds during field seed germination studies.

We buried seed packets in October 2002 at each of four forest floor conditions and monitored germination on a monthly basis at Site I. The four forest floor conditions were: (1) an unburned stand with uncleared soil with litter and organic material intact (unburned); (2) an unburned stand with litter and organic material of the forest floor removed by raking (unburned bare soil); (3) a moderately burned stand with some consumption of the forest floor and 30% or less crown scorch of the pine trees (moderate burn) and (4) a severely burned stand with a heavily burned forest floor dominated by ash and bare soil and 80–100% crown scorch or total crown consumption of the pine trees (severe burn). We included the unburned bare soil condition to evaluate the influence of physical disturbance of the forest floor on germination. We followed Ryan and Noste (1985) to determine ground char and Ryan (1982) to evaluate crown scorch.

At Site I, we buried two sets of nine seed packets, approximately 1.5 cm beneath the soil surface, in three clusters in each of the four forest floor conditions, for a total of 216 packets. We connected each seed packet with wire to a central post in the shape of a wheel with spokes for easy extraction and to prevent accidental loss of seed packets. No seeds were lost at Sites I or II. Beginning in April 2003, we retrieved one packet at each stake (six packets per forest floor condition) on a monthly basis until November 2003 and measured germination.

After collection of seed packets each month, we removed the seeds in the lab and counted the number of germinated seeds. If the radical was not visible, we used a dissecting microscope to inspect the seed for evidence of germination. Because seeds could have germinated at any time between burial and removal of packets and subsequently rotted, we included in our germination count seeds with cracked open seed coats even if the radical was not obviously present. Thus, our calculations represent a cumulative germination over all months of the study. After counting and removing the germinated seeds, we placed the remainder of the seeds in Petri dishes in the growth chamber for 21 days with the same environmental conditions used for the viability tests. We then calculated the field germination percent per seed packet by dividing the number of seeds germinated in the field by the total number of germinants.

We were unable to collect four seed packets at Site I from a control site (unburned) and an unburned bare soil site, due to frozen ground at the first collection in April 2003. We concluded that none of these seeds could have germinated because the soil was frozen and snow covered for several months prior to April. We counted these seed packets as having zero germination.

We measured air and soil temperatures periodically at all levels of burn severity at both sites using data loggers (Spectrum Technologies Inc., Plainfield, Illinois). At Site I, the data loggers recorded mean hourly temperatures at each cluster and each forest condition, for a total of 12 locations. We placed soil temperature probes 1.5 cm below mineral soil and air temperature was recorded at approximately 38 cm above the soil. At Site I, cattle damaged all the soil temperature probes in July 2003 except those in severely burned plots. Thus, most of our Site I soil temperature measurements ended in July 2003. We measured volumetric soil water content at a soil depth of 15 cm, using a Time Domain Reflectometer (TDR) (Soil Moisture Equipment Corp., Goleta, California), weekly between May and October 2003. At Site I, we measured soil water content at two locations per cluster for a total of 24 measurements per week. We averaged the measurements at each cluster per condition prior to statistical analysis.

The study design at Site II was slightly different than Site I. At Site II, we buried seed packets in late October 2003 in pile burn scars in a design that paired burn piles and adjacent unburned conditions. We placed two sets of six seed packets, each containing 20 seeds, 1.5 cm beneath the soil surface within the burn scar (approximately 40 cm from the edge) and adjacent to the scar (approximately 40 cm outside the edge). We replicated the design over five pile burn scars for a total of 120 seed packets. We collected seed packets (10 per treatment) monthly beginning in March and ending in August 2004 and measured seed germination as described for Site I. We also recorded hourly mean air and soil temperature within (pile burn scar) and adjacent (unburned) to each pile burn scar using the same data loggers described for Site I. We measured soil water content at each set of six seed packets for a total of 20 measurements per week. We averaged the two soil water content measurements at each set prior to analysis.

For Sites I and II, we collected soil samples for nutrient analyses. At Site I, we collected soil samples at a depth of 6 cm from each cluster and forest floor condition in June 2003, 13 months post-fire. Because unburned bare soil and unburned plots were close together, we combined the soil sample for both conditions, resulting in a total of nine soil samples. At Site II, we collected soil samples at a depth of 6 cm in April 2004, 14 months post-fire. We analyzed the following nutrients at both sites: total phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), nitrogen (N), extracted ammonium ( $\text{NH}_4\text{-N}$ ) and nitrate ( $\text{NO}_3\text{-N}$ ), and at Site I only pH. The NAU Analytical Services Laboratory prepared soils for analysis of total N, P and minerals using the Kjeldahl digest method (Parkinson and Allen, 1975). They measured concentrations of N and P by automated colorimetry using a Technicon Auto-Analyzer II and minerals (Ca, Mg and K) by flame atomic absorption spectrometry using a Perkin-Elmer 560 spectrophotometer (Parkinson and Allen, 1975). They extracted soils in two normal KCl and determined available N by analyzing for  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  by automated colorimetry again using a Technicon Auto-Analyzer II (Page, 1982).

## 2.2. Statistical analysis—germination study

The response variable for the germination study was percent germination. We used Shapiro–Wilk to test for normality and Levene to test for homogeneity of variance. For Site I we used an analysis of variance (ANOVA) with repeated measures for germination from each set of nine seed packets ( $n = 6$ ; d.f. = 3, 20) over all months to compare differences in seed germination among the four conditions. The time by condition interaction was not significant ( $P = 0.511$ ) for Site I, thus we subsequently ran ANOVA on means across time and used Tukey's Honestly Significant Difference (HSD) to separate mean germination among forest conditions. We also used repeated measures ANOVA for soil water content data over all months on data averaged for each cluster ( $n = 3$ ; d.f. = 3, 8). Germination and soil water content data over all nine months met both normality and homogeneity of variance assumptions. Similar to the germination data, the time by condition interaction was not significant ( $P = 0.467$ ) for soil water content, and thus we ran ANOVA on means across time and used Tukey's HSD

to separate average water content among forest conditions. We did not statistically analyze the temperature data because it was incomplete. Data logger failures occurred frequently likely due to electrical storms (personal communication Spectrum Technologies, 2003), and data were also lost due to damage from cattle. At Site I, we used ANOVA for each soil nutrient to compare concentration among forest conditions and Tukey's HSD to separate mean concentrations among the four conditions ( $n = 3$ ; d.f. = 2, 6).

