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Authors: Tad Weaver, J. Lichthardt, and D. Gustafson

This is a published article that originally appeared in Proceedings - Symposium on whitebark pine ecosystems: ecology and management of a high mountain resource, USDA Forest Service General Tech Report INT-270 in 1990. The final version can be found at https://doi.org/10.2737/INT-GTR-270.

T Weaver, J Lichthardt, and D Gustafson 1990. Exotic invasion of timberline vegetation, northern Rocky Mountains USA. p208-213. Schmidt, Wyman C.; McDonald, Kathy J., compilers. 1990. Proceedings - Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-GTR-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 386 p.

EXOTIC INVASION OF TIMBERLINE VEGETATION, NORTHERN ROCKY MOUNTAINS, USA

T. Weaver
J. Lichthart
D. Gustafson

ABSTRACT

Thirty-five exotic species were found in vegetation characteristic of Northern Rocky Mountain timberlines. At least 20 percent were intentionally introduced along roadsides. The diversity of invading exotics declined from subalpine to alpine vegetation. While exotic diversity generally increased with increasing disturbance, severe trampling excluded some species from road-shoulder sites. The exotics of greatest concern to wildland managers are Phleum pratense *(timothy) and* Poa pratensis *(Kentucky bluegrass) because they establish widely, spread vigorously, and usually escape early detection. Control of any exotic should involve its eradication and simultaneous introduction of desirable competitors to minimize reinvasion.*

INTRODUCTION

Timberline in the Northern Rocky Mountains is usually bordered above by alpine vegetation (Bamberg and Major 1968; Johnson and Billings 1962) and below by either subalpine forests—often subalpine fir-whortleberry (*Abies lasiocarpa-Vaccinium scoparium*, Daubenmire and Daubenmire 1968; Pfister and others 1977)—or subalpine meadows—often Idaho fescue-wheatgrass (*Festuca idahoensis-Agropyron caninum*, Mueggler and Stewart 1980). Whitebark pine often occurs at and below timberline and tends to dominate on relatively dry sites (Arno and Weaver, this proceedings). Since vegetation tends to vary continuously along environmental gradients, we believe that our observations of exotic weed invasion of adjacent forest, meadow, and tundra vegetation types also will apply to most timberline and whitebark pine vegetation types with similar understories.

Our studies of exotic invasion of major vegetation types of the Northern Rocky Mountains have concentrated on two questions:

1. Which exotics are capable of invading each environmental zone—habitat type (HT, Daubenmire 1968, 1970)?

2. Within an environmental zone, how much disturbance is required for success of the exotic; that is, does the plant require continuous disturbance or can it invade even undisturbed vegetation?

METHODS

To determine which exotics can invade major environmental zones of the Northern Rocky Mountains (question 1), we listed those present in each of 16 environmental types (= habitat types, HT's) ranging from dry grasslands up through forests to the alpine (Weaver and others 1989). Three of these HT's are found at timberline (*Abies lasiocarpa-Vaccinium scoparium* forests, *Festuca idahoensis-Agropyron caninum* meadows, and alpine tundra; Weaver and others 1989) and therefore represent whitebark pine understories. We sampled only roadside sites because these have a high probability of inoculation; that is, species absences there are likely due to the physical-biological environment rather than lack of seed. Ten sites were examined in each environmental zone (HT). At each site the five disturbance conditions described below were examined to ensure that exotics specific to any disturbance condition were included. As it turned out, this site reconnaissance—which examined far larger areas—identified few exotics not found in specific plots used to answer our second question.

Knowledge of the environmental zones (HT's) an exotic can occupy does not reveal the degree to which the plant will dominate the HT considered; will it occupy only highly disturbed areas or will it spread to undisturbed vegetation? To determine the capacity of an exotic to spread (question 2), we sampled sites experiencing the range of disturbance conditions (DC's) expected in the HT: constant heavy disturbance, periodic light disturbance, one-time heavy disturbance followed by primary succession, one-time light disturbance followed by secondary succession, and no disturbance. These DC's appear at roadsides in the form of shoulder, ditch slope, cutbank, logged right-of-way, and undisturbed vegetation of our National Parks, respectively. Exotic dominance was sampled in each DC in a 0.5- by 25-m macroplot running parallel to the road. Presence was recorded in each macroplot for plot constancy calculations; constancy indicates regional ubiquity and is calculated as the percent of the 10 sites in an environmental zone and across all disturbance conditions (HT) or a disturbance zone within

