CHAPTER 4

STUDYING PLANT INVASIONS IN PROTECTED AREAS

AT MULTIPLE SCALES: *Linaria vulgaris* **(SCROPHULARIACEAE)**

IN THE WEST YELLOWSTONE AREA

ABSTRACT

Invasive alien plants have long been recognized as a threat to low elevation, disturbed environments, but the case of *Linaria vulgaris* Mill. in Yellowstone National Park and Gallatin National Forest shows that invasions can also spread to high elevation natural reserves. Because invasions in protected areas are a product of complex processes occurring over a broad range of scales, we argue that a multi-scale research approach is needed to capture both patterns and potential mechanisms of the invasion process. Mapping *L. vulgaris* at the landscape scale, we found the species occupying a broad range of sites, apparently originating from just two historical sources. Analyzed at the stand scale, patches tend to be aggregated in newly invaded areas and become dispersed in heavily-infested areas. The data suggest that patches grow in size by clonal advance and in number by creation of new satellite patches. Radial patch growth rates are related to site characteristics. Clonal patch scale analysis shows that ramet densities and *Linaria*'s effects on native plants are highest in the patch centers. Both mean ramet height and reproductive vs. vegetative ramet height ratio are higher in patch cores. These results suggest that *L. vulgaris* may displace natural vegetation by maintaining vigor even in large and old clonal patches. Our results confirm that *L. vulgaris* is a significant threat to native biodiversity in open, human- or naturally-disturbed environments in protected areas of the Rocky Mountains. A multi-scale method can allow managers to better understand patterns of invasion and prioritize management activities to control invasive alien plants, especially in heterogeneous protected area landscapes.

INTRODUCTION

Invasive alien plant species threaten biodiversity worldwide (Mack et al. 2000, Sala et al. 2000, McNeely et al. 2001). Invasive alien plants not only change the composition of invaded communities, but also affect ecosystem processes such as disturbance regimes, wildlife interactions, evolutionary processes and biogeochemical cycles (Mack et al. 2000). Most invasive alien species are adapted to highly disturbed, nutrient rich, low elevation agricultural or urban environments (Hobbs 2000, Sax and Brown 2000, D'Antonio and Naiman 1994). In contrast, many protected areas or natural reserves, at least in temperate zones, occur at high elevations and relatively undisturbed environments (Noss and Cooperrider 1994, Scott et al. 2001). Consequently, the number and abundance of invasive alien plants is much lower in protected areas than in surrounding human dominated landscapes (Forcella and Harvey 1983, Lonsdale 1999, Pauchard and Alaback in review). However, these invasive species can still become a significant threat to ecosystems conserved in protected areas (MacDonald et al. 1989, Lesica and Ahlenshalager 1993, DeFerrari and Naiman 1994, Stohlgren et al. 1999, Ollif et al. 2001).

The high ecological value of protected areas and often low abundance of alien invasive plants pose unique challenges for monitoring and studying invasion processes. Most commonly used methods for monitoring weed populations are designed for highly disturbed and homogenous landscape elements where invasive plants are abundant (Cousens and Mortimer 1995). A conceptual framework for sampling invasive plant populations and their effects is needed for protected areas and their adjacent matrixes (sensu Lindemayer and Franklin 2002), recognizing both the complex and heterogeneous landscapes and the invaders' low numbers of initial populations.

To capture the underlying mechanisms of plant invasions in protected areas landscapes, it is necessary to consider the broad range of scales and processes involved (Stohlgren et al. 1999, Mack 2000, Chong et al. 2001). According to hierarchy theory, each scale involves a unique set of processes and mechanisms (Allen 1998). The description of any ecological phenomenon may be incomplete or misleading without assessment of related patterns at coarser scales. A fine-scale

approach (for example, monitoring an invasive plant using a 1-m^2 quadrat commonly used in agricultural weed studies) may illuminate specific elements of that species' population biology and effects on local biodiversity; however, that approach would likely overlook processes occurring outside the infested area, such as long distance dispersal. Conversely, landscape studies often fail to integrate fine-scale phenomena that may ultimately control landscape patterns. For managers, an assessment strategy that integrates methodologies across multiple scales may identify the dominant mechanisms governing the invasion process and thereby inform an effective control strategy (Table 1).

In the West Yellowstone area, *Linaria vulgaris* Mill. (common or yellow toadflax, "butter and eggs") is one of the most invasive alien plants, occupying heavily disturbed areas of the Gallatin National Forest and threatening to expand into more pristine areas in the adjacent Yellowstone National Park (Whipple 2001, Ollif et al. 2002). *Linaria vulgaris*, a member of the Scrophulariaceae family native to disturbed sites in Eurasia, was introduced in North America as an ornamental as much as 300 yr ago (Saner et al. 1995), but it has only recently become an important problem in natural areas of the Rocky Mountains. It is an aggressive perennial weed in agricultural and rangeland environments, reproducing by both sexual and asexual mechanisms (Saner et al. 1995, Nadeau et al. 1992). It invades from sea level to over 3000 m and up to 60 degrees latitude. It prefers open, wet environments, and usually grows on gravelly or sandy soils after heavy natural or human soil disturbance, creating discrete patches due to its clonal growth and predominantly short distance dispersal (Saner et al. 1995, Nadeau et al. 1991). A small proportion of its winged seed disperses long distances both by wind and animal vectors (Saner et al. 1995). Biocontrol insects may attack *L. vulgaris* from roots to seeds and have been extensively used with variable success (Saner et al. 1995).

Linaria vulgaris invasion in the West Yellowstone area serves as an ideal case study to demonstrate the utility and feasibility of the multi-scale approach framework to study invasions in protected areas. In this paper we report on our ongoing investigation into *Linaria vulgaris* invasion of Yellowstone National Park and Gallatin National Forest. *L. vulgaris* has the potential to invade new

high elevation environments in the Rocky Mountains, and we hypothesize that its ability to invade depends on several mechanisms occurring at the landscape, stand and patch scale. We relate spatial patterns and characteristics at these scales to factors of land use and site history. We discuss the advantages and disadvantages of our method and the conservation implications of studying plant invasions in protected areas using a multi-scale approach.

Study Area

The study area (Fig. 1) is located in the Madison Valley around the western entrance of Yellowstone National Park and the adjacent Gallatin National Forest (44°48'N, 111°12'W and 44°37'N, 111°00'W). The National Park boundary reflects a strong contrast in land use, while the two sides of the study area are similar in elevation, soil type and habitat type (Despain 1990, Hansen and Rotella 1999). Soils, formed on glaciofluvial outwash plains derived from rhyolite (Rodman et al. 1996), are sandy, well-drained, low in nutrients and highly susceptible to drought during the summer months. Climate is strongly influenced by high elevation (2000 m) with annual precipitation around 550 mm, mostly as snow. Mean temperature ranges from a low of –11.1 °C during January to a high of 15.2 °C in July (Western Regional Climate Center, 2001).

Pinus contorta forests and *Artemisia tridentata* semi-arid shrublands are the dominant vegetation types (Despain 1990). Fire is the main natural disturbance with catastrophic fires occurring every 400 to 600 years (Despain 1990). The 1988 Yellowstone fires burned an important portion of the study site inside the park but little on the Gallatin NF. Gallatin NF has been highly disturbed by logging during the past three decades, declining in the 90s (Susan LaMont personal communication). At present, an increasing number of tourists are visiting the area year round.

Beginning in the late 1800s, grazing, logging and transportation have facilitated the introduction of aggressive weeds like *Centaurea maculosa*, *Linaria vulgaris*, *Linaria dalmatica*, *Melilotus officinalis*, *Cirsium arvense* and *Verbascum thapsus* (Ollif et al. 2001). The harsh high

elevation climate restricts the intensity of weed invasion (Forcella and Harvey 1983). Nevertheless, plant invaders have colonized human-disturbed areas such as roads and campgrounds (Allen and Hansen 1999) and are progressively invading riparian habitats and other pristine environments. Both the Park Service and the Forest Service have developed management plans for controlling weed invasion, but *L. vulgaris* has only been targeted along major corridors (Ollif et al. 2001).

