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T. Weaver

Montana State University, Bozeman

D. Gusafson

Montana State University, Bozeman

J. Lichthardt

Conservation Data Center, Idaho Department of Fish and Game, Boise

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EXOTIC PLANTS IN EARLY AND LATE SERAL VEGETATION OF FIFTEEN NORTHERN ROCKY MOUNTAIN ENVIRONMENTS (HTs)¹

T. Weaver^{2,4}, D. Gustafson², and J. Lichthardt³

ABSTRACT.—We determined the capacity of exotic plants to invade major environmental types of the northern Rocky Mountains. We did this by observing their presence on disturbed and undisturbed sites in relatively well inoculated locations—corridors adjacent to highways—on transects across the mountains in Glacier National Park and Grand Teton National Park and on low-altitude sites between them. We draw 3 primary conclusions. First, of 29 exotics commonly found, the most dominant are intentionally introduced grasses (*Agrostis*, *Bromus*, *Dactylis*, and especially *Phleum pratense* and *Poa pratensis*) and legumes (*Melilotus*, *Medicago*, and *Trifolium*) rather than the forbs more often listed as noxious. Second, in the environmental types studied, disturbed sites are invadable, except in the alpine. Third, invasion of undisturbed sites declines from grasslands and open forests to alpine to moist forests. This gradient probably represents a decline in resource (light, water, nutrients) availability for herbs, except in the alpine, where a physical limitation is suggested by the poor performance of exotics on noncompetitive disturbed sites.

Key words: exotic plants, aliens, weeds, *Phleum pratense*, *Poa pratensis*, *Bromus inermis*, *Bromus tectorum*, *Trifolium*, *Melilotus*, *Centaurea*, *Chrysanthemum leucanthemum*, *habitat types*, *environmental types*, *Bouteloua gracilis*, *Agropyron spicatum*, *Artemisia tridentata*, *Pseudotsuga menziesii*, *Abies lasiocarpa*, *mountain meadows*, *alpine*, *seral stages*, *disturbance*, *climax*, *northern Rocky Mountains*, *Grand Teton National Park*, *Glacier National Park*, *Yellowstone National Park*.

National forests and parks have a mandate to manage against exotic plants both in their charters (U.S. Congress 1872) and recent executive directives (Clinton 1994, 1999).

Management of exotics requires their identification. Plants exotic to specific regions (e.g., Whitson 1992) and management units (e.g., Whipple 2001) have often been listed to facilitate recognition and identification. A listing by ecological zones within a region would refine this capacity.

In addition, a listing by environmental types within a region would provide a key to environments (or sites) the plant might invade or might already have invaded. Identification of occupiable environmental types will enable managers to concentrate control efforts in a fraction of the management area. Two environmental qualities are important. First, one considers environmental types (defined in Methods), determined by physical characteristics such as climate and substrate (Holdridge 1947, Daubenmire 1968, 1970, Whittaker 1975) and indicated locally by potential natural vegetation (Pfister et al. 1977, Mueggler and Stewart

1980, Steele et al. 1983). And, within each of these, one compares sites on the competitive spectrum from freshly disturbed (noncompetitive) to late seral (very competitive; Grime 1979, Despain 1990).

The objectives of this paper are thus to list the common exotics of the northern Rocky Mountains, to provide separate lists of the exotics present in major upland environmental types of the region, and to compare exotic presence in an early (less competitive) and late (more competitive) seral stage in each environmental type. A companion paper extends our results to separately map the potential distribution of major exotics on disturbed and undisturbed sites in Yellowstone National Park (Despain et al. 2001).

METHODS

Our term *environmental type* is synonymous with Daubenmire's (1968a, 1968b, 1970) *habitat type* (HT). (1) An environmental type (ET = HT) includes all environments (equivalent, but not identical) capable of supporting a climax

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²Ecology Department, Montana State University, Bozeman, MT 59717.

³Conservation Data Center, Idaho Department of Fish and Game, Boise, ID 83707.

⁴Corresponding author.

association (series of plant communities of the same kind). (2) The concept is useful because it groups discrete sites (or environments as opposed to plant communities) likely to respond similarly to similar management (Daubenmire 1968b, 1976, Pfister et al. 1977, Mueggler and Stewart 1980). (3) The term *environmental type* is preferred because it clarifies the concept that the types represent physical environment (e.g., moisture and temperature) rather than habitat for a particular organism, since the latter “habitat type” may either extend across several environmental types (e.g., wide-ranging plants in Table 3) or may not exist in the organism’s optimal environmental type (e.g., if vegetation of the seral stage present provides too much competition [Walter 1960] or fails to provide necessary nutrients, cover, or structure). Daubenmire (personal communication) recognized the environmental type/habitat type confusion—especially among zoologists—and wished he had called his types “environmental types.”