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

T. Weaver is Plant Ecologist and J. Lichthart and D. Gustafson are Ecologists, Department of Biology, Montana State University, Bozeman, MT 59717.

an environmental zone (HT-DC) occupied by the plant. Presence was also recorded in five 0.5- by 5-m subplots for frequency calculations; frequency indicates local ubiquity and is measured, for example, as the percent of five subplots in a macroplot occupied by the species. Cover was measured with 75 points lowered along the centerline of the macroplot; it indicates the degree to which the ground surface is covered by a particular species.

PRESENCE BY HABITAT

Our studies of vegetation above and below timberline suggest that 34 exotic species tolerate timberline environments of the Northern Rocky Mountains and show that these species differ considerably in the consistency of their presence among sites in an environmental type (constancy; table 1, column 2). Exotic diversity (richness)

Table 1—Constancy and infected site frequency of exotic species in three environmental types and five disturbance conditions. The species are listed in approximate order of their abilities to invade closed vegetation

	Constancy[2]	Disturbance condition[3] (infected site frequencies > 20 percent)				
Exotic species[1]	F.M.A.	Shoulder-constantly	Ditch-periodic	Roadcut-once (1°)	Logged-once (2°)	Climax-never dist.
Phleum pratense	99.99.36	FM	FM	FM		M
Poa pratensis	99.99.00	FM	FM	FM	F	M
Polygonum aviculare	60.60.00	FM	FM		F	M
Taraxacum officinale	99.99.91	FMA	FMA	FM	F	M
Descurainia pinnata	00.50.00		M	M		M
Festuca rubra	00.00.09					A
Madia glomerata	60.50.00	FM	FM	FM	F	
Lychnis alba	10.00.00			F		
Thlaspi arvense	00.10.00			M		
Tragopogon dubius	10.10.00		M	F		
Trifolium hybridum	99.90.00	FM	FM	FM		
Trifolium repens	90.30.00	FM	F	M		
Agrostis alba	60.40.00	FMA	FM	F		
Bromus inermis	50.99.36	FMA	FM	F		
Dactylis glomerata	50.00.00	F	F	F		
Matricaria matricari.	60.20.00	FM	FM	M		
Medicago lupulina	80.60.00	FM	FM	F		
Melilotus officinalis	40.70.00	F	FM	F		
Agropyron repens	30.00.00	F	F			
Arabis glabra	20.00.00	F	F			
Festuca pratensis	30.10.09	A	FM			
Plantago major	20.00.00	F	F			
Poa compressa	20.50.27	MA	FM			
Cirsium arvense	10.00.00		F			
Cirsium vulgare	10.00.00		F			
Lactuca serriola	10.00.00		F			
Medicago sativa	10.00.00		F			
Rumex crispus	20.00.00		F			
Tanacetum vulgaris	10.00.00		F			
Capsella bursa-past.	30.00.00	M				
Verbascum thapsus	10.00.00	F				
Alyssum alyssoides	20.00.00					
Rumex acetosella	00.00.36					
Trifolium pratense	20.00.00					

[1]Column 1 lists all exotics found in three HT's—a forest (F = *Abies lasiocarpa-Vaccinium scoparium*, Pfister and others 1977), a subalpine meadow (M = *Festuca idahoensis-Agropyron caninum*, Mueggler and Stewart 1980), and alpine tundra (Johnson and Billings 1962). Eleven alpine sites were sampled along the Beartooth Highway; 10 mountain meadows and 10 subalpine fir forests were sampled in and around Grand Teton National Park. Nomenclature follows Hitchcock and Cronquist (1973); abbreviated names are *C. bursa-pastoris* and *M. matricarioides*.

[2]Column 2 gives the constancy of each species in the forest (F), meadow (M), and alpine tundra (A) environments; that is, the percent of sites at which the exotic species was present in the area encompassed by five 0.5- by 25-m plots, one in each disturbance zone. In two cases a species, not present in the plots, was recorded outside; site constancies were slightly higher than plot constancies in these cases: *Taraxacum* 99.99.99 and *Bromus inermis* 50.99.45. Column 2 can be summarized by counting numbers of present exotics (cn > 10 percent, 30.17.07), common exotics (cn > 30 percent, 13.12.04), and universal exotics (cn > 30 percent, 05.05.01) in the forest, meadow, and alpine environments, respectively.