For the Site II field study, we used repeated measures ANOVA to compare average monthly germination percent ( $n = 5$ ; d.f. = 1, 8) between pile burn scars and unburned locations over all months. As in the Site I study, the time by condition interaction was not significant ( $P = 0.642$ ), and we therefore used a paired  $t$ -test of mean germination across time to compare differences between locations. Soil water content ( $n = 5$ ; d.f. = 1, 8) and soil nutrient analyses ( $n = 5$ ; d.f. = 1, 8) were conducted the same as for Site I. Germination and soil water content data across all months met normality and homogeneity of variance assumptions. We used JMP Version 5 for all statistical analyses (SAS Institute Inc., 2002).

### 2.3. Growth study

We extracted intact soil cores from Site I in fall 2002. The soil cores were approximately 10 cm in depth and 30 cm in diameter. We extracted the soil by pounding a piece of metal pipe (30 cm diameter  $\times$  30 cm depth) into the ground with a jackhammer. We extracted soil cores from areas lacking large rocks in two forest conditions, a severe burn and unburned. We extracted the cores intact and placed them into black plastic pots 28 cm deep and 34 cm in diameter. We pre-filled pots with sterile, unfertilized commercial potting soil to a depth of approximately 13 cm, which allowed the litter on the soil core to remain nearly even with the lip of the pot. Next, we transported the soil cores to the Rocky Mountain Research Station (RMRS) Greenhouse Facility in Flagstaff, and placed them outside on flat ground, covered with plastic to prevent existing ground cover from growing through the pots.

The RMRS Greenhouse Facility is located at approximately 2100 m elevation in a ponderosa pine forest. We placed pots in an unshaded area. Pots

received water only from precipitation. Some exotic species existed on site, such as cheatgrass (*Bromus tectorum* L.), prickly lettuce (*Lactuca serriola* L.), Russian thistle (*Salsola kali* L.), Dalmation toadflax (*Linaria dalmatica* (L.) P. Mill.) and diffuse and spotted knapweed. In the spring and summer of each year, we pulled nearby diffuse and spotted knapweed plants from the vicinity of the study area at the Greenhouse Facility to avoid contamination of experimental pots.

The experiment that used soil cores from Site I was a full factorial with four treatment combinations: two levels of forest floor conditions (unburned, burned)  $\times$  two levels of competition (present, absent). We included competition as a factor to determine potential effects of other plants on the growth of diffuse knapweed. The forest floor conditions included soil from a medium-density (740 trees/ha) unburned stand, and soil from a similar density severely burned stand (80–100% crown scorch or crown consumption of overstory trees) with heavily burned forest floor dominated by ash and bare soil.

We used 20 soil cores from each forest floor condition. We planted 15 diffuse knapweed seeds individually at an even spacing in each pot at a depth of 1.5 cm at the greenhouse. We randomly assigned competition levels to each pot. For the competition present treatment, we allowed plants to establish from the seed bank or existing plants in the extracted soil core to remain. For the no competition treatment, we clipped all non-knapweed plants at soil level. We began clipping in April when competing plants were approximately 2 cm in height. We clipped every 2 weeks in April and May, and once a week thereafter as needed.

When the first knapweed plants bolted and developed seed heads, we harvested all plants, and then separated and measured the dry weight of above- and below-ground portions. We harvested plants from the Site I soil core experiment between 31 July and 3 August 2003. We extracted whole plants from pots by washing soil from roots. For diffuse knapweed, we also separated and counted the number of seed heads. All plant parts were oven dried at 60 °C for 72 h before weighing.

In fall 2003, we conducted an experiment using soil cores from Site II in a paired design in which soil cores from within a pile burn scar were paired with unburned soil adjacent to the pile burn scar. Soil cores within pile burn scars were obtained no less than 25 cm from the

edge and cores adjacent were no more than 60 cm outside the edge of the scar in an unburned location ( $n = 20$  pairs). We used the same procedure to extract soil cores from Site II as described for Site I. We placed pots of soil in a partly shaded area at the RMRS greenhouse facility for the 2003 experiment to reduce high temperatures that occurred in the Site I soil core experiment. In October 2003, we planted 20 diffuse knapweed seeds in each pot at a depth of 1.5 cm. Because competition did not significantly affect knapweed growth in the Site I soil core experiment (see Section 3), we did not repeat the competition treatment. We harvested all plants between 9 and 14 September 2004 in the same manner described for the Site I experiment.

In both experiments, we identified all plant species that emerged in the pots to genus and to species when possible, and counted the number of surviving individuals. For the Site II soil core experiment, we measured volumetric soil water content at 15 cm in a subset of pots ( $n = 2$  for each treatment combination; d.f. = 3, 4) once per week beginning in May using a TDR, and measured mean hourly air and soil temperatures ( $n = 2$ ; d.f. = 3, 4) with data loggers as described for the seed packet study. We performed the same measurements for Site II soil cores as for Site I (temperature  $n = 2$ ; d.f. = 3, 4 and soil water content  $n = 5$ ; d.f. = 1, 8).

