

PLANT INVASIONS IN PROTECTED AREAS AT MULTIPLE SCALES:
LINARIA VULGARIS (SCROPHULARIACEAE)
IN THE WEST YELLOWSTONE AREA

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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 2 historical sources, colonizing both human-caused and natural disturbances. Analyzed at the stand scale, patches tend to aggregate in newly invaded areas and disperse in heavily infested areas. The data suggest that patches grow in size by clonal growth 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 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.

Key words: exotic plant species invasion, protected areas, multi-scale method, *Linaria vulgaris*, Yellowstone National Park, Gallatin National Forest, boundary issues, landscape analysis, clonal patch, spatial distribution.

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 (D'Antonio et al. 1999, Hobbs 2000, Sax and Brown 2000). 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 2004). However, invasive species can still become a significant threat to ecosystems conserved in protected

areas (MacDonald et al. 1989, Lesica and Ahlenhalager 1993, DeFerrari and Naiman 1994, Stohlgren et al. 1999, Olliff 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 Lindenmayer and Franklin 2002), recognizing both the complex and heterogeneous landscapes, and the invaders' contagious distributions and low population density.

To identify the underlying mechanisms of plant invasions in protected area landscapes, we must consider the broad range of scales and processes involved (Stohlgren et al. 1999,

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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 (Dixon et al. 2002). A fine-scale approach (for example, monitoring an invasive plant using a 1-m² 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 help identify the dominant mechanisms governing

the invasion process and thereby provide 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 plant species, 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, Olliff et al. 2002). *Linaria vulgaris*, a member of the Scrophulariaceae family native to disturbed sites in Eurasia, was introduced to North America as an ornamental perhaps 300 years 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 (Nadeau and King 1991, Nadeau et al. 1991, 1992, Saner et

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 geoeological 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 and 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 spatial arrangement of patches • Patterns of short distance dispersal	• Individual ramet 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	• Detect and prioritize 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

al. 1995). It invades from sea level to over 3000 m and up to 60 degrees N 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 (Nadeau et al. 1991, Saner et al. 1995). 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 to study invasions in protected areas since *L. vulgaris* is a rapidly spreading early invader and is easy to detect at both community and landscape scales. In this paper we report on our ongoing investigation into *Linaria vulgaris* invasion of Yellowstone National Park and Gallatin National Forest. *Linaria 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 advantages and disadvantages of our method and conservation implications of studying plant invasions in protected areas using a multi-scale approach.

STUDY AREA

The study area (Fig. 1) is in the Madison Valley near the western entrance of Yellowstone National Park (NP) and the adjacent Gallatin National Forest (NF; 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 2 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 in the form of snow. Mean tem-

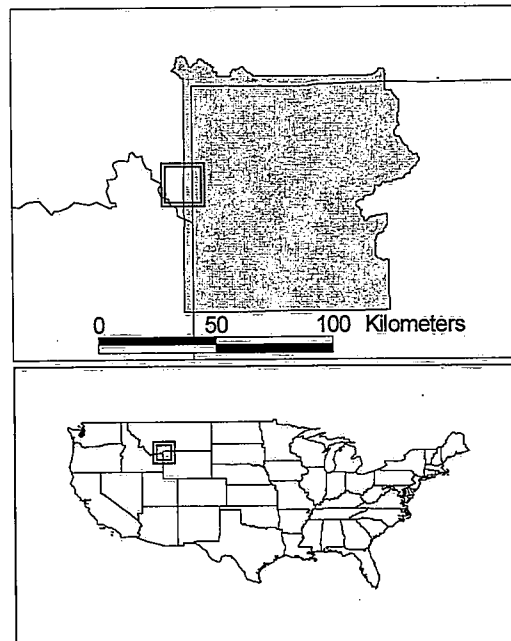


Fig. 1. Map of the study area in West Yellowstone, Montana. The square indicates the location of the study area. A detailed map of the study area is presented in Figure 2.

perature 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* semiarid shrublands are dominant vegetation types (Despain 1990). Catastrophic fires occur at least every 300 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 3 decades, declining in the 1990s (Susan LaMont, USDA Forest Service, West Yellowstone, personal communication). Increasing numbers of tourists are visiting the area year-round.