[3]Columns 3 through 7 indicate the disturbance conditions where, at infected sites, the species had a frequency higher than 20 percent; that is, the species occurred in more than 20 percent of the 1- by 5-m plots sampled at infected sites in that disturbance condition. The disturbance conditions considered include undisturbed (Climax-never dist.), secondary succession on cleared right-of-way (Logged once (2°)), primary succession on roadcuts (Roadcut-once (1°)), periodically disturbed ditch slope (Ditch-periodic), and constantly disturbed road shoulder (Shoulder-constantly). The environments where the frequency exceeded 20 percent are indicated by F (forest), M (meadow), and A (alpine tundra).

declines from 30 species in subalpine forests to 17 species in subalpine meadows, to seven species in alpine tundra. Wildland managers should notice that 20 to 30 percent of the high-frequency exotics (table 1, columns 3 through 7) have been intentionally introduced in roadside seedings.

Vaccinium scoparium (whortleberry) dominates the understories of the major forest habitats, such as *Abies lasiocarpa-Vaccinium scoparium, Pinus albicaulis-Vaccinium scoparium, Abies lasiocarpa-Pinus albicaulis-Vaccinium scoparium* (Pfister and others 1977). In this vegetation we found 30 exotic associates, of which 13 occurred in over 30 percent of the stands and five occurred in over 80 percent of the stands (table 1).

Festuca idahoensis-Agropyron caninum meadows occupy drier sites in the subalpine zone and serve as an understory in *Pinus albicaulis-Festuca idahoensis* woodlands. These meadows contained 17 exotic species, of which 12 occurred at over 30 percent of the sites, five occurred at over 80 percent of the sites, and only two—*Descurainia pinnata* (tansey mustard) and *Thlaspi arvense* (pennycress)—were not observed as colonizers in whortleberry understories (table 1).

Alpine vegetation appears around and among trees—whitebark pine (*Pinus albicaulis*), subalpine fir, and Engelmann spruce (*Picea engelmannii*) at upper timberline. In this vegetation we found seven exotic species, of which four appeared in over 30 percent of the stands, one appeared in over 80 percent of the stands, and only two, *Festuca rubra* (red fescue) and *Rumex acetosella* (sheep sorrel), were not observed in whortleberry understories (table 1).

PRESENCE BY DISTURBANCE CONDITION

Exotic species that invade undisturbed climax vegetation are of greatest concern to managers opposed to the modification of natural vegetation. We recorded no exotic colonization of forests with undisturbed whortleberry understories (table 2); the absence of exotics in closed forest stands is probably due to the high sun requirements of the plants introduced. Six exotic species were present in over 30 percent of the meadow sites occupied by the exotic species (table 3). Three species, *Festuca rubra, Poa compressa* (Canada bluegrass), and *Taraxacum officinale* (dandelion), were present in over 30 percent of the occupied alpine sites (table 4). Most of these colonizers had frequencies over 20 percent; that is, they occurred in over 20 percent of the 0.5- by 5-m quadrats sampled. Throughout this section, and in tables 2, 3, and 4, disturbed site constancy is expressed on the basis of infected sites because our object is to express the capacity of species present to invade variously disturbed zones. If readers want to calculate conventional constancies they can use disturbed site constancy and total constancy (from table 1) to do so; for example, if the disturbed site infected-constancy were 50 percent and the total constancy were 50 percent the disturbed site total-constancy would be 25 percent.

Exotic species that colonize secondary succession sites such as logged or burned sites are also of concern because large areas are involved and their dominance might slow succession. Of 13 invaders found on logged *Abies lasiocarpa-Vaccinium scoparium* sites, six had constancies over 30 percent and four had frequencies of 20 percent or more (table 2). While this disturbance condition does not exist in meadow and alpine sites, it exists potentially (unstudied) in high-altitude whitebark or limber pine (*Pinus flexilis*) woodlands.

Topsoil removal leading to primary succession, while less common than the community destruction considered above, does occur on roadcuts, riverbanks, and landslides. Fourteen, 10, and two exotic species had constancies over 30 percent on roadcuts in forest, meadow, and alpine zones respectively (tables 2, 3, and 4). Sixteen species had frequencies of over 20 percent on primary succession sites in at least one environmental type (table 1). Two exotics—*Lychnis* (campion) and *Thlaspi* (pennycress)—that were restricted to primary succession sites in our sample are known to occupy repeatedly disturbed sites elsewhere.