METHODS

Linaria vulgaris invasion and its effects were studied at three scales: landscape, stand and clonal patch (Table 1). Each scale was defined arbitrarily to capture a unique set of processes, and the specific methods used varied with scale (Table 1). The landscape scale was defined to understand dispersal processes and habitat invasibility in the portion of the Madison Plateau where *L. vulgaris* was abundant in both the Gallatin NF and Yellowstone NP (ca. 20 by 10 km, Fig. 1, Fig. 2). Short distance dispersal processes, infilling of infestations and interactions with local site characteristics were studied using the stand scale. The sampling size unit was defined as a macroplot of 50 m by 100 m, sufficient to evaluate the structure and dynamics of groups of clonal patches. At the finest scale, the clonal patch varies from 50 cm to 25 m in diameter. A 20 by 50 cm sample unit was used at this scale to evaluate processes including population structure of *L. vulgaris* and the species interaction with native vegetation.

Landscape Scale

In the summer of 2001, a census was completed of the locations and attributes of 300 clusters of *L. vulgaris* clonal patches. Regions of patch clusters were searched systematically in an effort to capture the majority of existing patches. Differential GPS positions were recorded with a Trimble GeoExplorer 2. Patch clusters were considered separate units when the distance to the nearest *L. vulgaris* plant was more than 5 m. Large areas with solid infestations (clusters larger than 50m) were recorded as polygons instead of as individual clusters. Attributes collected for each

cluster were (Table 2): land use class; longest diameter and longest perpendicular axis length; azimuth of the longest diameter; ramet density in a randomly located 50 x 20 cm microplot; average dominant height; visually estimated percent of reproductive ramets; soil disturbance; fire intensity; tree height; and visually estimated canopy cover %, shrub cover %, and plant cover %, excluding *L. vulgaris*, both inside and outside the cluster. Location and cluster attributes were plotted in ArcView 3.2. SPSS 10.0 was used to characterize diameter, land use, soil disturbance and fire intensity variables.

Stand Scale

In August of 2000, we recorded spatial attributes of *L. vulgaris* patches in five 50 x 100 m macroplots. In the Gallatin NF, three macroplots were located in old clearcuts (logged between 1978 and 1982), and one in a newer clearcut (logged in 1992). In Yellowstone NP one macroplot was located on a riverbank of the Madison River. The three old clearcut macroplots were randomly selected from areas with high levels of *L. vulgaris* infestation. The newer clearcut and riverbank macroplots, on the other hand, represented unique characteristics of early invasion that were impossible to replicate and were therefore considered study cases. We recorded the longest length, perpendicular longest width and azimuth for each patch in each macroplot. Plants separated more than 50 cm were considered as different patches. Patch corners and centers were permanently marked with metal stakes. Polygons were built in ArcInfo 8.0 and plotted in ArcView 3.2. In August of 2001, we returned to each patch and recorded its positive or negative radial (horizontal) growth along the previously-measured axes. New patches in the macroplots were added to the spatial data. We also recorded the substrate condition in 4 categories: *Pinus contorta* litter (>50%), herbaceous plant cover (>25%), bare soil (>75%), and coarse woody debris (>50%).

We assessed spatial patterns in the 2000 data using two macroplots, one in an old clearcut under severe invasion and one in a newer clearcut at early stages of invasion. We conducted point pattern analyses using patch centroids within macroplots. Patches were classified as clustered,

random, or dispersed using a nearest neighbor R-statistic (Fotheringham et al. 2000). For old clearcuts, differences in mean patch radial growth were tested using a Kruskal-Wallis nonparametric test for each factor (macroplot, land use, substrate) and a Mann-Whitney test for pairwise comparisons (significant when p<0.05). A linear model tested correlation between radial growth and longest patch diameter (significant when p<0.01).

Clonal Patch Scale

In August of 2000, patches were randomly selected in each macroplot to locate 20 x 50 cm microplots (Daubenmire 1968). Patches were stratified into small, medium and large classes. For medium (5-10 m long) and large patches (> 10 m long), seven one-meter microplots were located along the longest patch axis: two outside the edge, two within the patch along the edges, two in the interior and one in the middle (Fig. 3). In small patches (less than 5 m long), only 5 microplots were located (Fig. 3). Microplots were marked permanently using metal stakes. In each microplot, every ramet was recorded along with its height class (10 cm) and reproductive stage (vegetative, reproductive) based on the presence of reproductive structures. Cover for each plant species was assigned to the five cover classes of Braun-Blanquet (described in Mueller-Dombois and Ellemberg 1974). Microplots were remeasured in August of 2001.

Differences in microplot variables at the outside, edge, interior and middle of patches were tested in medium and large patches combined using only the data for old clearcuts (N=12 patches, n=84 microplots). Variables tested were ramet density, ramet density by reproductive stage, ramet height, *L. vulgaris* cover %, species richness and total cover % of other plants. In all cases, because the data were not normally distributed (Kolmogorov-Smirnov, p<0.01), non-parametric tests were used (Kruskal-Wallis and Mann-Whitney for pairwise comparisons, significant when p < 0.05).

RESULTS

Landscape distribution

At the landscape scale, *Linaria vulgaris* occupies a wide variety of environments in the Gallatin NF, from clearcuts to sagebrush communities, while in Yellowstone NP it is constrained to roadsides, riverbanks and isolated areas in burned sites (1988 fires) and rocky hillsides (Fig. 2). Patch size distribution followed an inverted exponential curve, indicating a continuous recruitment of new patches (Fig. 4). In the study area, most patches occurred in logged areas (39.3%), roadsides (35.3%) and within 10 m of a road (20.3%), while just a fraction occurred in more pristine lake or river environments (3.2%) or in other natural vegetation (1.7%). The majority of recorded clusters were located in and around a heavily-infested area 6 km west of West Yellowstone around Highway 12 (Fig. 2). This area has been intensively logged in the last 20 years, favoring the establishment of *L. vulgaris*, and several infestations are dense enough to not have been recorded as separate patch clusters (Fig. 2). In addition, a small number of patches and a heavily-infested area were mapped along the sandy shores of Hebgen Lake (Fig. 2).

Linaria vulgaris is abundant in loose and bare soils with more than 52% of the recorded clusters in periodically disturbed sites such as roadsides (Fig. 4). *Linaria vulgaris* was also abundant in fire piles or areas that had been subject to intense fire, with almost 10% of the patches developing in areas with signs of severe burn, which are frequent in logging areas, but may also occur following natural fires (Fig. 4).

A total of 19 patch clusters (6.3%) were found in the interior of Yellowstone NP. In the park, clusters were found along the highway (58%), in riverbanks (21%), secondary roads (11%) and in natural vegetation, including a burn area and a hillside (Fig. 2).

Stand scale

The spatial distribution of *L.vulgaris* patches in the old clearcut and new clearcut macroplots suggested clear differences in patch patterns (Fig. 5). Patches covered 12.5% of the total area of the

old clearcut, but only 1.3% of the new clearcut. Patch density was also higher in the old clearcut

(58/ha) compared to the new clearcut (20/ha). Mean patch size differed significantly between the old

(26.3 m^2) and the new clearcut (6.7 m^2) (Mann-Whitney, p<0.01).

Within the new clearcut, the centroids of the 10 mapped patches were significantly

aggregated (nearest-neighbor R = 0.53, p<0.05) (Fig. 5b). Clonal patches of *L. vulgaris* occurred in

only three areas of the clearcut, and in two of those areas clusters of 3-4 small patches (<1 m

diameter) were found in close proximity to individual large patches (diameter >5 m). Within the old

clearcut, on the other hand, patch centers inside the 50m x 100m macroplot showed statistically

significant dispersion (nearest-neighbor R = 1.34, p <0.005) (Fig. 5a). Because most patches in the

old clearcut measured at least 5-10 m in one or both diameters, the frequency of closely-neighboring

patch centers was reduced below the rate that would be found in a random point distribution.