Since 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* (Olliff et al. 2001). Although the harsh, high-elevation climate restricts the intensity of weed invasion (Forcella and Harvey 1983), plant invaders nevertheless have colonized human-disturbed areas such as roads and campgrounds

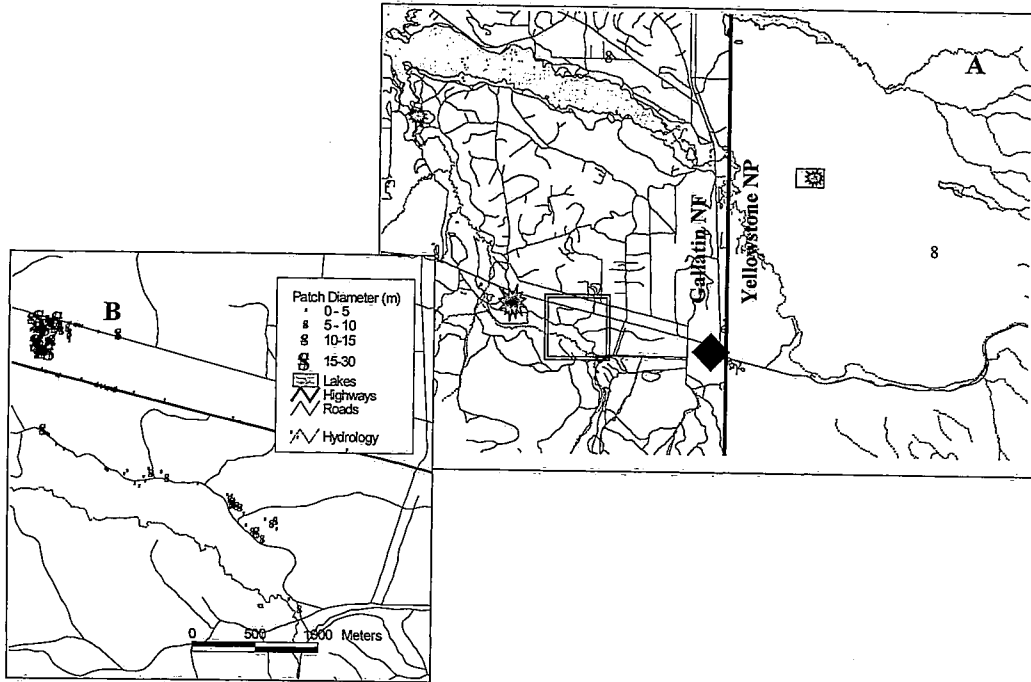


Fig. 2. Landscape distribution of *Linaria vulgaris* patch clusters in the study site: A, West Yellowstone study site (rhomboid indicates town of West Yellowstone; the square is enlarged in part B); B, an example of spatial cluster distribution at the landscape scale, with clusters classified by size.

(Allen and Hansen 1999) and are progressively invading riparian habitats and other pristine environments. Both the National Park Service (NPS) and the U.S. Forest Service have developed management plans for controlling weed invasion (Olliff et al. 2001).

METHODS

Linaria vulgaris invasion and its effects were studied at 3 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 study area for the landscape scale was defined to determine *L. vulgaris* dispersal processes and habitat invasibility in the Madison Plateau (approximately 20×10 km; Figs. 1, 2). The area includes portions of Galatin NF and Yellowstone NP. 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 50×100 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 20×50 -cm sample unit was used at this scale to evaluate processes including population structure of *L. vulgaris* and the species interactions with native vegetation.

Landscape Scale

In the summer of 2001, we completed a census 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. We recorded differential GPS positions with a Trimble GeoExplorer 2 (3–5 m accuracy); 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 >50 m) were recorded as polygons rather than individual clusters. We noted the following attributes for each cluster: land use class; longest diameter and longest perpendicular axis length; azimuth of the longest diameter; ramet density in a

TABLE 2. Scale definition for 3 attributes of the landscape-scale assessment of *Linaria vulgaris* patch clusters.