Ditch slopes are periodically influenced by humans; they may be mowed, watered, sanded, lightly compacted, sprayed with herbicide, or salted. Twenty-eight, 13, and four species had constancies over 30 percent on infected sites in forest, meadow, and alpine respectively (tables 2, 3, and 4). Infected site frequencies of 20 percent or more were observed for 20 species in this disturbance condition (table 1).

Road shoulders are constantly disturbed by people with heavy trampling, mowing, watering, sanding, heavy compaction, herbicides, or salt. Twenty-two, 15, and six species had constancies over 30 percent on infected sites in forest, meadow, and alpine zones, respectively (tables 2, 3, and 4). Infected site frequencies over 20 percent were observed for 21 species in this disturbance condition (table 1).

Numbers and frequencies of species generally increase as one moves from undisturbed to regularly disturbed sites (right to left in tables 1 to 4). We believe such increases occur primarily because resources are more available to individuals on more disturbed sites—both because competition is increasingly reduced and because supplements, especially runoff water, begin to appear. Diversity increases might also be due to a constant reintroduction of species, such as *Chenopodium album* (lambsquarter), which are unlikely to reproduce or spread away from the road. At timberline, half of the exotics such as *Plantago major* (broadleaf plantain) are restricted to high-resource, low-competition shoulder and ditch sites (table 2).

Due to the interaction of disturbance and trampling, the increase in species richness ceases when one moves to the road shoulder (tables 1 to 4). Further increases in water and sun, decreased competition, or continual introduction support the increase of several species such as *Capsella bursa-pastoris* (shepherdspurse), *Chenopodium album* (lambsquarter), and *Verbascum thapsas* (mullien).

Table 2—Exotic invasion of five disturbance zones in ABLA-VASC forests as indexed by percent constancy, percent frequency, and percent cover at infected sites. Blanks separated by periods indicate zeros

	Disturbance zone[1] and presence[2]				
	Shoulder-constantly	Ditch-periodic	Roadcut-once (1°)	Logged-once (2°)	Climax-never dist.
Exotic species[2]	cn fq cv	cn fq cv	cn fq cv	cn fq cv	cn fq cv
Verbascum thapsus	99.20. 0.	. . .	. . .	. . .	. . .
Agropyron repens	33.27. 2.	99.40. 5.	. . .	. . .	. . .
Alyssum alyssoides	50.10. 0.	50.10. 0.	. . .	. . .	. . .
Arabis glabra	99.20. 0.	99.30. 1.	. . .	. . .	. . .
Capsella bursa-past.	67.20. 0.	33. 7. 0.	. . .	. . .	. . .
Chenopodium album	50.10. 0.	50.10. 0.	. . .	. . .	. . .
Festuca pratensis	33.13. 0.	67.33. 2.	. . .	. . .	. . .
Matricaria matricari.	83.53. 1.	67.30. 2.	. . .	. . .	. . .
Plantago major	99.40. 1.	99.50. 1.	. . .	. . .	. . .
Cirsium arvense	. . .	99.40. 0.	. . .	. . .	. . .
Cirsium vulgare	. . .	99.20. 0.	. . .	. . .	. . .
Lactuca serriola	. . .	99.20. 0.	. . .	. . .	. . .
Medicago sativa	. . .	99.99.12.	. . .	. . .	. . .
Poa compressa	. . .	99.30. 1.	. . .	. . .	. . .
Rumex crispus	. . .	99.20. 1.	. . .	. . .	. . .
Tanacetum vulgare	. . .	99.20. 0.	. . .	. . .	. . .
Lychnis alba	. . .	. . .	99.40. 0.	. . .	. . .
Tragopogon dubius	. . .	. . .	99.20. 0.	. . .	. . .
Agrostis alba	99.53. 7.	83.57.13.	67.23. 0.	17. 7. 0.	. . .
Bromus inermis	99.64. 8.	80.60. 6.	80.56. 5.	60.16. 1.	. . .
Dactylis glomerata	99.48. 4.	99.48. 4.	40.28. 0.	20. 4. 0.	. . .
Madia glomerata	67.33. 1.	83.63. 4.	83.43. 1.	33.20. 0.	. . .
Medicago lupulina	63.55. 3.	75.50. 2.	50.30. 2.	13. 5. 0.	. . .
Melilotus officinalis	99.50. 2.	75.75. 5.	75.60.17.	25.15. 1.	. . .
Phleum pratense	90.82. 7.	90.68. 5.	80.50. 1.	30. 6. 0.	. . .
Poa pratensis	90.74.11	90.54. 3.	40.30. 1.	30.20. 0.	. . .
Polygonum aviculare	83.47. 2.	67.47. 2.	67.17. 0.	50.23. 0.	. . .
Taraxacum officinale	99.76. 5.	99.82. 4.	80.64 . 3.	80.48. 2.	. . .
Trifolium hybridum	80.54. 7.	60.58. 9.	80.60. 7.	40.16. 0.	. . .
Trifolium pratense	50.10. 0.	50.10. 0.	0. 0. 0.	50.10. 0.	. . .
Trifolium repens	44.31. 3.	89.62. 9.	44.18. 0.	11. 7. 0.	. . .