#### 2.4. Statistical analysis—growth study

We used total diffuse knapweed plant biomass (dry weight in gram) per pot as the response variable for the experiment based on Site I. We used Shapiro–Wilk to test for normality and Levene to test for homogeneity of variance for both experiments. We used a two-way ANOVA ( $n = 6$  burn with competition,  $n = 4$  unburned with competition,  $n = 6$  burned and  $n = 4$  unburned; d.f. = 3, 16) to test main effects and the interaction between forest floor condition and competition. We excluded pots with no knapweed biomass from the analyses. Data met ANOVA assumptions, except for a departure from normality (Shapiro–Wilk  $P = 0.008$ ). Although there are non-parametric methods to test for burn and competition effects individually, there is no non-parametric method to test for interaction between the two. Because ANOVA is relatively robust to this type of violation (Steel and Torrie, 1980) and we

wanted to test interaction effects, we accepted non-normal data. We also used mean diffuse knapweed biomass per plant (dry weight in gram) as a response variable to test for differences in plant size among conditions. These data met assumptions for homogeneity of variance. However, because these data so strongly violated the assumption of normality (Shapiro–Wilk  $P < 0.001$ ), we used the non-parametric Kruskal–Wallis rank test to compare individual knapweed biomass among the four condition/treatment combinations (Hollander and Wolfe, 1999), and did not test the interaction. Mean knapweed biomass per plant met assumptions for Kruskal–Wallis, which include independent, random samples and similarity of sample distributions. Soil water content data met parametric assumptions, thus we used repeated measures ANOVA.

For soil cores from Site II, data for total biomass per pot met assumptions of normality and homogeneity of variance. We used a one-way ANOVA to test for differences in total knapweed biomass per pot between pile burn scars and unburned locations. Data for mean biomass per plant strongly violated the normality assumption (Shapiro–Wilk  $P < 0.001$ ), and we used the non-parametric Benard–van Elteren rank test that accounts for blocking and unequal sample sizes (Benard and van Elteren, 1953; Norwood et al., 1989). For soil cores from both sites, we categorized species as native or non-native (USDA NRCS, 2004), and compared the proportion of non-native plants that survived with native plant survival across treatments using pots as the experimental unit, excluding those pots that contained no plants throughout the study. We used Kruskal–Wallis to test for significant differences between native and non-native survival for both years. We compared differences in soil water content with repeated measures ANOVA. For all ANOVA we used JMP 5 (SAS Institute Inc., 2002). Finally, we reported the number of knapweed plants, as well as the percentage of plants that died throughout the study.

### 3. Results

#### 3.1. Seed viability

Germination tests in the growth chamber revealed similar viability of diffuse knapweed seeds from local

Flagstaff populations as reported in other studies when conditions are optimal (Watson and Renney, 1974). When we incubated our random sample of collected seeds for viability tests, mean ( $\pm$ S.E., here and throughout) percent germination of loose seeds was  $85.5 \pm 2.2\%$  in 2002 and  $94 \pm 1.7\%$  in 2003. Germination in viability test seed packets was  $85 \pm 2.2\%$  in 2002, the only year we tested this, when incubated under the same conditions.

### 3.2. Seed germination study

Mean seed germination by month at Site I was higher ( $P = 0.017$ ) over time in the severely burned condition than the unburned condition. In April, germination in the severe burn appears to be greater than all other conditions (Fig. 2a). Across all months, germination in the unburned condition ranges from a low of 33% in April to a high of 72% in September. Overall mean germination was higher (76%) in the severe burn compared with the unburned condition (59%) ( $P = 0.017$ ; Fig. 2b). The moderate burn and unburned bare soil conditions were similar to both the severe burn and unburned conditions (Fig. 2b).

There were differences in soil water content among the four forest floor conditions at Site I (Fig. 3). Volumetric soil water content ranged from lows of 9.8% in the unburned and 17.0% in the severely burned condition the first week of July at the peak of the dry season to highs of 37.5% in the unburned and 32.2% in the severely burned condition in September following late season rain. Volumetric soil water content was significantly greater ( $P = 0.002$ ) in the severely burned condition compared to the unburned condition (Fig. 3a). Overall average soil water content in the moderate burn and unburned bare soil conditions was similar to other conditions, whereas it was greater in the severe burn compared to the unburned ( $P = 0.035$ ) (Fig. 3b).

Although we did not statistically analyze temperature data, the unburned condition appeared to have the lowest average weekly maximum soil temperature of all treatments. For example, from May to July when we have the most data, the average weekly maximum soil temperature in the severe burn, moderate burn and unburned bare soil conditions were 25.4, 22.4 and 21.6 °C, respectively, while the unburned condition was only 13.2 °C. Average hourly air temperatures

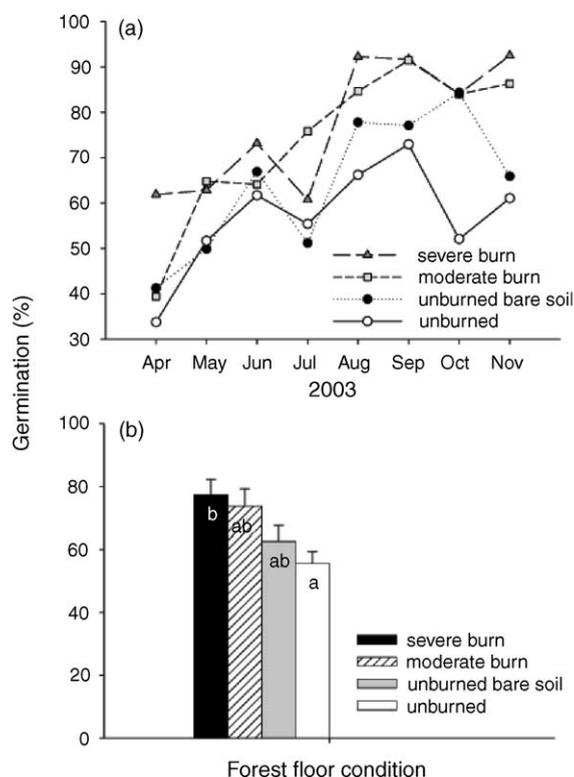


Fig. 2. Average monthly (a) and overall mean ( $\pm$ S.E.) (b) percent germination of diffuse knapweed seeds in four ponderosa pine forest floor conditions at Site I. For (b), bars with different letters indicate significant differences.

ranged from a low of  $-13.3$  °C under the moderately burned condition in April to a high of  $35.8$  °C under the severely burned condition in July (data on air and soil temperatures are not shown). Average hourly soil temperatures ranged from a low of  $-0.8$  °C in April to a high of  $34.5$  °C in July, both under the severe burn condition. Germination occurred within this range of temperatures, evidenced by fresh radicles at collection.

