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# Spotted Knapweed in Natural Area Fescue Grasslands: An Ecological Assessment

## Abstract

Spotted knapweed (*Centaurea maculosa*) is an introduced species to the Pacific Northwest, and competitor with native species. This study assessed 1) the capability of spotted knapweed to invade fescue grasslands in Glacier National Park (USA) and 2) the effects of spotted knapweed on these indigenous communities. Transects were established in roadside areas and adjoining grassland communities on three sites from 1984-87. Spotted knapweed stem densities, the occurrence of associated species, and spotted knapweed seed production were observed within quadrats along these transects. Seed production in roadside areas was relatively high, presumably facilitating knapweed invasion into adjacent grassland vegetation. Stem densities in transects along the outer areas of each colony increased significantly during the study, suggesting that spotted knapweed is capable of successfully expanding within the park's fescue grasslands. Species richness and the frequency of several species were inversely related to spotted knapweed stem density, suggesting that spotted knapweed invasion is capable of altering plant community composition. Though these trends should be evaluated over a longer time span and in other areas, there seems to be sufficient reason for concerrn about spotted knapweed's disruptive potential in natural area grassland communities in this region.

## Introduction

Spotted knapweed (Asteraceae: *Centaurea maculosa* Lam.) is an Eurasian species common in a number of rangeland areas of the Pacific Northwest. It apparently was introduced into this region around 1900 and now occupies over 800,000 ha in Montana alone (French and Lacey 1983). Reported negative effects exerted by spotted knapweed and a closely related species, diffuse knapweed (*C. diffusa*), include allelopathic suppression of seed germination and seedling growth (Fletcher and Renney 1963, Muir and Majak 1983, Kelsey and Locken 1987, but see also Locken and Kelsey 1987), reduced forage yield (Watson and Renney 1974, Myers and Berube 1983), and possible increased soil erosion from displacement of perennial grasses (French and Lacey 1983).

Spotted knapweed is capable of vegetative reproduction, though lateral shoots do not become detached from the parent root stock (Watson and Renney 1974). Colony expansion is thus dependent on seed dispersal and is facilitated by substrate disturbance and excessive livestock grazing (Watson and Renney 1974, French and Lacey 1983). As is the case for other alien species in western Montana (Forcella and Harvey 1983), roadside habitats appear to be especially suitable for spotted knapweed colonization (French and Lacey 1983; Tyser, personal observation).

Spotted knapweed is usually studied from an agricultural perspective (e.g., Watson and Renney 1974, Shirman 1981, Myers and Berube 1983). There is reason, however, to be concerned about its occurrence in natural area grasslands, that is, grasslands protected from agricultural use and significant human disturbance (Weaver and Woods 1985). Invasion of diffuse knapweed may be reduced in areas seeded with grass (e.g. *Agropyron cristatum*), though the extent of this reduction appears to be affected by grass species and precipitation (Berube and Myers 1982). These observations raise the possibility that natural area grassland communities, if not disturbed by humans or livestock, may successfully resist spotted knapweed invasion.

The present study considers the invasive potential of spotted knapweed in grasslands dominated by *Festuca scabrella* and *F. idahoensis* in the St. Mary area of Glacier National Park, USA. Prior to establishment of Going-to-the-Sun Highway in the mid-1930's, these areas were likely subjected to some degree of grazing from pack horses used in touring the park. Trespassing livestock, primarily cattle, are occasionally sighted in these grasslands, but apparently exert minimal impact (Clifton 1977). Because of limited livestock grazing and restricted human-related substrate disturbance (e.g. road and trail construction), these grasslands have been subjected to relatively little human disturbance since the park was established in 1910.

Spotted knapweed was first observed in the park in the mid-1960's (R. Wassem, personal communication). It is now widely distributed in the park, but is primarily restricted to roadside areas. In several locations, however, spotted knapweed colonies have expanded from the roadside into the edge of adjacent fescue grasslands (Weaver and Woods 1985; Tyser, personal observation). While no federally listed rare, threatened, or endangered species are known to occur in these grasslands (Lesica *et al.* 1984), the ultimate esthetic and biological impact of spotted knapweed on these areas is a legitimate concern.

This investigation, which examined several locations where spotted knapweed occurred in the grassland-roadside ecotone, had two primary objectives: 1) to determine if spotted knapweed is capable of significant dispersal into Glacier's natural area fescue grasslands, and 2) to assess the potential effects that spotted knapweed has on the plant community composition of these grasslands.