Attribute Class	Scale definition
Land use	
Road	Area located 10 m from a road or highway
Logged area	Area has been clearcut or intensively logged during the last 30 years
Riverside	Area is near a river, lake, or in riverbanks
Natural vegetation	Area does not show signs of heavy human disturbance
Fire intensity	
1	Area with no historical record or physical sign of fire
2	Area with historical record of fire but no physical signs
3	Area with scattered physical signs of fire such as coarse, woody debris charcoal
4	Area with high density of coarse, woody debris charcoal (burn piles in logging operations)
Soil disturbance	
1	Presence of bare soil, but no signs of soil turnover
2	Presence of bare soil, signs of turnover disturbance, but >25% herbaceous cover
3	High levels of soil turnover (e.g., gopher mounds), <25% herbaceous cover
4	Soil disturbed periodically, <5% plant cover (e.g., roads, trails)

randomly located 50 × 20-cm microplot; average dominant height; visually estimated percent of reproductive ramets; soil disturbance; fire intensity; tree height; and visually estimated percent canopy cover, percent shrub cover, and combined herb and grass percent cover, excluding *L. vulgaris*, both inside and outside the cluster (Table 2). Location and cluster attributes were plotted in ArcView 3.2. We used SPSS 10.0 to statistically analyze variability in cluster size, land use, soil disturbance, and fire intensity variables.

Stand Scale

In August 2000 we recorded spatial attributes of *L. vulgaris* patches in five 50 × 100-m macroplots. In the Gallatin NF we located 3 macroplots in old clearcuts (logged between 1978 and 1982), and 1 in a newer clearcut (logged in 1992). In Yellowstone NP a single macroplot was located on a riverbank of the Madison River. The 3 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 as study cases. We recorded the longest length, perpendicular longest width, and azimuth for each patch in each macroplot. Plants separated by more than 50 cm were considered to be different patches. Patch corners and centers were permanently marked with metal stakes. Field measurements and trigonometric functions were used to cre-

ate polygons in ArcInfo 8.0 and ArcView 3.2. In August 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 2 macroplots, 1 in an old clearcut under severe invasion and the other in a newer clearcut at early stages of invasion. We conducted point pattern analyses using patch centroids within macroplots. Using a standardized nearest-neighbor distance (*R*-statistic; Fotheringham et al. 2000), we classified patches as clustered ($R < 1$), random ($R = 1$), or dispersed ($R > 1$). 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 $P < 0.05$). The correlation between radial growth and longest patch diameter was tested using a linear regression model (significant when $P < 0.01$).

Clonal Patch Scale

In August 2000 patches were randomly selected in each macroplot to locate 20 × 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 1-m microplots were located along the longest patch axis: 2 outside the edge, 2 within the patch along the edges, 2 in the interior, and 1 in the middle (Fig. 3). In small patches (<5 m long), only 5 microplots were located (Fig. 3). Microplots were marked permanently using metal stakes. In each microplot we recorded every ramet 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 5 cover classes of Braun-Blanquet (described in Mueller-Dombois and Elleberg 1974). Microplots were remeasured in August 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 included ramet density, ramet density by reproductive stage, ramet height, *L. vulgaris* percent cover, species richness, and total percent cover of other plants. In all cases, because the data were not normally distributed (Kolmogorov-Smirnov, $P < 0.01$), nonparametric 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 NE, 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). Most patches in the study area occurred in logged areas (39.3%), along roadsides (<2 m from the road; 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%). Most recorded clusters were 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 not to have

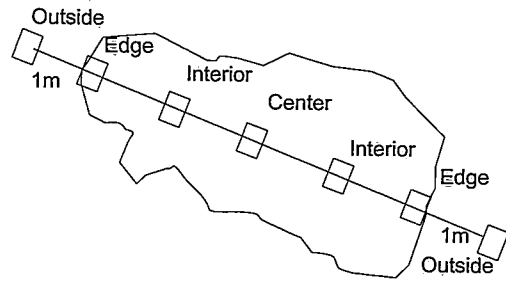


Fig. 3. Schematic diagram showing the location of 7 microplots (50 × 20 cm) used in large and medium-sized patches of *Linaria vulgaris*. Spacing between plots is 1/4 of patch length. In small patches (<5 m) only 5 microplots were located (2 outside, 2 along the edges, and 1 in the center).

been recorded as separate patch clusters (Fig. 2). In addition, a small number of patches and a heavily infested area were found along the sandy shores of Hebgen Lake (Fig. 2).

Linaria vulgaris is abundant in loose and bare soils with >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. Almost 10% of the patches occurred in areas with signs of severe burn, which are frequent in logging areas, but may also occur in natural fires (Fig. 4).

Nineteen patch clusters (6.3%) were found in the interior of Yellowstone NP. Clusters were found in the park along the highway (58%), in riverbanks (21%), on secondary roads (11%), and in natural vegetation, including a burned area and a hillside (Fig. 2).