Concentrations of some soil nutrients differed among forest floor conditions 13 months after the wildfire at Site I (Table 1(A)). Total Ca was greater in the severely burned condition than in either the moderately burned or unburned conditions ( $P < 0.001$ ). Extracted  $\text{NH}_4\text{-N}$  was also significantly greater in the severely burned condition than in the unburned condition ( $P = 0.038$ ). Extracted  $\text{NH}_4\text{-N}$  was 4.8 times greater in the severe burn than the unburned condition. Total pH was greatest in the severely burned condition,

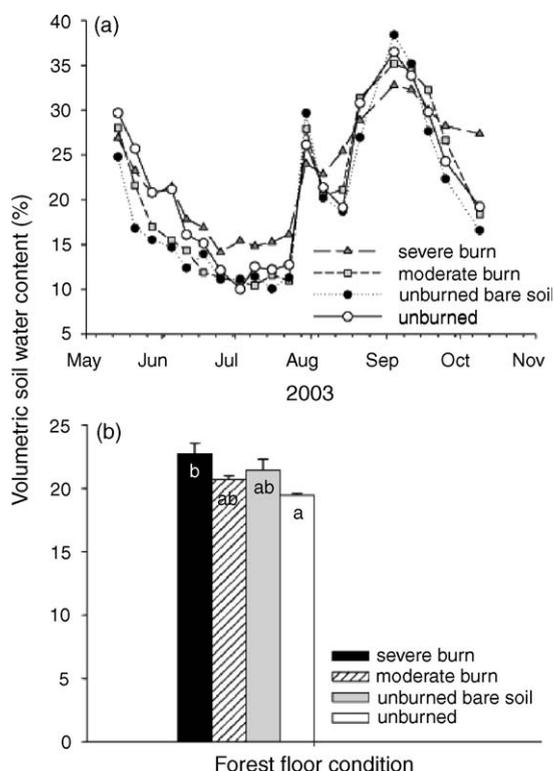


Fig. 3. Average monthly (a) and overall mean (+1S.E.) (b) volumetric soil water content in four ponderosa pine forest floor conditions at Site I. For (b), bars with different letters indicate significant differences.

intermediate in the moderately burned condition and lowest in the unburned condition ( $P < 0.001$ ).

At Site II, germination within pile burn scar locations was significantly higher ( $P = 0.003$ ) than adjacent unburned locations (Fig. 4a). Germination ranged from a low of 21.3% in the unburned locations in March to a high of 87.3% in pile burned locations in August. Overall mean germination for Site II was  $67.5 \pm 6.0\%$  for pile burned locations and  $38.2 \pm 4.6\%$  for unburned locations.

Soil water content at Site II was significantly higher ( $P = 0.002$ ) in the pile burn locations than in the unburned locations with no significant time  $\times$  location interaction (Fig. 4b). Volumetric soil water content ranged from lows of 8.1% in unburned locations and 11.3% in pile burn scars in late June to highs of 23.0% in unburned locations and 29.2% in pile burn scars in July following the onset of the summer rainy season. Average hourly soil temperature at Site II ranged from a low of 0.6 °C in March to a high of 33.6 °C in June (data on air and soil temperatures are not shown). Average hourly air temperature ranged from  $-5.6$  to 32.8 °C in March and June, respectively. Germination occurred within these temperature ranges.

Concentrations of two soil nutrients differed between pile burn scars and unburned locations 14 months after burning at Site II (Table 1(B)). Total K and total Mg were greater in pile burn scars than

Table 1

Nutrient concentrations and pH of soil samples collected from (A) three ponderosa pine forest floor conditions 13 months after burning at Site I and (B) two forest floor conditions 14 months after burning at Site II

Forest floor condition	Response variable (units)															
	N		P		K		Mg		Ca		NH <sub>4</sub> -N		NO <sub>3</sub> -N		pH	
	(mg/g)	(mg/g)	(mg/g)	(mg/g)	(mg/g)	(mg/g)	(mg/g)	(mg/g)	(μg/g)	(μg/g)	(μg/g)	(μg/g)				
	Mean	1S.E.	Mean	1S.E.	Mean	1S.E.	Mean	1S.E.	Mean	1S.E.	Mean	1S.E.	Mean	1S.E.	Mean	1S.E.
(A) Site I																
Unburned	1.96	0.03	1.81	0.06	5.03	0.24	14.43	1.76	<b>2.43a</b>	0.02	<b>25.06a</b>	16.91	1.12	1.12	<b>5.18a</b>	0.10
Moderate burn	1.79	0.04	1.66	0.06	4.50	0.17	13.17	0.86	<b>2.71a</b>	0.06	<b>48.23ab</b>	19.47	1.38	0.63	<b>5.55b</b>	0.02
Severe burn	2.14	0.27	1.70	0.12	5.30	0.37	9.24	1.53	<b>3.26b</b>	0.11	<b>121.47b</b>	24.78	4.29	1.86	<b>6.33c</b>	0.01
P-value	0.352	–	0.439	–	0.193	–	0.096	–	<b>&lt;0.001</b>	–	<b>0.038</b>	–	0.241	–	<b>&lt;0.001</b>	–
(B) Site II																
Unburned	1.28	0.20	0.86	0.10	<b>4.53a</b>	0.11	<b>2.41a</b>	0.09	3.93	0.43	5.97	10.57	0.99	0.99	–	–
Burn pile scars	1.08	0.26	1.06	0.12	<b>5.08b</b>	0.20	<b>2.99b</b>	0.12	4.85	0.32	25.12	1.25	1.97	0.59	–	–
P-value	0.558	–	0.246	–	<b>0.041</b>	–	<b>0.005</b>	–	0.123	–	0.109	–	0.423	–	–	–

Means and ANOVA  $P$ -values for significant ( $P \leq 0.05$ ) treatment effects indicated in boldface; means followed by the same letter (a–c) in a column for a given Site (I or II) are not significantly different ( $P \leq 0.05$ ).