## Methods

### Study Sites

Three sites were studied in Glacier National Park from 1984-87. Each of the sites was in Glacier's St. Mary valley region and consisted of spotted knapweed stands grading into grasslands dominated by native fescue species (*Festuca idahoensis* and *F. scabrella*). These grasslands are classified as short grass prairies (Kaul 1986) and are representative of the *F. scabrella/F. idahoensis* habitat type of Mueggler and Stewart (1980). Timothy (*Phleum pratense*), an alien Eurasian species, is widely distributed throughout the grasslands in this region and was common in each study site. Mean annual precipitation in this area is approximately 65 cm (Finklin 1986).

In two sites, the Triple Divide turnout ("TDT") and Two Dog Flats ("TDF") sites, spotted knapweed had dispersed about 10-20 m from the roadside ditch into grasslands bordering Going-to-the-Sun Highway. The sites were located about 5.5 km and 3.0 km, respectively, southwest of the St. Mary entrance station. With the exception of the roadside ditch bordering these sites and some substrate slumping associated with the roadbed cut in the TDT site, no human-related substrate disturbance was evident in either site. In addition to *Phleum pratense*, four relatively uncommon alien species (*Cirsium arvense, Poa pratensis, Taraxacum officinale,* and *Tragopogon dubius*) also occurred in the TDF site. The third site ("STM"), located approximately 0.5 km east of the St. Mary entrance station, was adjacent to the intersection of an access road with Going-to-the-Sun Highway. The substrate in the central part of this site had been disturbed by sewer line construction in 1980 (J. Vekasy, personal communication).

### Sampling Procedures

Transects (40-50 m in length) were placed in three locations within each site: 1) in the center of the spotted knapweed colony ("core" transects), 2) 1-2 m immediately inside the colony perimeter ("fringe" transects), and 3) parallel to the fringe transect along the perimeter of the colony ("perimeter" transects). Permanent stakes allowed consistent placement of transects within each site from year to year. In addition, roadside transects were established between the core transect and the road in the TDT and in TDF sites. Spotted knapweed stem densities were determined each year in 20 x 50 cm (0.1 $m^2$) quadrats placed at 0.5 or 1.0 m intervals along these transects. Because multiple stems may be produced from the root crown of a single spotted knapweed genet (Watson and Renney 1974), stem density can not be considered as an estimator of population density.

Spotted knapweed stems were collected along the roadside and core transects at the TDF site in late August in 1984 and 1985 and at TDT site in 1985. Collections were made after flowering was completed, but before opening of seed head bracts. Estimates of seed production densities along these transects were calculated by multiplying stem density x seed heads/stem x seeds/seed head (Schirman 1981).

The occurrence of vascular species (excluding *Carex* spp.) was noted in the core, fringe, and perimeter quadrats at the TDF site, but not at the TDT or STM sites. Frequencies of individual species, defined as the percent of quadrats in which a species was observed, were determined each year. Species frequency categories were designated as follows: common species (species occurring in > 50 percent of the quadrats), uncommon species (species occurring in 5-50 percent of the quadrats, and rare species (species occurring in < 5 percent of the quadrats). Species nomenclature follows Hitchcock and Cronquist (1973).

In 1987 the percent surface area of recently disturbed soil (loose, unvegetated soil) was estimated along each transect in the three study sites. Presence or absence of recently disturbed soil was noted at three points at 0.5 m intervals: one point on each 0.5 m transect mark and two points 0.25 m perpendicular to each 0.5 m mark.

### Statistical Analysis

Linear regression slopes were calculated and statistically evaluated to assess 1) yearly trends in spotted knapweed stem densities at each site, 2) yearly trends in species richness at the TDF site, and 3) the relationship between spotted knapweed stem density and number of non-knapweed species per quadrat at the TDF site. Stem densities in a number of transects were non-normally distributed and could not be transformed by standard logarithmic or square root transformations. Therefore, stem densities were rank-transformed and the ranks were evaluated by linear regression (Conover and Iman 1981).

Two-way analysis of variance was used to analyze species richness patterns with respect to two factors: transect location (three levels: core, fringe and perimeter) and year (four levels). The Newman-Keuls test was used to determine differences between the means of each level for each factor found to be significant (Zar 1984). Core versus perimeter frequencies of individual species were compared using 2 x 2 contingency tables analyzed with the Fisher exact test. This test was used rather than the chi-square or the G-test because it is preferable when cell frequencies are small (Zar 1984: 65), which was the case for a number of species. Between transect differences in number of points hitting disturbed soil were compared using chi-square.