To determine which exotics might invade a specific environmental type (e.g., a montane environment occupied by *Pseudotsuga menziesii/Symphoricarpos albus* at climax), we needed to observe exotic colonization of well-inoculated sites in that type. Thus, we sampled several (7–11) sites jointly in that type and near a major highway that has long delivered seed to it (Table 1).

To determine which “seral” vegetation types in that environmental type could be invaded, we needed to compare invasion of highly disturbed (low competition), less disturbed (early seral), and high competition (late seral) sites (Grime 1979) occupying that physical environment. Thus, we sampled relatively gentle road cuts, logged right-of-way (not reported here), and nearby undisturbed vegetation at each of the 7–11 sites studied. The fact that our work was primarily in national parks facilitated location of undisturbed sites adjacent to highly disturbed sites. The relatively low establishment of a species on a late seral site, perhaps 20–30 m away, is attributed to competition but could also be due to failure to disperse. We attribute most of the deficiency to competition, however, both because differences in distances from the highway are short and because dispersal is a characteristic selected for in opportunistic species.

To complete the list of exotics likely to invade our region, we needed to sample other major environmental types representative of the environmental gradient from steppe upward through forest to the alpine. Thus, we sampled 15 environmental types along highways crossing the mountains in Glacier and Grand Teton national parks (1984–1985) and in intervening lowland areas (in 1986). We identified major environmental types by using late seral vegetation as indicators (Holdridge 1947, Daubenmire 1968a, 1968b, 1970, Whittaker 1975). While our exotic lists for major environmental types approach completeness, our regional list is incomplete because we omitted less widespread types such as those along streams or on unusual substrates. The environmental types (HTs) sampled are listed, in altitudinal order, in Table 1, with abbreviations, general locations, and sample size (~10). Underlying changes in climate and soils along the gradient are compared in Table 2, as well as by Daubenmire (1968a, 1970), Pfister et al. (1977), Mueggler and Stewart (1980), and Steele et al. (1983).

Thus, our sample design included 15 environmental types (HTs), 2 treatments reported here (and 3 others [Weaver et al. 1993]), and approximately 10 replications (sites). Vegetational characteristics of each of the approximately 800 sites studied were recorded with measures of presence, frequency, and cover of both native and exotic species present. (1) Presence was recorded by listing all exotic and native plant species present in a 1 × 25-m plot representative of the zone and parallel to the highway traveled. We separately noted any other species present in adjacent similar vegetation. Natives in the plots, not discussed here, are listed in Weaver et al. (1993). (2) Cover of a species was measured by recording the percentage of 75 points covered by that species. The 75 points were located by lowering 3 pins into the vegetation in each meter point along the plot’s center line. Cover was integrated over a type by averaging cover measurements across sites, but only at sites where the species occurred. We omitted unoccupied plots in these calculations to measure the success of species at sites where they did occur. If desired, cover values for the environmental zone as a whole can be calculated by multiplying cover values presented by the associated *constancy value*; this will correct the cover

TABLE 1. Environmental types (HTs), locations, and sizes of samples in which exotic distributions were observed. Environmental types are listed in approximate order of altitude, from low to high.

Environmental type (HT) ^a	Abbreviation ^b	Location ^c	Sample ^d
GRASSLANDS/ SHRUBLANDS			
<i>Stipa comata</i> / <i>Bouteloua gracilis</i>	STCO/ BOGR	Broadwater MT	7
<i>Agropyron spicatum</i> / <i>Bouteloua gracilis</i>	AGSP/ BOGR	Broadwater MT	8
<i>Artemisia arbuscula</i> / <i>Festuca idahoensis</i>	ARAR/ FEID	Teton WY	10
<i>Artemisia tridentata</i> / <i>Festuca idahoensis</i>	ARTR/ FEID	Meagher, Gallatin MT	10
<i>Festuca scabrella</i> / <i>Festuca idahoensis</i>	FESC/ FEID	Glacier MT	10
DRY FORESTS			
<i>Pseudotsuga menziesii</i> / <i>Symphoricarpos albus</i>	PSME/ SYAL	Meagher, Gallatin MT	10
<i>Pseudotsuga menziesii</i> / <i>Physocarpus malvaceus</i>	PSME/ PHMA	Gallatin MT, Park WY	6
WARM MOIST FORESTS			
<i>Populus tremuloides</i> / <i>Calamagrostis rubescens</i>	POTR/ CARU	Flathead MT	8
<i>Tsuga heterophylla</i> / <i>Clintonia uniflora</i>	TSHE/ CLUN	Flathead MT	10
<i>Abies lasiocarpa</i> / <i>Clintonia uniflora</i>	ABLA/ CLUN	Flathead MT	9
<i>Abies lasiocarpa</i> / <i>Xeophyllum tenax</i>	ABLA/ XETE	Flathead MT	10
COOL CONIFER FORESTS			
<i>Abies lasiocarpa</i> / <i>Arnica cordifolia</i>	ABLA/ ARCO	Teton WY	10
<i>Abies lasiocarpa</i> / <i>Vaccinium scoparium</i>	ABLA/ VASC	Teton WY	10
HIGH GRASSLANDS AND TUNDRA			
<i>Festuca idahoensis</i> / <i>Agropyron caninum</i>	FEID/ AGCA	Teton WY	10
<i>Deschampsia caespitosa</i> / <i>Carex</i> spp.	DECA/ CASP	Park WY, Carbon MT	11