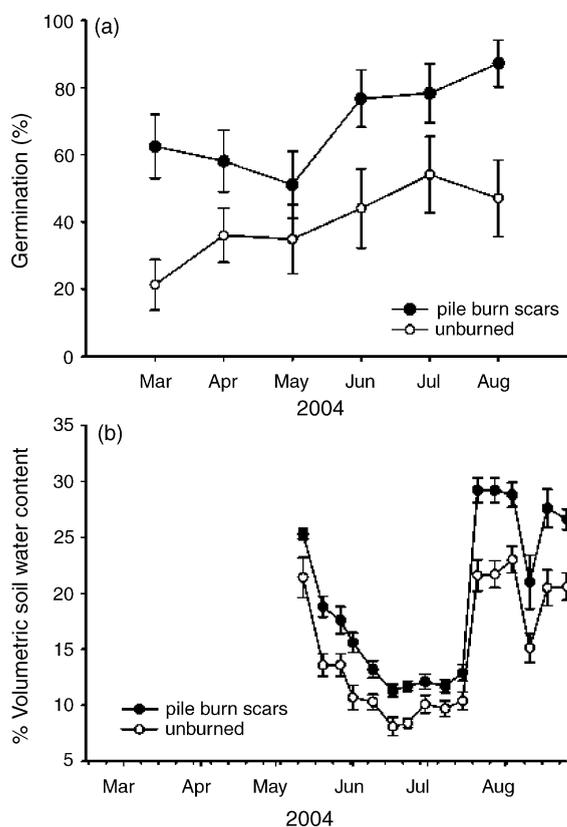


Fig. 4. Mean ( $\pm$ 1S.E.) diffuse knapweed seed germination (a) and mean ( $\pm$ 1S.E.) volumetric soil water content (b) over time at Site II.

unburned locations ( $P = 0.041$  and  $0.005$ , respectively). Although concentration of  $\text{NH}_4\text{-N}$  was 4.2 times higher in pile burn scars than in unburned soil, this difference was not significant ( $P = 0.109$ ).

### 3.3. Growth study

For the experiment based on soil cores from Site I, only 50% of all soil cores produced knapweed plants; 60% of those that produced knapweed were from burned soil and 40% from unburned soil. These percentages were evenly split between competition and no competition treatments. For knapweed plants that survived through the end of the experiment, unburned soil cores produced an average of 1.0 plant per core, while burned cores produced an average of 2.0 plants per core. Total knapweed biomass per pot was significantly greater ( $P = 0.035$ ) in soil cores from

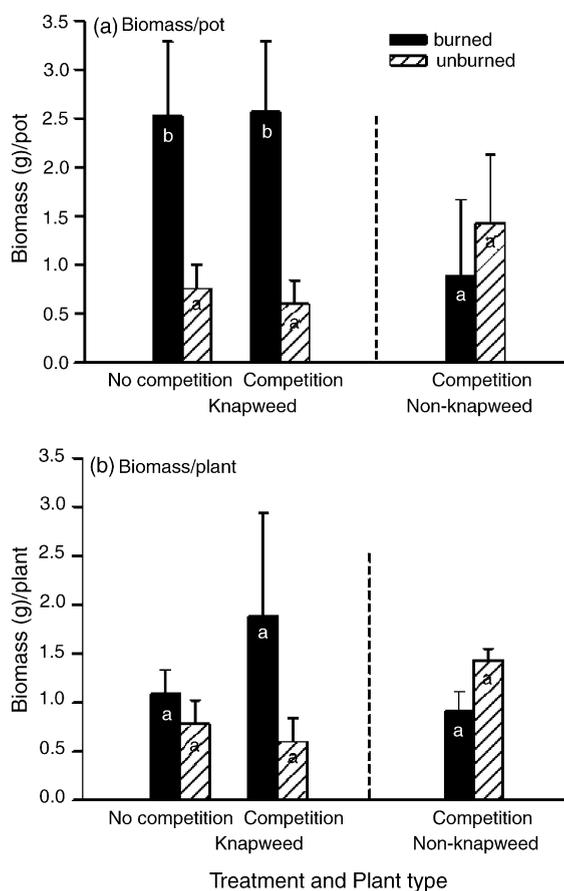


Fig. 5. Mean ( $\pm$ 1S.E.,  $n = 6$  samples per bar for burned and 4 samples per bar for unburned) plant biomass per pot (a) and per plant (b) for diffuse knapweed and other plant species that grew in soil cores collected in 2002 from two ponderosa pine forest floor conditions at Site I. Bars with different letters indicate significant differences. We did not statistically compare knapweed with non-knapweed.

the burned condition than the unburned condition for pots where knapweed grew (Fig. 5a). Competition had no effect on total knapweed biomass per pot ( $P = 0.905$ ) and there was no interaction between burn condition and competition ( $P = 0.891$ ). Total knapweed biomass per pot ( $2.6 \pm 1.0$  g) was 189% greater than non-knapweed biomass ( $0.9 \pm 0.8$  g) in burned soil (Fig. 5a). In unburned soil the opposite occurred; knapweed biomass per pot ( $0.6 \pm 0.2$  g) was 58% lower than non-knapweed biomass per pot ( $1.4 \pm 0.7$  g). Knapweed biomass per plant did not differ significantly among the four treatment combi-

nations ( $P = 0.673$ ) (Fig. 5b). Neither total biomass per pot, nor average biomass per plant of non-knapweed differed between burned and unburned soils ( $P = 0.927$  and  $0.579$ , respectively) (Fig. 5a and b).

Volumetric soil water content for the experiment based on soil cores from Site I ranged from a high of 18.0% in early May to a low of 3.1% in mid-July before summer rains began. Soil water content varied greatly among pots and no significant differences occurred among treatments ( $P = 0.408$ , time  $\times$  condition interaction  $P = 0.592$ ). Knapweed seedlings in this experiment survived air temperatures between  $-8.2$  and  $41.6$  °C and soil temperatures between  $-1.3$  and  $38.5$  °C.