## Results

### Stem Densities

Spotted knapweed densities increased significantly from 1984-87 in each of the fringe and perimeter transects at the three study sites (Figure 1). Even in the colony core areas, where knapweed stem densities were highest and presumably closest to equilibrium levels, densities increased in two of the three study sites (the TDT and STM sites). Spotted knapweed colony fronts at the study sites advanced less than 10 m during the study. However, it is likely that seed dispersal exceeded this distance.

The mean stem densities in the colony core areas for the TDT, TDF, and STM knapweed colonies in 1987 were 7.1, 7.6, and 6.6 stems/0.1 $m^2$, respectively. Though it is difficult to predict what density spotted knapweed is capable of attaining in these grasslands, these data suggest that equilibrium stem densities exceed 7.0 stems/0.1 $m^2$.

### Seed Production Estimates

Seed production estimates from stems collected along the core and roadside transects at the TDF site in 1984 and 1985 are summarized in Table 1. Unmowed roadside knapweed plants were notably larger and produced more seed heads per stem compared to mowed plants. However, after mowing in June 1985, spotted knapweed plants produced an increased number of relatively small lateral stems which offset the fewer number of seed heads per stem (Table 1). As a result, calculated seed production along the roadside transect was fairly constant in both years, and was significantly higher than that along the core transect. Similar results were noted at the TDT site, where seed production in 1985 was calculated as 881 and 2,471 seeds/0.1 $m^2$ in the core and roadside quadrats, respectively.

### Species Richness Observations (TDF Site)

Species richness patterns at TDF showed significant between-transect and between-year differences (Table 2). Transect species richness means differ significantly from one another (perimeter > fringe > core; Newman-Keuls test, $p < 0.05$), indicating the presence of a spatial species richness gradient which is inversely related

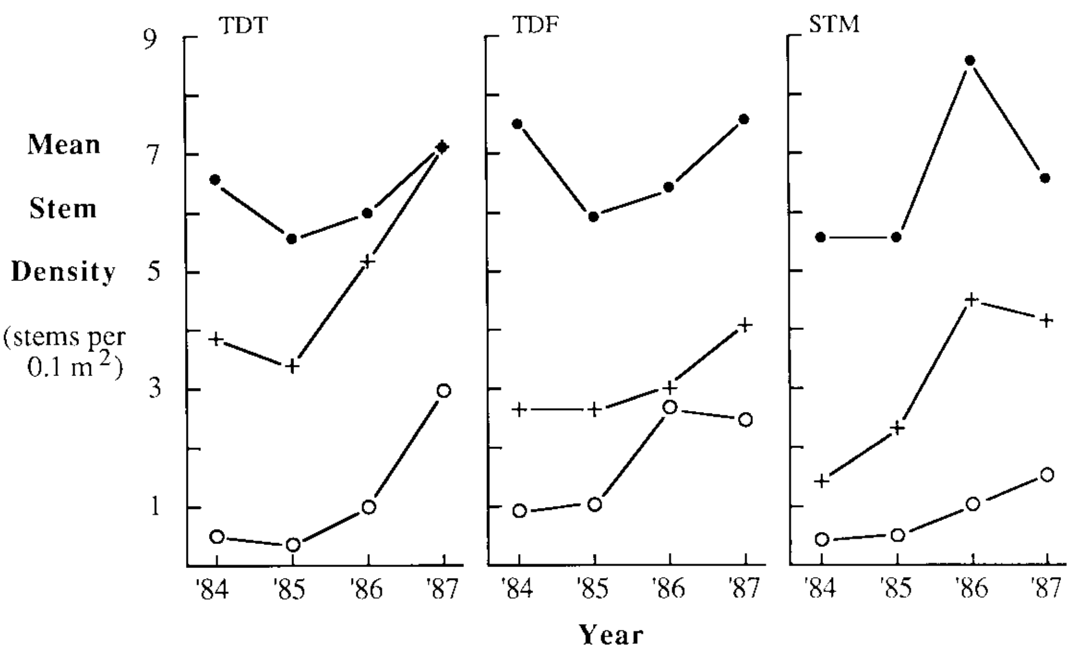


Figure 1. Trends in spotted knapweed stem densities in the core (•), fringe (+), and perimeter (o) transects in the three study sites (TDT, TDF, STM). With the exception of the TDF core transect, stem densities increased significantly (linear regression slopes $\neq 0.0$, $p < 0.05$) along each transect from 1984-87.