In the period 2000-2001, there were no significant differences in mean radial growth

between the three old clearcut macroplots (Kruskal-Wallis, p>0.05). Mean radial growth in the old

clearcuts was 21.2 ± 1.4 cm (Fig. 6a), significantly higher than the growth rate in the new clearcut

(32.8 ± 3.8 cm) (Mann-Whitney, p<0.01).   Meanwhile, mean radial growth in the riverbank

macroplot (28.5 ± 4.6 cm) was not significantly different from either of the other land use types

(Mann-Whitney, p>0.05). In old clearcuts, substrate was a significant factor in determining radial

growth (Kruskal-Wallis, p<0.01) (Fig 6). However, the only pairwise significant difference was

between bare soil and *Pinus contorta* canopy (p <0.01), which had the highest and lowest growth

respectively.

Clonal Patch scale

In old clearcuts, *Linaria vulgaris* cover and ramet density were affected by position within

the patch longest axis (Kruskal-Wallis, p<0.01), and were higher in the interior and center than in the

edges of clonal patches (Mann-Whitney p<0.01) (Fig. 7a, c). The total cover of other species was

also related to position (Kruskal-Wallis, p<0.01), but tended to decrease in patch cores (Mann-

Whitney, p<0.05) (Fig. 7b). Species richness was not related to position in the *L.vulgaris* patches (Kruskal-Wallis, p>0.05).

In old clearcuts, the density of vegetative ramets in patch edges was significantly greater than the density of reproductive ramets (Mann-Whitney, p<0.05) (Fig. 7d). At patch centers and interiors, reproductive and vegetative ramet densities were not significantly different (Mann-Whitney, p>0.05). Overall, plants were taller in the patch centers (Fig. 8a). However, when ramets were classified by reproductive stage, average height for vegetative and reproductive ramets did not vary with position (Fig 8b). Therefore, differences in average height corresponded mainly to differences in the proportion of reproductive vs. vegetative ramets.

DISCUSSION

Our method proved to be useful in understanding invasion processes at each of the three scales and evaluating the overall potential threat of the species over ecosystems of the West Yellowstone area. Long-distance dispersal and patterns of overall invasion at the landscape scale, rapid patch expansion at the stand scale and loss of native vegetation at the patch scale indicate that *Linaria vulgaris* can strongly impact ecosystems both through its rapid expansion and its competitive ability. These results suggest a strong potential of *L. vulgaris* to invade high-elevation protected areas in the Rocky Mountains. The species can follow road corridors and establish new patches in a wide range of disturbance regimes and habitats. Once established in a new environment it continues to grow, in term of number of patches, density of patches and regularity of patch distribution, ultimately causing the decline of native plant species.

Landscape Scale

Linaria vulgaris is widely dispersed across the landscape, but patch cluster density is highly variable. Management differences between Gallatin NF and Yellowstone NP appear to be key factors in *L. vulgaris* invasion. Patterns of cluster distribution are consistent with the presence of one major

source of propagules in the Gallatin NF. We hypothesize that an old ranch (late 1800s) located on the western edge of the study site has been the major source of propagules (Susan LaMont personal communication). There is also evidence that a small population was established in the park for aesthetic purposes and now is responsible for at least one wild population in the riverbank of Madison River (McClure personal communication). However, most clusters inside the park appear to have been initiated from propagules brought by vehicle flow along the entrance highway, which passes through the main infestations in the Gallatin NF (10 km apart). Long term monitoring and additional spatial analysis of cluster distribution is needed to understand the invasion dynamics at this scale. Since invaders show rapid genetic change, genetics techniques may also help to elucidate flow of propagules in the landscape (Lee 2002, Sakai et al. 2001).

Our landscape assessment supplemented previous reports that were qualitative and incomplete, missing *L. vulgaris* clusters in more pristine areas (Susan LaMont, Craig McClure personal communication). The landscape scale analysis also helped us to develop hypotheses as to where the initial infestation occurred and which were at present the major sources of propagules for long-distance dispersal. One of the major constraints of our method at the landscape scale is the lack of true replicates, which reduces the feasibility of using statistical tools. While we were able to document general landscape patterns with our intensive census technique, for future studies we recommend a broader coarse-scale assessment of weed populations utilizing for example long transects, to provide statistically robust and complete information on the distribution of critical new populations. Simple qualitative measures of weed presence extended over extensive areas would provide more useful information on locations of rare and small new populations, compared to more detailed but less extensive surveys (Maxwell et al. 2001).

Stand Scale

At the stand scale, we hypothesize that a clumped distribution is indicative of an early stage of invasion, as shown in the case of the new clearcut. Aggregation caused by clonal growth and poor

dispersal (Saner et al. 1995, Nadeau et al. 1991) may be an ecological strategy to overcome interspecific competition and assure persistence (Murrel et al. 2001). After overcoming local dispersal barriers by sufficient propagule production and colonization of the majority of suitable sites, the invasion process leads to a more random, and in some cases, dispersed distribution, as is the case in old clearcuts. These areas generally show dense and sometimes continuous *L. vulgaris* patches that are controlled mainly by environmental conditions rather than by the propagule availability. Our monitoring data suggests that new patches tend to be established as satellite patches and in some cases are absorbed into the parental patch. Even in heavily-infested areas, new patches can become established in the remaining non-invaded sites. These findings suggest that given sufficient time *L. vulgaris* will be able to dominate all areas with suitable conditions.

The higher radial growth of *L. vulgaris* in the new clearcut confirms its aggressive vegetative growth in recently disturbed soils. The relatively low overall average rate of growth (ca. 20-30 cm) reflects the harsh natural environment (cf. up to 2 m/yr growth of *L. vulgaris* in recently disturbed barley crops [Nadeau et al. 1991b]). The lower radial growth in *Pinus contorta* litter suggests that *Linaria* is not a good competitor in tree-shaded environments. The lack of relationship between patch diameter and radial growth shows that the potential for patch expansion does not diminish in older patches, confirming that a patch could persist indefinitely as long as the overall environmental conditions do not change (Lajeunesse 1999). Negative radial growth in a few patches could indicate a temporal dynamic in spatial distribution related to climate variations (e.g. intense summer drought), competition with native plants, the presence of herbivory or a combination of these factors (Saner et al. 1995, Pauchard and Alaback, unpublished data). We expect that our monitoring data will eventually help to answer those questions. The presence of both native and introduced insect predators may be the major factor controlling the expansion of these populations, but data are not yet available to confirm assess this factor (Bruce Maxwell personal communication, Saner et al. 1995).

Our method was efficient in evaluating the spatial distribution of *L. vulgaris* patches, determining overall characteristics of patch populations, and showing how stand structure converged from clumps to random distribution over time. However, our methods at the stand scale presented difficulties in assessing patch shape, because of irregular shapes that are more difficult to characterize than an ideal ellipse. Also, as we have observed in the monitoring process, patches tend to grow unevenly, changing their shape and orientation year by year so that re-mapping may be needed (Lajeunesse 1999). Replication of macroplots in early stages of invasion is needed because these areas probably have the most rapidly changing populations.

Clonal Patch Scale

At the patch scale, higher ramet density in patch cores compared to edges indicates that patches are expanding and maintaining a high ramet density. We found mean densities of almost 200 ramets/m^2, slightly higher than those found by Clements and Cover (1990 in Saner et al. 1995) in Ontario natural grasslands, but lower than the 300-700 plants/m^2 found in agricultural crops (Nadeau et al. 1991). The high ramet density in patch centers suggests that this species does not experience significant die-off after reaching maximum densities. *L. vulgaris* thereby presents a more difficult control problem than *Linaria dalmatica*, which has shown die-off or ring growth (Vujnovic and Wein 1997).

As it appears in old clearcuts, *L. vulgaris* is diminishing the cover of native plants in the core of the patches but not reducing species richness. We do not know if this pattern is due to rapid colonization of bare soils or if it really implies a displacement of the native species. The higher ramet density and mean height in the interior of the patches shows a trend of increasing biomass as the patches expand. This may reduce the available resources and lead to impoverishment of the native plant community. However, preliminary soil tests on patch centers and exteriors show no significant trend in nutrient availability. Even at higher densities, *L. vulgaris* height is not affected by intraspecific competition in patch cores; the tallest ramets grow in the densest areas of the patches.

Similarly, the height of reproductive ramets does not decrease with intraspecific competition. Therefore, we could expect a proportional relationship between patch area and propagule output.