The overall average survival of diffuse knapweed plants that germinated in soil cores from Site I was 86.8% in August 2003 at the end of the experiment. Diffuse knapweed plants emerged as early as the first week of March 2003. Sixty-five percent of the non-

knapweed plants died before the end of the experiment, mostly during a period of low soil moisture and high temperatures in late June and early July, while only 13.2% of the knapweed plants died under the same environmental conditions. The total number of native plants that emerged from Site I soil cores, including Wright's deervetch (*Lotus wrightii* (Gray) Greene), common yarrow (*Achillea millefolium* L.) and Arizona fescue, had lower survival rates than the total number of non-native plants including Russian thistle and prickly lettuce (Kruskal–Wallis  $P = 0.001$ ) (Table 2(A)). Of these non-knapweed plants, mean survival of native plants was 17.2% while 100% of the non-native plants survived. Of the 33 knapweed plants that survived until the end of the experiment, 25 grew in cores from burned soil, while only 8 grew in cores from unburned soil. Fifteen percent of all knapweed plants (5 of 33) bolted and produced seed, all occurred in cores from burned soil. The number of knapweed

Table 2

Number of plants and survival of plant species other than diffuse knapweed that emerged from soil cores collected from (A) Site I (2002–2003) and (B) Site II (2003–2004), and then moved to the RMRS Greenhouse Facility for experiments

Family	Scientific name	Common name	Total no. plants	% Survival
(A) Site I (2002–2003) soil cores (diffuse knapweed survival = 86.8%)				
Asteraceae	<i>Achillea millefolium</i> L.	Common yarrow	1	0
	<i>Lactuca serriola</i> L. <sup>a</sup>	Prickly lettuce	1	100
	<i>Taraxacum officinale</i> <sup>a</sup> G.H. Weber ex Wiggers	Common dandelion	1	100
Chenopodiaceae	<i>Chenopodium</i> <sup>b</sup> sp.	Goosefoot	1	100
	<i>Salsola kali</i> L. <sup>a</sup>	Russian thistle	3	100
Fabaceae	<i>Lotus wrightii</i> (Gray) Greene	Wright's deervetch	1	0
Poaceae	<i>Elymus elymoides</i> (Raf.) Swezey	Squirreltail	3	67
	<i>Festuca arizonica</i> Vasey	Arizona fescue	10	20
Rosaceae	<i>Potentilla</i> <sup>b</sup> sp.	Cinquefoil	11	18
(B) Site II (2003–2004) soil cores (diffuse knapweed survival = 74.6%)				
Asteraceae	<i>Bahia dissecta</i> (Gray) Britt.	Ragleaf bahia	4	25
	<i>Cirsium vulgare</i> <sup>a</sup> (Savi) Ten.	Bull thistle	3	67
Brassicaceae	<i>Descurainia</i> <sup>c</sup> sp.	Tansymustard	3	0
Chenopodiaceae	<i>Salsola kali</i> L. <sup>a</sup>	Russian thistle	1	100
Onagraceae	<i>Epilobium brachycarpum</i> K. Presl	Tall annual willowherb	6	17
Poaceae	<i>Bromus tectorum</i> <sup>a</sup> L.	Cheatgrass	1	100
	<i>Elymus elymoides</i> (Raf.) Swezey	Squirreltail	13	54
	<i>Festuca arizonica</i> Vasey	Arizona fescue	12	17
	<i>Muhlenbergia ramulosa</i> (Kunth) Swallen	Green muhly	1	100
Polygonaceae	<i>Polygonum douglasii</i> Greene	Douglas' knotweed	7	14
Scrophulariaceae	<i>Verbascum thapsus</i> L. <sup>a</sup>	Common mullein	11	64

<sup>a</sup> Non-native to the U.S. (USDA NRCS, 2004).

<sup>b</sup> These genera have both non-native and native species in northern Arizona.

<sup>c</sup> Because these plants died before flowering, it was not possible to identify to species, and thus not possible to determine nativity.

seed heads from plants that bolted ranged from 6 to 117 per plant, with a mean of  $34.4 \pm 20.8$  seed heads.

For the experiment based on soil cores from Site II, 87.5% of all soil cores produced knapweed; 47.5% of those that produced knapweed were from pile burn scars and 42.5% were from unburned soil. Unburned soil cores produced an average of 2.8 knapweed plants per core, while pile burn cores produced 2.3 plants per core. Total knapweed biomass per pot tended to be higher in soil from pile burn scars ( $3.30 \pm 0.63$  g) compared to unburned locations ( $2.50 \pm 0.42$  g), but this difference was not significant ( $P = 0.317$ ) (Fig. 6a). Diffuse knapweed biomass per plant was  $1.7 \pm 0.5$  g in soil from pile burn scars and  $0.97 \pm 0.24$  g in soil from unburned locations (Fig. 6b). However, this difference was not significant ( $P = 0.617$ ). For plants other than knapweed, neither total biomass per pot ( $P = 0.207$ ) nor average biomass per plant ( $P = 0.223$ ) differed significantly between soil from pile burn scars and unburned locations (Fig. 6a and b). High variability of non-knapweed in pile burn soil cores is primarily due to one Russian thistle plant weighing 13.0 g (Fig. 6b).

Volumetric soil water content ranged from a low of 6.7% in early August during a break in the summer rains to a high of 19.0% in late August for the experiment based on cores from Site II. Volumetric soil water content did not differ between pile burned or unburned soil cores ( $P = 0.660$ , time  $\times$  treatment interaction  $P = 0.906$ ). After emergence, diffuse knapweed plants survived air temperatures between 5.1 and 41.6 °C and soil temperatures between 1 and 36.6 °C; there were no obvious differences in air or soil temperatures between burned and unburned cores ( $n = 2$ , data not shown).