Stand Scale

Linaria vulgaris patches showed a different spatial arrangement in the old clearcut compared with the new clearcut (Fig. 5). Patches covered 12.5% of the macroplot area in the old clearcut, but only 1.3% in the new clearcut. Patch density was also higher in the old clearcut ($58 \cdot \text{ha}^{-1}$) compared with the new clearcut ($20 \cdot \text{ha}^{-1}$). 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 3 areas of the clearcut, and in 2 of those

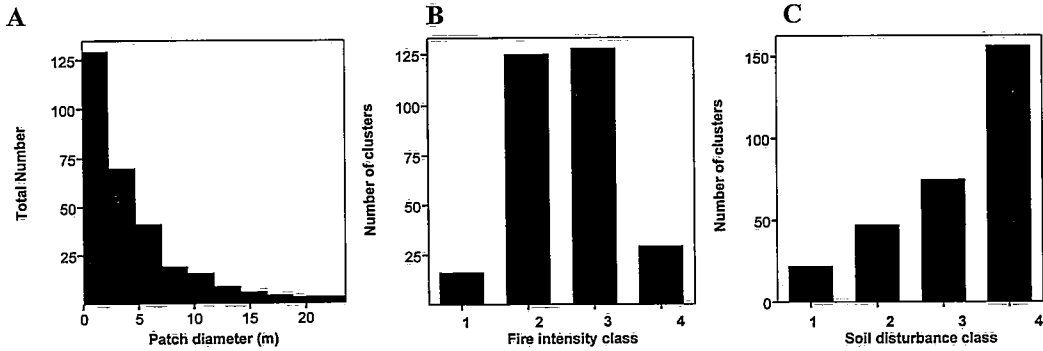


Fig. 4. Attribute histograms for 300 *Linaria vulgaris* clusters in the West Yellowstone area: A, patch diameter; B, fire history class (1 = minimal signs of historical fire to 4 = signs of severe fire; see Table 2 for details); C, soil disturbance class (1 = no disturbance to 4 = periodically disturbed soil; see Table 2 for details).

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 50 × 100-m 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 either or both directions, the frequency of closely neighboring patch centers was reduced below the rate that would be found in a random point distribution.

There were no significant differences in mean radial growth between the 3 old clearcut macroplots in the period 2000–2001 (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

Linaria vulgaris percent cover and ramet density in old clearcuts were higher in interiors and centers than in the edges of clonal patches (Kruskal-Wallis, $P < 0.01$; Mann-Whitney, $P <$

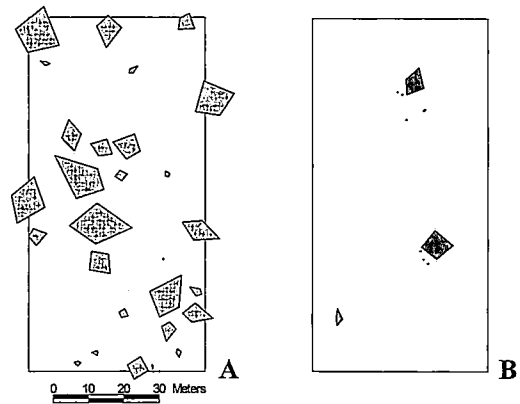


Fig. 5. Clonal patch spatial arrangement in the Gallatin National Forest: A, an old clearcut; B, a new clearcut. The macroplot is 50 × 100 m; total number of patches is 27 for A and 10 for B.

0.01; Figs. 7A–C). Total cover of other species was also related to position (Kruskal-Wallis, $P < 0.01$), but decreased 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 patch centers (Fig. 8A). However, when ramets were classified by reproductive stage, average height for vegetative and reproductive