Data from the clonal patch scale suggest a negative effect of *L. vulgaris* on native vegetation and confirm that the species maintains high densities, even years after patch establishment. This scale is crucial to understand the behavior of the invader and its interaction with native vegetation (Table 1). Our ability to determine population structure is limited due to the dominant vegetative reproduction of *L. vulgaris*. The proportion of ramets and genets is impossible to calculate with our method, and thereby it is difficult to assess the importance of sexual reproduction in the dynamics of patch expansion. Overall, the clonal patch scale provides the most information on the dynamics of interaction between the invasive plant and native species. From a monitoring perspective, this type of data may reveal how the invader diminishes the cover of other plants to the point of reducing local species richness.

Conservation Implications: Integrating Scales

Linaria vulgaris invasion in the West Yellowstone area illustrates that invasive plant species are becoming a threat not only to low-elevation disturbed environments, but also to remote, high-elevation protected areas. Ecological phenomena such as invasions do not distinguish political boundaries (Landres et al. 1998, Lindenmayer and Franklin 2002), and thus land use practices that favor invasive species in adjacent land may be the starting point of invasion processes in protected areas. The distribution, abundance and growth trends of *L. vulgaris* in the Yellowstone area, as deduced from our multi-scale approach, suggest that this species has the potential to invade both pristine and human-disturbed areas in high elevation environments in the Rocky Mountains. Furthermore, the increase in visitation and development around protected areas is facilitating the spread of alien invasive species invaders into natural communities even under harsh climatic conditions. Anecdotal data from other areas confirm this trend. *L. vulgaris* is an important problem in Rocky Mountain National Park, Colorado, where it occurs up to 3,600 m elevation in naturally

disturbed ground (Jeff Connor personal communication). In the Northern Rockies, Forest Service weed specialists have observed *L. vulgaris* populations between 1,000 and 2,000 m in a number of National Forests (Pauchard unpublished data).

The overall effect of *L. vulgaris* invasion on native communities is difficult to assess. However, our findings suggest high *L. vulgaris* densities reduce plant cover of other species. Other effects such as impacts on wildlife may be expected as *L. vulgaris* displaces native plants. Global warming may also enhance weeds' invasiveness (Dukes and Mooney 1999). We have also found what appear to be natural hybrids of *L. vulgaris* and *L. dalmatica* in our study area (Saner et al. 1995, Vujnovi and Wein 1997; genetic analyses are in progress). These hybrids may pose a new threat due to plasticity and rapid genetic change (Sakai et al. 2001).

In Yellowstone NP, *L. vulgaris* could easily expand into other open areas such as riverbanks, burned areas, meadows or sagebrush shrublands. We have already found patches far from human corridors in naturally disturbed grounds. Activity of both gophers and large herbivores seems to favor *L. vulgaris* establishment (Bruce Maxwell personal communication). Increased recreation and visitation could promote further dispersal into remote areas. Identifying correlations of *L. vulgaris* invasion with habitat characteristics (e.g. disturbance regime) and dispersal constraints (e.g. distance from nearest seed source) would help to predict future infestations.

Our multi-scale results suggest that *L. vulgaris* control would be most efficient by emphasizing control on new populations and dispersal corridors. Disturbed environments close to major dispersal corridors should be emphasized in monitoring activities. At present, Yellowstone NP applies herbicides to all *L. vulgaris* patches that are sources of seeds that may be dispersed by vehicles or pedestrians (Ollif et al. 2001, Craig McClure personal communication). A similar control approach is used by the Gallatin NF and Gallatin County. Biocontrol agents have been released in Gallatin NF during the last two decades (Susan LaMont personal communication) and some have dispersed into *L. vulgaris* patches inside Yellowstone NP (Ollif et al. 2001). Even so, *L. vulgaris*

expansion continues, especially in isolated areas of the southern corner of Yellowstone National Park (Whipple 2001).

Conclusion

Protected areas and their contiguous matrixes represent a unique setting for studying the interactions between major causes of invasion such as disturbance, environmental factors and dispersal strategies, all of which tend influence the invasion process at specific scales. A multi-scale method may help to promote integration in our understanding of invasion processes in complex natural landscapes since it allows consideration of coarse scale phenomena such as patterns of spread along dispersal corridors and effects of land use or disturbance regimes on invisibility, along with fine-scale phenomena such as population dynamics and native species decline as related to more site specific factors. A multi-scale method may lead to more successful invasion management in these particularly sensitive and critical natural areas. To allocate limited resources, a multi-scale method should be used to determine which mechanisms exert the greatest influence in the invasion process.

REFERENCES

ALLEN, K., AND K. HANSEN. 1999. Geography of exotic plants adjacent to campgrounds, Yellowstone National Park, USA. Great Basin Naturalist 59:315-322.

ALLEN, T.F.H. 1998. The landscape "level" is dead: persuading the family to take it off the respirator. Pages 35-54 *in* D.L. Peterson and V.T. Parker, editors, Ecological scale: theory and applications. Columbia University Press, New York.

CHONG, G.W., R.M. REICH, M.A. KALKHAN, AND T.J. STOHLGREN. 2001. New approaches for sampling and modeling native and exotic plant species richness. Western North American Naturalist 61:328-335.

COUSENS, R., AND M. MORTIMER. 1995. Dynamics of weed populations. Cambridge University Press, Cambridge.

D'ANTONIO, C.M., T.L. DUDLEY, AND M. MACK. 1999. Disturbance and biological invasions: direct effects and feedbacks. Pages 413-452 *in* L.R. Walker, editor, Ecosystems of disturbed ground. Elsevier, Amsterdam.

DAUBENMIRE, R. 1968. Plant communities. A textbook of plant synecology. Harper and Row, New York.

DEFERRARI, C.M., AND R.J. NAIMAN. 1994. A multi-scale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. Journal of Vegetation Science 5:247-258.

DESPAIN, D.G. 1990. Yellowstone vegetation. Roberts Rinehart Publishers, Boulder, Colorado.

DUKES, J.S., AND H.A. MOONEY. 1999. Does global change increase the success of biological invaders? Trends in Ecology and Evolution 14:135-139.

FORCELLA, F., AND S.J. HARVEY. 1983. Eurasian weed infestation in western Montana in relation to vegetation disturbance. Madroño 30:102-109.

FORMAN, R.T.T. 1995. Land mosaics: the ecology of landscape and regions. Cambridge University Press, Cambridge.

FOTHERINGHAM, A.S., C. BRUNSDON, AND M. CHARLTON. 2000. Quantitative geography: perspectives on spatial data analysis. Sage Publications. London.

HANSEN, A.J., AND J.J. ROTELLA. 1999. Nature reserves and land use: implications of the "Place" principle. Pages 57-75 *in* V. Dale and R. Haeuber, editors, Applying ecological principles to land management. Springer Verlag, New York.

LAJEUNESSE, S. 1999. Dalmatian and yellow toadflax. Pages 202-216 *in* R.L. Sheley and J.K. Petroff, editors, Biology and management of noxious rangeland weeds. Oregon State University Press, Corvallis.

LANDRES, P.B., R.L. KNIGHT, S.T.A. PICKETT, AND M.L. CADENASSO. 1998. Ecological effects of administrative boundaries. Pages 39-64 *in* R.L. Knight and P.B. Landres, editors, Stewardship across boundaries. Island Press, Washington D.C.

LEE, C.E. 2002. Evolutionary genetics of invasive species. Trends in Ecology and Evolution 17:386-391.

LESICA, P., AND K. AHLENSHALAGER. 1993. New vascular plant records and the increase of exotic plants in Glacier National Park, Montana. Madroño 40:126-131.

LINDENMAYER, D.B., AND J.F. FRANKLIN. 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington D.C.

LONSDALE, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522-1536.

MACDONALD, I.A.W., L.L. LOOPE, M.B. USHER, AND O. HAMANN. 1989. Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. Pages 215-255 *in* J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek, and M. Williamson, editors, Biological invasions: a global perspective. Wiley, New York.

MACK, N.M. 2000. Assessing the extent, status and dynamism of plant invasions: current and emerging approaches. Pages 141-169 *in* H.A. Mooney and R.J. Hobbs, editors, Invasive species in a changing world. Island Press, Washington D.C.