The average overall survival of diffuse knapweed plants that germinated in soil cores from Site II was 74.6% in September 2004 at the end of the experiment. Diffuse knapweed plants emerged as early as the last week of March 2004. During the experiment based on Site II soil cores, 61% of the non-knapweed plants died, while only 26.4% of all knapweed plants died. Most plants died during a period of low soil moisture and high temperatures in late June. Most knapweed plants died before they could form drought tolerant rosettes. The total number of native plants, including ragleaf bahia (*Bahia dissecta* (Gray) Britt.) and squirreltail, had lower survival than the total number of non-native plants, including Russian thistle and

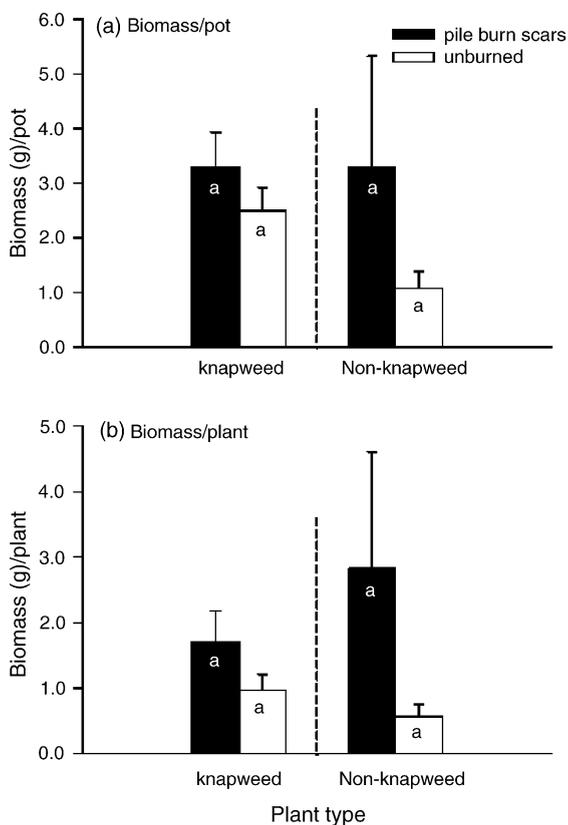


Fig. 6. Mean (+1 S.E.,  $n = 19$  samples per bar for pile burn scars and  $n = 16$  samples per bar for unburned) plant biomass per pot (a) and per plant (b) for diffuse knapweed and other species of plants that grew in soil cores collected in 2003 from two ponderosa pine forest floor conditions at Site II. Bars with different letters indicate significant differences. We did not statistically compare knapweed with non-knapweed.

common mullein (*Verbascum thapsus* L.) (Kruskal–Wallis  $P = 0.037$ ) (Table 2(B)). Of these non-knapweed plants, mean survival of native plants was 24.0% while 55.6% of non-native plants survived. Of the 92 knapweed plants that survived until the end of the experiment, 44 occurred in cores from burned soil and 48 grew in cores from unburned soil. Only 1 of all 92 knapweed plants (1.1%) bolted and produced seed; it grew in a burned soil core and produced 38 seed heads.

#### 4. Discussion

Both wildland fires and fuel reduction treatments disturb large areas of ponderosa pine forests of

Arizona, and these disturbances are predicted to increase in the future (Covington and Moore, 1994; Covington et al., 2001). Our results strongly suggest that wildfires and slash pile burning in northern Arizona can promote the germination and success of diffuse knapweed.

We observed an opportunistic and drought tolerant life strategy in diffuse knapweed during our studies. Knapweed germination at Site I in April was greatest under severely burned compared with unburned conditions at a time when few other plants germinate at elevations above 2400 m. Results were similar in March at Site II at a lower elevation (2300 m) where germination was higher in pile burn scars than unburned locations. Early diffuse knapweed germinants have been reported to have higher survival than late germinants in other regions (Schirman, 1981). Diffuse knapweed also survived extremes in temperature and soil water content in our soil core experiments. Although knapweed germination was higher in burned than unburned locations, germination did occur at moderate rates within unburned locations and under considerable shade at Site I. These characteristics of diffuse knapweed may enable it to gain an early competitive advantage and fill niches previously occupied by native plants, especially in sites disturbed by severe fire.

Earlier and higher knapweed germination in severely burned locations can be explained by increased soil water content and temperature following severe fire. Soil water content in the field studies was greater under severely burned conditions at Site I and in pile burn locations at Site II, compared with unburned conditions. At Site I, the death of large trees in severely burned stands likely reduced interception, transpiration and shading, but increased evaporation (DeBano et al., 1998; Smit and Rethman, 2000; Simonin, 2003). At Site II, thinning associated with the fuel reduction project likely increased soil water content (Smit and Rethman, 2000; Simonin, 2003; Skov et al., 2004) in both pile burn scars and unburned locations, but lack of immediate colonization of pile burn scars by native plants due to seedbank degradation (Korb et al., 2004), probably further increased soil moisture availability to diffuse knapweed seeds compared to unburned locations. If severely burned areas have high soil moisture, yet have little to no remaining native plant seed bank, diffuse knapweed

germination and growth should be stimulated. Diffuse knapweed is severely limited by water availability at only one period during its life cycle from germination until it forms a rosette. Once it reaches the rosette stage, it is extremely drought resistant in some studies (Berube and Myers, 1982); therefore, it may survive even at low soil moisture levels. At Site I, severely burned locations appeared slightly warmer than unburned locations, which in combination with higher soil water content, promoted higher germination of knapweed seeds. In contrast, Riba et al. (2002) reported lowest germination rates of seeds of a spotted knapweed subspecies under full light burned conditions in a greenhouse study comparing varying levels of light for burned and unburned soils.

The difference in germination was greatest between the severely burned and the unburned condition, whereas germination in the moderately burned and unburned bare soil conditions were similar. Perhaps, the temperature and soil moisture increases were less under the moderately burned than in the severely burned condition due primarily to the fact that trees survived the fire and were able to transpire (Smit and Rethman, 2000; Simonin, 2003; Skov et al., 2004). Crawford et al. (2001) reported that plant species richness and cover of a number of ruderal plants, some of which are exotic, were higher in severely burned areas than unburned; however, they reported no significant differences between moderately burned and unburned areas. In another study, exotic species abundance was greater in a severe wildfire versus three other treatments: unmanaged, thinned and thinned and burned, which were all statistically similar (Griffis et al., 2001). Conditions created by a severe fire, given adequate soil moisture, may provide more suitable growing conditions for diffuse knapweed and some other exotic plants in this region than moderately burned or unburned areas.