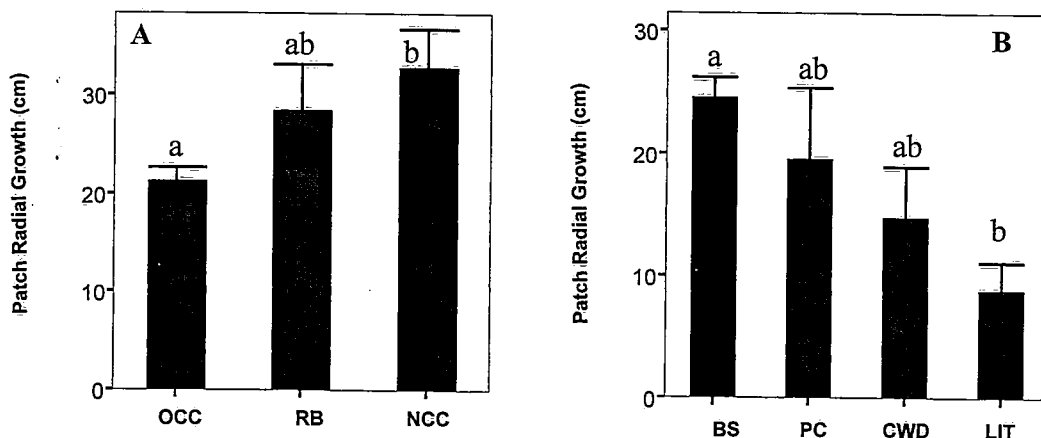


Fig. 6. Radial growth ($\pm s_x$) of *Linaria vulgaris* clonal patches, 2000–2001. A, Patch growth by land use. Patch growth in new clearcuts (NCC, number of patches = 10, corners = 36) was significantly greater than in old clearcut patches (OCC, $n = 70$, corners = 271; Mann-Whitney, $P < 0.01$). Growth 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 $4 \times$ total number of patches. B, Patch growth (2000–2001) in old clearcuts by substrate (BS = bare soil, PC = $>25\%$ plant cover, CWD = $>50\%$ coarse woody debris, LIT = $\geq 50\%$ cover of *Pinus contorta* litter). Only canopy and bare soil were significantly different (Mann-Whitney, $P < 0.05$).

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 is useful in understanding invasion processes at each of the 3 scales and evaluating the potential threat of this species in West Yellowstone ecosystems. 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 affect ecosystems both through its rapid expansion and its competitive ability. *L. vulgaris* is able to invade high-elevation, protected areas in the Rocky Mountains, following road corridors and establishing new patches in a wide range of disturbance regimes and habitats. Once established in a new location, this species expands the number and density of patches and increases its ramet density within patches, affecting native plant communities.

Landscape Scale

Linaria vulgaris is widely dispersed across the landscape, but patch cluster density is highly variable. Management and land use appear to

be key factors in determining the concentration of *L. vulgaris* infestations in the developed areas of Gallatin NF. Patterns of cluster distribution are consistent with the presence of a major source of propagules in the Gallatin NF. A late-1800s ranch on the western edge of the study site has probably 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 1 wild population along the Madison River (Craig McClure, NPS, personal communication). However, most clusters inside the park occur near the entrance highway and were probably initiated from propagules brought by vehicles from the extensive infestations in the Gallatin NF (<10 km apart) and/or contaminated sand and gravel used for road maintenance. Long-term monitoring and additional spatial analysis of cluster distribution are needed to understand invasion dynamics at this scale. Since many invaders show rapid genetic change, genetics techniques may also help to elucidate flow of propagules in the landscape (Sakai et al. 2001, Lee 2002).

Our landscape assessment supplemented previous reports that did not provide quantitative data and missed the occurrence of *L. vulgaris* in less developed areas (Susan LaMont