MACK, R.N., D. SIMBERLOFF, W.M. LONSDALE, H. EVANS, M. CLOUT, AND F.A. BAZZAZ. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10:689-710.

SAKAI, A.K., F.W. ALLENDORF, J.S. HOLT, D.M. LODGE, J. MOLOFSKY, K.A. WITH, S. BAUGHMAN, R.J. CABIN, J.E. COHEN, N.C. ELLSTRAND, D.E. MCCAULEY, P. O'NEIL, I.M. PARKER, J.N. THOMPSON, AND S.G. WELLER. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32: 305-33.

SANER, M.A., D.R. CLEMENTS, M.R. HALL, D.J. DOOHAN, AND C.W. CROMPTON. 1995. The biology of Canadian weeds 105: *Linaria vulgaris* Mill. Canadian Journal of Plant Science 75:525-537.

SAX, D.F., AND J.H. BROWN. 2000. The paradox of invasion. Global Ecology and Biogeography 9:363-371.

SCOTT J.M., F.W. DAVIS, R.G. MCGHIE, R.G. WRIGHT, C. GROVES and J. ESTES. 2001. "Nature reserves: Do they capture the full range of America's biological diversity?" Ecological Applications, 11(4): 999-1007.

STOHLGREN, T.J., D. BINKLEY, G. W. CHONG, M. A. KALKHAN, L. D. SCHELL, K. A. BULL, Y. OTSUKI, G. NEWMAN, M. BASHKIN, AND Y. SON. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69:25-46.

VUJNOVIC, K., AND W.W. ROSS. 1997. The biology of Canadian weeds 106: *Linaria dalmatica* (L.) Mill. Canadian Journal of Plant Science 77:483-491.

WESTERN REGIONAL CLIMATE CENTER. 2001. West Yellowstone Climate Summary. Retrieved on 09/15/2001 from the World Wide Web http://www.wrcc.dri.edu/.

WHIPPLE, J.J. 2001. Annotated checklist of exotic vascular plants in Yellowstone National Park. Western North American Naturalist 61:336-346.

MAXWELL, B., R. ASPINALL, T. WEAVER, D. DESPAIN, AND L. CAMERON. 2001. Methods to Inventory Weed Populations in Remote Areas. CIPM Proposal Abstracts. Viewed 08/30/02 at http://www.weedcenter.org/.

MCNEELY, J.A., H.A. MOONEY, L.E. NEVILLE, P. SCHEI, AND J.K. WAAGE. 2001. Strategy on invasive alien species. IUCN in collaboration with the Global Invasive Species Programme. Gland, Switzerland and Cambridge, UK.

MUELLER-DOMBOIS, D., AND H. ELLEMBERG. 1974. Aims and methods in vegetation ecology. John Willey and Sons, Chichester.

MURRELL, D.J., D.W. PURVES, AND R. LAW. 2001. Uniting pattern and processes in plant ecology. Trends in Ecology and Evolution 16:529-530.

NADEAU, L.B., AND J.R. KING. 1991. Seed dispersal and seedling establishment of *Linaria vulgaris* Mill. Canadian Journal of Plant Science 71:771-782.

NADEAU, L.B., M.R.T. DALE, AND J.R. KING. 1991b. The development of spatial patterns in shoots of *Linaria vulgaris* (Scrophulariaceae) growing on fallow land or in a barley crop. Canadian Journal of Botany 69:2539-2544.

NADEAU, L.B., J.R. KING, AND K.N. HARKER. 1992. Comparison of growth of seedlings and plants grown from root pieces of Yellow Toadflax *Linaria vulgaris*. Weed Science 40:43-47.

NOSS, R.F., AND A.Y. COOPERRIDER. 1994. Saving nature's legacy: protecting and restoring biodiversity. Island Press, Washington D.C.

OLLIFF, T.R., C. MCCLURE, P. MILLER, D. PRICE, D. REINHART, AND J. WHIPPLE. 2001. Managing a complex exotic vegetation program in Yellowstone National Park. Western North American Naturalist 61:347-358.

REICHMAN, O.J., AND E.W. SEABLOOM. 2002. The role of pocket gophers as subterranean ecosystems engineers. Trends in Ecology and Evolution 17:44-49.

RODMAN, A., H.F. SHOVIC, AND D. THOMAS. 1996. Soils of Yellowstone National Park. Yellowstone Center for Resources, Yellowstone National Park, Wyoming.

SALA, O.E., F.S. CHAPIN III, J.J. ARMESTO, E. BERLOW, J. BLOOMFIELD, R. DIRZO, E. HUBER-SANWALD, ET AL. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770-1774.

Table 1. Theoretical multi-scale framework for assessing alien plant invasions. At each scale, a different set of processes can be evaluated and unique management strategies can be designed.

Element/Scale	Landscape	Stand	Invader Patch
Spatial dimensions	- Defined by geoecological system (Over 10^6 m^2)	- Area of the stand and large plots (1,000-10,000 m^2)	- Patch size and microplots (0.1-500 m^2)
Temporal scale	- Events that occur over hundreds of years	- Events occur in decades	- Events occur yearly
Key processes & structures affecting invasion	-Topography, winds -Land-use and history -Macroclimate	-Soil series -Disturbance regimes -Microclimate -Plant community types	-Microsite variation (e.g. soil disturbance, coarse woody debris) -Plant interactions -Plant-animal interactions
Spatial pattern detection	-Identify infection loci and sinks, and dispersal corridors.	- Identify patches' spatial arrangement. - Patterns of short distance dispersal.	- Individual ramets' distribution - Density patterns
Processes studied	- Long term dispersal and interactions with landscape structure (e.g. long-term patterns of spread along corridors)	- Interaction between invasion and disturbance and site characteristics.	-Population dynamics -Interaction with native plants
Monitoring	- Identify key loci of infection and detect new isolated patches.	- Monitor infilling of colonized stands - Monitor successional changes	-Monitor population characteristics -Monitor effects on native species
Conservation and management applications	- Detection and prioritization of infested areas.	- Test efficacy of control methods and their interactions with site factors - Determine invasion effects on overall native plant community	-Quantify control effects on population dynamics -Determine the effects of control in native plants

Table 2. Scale definition for three attributes of the landscape scale assessment of *Linaria vulgaris* patch clusters.