TABLE 1. Comparison of spotted knapweed seed production in the core area of the Two Dog Flats site versus the adjacent roadside. Number of observations—seed heads dissected, stems collected, and quadrats examined—are indicated in parentheses.

| | Core Area | | Roadside | |
|---|---|---|---|---|
| | 1984 | 1985 | 1984 | 1985[a] |
| $\bar{X}$ seeds/seed head | 23.5 (106) | 29.1 (144) | 25.4 (364) | 28.5 (309) |
| $\bar{X}$ seed heads/stem | 4.8 (51) | 4.7 (50) | 16.9 (51) | 5.2 (50) |
| $\bar{X}$ stems/0.1 m² | 5.6 (41) | 5.9 (41) | 8.7 (41) | 16.0 (41) |
| Calculated seeds/0.1 m² | 846 | 806 | 3,734 | 2,629 |

[a]Transect mowed in June 1985

TABLE 2. Species richness (mean number of species—excluding spotted knapweed and *Carex* spp.—per 0.1 m² quadrat) patterns in the TDF knapweed colony. Species richness varied significantly with respect to both location and year (two-way ANOVA, $p < 0.05$).

| Transect Location | 1984 | 1985 | 1986 | 1987 | Transect Mean | Number of Quadrats |
|---|---|---|---|---|---|---|
| Core | 6.5 | 6.9 | 6.3 | 6.4 | 6.5 | 41 |
| Fringe | 7.6 | 8.1 | 7.3 | 7.0 | 7.5 | 46 |
| Perimeter | 8.6 | 8.9 | 8.4 | 8.3 | 8.6 | 50 |
| Yearly Mean | 7.7 | 8.0 | 7.4 | 7.3 | | |

to spotted knapweed stem density. In addition, linear regression using the 1987 TDF observations indicated a highly significant negative relationship between knapweed stem density and number of non-knapweed species per quadrat: $y = 8.01 - 0.16x$, where y = number of non-knapweed species/quadrat and x = number of spotted knapweed stems/quadrat (slope $\neq 0.0$, $t_{135df} = 4.526$, $p < 0.001$). Except for the clear association with spotted knapweed stem densities, no other prominent environmental correlate appeared to be associated with this species richness gradient. For example, no significant between-transect differences in substrate disturbance were observed (see below).

Comparable analysis of the differences in yearly species richness means show less prominent patterns, though 1985 values were significantly higher than the 1984 and 1986-87 values (Newman-Keuls test, $p<0.05$). In addition, regression analyses suggest that no significant changes in species richness occurred within either the core or perimeter quadrats from 1984-87. However, a small, but significant, decline in species richness occurred in the fringe quadrats (regression slope $= -0.28$, $t_{182df} = 2.073$, $p < 0.05$) during this period.

## Species Frequency Patterns (TDF Site)

*Alien Species.* Spotted knapweed frequencies were relatively high at the TDF site, with mean yearly frequencies of 99.4, 82.6, and 74.0 percent in the core, fringe and perimeter quadrats, respectively. In addition to spotted knapweed, three other alien species (*Phleum pratense, Poa pratensis,* and *Tragopogon dubius*) were observed in the TDF quadrats. Mean yearly frequencies of *P. pratensis* and *T. dubius* were relatively low (*P. pratensis:* 11.6, 0.5, and 6.0 percent, *T. dubius*: 0.6, 5.4, and 6.5 percent for the core, fringe, and perimeter transects, respectively). Mean yearly frequencies of *P. pratense* were relatively high (68.3, 85.9, and 82.5 percent for the core, fringe, and perimeter transects, respectively).