Diffuse knapweed may respond positively to a lack of competition and absence of mycorrhizae after severe fire (Keeley et al., 1985; Korb et al., 2004). Korb et al. (2004) reported that slash pile burning in a ponderosa pine forest nearly eradicated the native seed bank as well as arbuscular mycorrhizae. Although native plants may be dependent on mycorrhizae to succeed, some non-native plants may not. In fact, association with mycorrhizae may have a negative impact on diffuse knapweed plants as evidenced by increased root beetle attack (Harris and Clapperton,

1997). Callaway et al. (2003) reported that Maltese star-thistle (*Centaurea melitensis* L.) plants grown with an intact microbial community were 50% smaller than those grown in an environment with reduced arbuscular mycorrhizae fungi due to fungicide application. Given this evidence, reduced mycorrhizae in burned soil cores may have been a factor in greater diffuse knapweed biomass compared to unburned soil cores with an intact soil community. If a diffuse knapweed seed source exists near ponderosa pine forests burned by severe wildfire or pile burns, colonization may occur easily and rapidly after fire.

Diffuse knapweed growth may respond to a variety of factors after fire including increases in soil nutrient availability. Initial soil nutrient changes caused by the wildfire and pile burns in our study were likely diminishing by the time we sampled soils 13 and 14 months post-fire (DeBano et al., 1998). Nonetheless, we detected a difference in the concentration of plant-limiting nutrients between burned and unburned locations at both sites. At Site I, soil pH, Ca and  $\text{NH}_4\text{-N}$  concentrations were highest in the severely burned condition 13 months post-fire. At Site II soil K and Mg concentrations were higher in the pile burn scars than unburned locations.  $\text{NH}_4\text{-N}$  was 4.2 times greater in pile burn scars than unburned soil at Site II, but overall levels were much lower than those at Site I. Significant soil nutrient differences between pile burns and nearby unburned soil have been reported as long as 20 months after fire (Korb et al., 2004). Although soil nutrient sampling was performed long after fire, nutrient increases in burned locations may have stimulated growth of knapweed in burned compared with unburned soils, but probably did not affect germination.

Diffuse knapweed biomass per pot was greater in severely burned soil cores compared with unburned cores in the Site I experiment, most likely due to a greater number of plants per pot. Although results for knapweed biomass from Site II soil cores were inconclusive, there was a tendency for more biomass in burned soil. A greater number of knapweed plants grew in soil cores from Site II compared with Site I, but fewer bolted and produced seed from Site II. Limited reproduction has been associated with high plant density (Powell, 1990). There were several knapweed plants in soil cores from Site I that produced seed in the first year, all of which occurred in severely

burned soil cores. Rapid seed production of diffuse knapweed in burned forests could decrease the time needed for establishment of new populations.

There are several potential explanations for the greater stimulation of knapweed biomass by burned soil from the Site I wildfire compared with the Site II pile burns. Increases in  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  between unburned and severely burned locations were greater at Site I (385 and 283%, respectively) than Site II (320 and 99%, respectively). Overall  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  concentrations were also greater at Site I than at Site II. It is also possible that the intensity and long fire residence time associated with pile burning initially decreased soil nutrient availability. We obtained our unburned soil cores about 60 cm from the edge of the pile burn scar at Site II, and this area may have experienced heating while the piles were burning, thus obscuring differences between burned and unburned results. According to Korb et al. (2004), there were significant soil nutrient differences between pile burn scar edges and 3 m outside scars. At distances less than 3 m, soil nutrient levels may be affected, depending on the fire residence time.

Diffuse knapweed seedlings survived relatively extreme temperature and soil moisture conditions in our soil core experiments while many non-knapweed plants did not. Mean survival of non-knapweed plants for both years was only 38%, while mean survival of knapweed was 81%. Knapweed mortality was lower in soil cores from Site I than Site II where more plants grew. Powell (1990) observed higher mortality rates in diffuse knapweed seedlings and rosettes in dense knapweed populations than in sparse populations. Competition from non-knapweed plants had no effect on knapweed in our study; however, most of the competition died early in the study likely because of drought conditions. High non-knapweed mortality may also be due in part to our method of soil core extraction. During this process, it is possible we cut off some root mass of existing perennial plants below 10 cm. Of the species that survived the experiments, most were non-native, such as Russian thistle, prickly lettuce and common dandelion. With the low survival of plants other than knapweed, the actual effect of competition in this experiment was likely very minimal. Future experiments should consider isolating allelopathic effects (Muir and Majak, 1983) on non-knapweed plants, and conducting in situ experiments

in existing knapweed populations. Supplemental water, especially during droughts, may also provide a more accurate measure of competition effects.

Overall, diffuse knapweed is a serious threat to northern Arizona ponderosa pine forests burned by wildfire and slash piles, as well as threatening unburned areas. Knapweed's ability to germinate under varying temperature and soil moisture conditions in both burned and unburned stands has important implications for land managers. Diffuse knapweed germination was stimulated by severe fire, resulting from both wildfire and slash pile burning. Knapweed plants produced more biomass in soils severely burned by wildfire compared with unburned soils. Knapweed plants survived extremes of temperature and soil moisture better than most native plants. As populations of diffuse knapweed move closer to northern Arizona forests, the risk of invasion into the WUI, and eventually interior forests will increase because current management practices, such as slash pile burning, promote germination and seedling success. We encourage managers to include control of invasive exotic plants in all burn and fuel reduction plans. Knapweed seeds can remain viable for long periods (Davis et al., 1993); therefore, it is important to remove plants even after they produce seed and die, thus preventing them from spreading seed into the WUI. Growing knapweed populations in Flagstaff and similar western U.S. towns suggest high potential for spread into the WUI. Quick action is necessary in these areas to keep knapweed and other exotic invasive plants out of the WUI (Dombeck et al., 2004). Failure to treat exotic invasive plants prior to or during fuel reduction and wildfire rehabilitation may result in trading one undesirable condition, fire danger, for another, weed infestation (Sieg et al., 2003). Because the WUI often forms the border between federal and/or state and local land management agencies, integrated management policy among these agencies (Dombeck et al., 2004; USDA Forest Service, 2004) will aid in lessening the likelihood of diffuse knapweed and other exotic plants expanding into WUI treatment areas.

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