Attribute	Classes			
Land use	Roads: areas located 10 m from a road or highway	Logged areas: areas that have been clearcutted or intensively logged during the last 30 years	Riversides: areas that are near a river, lake or in riverbanks	Natural vegetation: Areas that do not show signs of heavy human disturbance
Fire Intensity	1: Areas with no historical record or physical sign of fire	2: Areas with historical record of fire but no physical signs	3: Areas with scattered physical signs of fire such as coarse woody debris charcoal	4: Areas with high density of coarse woody debris charcoal (burn piles in logging operations)
Soil Disturbance	1: Present of bare soil, but no signs of soil turn over	2: Presence of bare soil, signs of turnover disturbance but more than 25% herbaceous cover	3: High levels of soil turnover (e.g. gophers mounds), less than 25% herbaceous cover.	4: Areas where soil is disturbed periodically with less than 5% of plant cover (e.g. roads, trails).
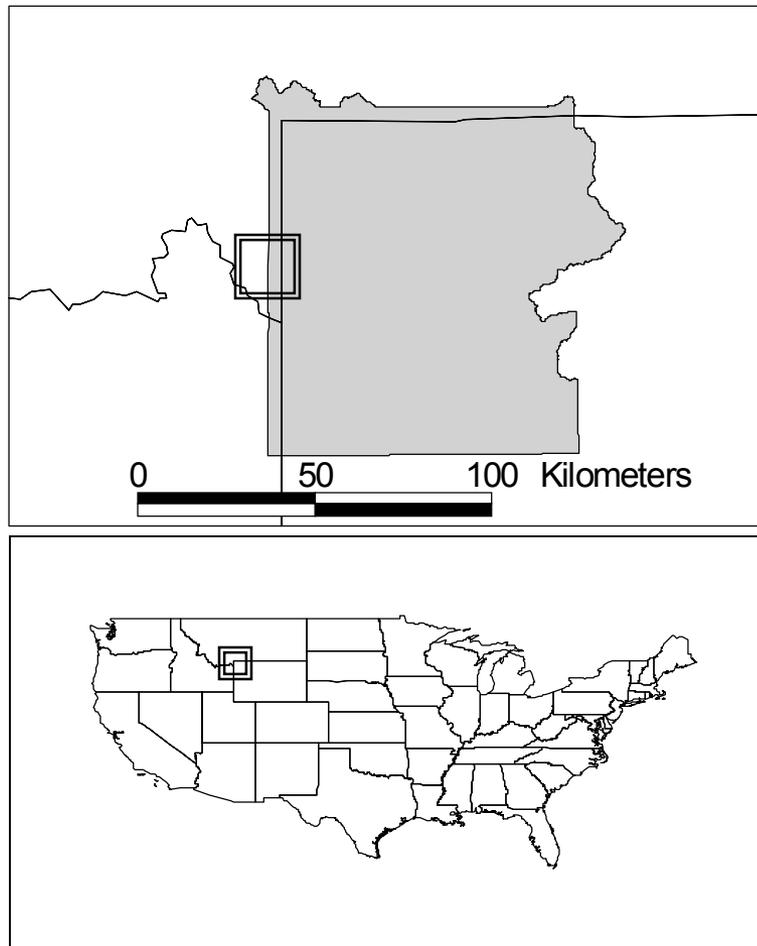
Fig. 1. Map of the study area in West Yellowstone, Montana. The square indicates the location of the study area. A detailed map of the study area is presented in Fig. 2.
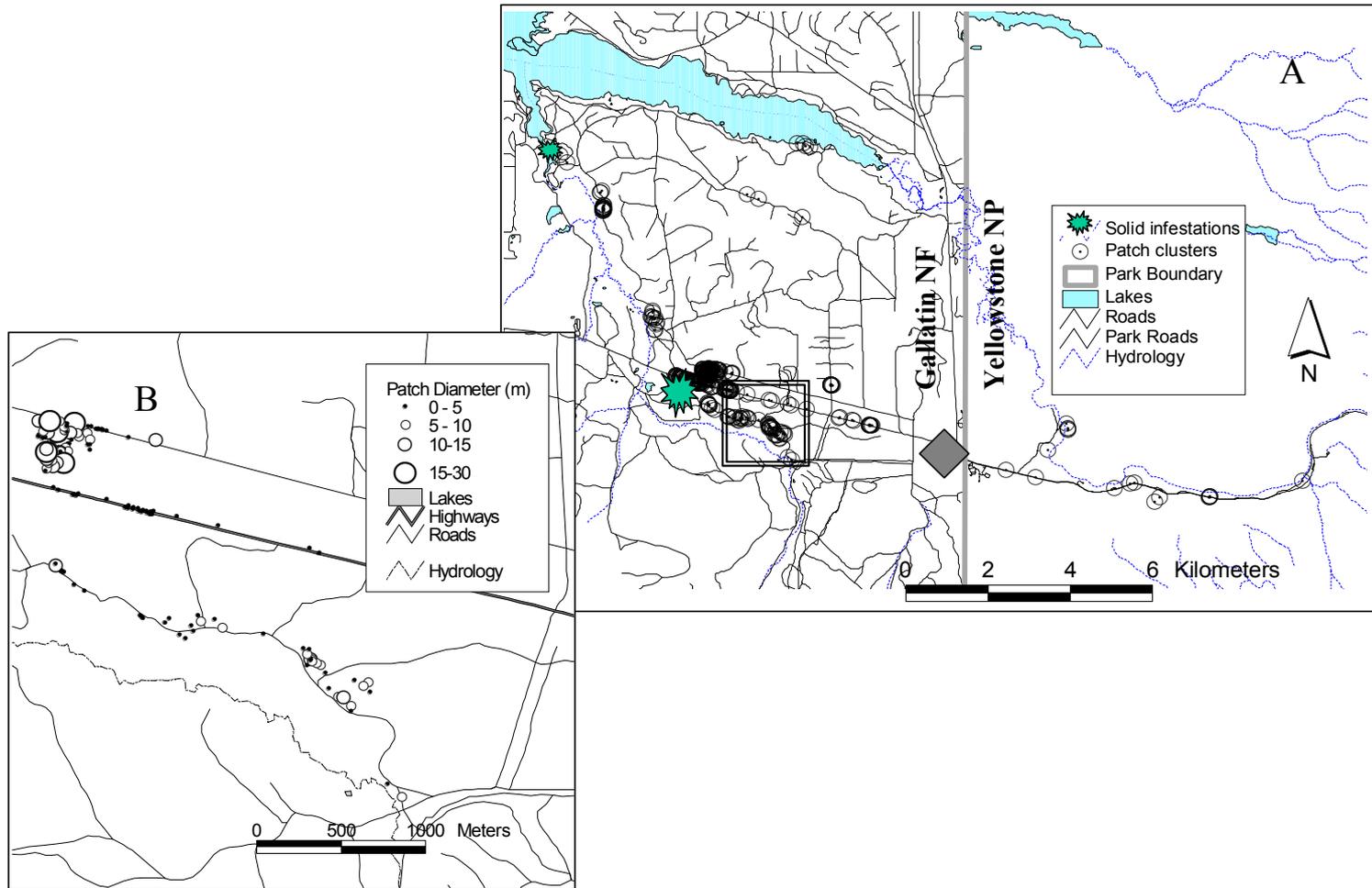
Fig. 2. Landscape distribution of *Linaria vulgaris* patch clusters in the study site. A. West Yellowstone Study site (the rhomboid indicates the town of West Yellowstone; the square is enlarged in part B). B. An example of spatial cluster distribution at the landscape scale, with clusters classified by size.
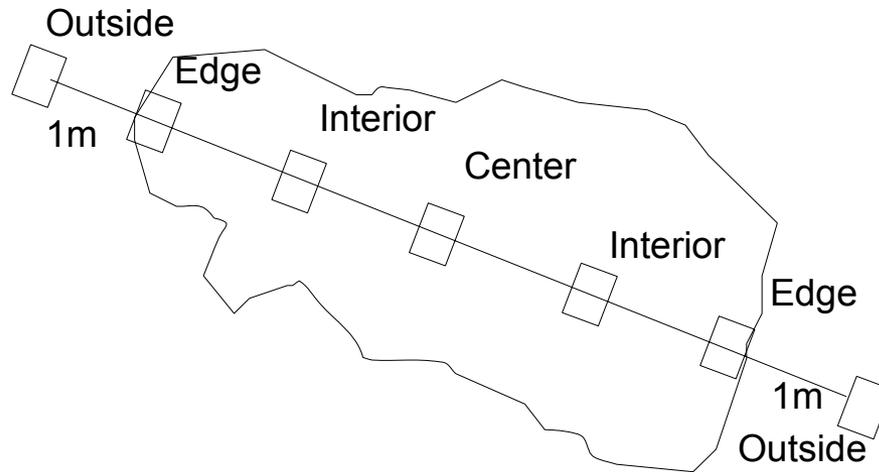