*Frequency Patterns in the Fringe Transect.* Comparison of 1984 and 1987 fringe transect frequencies (Figure 2) reveals changes associated with the species richness decline noted earlier for this transect. Of the 38 species observed in the fringe quadrats in 1984, 31 were reclassified at the same frequency level in 1987. However, 7 of the original 38 species were reclassified into lower frequency categories in 1987 (*Galium boreale, Hieracium umbellatum, Potentilla*

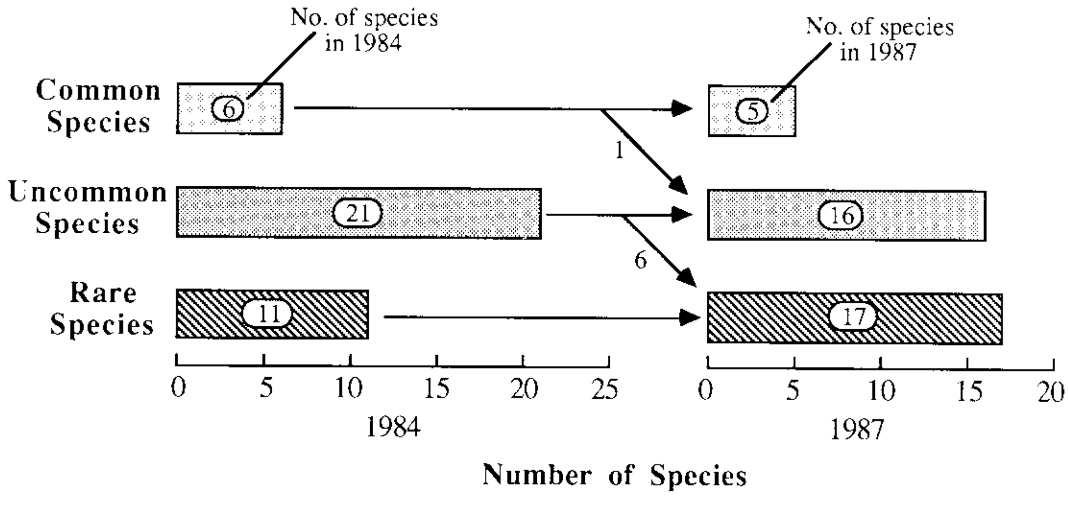


Figure 2. Number of species in three frequency categories in the 1984 versus 1987 fringe transect. Of the seven frequency category changes which occurred, each was from a higher to a lower category. For example, of the 21 species classified as "uncommon" in 1984, six were reclassified as "rare" in 1987. (Common, uncommon, and rare species occurred in >50%, 5-50%, and <5%, respectively, of the fringe quadrats.)

arguta, Potentilla gracilis, Silene parryi, Stipa occidentalis,* and *Tragopogon dubius*). No species were reclassified into higher frequency classes.

In addition, five "rare" species (*Agropyron spicatum, Castilleja cusickii, Collomia linearis, Heuchera cylindrica,* and *Lithospermum ruderale*) and two "uncommon" species seen in 1984 (*Stipa occidentalis* and *Tragopogon dubius*) were not observed in any of the fringe quadrats in 1987. By comparison, only one species (*Poa pratensis*) was observed in the fringe quadrats in 1987 which was not observed in 1984. Thus, the decline in species richness which occurred in the fringe area of the TDF knapweed colony is consistent with changes observed in frequencies of individual species.

*Core versus Perimeter Frequency Comparisons.* If spotted knapweed affects native species, the frequencies of affected species may differ between quadrats with high knapweed stem densities (core quadrats) and quadrats with low knapweed stem densities (perimeter quadrats). Core versus perimeter comparisons at the TDF site indicate that frequencies of four to seven native species showed significant differences each year (Table 3).

In all but three instances (*Berberis repens* in 1984 and 1985, and *Rosa* spp. in 1984), species showing significant differences were more frequent in the perimeter transect than the core transect. Interestingly, in two instances the frequencies of alien species (*Tragopogon dubius* in 1984 and *Phleum pratense* in 1986) were significantly higher in the perimeter quadrats than in the core quadrats, suggesting that spotted knapweed may also negatively affect the distribution of other alien species.

Only two of the species listed in Table 3, *Festuca idahoensis* and *Phleum pratense*, were common (frequency >50%) in the perimeter transect during each year of the study. Hence, most of the differences summarized in Table 3 pertain to species which were either uncommon or rare. Four other species (*Achillea millefolium, Cerastium arvense, Festuca scabrella,* and *Galium boreale*) were also common in the perimeter transect. With the exception of *Galium boreale* in 1987, frequencies of each of these species were higher in the perimeter transect than in the core transect, though these differences were not significant (Fisher exact test, $p > 0.05$).