[1]Site and type of disturbance were: constantly and heavily disturbed road shoulder (Shoulder-constantly), periodically and lightly disturbed ditch (Ditch-periodic), once heavily disturbed with soil removal (Roadcut-once 1°), once moderately disturbed without soil removal (Logged-once 2°), and undisturbed climax (Climax-never dist.).

[2]Exotic presence at infected sites is reported with constancy (cn = percent of infected sites occupied), frequency (fq = percent of 0.5- by 5-m subsites occupied at infected sites), and cover (cv = percent of ground covered at infected sites). Data are based on 10 sites sampled in the Grand Teton National Park area.

Simultaneously, trampling at the road shoulder eliminates brittle-stemmed species such as *Cirsium* (thistle), *Lactuca* (lettuce), and *Tanacetum* (tansey) that would undoubtedly thrive in its absence. Species that do survive on roadshoulders seem to do so (Dale and Weaver 1974) via flexibility (as with grasses and clovers, especially bluegrass, timothy, clover, and sweetclover), stemless forms (such as plantain, dandelion, and mullien), creeping forms (such as knotweed), and avoiding destruction with short life cycles or growth in the off-season (as illustrated by rockcress and shepherdspurse).

MANAGEMENT

As noted above, the exotics of greatest concern are those capable of leaving the roadsides and invading little-disturbed or undisturbed native vegetation. For the upper forest and alpine zones these include *Phleum pratense* (timothy), *Poa pratensis* (Kentucky bluegrass), *Polygonum aviculare* (prostrate knotweed), *Taraxacum officinale* (dandelion), *Descurainia pinnata* (tansey mustard), and *Festuca rubra* (red fescue). *Phleum pratense* and *Poa*

Table 3—Exotic invasion of five disturbance zones in FEID-AGCA meadows as indexed by percent constancy, percent frequency, and percent cover at infected sites. Dashes indicate a nonexistent zone and blanks separated by periods indicate zeros

Exotic species[2]	Shoulder-constantly	Ditch-periodic	Roadcut-once (1°)	Logged-once (2°)	Climax-never dist.
	Disturbance zone[1] and presence[2]				
	cn fq cv	cn fq cv	cn fq cv	cn fq cv	cn fq cv
Chenopodium album	99.40. 0.	. . .	. . .	- - -	. . .
Agrostis alba	25.20. 1.	99.30. 1.	. . .	- - -	. . .
Bromus inermis	80.50. 4.	80.36. 2.	. . .	- - -	. . .
Festuca pratensis	. . .	99.40. 0.	. . .	- - -	. . .
Tragopogon dubius	. . .	99.20. 1.	. . .	- - -	. . .
Matricaria matricari.	50.30. 1.	50.30. 1.	50.20. 1.	- - -	. . .
Poa compressa	60.28. 2.	60.32. 2.	20. 4. 0.	- - -	. . .
Trifolium hybridum	78.44. 2.	78.60. 5.	67.24. 1.	- - -	. . .
Trifolium repens	67.27. 1.	33. 7. 0.	33.27. 1.	- - -	. . .
Thlaspi arvense	. . .	. . .	99.20. 0.	- - -	. . .
Descurainia pinnata	20.12. 0.	40.20. 1.	40.32. 1.	- - -	80.28. 1.
Madia glomerata	40.20. 0.	80.56. 1.	40.28. 0.	- - -	40.12. 0.
Melilotus officinalis	71.17. 1.	57.20. 0.	14.11. 0.	- - -	14. 6. 0.
Phleum pratense	60.32. 0.	99.60. 1.	70.40. 1.	- - -	60.30. 0.
Poa pratensis	90.76. 3.	90.68. 3.	70.40. 3.	- - -	50.22. 0.
Polygonum aviculare	33.20. 2.	83.40. 2.	0. 0. 0.	- - -	33.23. 0.
Taraxacum officinale	90.88. 7.	99.88. 5.	99.60. 1.	- - -	60.32. 0.