Fig. 3. Schematic diagram showing the location of 7 microplots (50 by 20 cm) used in large and medium-sized patches of *Linaria. vulgaris*. Spacing between plots is 1/4 of patch length. In small patches (<5m) only 5 microplots were located (2 outside, 2 along the edges and one in the center).
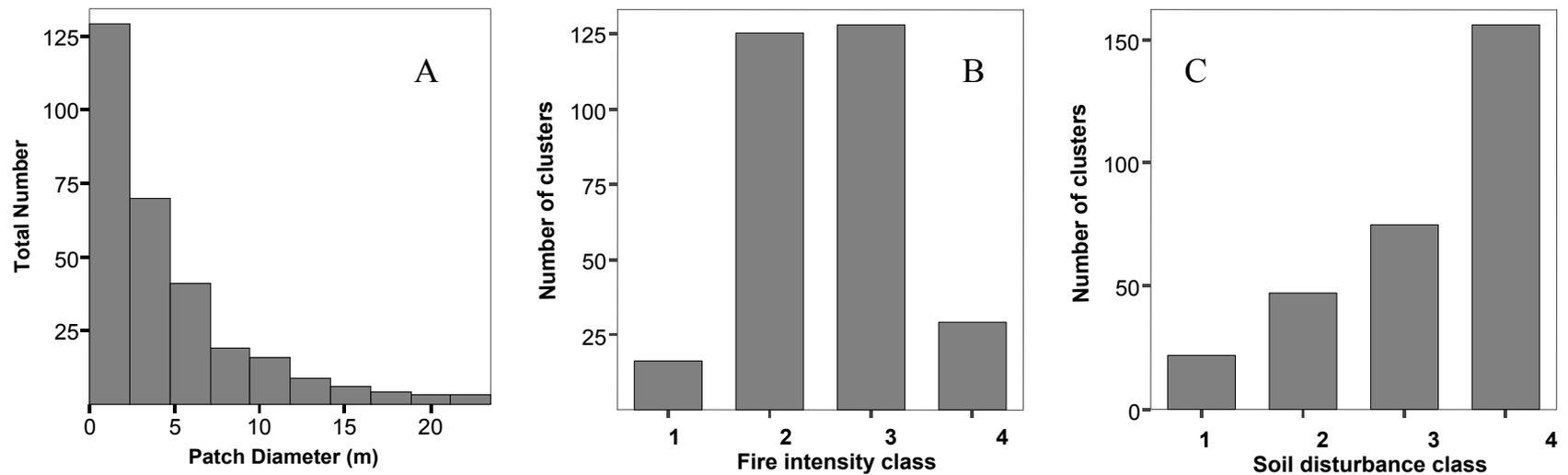
Fig. 4. Attributes histograms for 300 *Linaria vulgaris* clusters in the West Yellowstone area. A. Patch diameter, B. Fire history class (1: minimal signs of historical fire, to 4: signs of severe fire; see Table 2 for details). C. Soil disturbance class (1: no disturbance, to 4: periodically disturbed soil; see Table 2 for details).
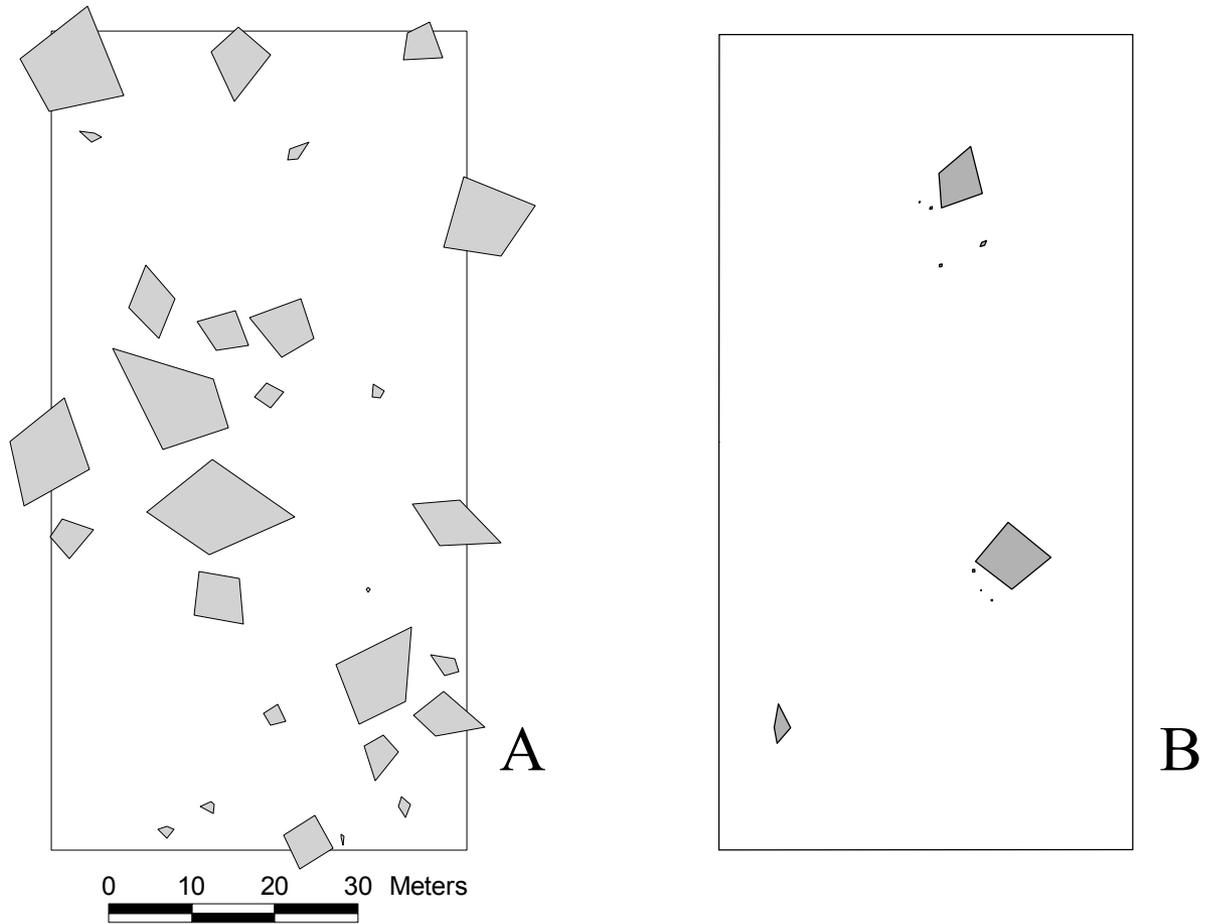
Fig. 5. Clonal patch spatial arrangement in A) an old clearcut, B) a new clearcut, both in the Gallatin National Forest. The macroplot is 50 by 100 m and the total number of patches is 27 for A and 10 for B.
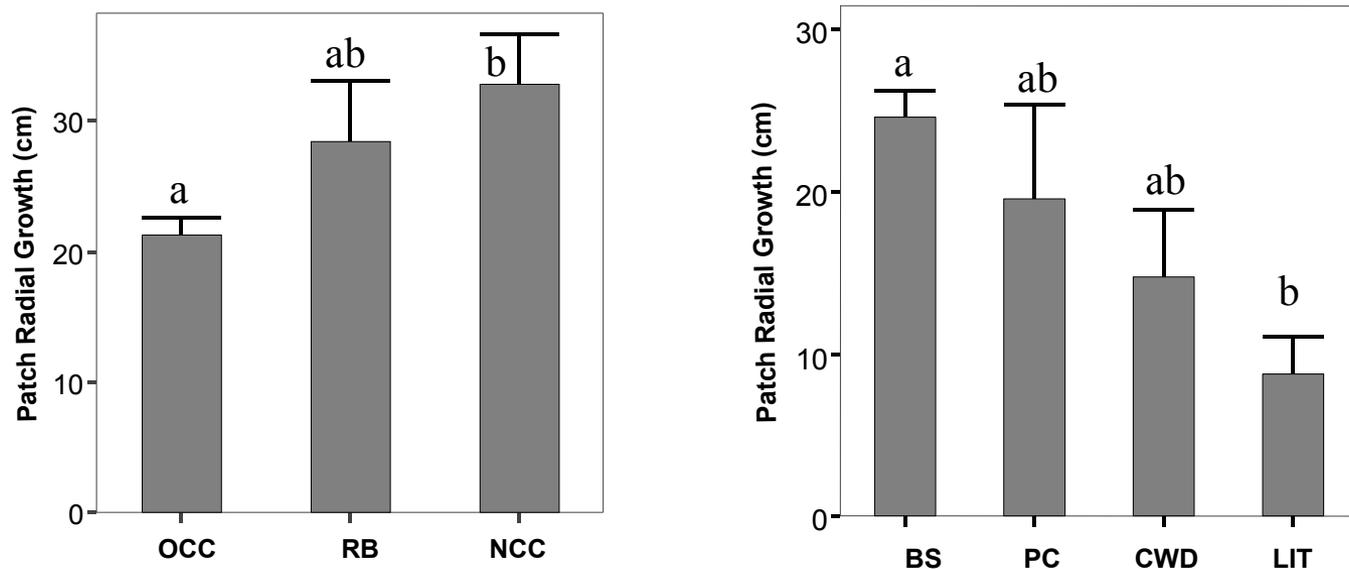
Fig. 6. Radial growth (+SE) of *Linaria vulgaris* clonal patches from 2000-2001. A. Patch growth by land-use. Patch growth in new clearcuts (NCC, number of patches n=10, corners=36) was significantly greater than in old clearcut patches (OCC, n=70, corners=271) (Mann-Whitney, p<0.01). The growth in the riverbank macroplot (RB, n=8, corners=28) was not significantly different from either of the other land use types. Because some patches had merged in 2001, the number of corners is less than 4x the total number of patches. B. Patch growth (2000-2001) in old clearcuts by substrate (BS: bare soil, PC: more than 25% plant cover, CWD: more than 50% coarse woody debris, LIT: 50% or more cover of *Pinus contorta* litter). Only Canopy and bare soil were significantly different (Mann-Whitney, p<0.05).