## Substrate Disturbance Observations

A significant proportion of substrate surface consisted of recently disturbed soil at each site. The percent coverage of disturbed soil was quite similar along each transect at the TDF site (9.4, 8.2, and 7.8 percent for the core, fringe, and perimeter transects, respectively) and showed no significant between-transect differences ($\chi^2_{2df} = 0.47$, $p > 0.75$). Corresponding observations at the other two sites were 20.4, 8.7, and 9.6 percent (TDT site), and 4.2, 11.1, and 5.0 percent (STM site). The relatively large proportion of disturbed soil in the TDT core area apparently resulted from slumping associated with the roadbed cut. Otherwise, recent soil disturbance in the three sites resulted from occasional Columbian

TABLE 3. Year-by-year listing of species showing significantly different (Fisher exact test, $p < 0.05$) core versus perimeter frequencies at the TDF site. The species listed represent 9.5 – 16.7% of the total number of species observed per year in the two transects. Except as indicated,[a] the frequency of each species was higher in perimeter quadrats than in core quadrats.

| 1984 | 1985 | 1986 | 1987 |
|---|---|---|---|
| *Berberis repens*[a] | *Berberis repens*[a] | *Agoseris glauca* | *Festuca idahoensis* |
| *Campanula rotundifolia* | *Festuca idahoensis* | *Lupinus sericeus* | *Koeleria cristata* |
| *Festuca idahoensis* | *Gaillardia aristata* | *Festuca idahoensis* | *Lupinus sericeus* |
| *Gaillardia aristata* | *Koeleria cristata* | *Phleum pratense* | *Solidago missouriensis* |
| *Lupinus sericeus* | *Lupinus sericeus* | *Potentilla gracilis* | |
| *Rosa* spp.[a] | *Stipa occidentalis* | | |
| *Tragopogon dubius* | *Lomatium triternatum* | | |

ground squirrel (*Spermophilus columbianus*) burrow diggings and other disturbances, presumably from ground squirrel or wintering elk foraging activities. Old, apparently abandoned, Columbian ground squirrel and badger (*Taxidea taxus*) burrows were also present at the study sites. In several instances, relatively high spotted knapweed stem densities occurred on excavations associated with these burrows.

In addition, two small isolated spotted knapweed stands were observed on ground squirrel burrow mounds at the TDF site which were >100 m from the nearest knapweed colony. It is possible that these disjunct colonies resulted from seed heads transported by Columbian ground squirrels (see also Mittelbach and Gross 1984).

## Discussion

This study suggests that spotted knapweed in Glacier National Park is capable of i) colonizing fescue grasslands adjacent to roadside knapweed populations, and ii) subsequent dispersal within these grasslands. Roadside populations appear to have relatively high levels of seed production (Table 1 and Schirman 1981), which presumably facilitates grassland colonization. Post-colonization dispersal of spotted knapweed within these grasslands may be characterized as a gradual, broad, frontal expansion along colony borders. Seedfall for this species occurs within 1 m of the parent plant, whereas diffuse knapweed plants break off at ground level and disperse seeds in a "tumble-weed" manner (Watson and Renney 1974). These differences in seed dispersal probably account for the relatively slow, gradual colony expansion noted for spotted knapweed in this study compared to the approximately 40 m/year rate of advance by diffuse knapweed observed by Myers and Berube (1983). However, animal-aided long-distance seed dispersal and subsequent establishment of disjunct spotted knapweed colonies appear to also occur.

The increase in spotted knapweed stem densities in the TDF fringe quadrats coincided with a decline in the frequency of some species (Figure 2) and a small, but significant decline in species richness in the same quadrats. These trends were consistent with a number of other observations, including the between-transect spatial patterns of species richness noted in Table 2, and the perimeter versus core frequency differences of various common and less common species summarized in Table 3. Parallel patterns were also observed in another grassland site studied in Glacier composed largely of *Agropyron caninum* and *Poa* spp. (Tyser, personal observation). While it is likely that additional contributing factors may exist, these observations strongly suggest that spotted knapweed is capable of altering the community composition of Glacier's fescue grasslands.

Although a number of significant questions remain (e.g., to what extent will spotted knapweed's expansion continue?), it is useful to consider what factors may contribute to spotted knapweed's apparent success in Glacier's fescue grasslands. One component of this success is spotted knapweed's presence in the park's roadside areas, which appears to precede dispersal into adjacent grasslands. Exotics are often well-represented in roadside plant communities (Frankel 1970, Forcella and Harvey 1983), including roadsides in natural areas such as Glacier and Teton National Parks (Weaver and Woods 1985, 1986). As with other exotics, spotted knapweed establishment appears to be facilitated by vehicle traffic and soil disturbance (Watson and Renney 1974, French and Lacey 1983) associated with road construction and maintenance activities.