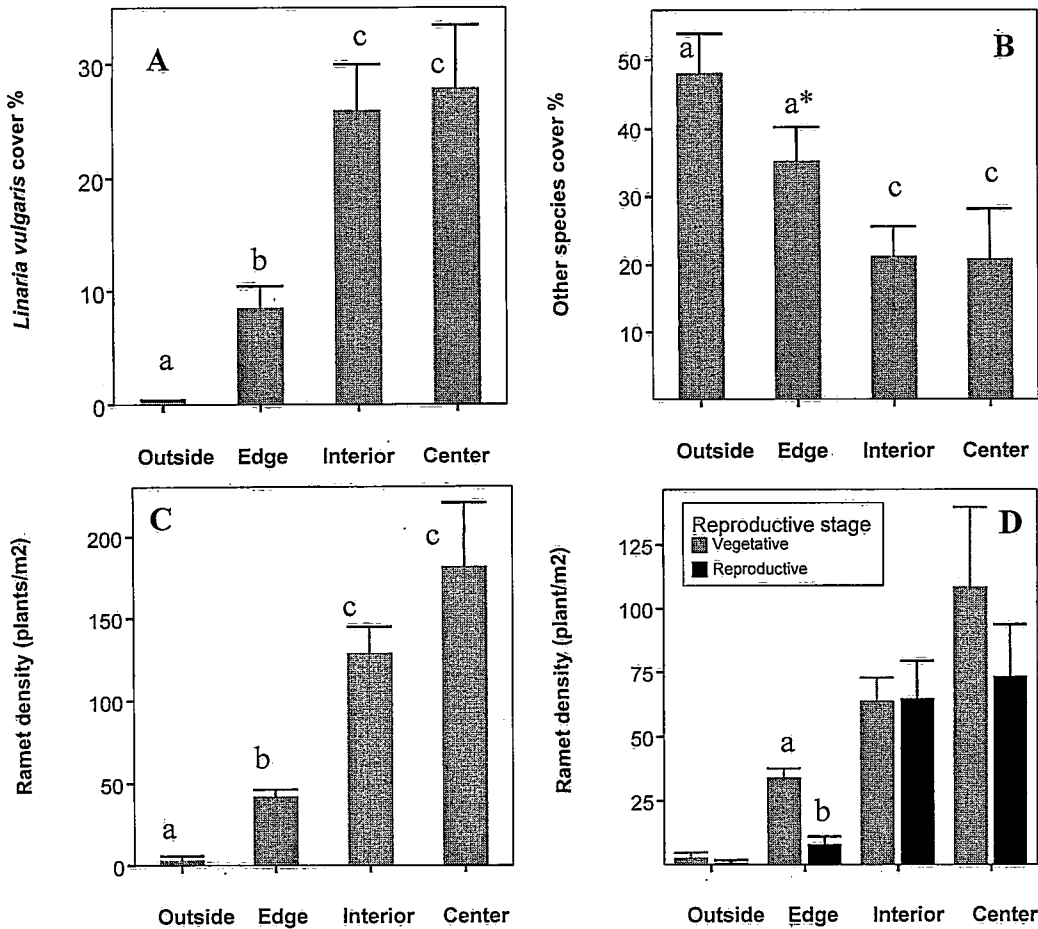


Fig. 7. Microplot variables (mean \pm $s_{\bar{x}}$) from outside (1 m) to center in large and medium *Linaria vulgaris* clonal patches from clearcuts and riverbanks ($n = 12$; center plots = n , all others = $2n$). A, *L. vulgaris* cover percentage; B, other species cover percentage; C, *L. vulgaris* ramet density; D, *L. vulgaris* ramet density separated by reproductive stage. *L. vulgaris* percentage, other species cover, and ramet density were significantly correlated with location in the patch (Kruskal-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 significantly different only in patch edges.

personal communication, Craig McClure personal communication). From the landscape-scale analysis we were able to hypothesize the location of both the initial infestation and the current major sources of propagules. One of the major constraints of our method at the landscape scale is the lack of true replicates, preventing statistical analysis. In future studies we recommend use of a broader coarse-scale assessment of weed populations, perhaps using randomly located long transects. This would provide statistically robust data on weed presence over extensive areas, with critical information on the locations of rare and small new populations (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 is caused by clonal growth or poor dispersal and may be an ecological strategy to overcome interspecific competition and assure persistence (Nadeau et al. 1991, Saner et al. 1995, Murrell 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