[1]Site and type of disturbance were: constantly and heavily disturbed road shoulder (Shoulder-constantly), periodically and lightly disturbed ditch (Ditch-periodic), once heavily disturbed with soil removal (Roadcut-once 1°) once moderately disturbed without soil removal (Logged-once 2°), and undisturbed climax (Climax-never dist.)
[2]Exotic presence at infected sites is reported with constancy (cn = percent of infected sites occupied), frequency (fq = percent of 0.5- by 5-m subsites occupied at infected sites), and cover (cv = percent of ground covered at infected sites). Data are based on 10 sites sampled in the Grand Teton National Park area.

Table 4—Exotic invasion of five disturbance zones in the alpine tundra environment, as indexed by percent constancy, percent frequency, and percent cover at infected sites. Dashes indicate a nonexistent zone and blanks separated by periods indicate zeros

Exotic species[2]	Shoulder-constantly	Ditch-periodic	Roadcut-once (1°)	Logged-once (2°)	Climax-never dist.
	Disturbance zone[1] and presence[2]				
	cn fq cv	cn fq cv	cn fq cv	cn fq cv	cn fq cv
Festuca pratensis	99.20. 0.	. . .	. . .	- - -	. . .
Bromus inermis	75.25. 0.	25. 5. 0.	. . .	- - -	. . .
Phleum pratense	50.10. 0.	50.10. 0.	25. 5. 0.	- - -	. . .
Poa compressa	67.40. 0.	33. 7. 0.	0. 0. 0.	- - -	33. 7. 0.
Taraxacum officinale	90.62. 1.	80.60. 1.	40.10. 0.	- - -	10. 2. 0.
Rumex acetosella	50. 5. 0.	50.15. 0.	25.15. 0.	- - -	75.15. 0.
Festuca rubra	. . .	. . .	99. 0. 0.	- - -	99.40. 0.

[1]Site and type of disturbance were: constantly and heavily disturbed road shoulder (Shoulder-constantly), periodically and lightly disturbed ditch (Ditch-periodic), once heavily disturbed with soil removal (Roadcut-once 1°) once moderately disturbed without soil removal (Logged-once 2°), and undisturbed climax (Climax-never dist.)
[2]Exotic presence at infected sites is reported with constancy (cn = percent of infected sites occupied), frequency (fq = percent of 0.5- by 5-m subsites occupied at infected sites), and cover (cv = percent of ground covered at infected sites). Data are based on 10 sites sampled in the Beartooth Plateau area.

pratensis are of special concern because they often dominate the areas they occupy. Because we sampled along long-established roads, we believe that most invaders that have occupied the region for long periods of time have been introduced, have been naturally tested, and are unlikely to invade further. Any plants currently establishing in the region, however (like, but probably not including leafy spurge [*Euphorbia esula*]), have not been tested naturally and could conceivably become important at timberline. While most new introductions fail to establish, some establish in limited areas and small numbers and, presumably after either a "fitting mutation" or some natural or human-caused environmental change, spread widely (Krebs 1985). Plants that have only established well on roadsides in timberline environments are of little concern in this vegetation zone (because they occupy little area and have been well tested for escape), but should perhaps be controlled if roadsides through this zone serve as corridors for invasion of other habitats. Control of any exotic species should involve both elimination and simultaneous introduction of a desirable competitor to minimize reinfection.

ACKNOWLEDGMENTS

The project was designed by T. Weaver; field sampling was done by B. Woods (below timberline) and J. Lichthart (above timberline); data analysis and interpretation are due primarily to T. Weaver and D. Gustafson. The field work was supported by National Park Service grant CX125-4-A038.

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