Abiotic features intrinsic to grassland ecosystems may represent another component of spotted knapweed's apparent success in Glacier. Grasslands consist of open areas having frequent breaks in cover with relatively warm-dry climates. These climatic factors appear to facilitate invasion of a number of alien species introduced into North America (Lindsay 1955, Forcella and Harvey 1983, Weaver and Woods 1985, Baker 1986, Mooney *et al.* 1986), which are likely preadapted to these conditions (see also Mack 1986).

Natural biotic features characteristic of native grasslands may also facilitate alien dispersal into Glacier's grasslands. For example, mammal (e.g., *Spermophilus*) burrowing activities create microhabitats suitable for spotted knapweed colonization, and subsequent foraging activities appear to disperse knapweed seeds to such microhabitats. Native ungulates represent another possible contributing factor. Overgrazing by wintering elk (*Cervus elaphus*), which are reaching historically high levels in the park's

St. Mary valley grasslands (Martinka 1982 and personal communication), may reduce the competitive ability of native grassland species by selectively feeding on these species. Seeds or seed heads lodged in the fur of ungulates may also facilitate the dispersal of alien species.

In addition to the presence of such biotic factors, the obvious *absence* of other biotic factors (parasites, pathogens, etc.) likely contributes to the success of alien species such as spotted knapweed. Although concern about the introduction of biocontrol agents into North American natural areas is understandable, initial attempts at spotted knapweed biocontrol have met with some success (Harris 1980, Story and Nowierski 1984). Such introductions may reduce the competitive effectiveness of aliens such as spotted knapweed, thereby enhancing populations of indigenous species.

Because other natural area grasslands in this region are characterized by many of these biotic and abiotic features, it is reasonable to suspect that they may also be vulnerable to invasion by spotted knapweed. Few similar studies of natural area grasslands are available; however, spotted knapweed stem densities (5.1-5.9 stems/0.1 $m^2$) and seed production densities (ca. 880-960/0.1 $m^2$) reported for "ungrazed rangeland" in northern Idaho (Schirman 1981: site 11) are similar to those observed in the core areas in this study. Schirman's site, dominated by *Festuca idahoensis,* was located in a state park which had not been significantly disturbed for $>30$ years prior to his observations (Schirman, personal communication).

The rather short term nature of this present study (four years) and the general lack of comparable studies prohibit definitive conclusions, but there seems to be sufficient reason for concern about the potential effects of spotted knapweed in natural area grasslands of this region. While spotted knapweed control actions may raise legitimate concerns about potential disruption of native communities, we offer several general comments about management of spotted knapweed in natural areas.

Because establishment of this species appears to be commonly associated with human-related substrate disturbances (e.g., road construction and maintenance, laying underground cables, etc.), natural area managers should minimize the extent to which these disturbances are allowed to occur. In the event of such disturbances, we suggest using construction materials free of knapweed seed, encouraging rapid establishment of native plant cover, and immediate follow-up treatment of colonizing knapweed plants.

If spotted knapweed is already established in roadside areas or in native communities, various ongoing integrated management actions aimed at minimizing seed production (mowing, introduction of *Urophora* gall flies and other biocontrol agents, herbicide treatment, etc.) should be carefully considered. Mowing after bud formation but prior to seed production may be an effective method of reducing seed production. Studies by Harris (1980) show that *Urophora affinis* and *Urophora quadrifasciata* gall flies may also be helpful in reducing seed production, though not in reducing established spotted knapweed populations (Schirman 1981). Lacey *et al.* (1986) offer useful suggestions about herbicide control strategies.

In formulating management actions, natural area managers should consider key natural history features of spotted knapweed, including seed and pre-flowering rosette stage longevities. Ongoing observations of marked plants (Tyser, personal observation) suggest that spotted knapweed rosettes in this region are capable of persisting four years or longer before developing their initial floral stalk (see also Boggs and Story 1987). Studies of spotted knapweed seed longevity (Chicoine and Fay 1984; Fay, personal communication) suggest that seeds of this species can persist in excess of six years in the soil. We know of no observations of how mowing influences spotted knapweed mortality, but suspect the life span of mowed plants is multi-yeared. Each of these observations suggests that a successful spotted knapweed control strategy necessitates a sustained, site-specific commitment extending over a number of years.

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