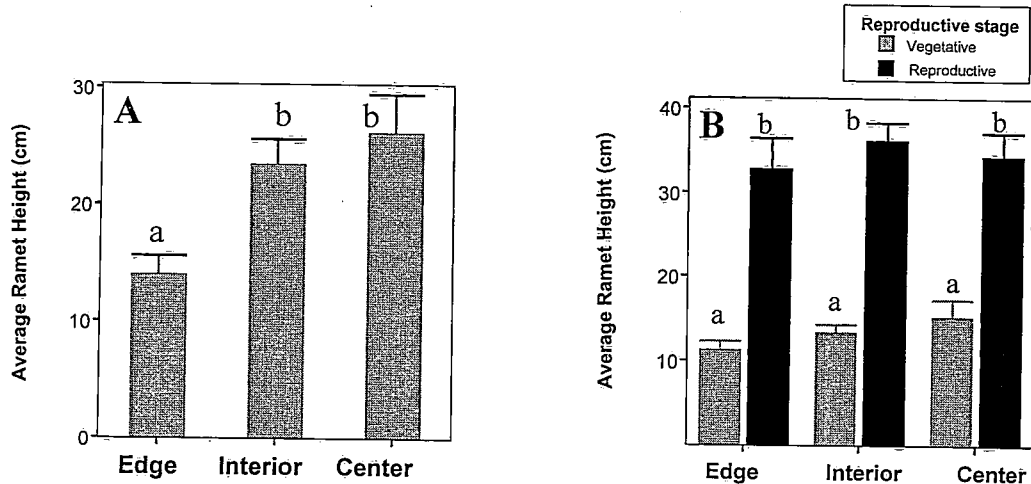


Fig. 8. Microplot mean averages of height ($\pm s_{\bar{x}}$) in the edge, interior, and center in large and medium *Linaria vulgaris* clonal patches ($n = 12$; center plots = n , all others = $2n$). A, Average height considering both vegetative and reproductive ramets is significantly different from edge to center (Kruskal-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 or reproductive stages across the 3 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, $P < 0.01$).

in old clearcuts. These areas generally show dense and sometimes continuous *L. vulgaris* patches that are controlled mainly by environmental conditions rather than by propagule availability. Our monitoring data suggest 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 become established in the remaining noninvaded sites.

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 $2 \text{ m} \cdot \text{yr}^{-1}$ growth of *L. vulgaris* in recently disturbed barley crops; Nadeau et al. 1991). 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 distri-

bution 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 2002). We believe that our monitoring data will eventually help to answer those questions. The presence of both native and introduced insect predators may be a major factor controlling the expansion of these populations (Bruce Maxwell, Montana State University, 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 with edges indicates that patches are expanding and maintaining a high ramet density. We found mean densities of almost 200 plants \cdot 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 \cdot m⁻² found in agricultural crops (Nadeau et al. 1991). The high ramet density in patch centers suggests that this species does not undergo significant die-off after reaching maximum densities. *Linaria 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 cover of native plants in patch cores 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 patches show a trend of increasing biomass as the patches expand. This may reduce 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; tallest ramets grow in densest areas of the patches. Similarly, height of reproductive ramets does not decrease with intraspecific competition. Therefore, we expect that patch area and propagule output will be proportionally related. However, our ability to determine population structure was limited due to the dominant vegetative reproduction of *L. vulgaris*. The proportion of ramets and genets is impossible to calculate with our method and thus difficult to assess the importance of sexual reproduction in the dynamics of patch expansion. Alternative methods such as excavation of all ramets and genets and genetic testing could be used to solve this limitation.

The study of ecological phenomena at this fine scale is crucial in understanding the behavior of the invader and its interaction with native vegetation (Table 1). Overall, the clonal patch scale provides the most information on the dynamics of interaction between invasive plant and native species.

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 into natural communities even under harsh climatic conditions. Anecdotal data from other areas confirm this trend. *Linaria vulgaris* is an important problem in Rocky Mountain National Park, Colorado, where it occurs up to 3600 m elevation in naturally disturbed ground (Jeff Connor personal communication). In the Northern Rockies, U.S. Forest Service weed specialists have observed *L. vulgaris* populations between 1000 m and 2000 m on national forest lands (Pauchard unpublished data).

In Yellowstone NP, *L. vulgaris* could easily expand into other open areas such as riverbanks, fires, meadows, or sagebrush shrublands. We already have found patches far from human corridors in naturally disturbed grounds. 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. Also, the role of natural fine-scale disturbances in *L. vulgaris* expansion needs to be studied, especially the effects of pocket gophers and large herbivores (e.g., Reichman and Seabloom 2002). The presence of natural hybrids of *L. vulgaris* and *L. dalmatICA* in our study area increases the risk of invasion due to hybrid vigor and rapid genetic change (Saner et al. 1995, Vujnovic and Wein 1997, Sakai et al. 2001).

The multi-scale data suggest that *L. vulgaris* management 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 (Olliff et al. 2001, Craig McClure personal communication). A similar control approach is used by the Gallatin NF and Gallatin County. Bio-control agents have been released in Gallatin NF during the last 2 decades (Susan LaMont personal communication), and some have dispersed into *L. vulgaris* patches inside Yellowstone NP (Olliff et al. 2001). Even so, *L. vulgaris* expansion continues, especially in isolated areas of the southern corner of Yellowstone National Park (Whipple 2001).

Our multi-scale method enhances understanding of invasion processes in complex natural landscapes by integrating coarse-scale phenomena (e.g., dispersal and disturbance effects) with fine-scale phenomena (e.g., invader population dynamics and native species response). This multi-scale approach may lead to more successful and efficient management of alien invasions in natural areas.

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