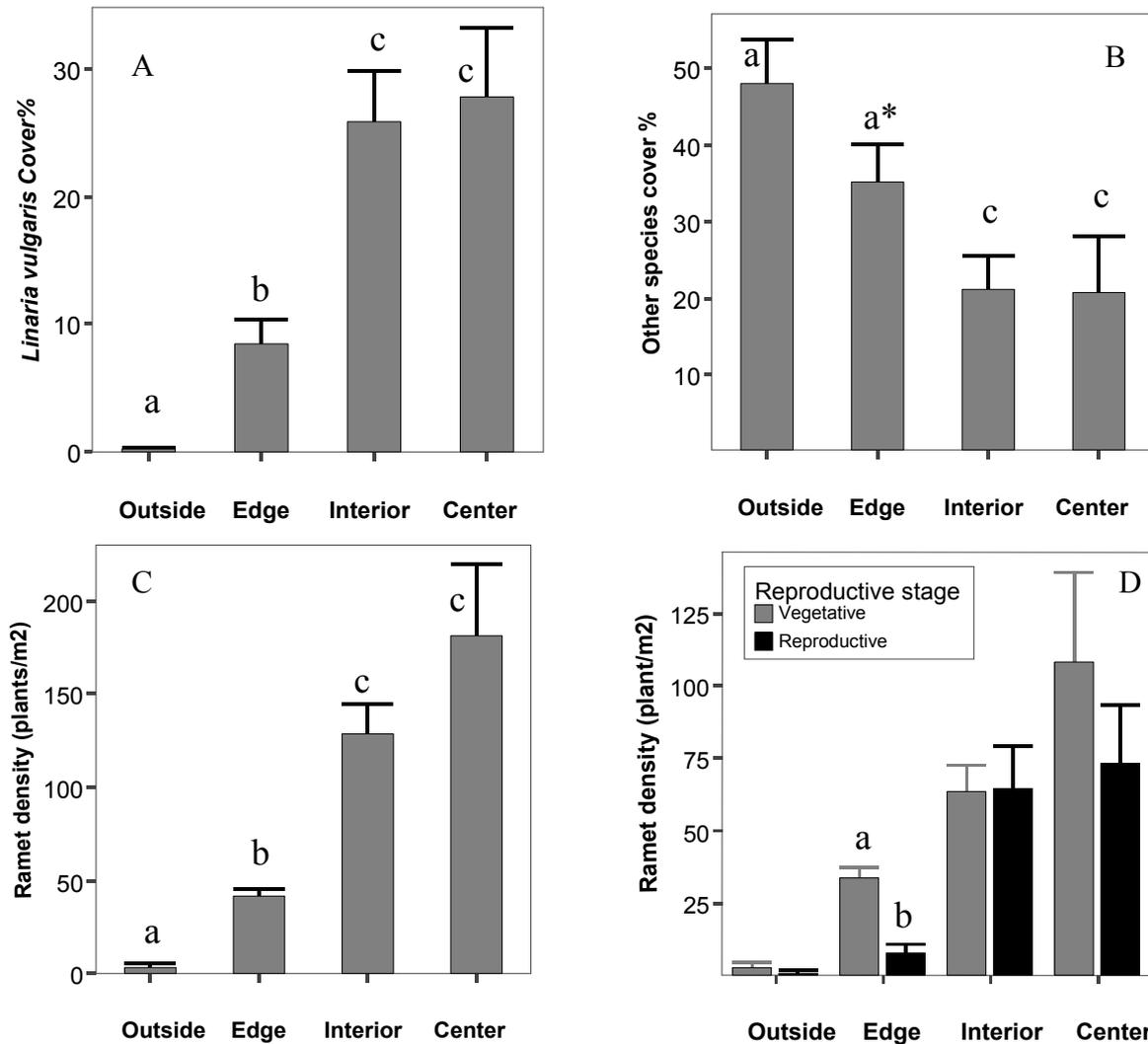
Fig. 7. Microplot variables (mean +SE) from outside (1m) to the center in large and medium *Linaria vulgaris* clonal patches from clearcuts and riverbanks (N=18; center plots=N, all others=2N). A. *L. vulgaris* cover %. B. Other species cover %. C. *L.vulgaris* ramet density. D. *L. vulgaris* ramet density separate by reproductive stage. *L. vulgaris* cover %, others species cover and ramet density were significantly correlated with location in the patch (Kruskall-Wallis, p<0.01). Lowercase letters indicate significant pairwise differences (Mann-Whitney, p<0.01, * indicates p<0.05). Mean vegetative and reproductive ramet densities were only significantly different in the patch edges.
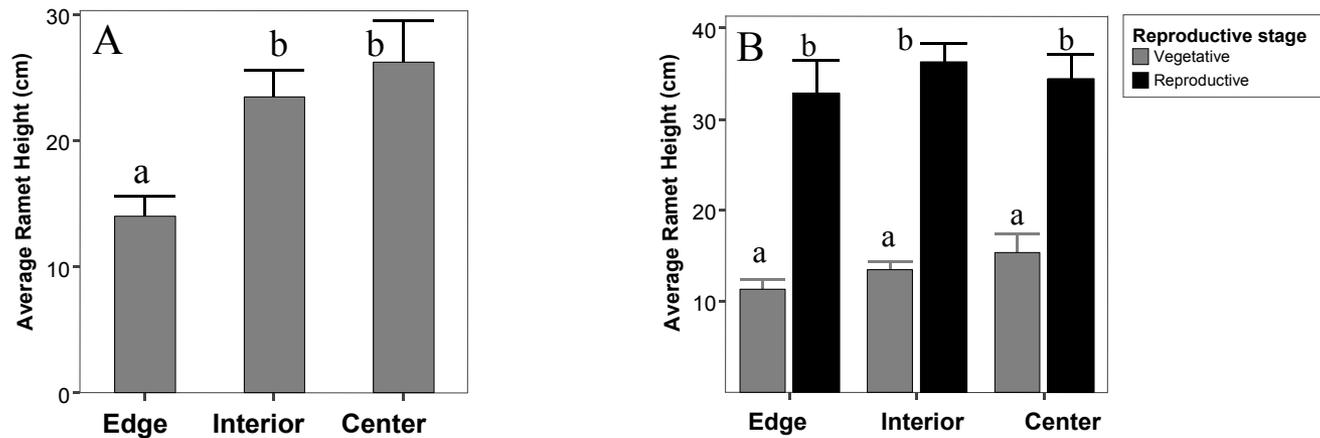
Fig. 8. Microplot mean average height (±SE) in the edge, interior and center in large and medium *Linaria vulgaris* clonal patches (n=24 for edge, interior; n=12 for center). A. Average height considering both vegetative and reproductive ramets is significantly different from the edge to the center (Kruskall-Wallis, p<0.01). Lowercase letters indicate significant differences (Mann-Whitney, p<0.01). B. Average height by reproductive stage. Height differences are not significant for either vegetative and reproductive stages across the the three positions (Kruskal-Wallis, p>0.05). However, mean height of vegetative ramets is always significantly different from the mean of reproductive ramets (Mann-Whitney, p<0.01). Lowercase letters indicate significant differences (Mann-Whitney, p<0.01).