^aEnvironmental types are those of Pfister et al. (1977) and Meuggler and Stewart (1980).

^bAbbreviations provide a key to Table 3. They represent dominant species by reporting initial letters (2) from genus and species names.

^cLocations are specified by county. Glacier and Flathead are in the Glacier National Park area. Broadwater and Meagher are adjacent to the Bridger/Big Belt Mountains. Gallatin, Park, and Carbon are at the north edge of Yellowstone. Teton includes Grand Teton National Park.

^dEach environmental type was sampled at 7–11 sites. At each site 5 environments were sampled with 5 parallel quadrats. Of these, those representing roadcuts and undisturbed vegetation are discussed here.

value downward for sites at which the species did not occur (Table 3). (3) Constancy was calculated as the percentage of sites in the environmental type at which the species occurred.

We hypothesized that a strong presence of an exotic in roadside samples would result in a strong presence in adjacent undisturbed vegetation because a strong presence at the roadside indicates both good adaptation to the environment and production of many propagules for colonization of nearby sites. We tested this hypothesis, using both constancy and cover data, by comparing the presence of each exotic in disturbed vegetation on sites adjacent to occupied vs. unoccupied native vegetation. The Mann-Whitney test, a non-parametric *t* test, was used (Gibbons 1985). An alternative test, regression/correlation, was forgone because quantitative data from the undisturbed sites are currently unavailable.

In a companion paper (Despain et al. 2001), we map the potential range of an exotic in a region by using a map of the environmental types (HTs) of the region (e.g., Despain 1990b) as a base and shading ETs invisable by the species studied. We expect the range mapped

on disturbed sites to enclose the range on undisturbed sites because competition is less rigorous on disturbed sites.

RESULTS

Our observations of exotic plant presence on roadcuts (outslopes) and adjacent undisturbed vegetation of 15 environmental types are summarized in Table 3. (1) Vertically, table segments list groups of exotic species found, according to their ranges on the altitudinal gradient studied: those with narrow, moderate, or broad amplitude and those with an interrupted range. (2) The elevational gradient ranges from dry steppe, through warm dry forests, warm moist forests, cool forests, to mountain meadows and alpine tundra. Fifteen segments (environmental types or habitat types) on this gradient are listed horizontally. These are named and characterized in Table 1. (3) Entries in Table 3 specify the presence of exotics, both on disturbed sites in corridors along which propagules are expected to move and on adjacent undisturbed sites. Presence on roadsides is indicated by constancy (the percent of occupied

TABLE 2. Comparison of environments in major Rocky Mountain ecosystems. Standard errors, as well as additional data, are available in Weaver (1978, 1980, 1990, 1994).

Parameter	Temperatures (C) ^b			Water availability (mm) ^c				GS ^d mo
	Jan min	T _{gs} mean	July max	Pptn ann	Drt mo	HOH deficit	Soil WHC	
Alpine tundra ^a	-16	6	12	778	0	0	38	3.6
<i>Abies lasiocarpa</i>	-18	12	22	820	0	0	30	4.5
<i>Pseudotsuga menziesii</i>	-16	12	27	580	0	1	103	3.6
<i>Festuca idahoensis</i>	-12	12	27	380	1	6	101	5.1
<i>Agropyron spicatum</i>	-13	12	28	380	1	17	117	4.9
<i>Bouteloua gracilis</i>	-15	14	31	350	2	25	117	4.4

^aThe ecosystems compared range from alpine down through high forests (ABLA), low forests (PSME), and grasslands (FEID, AGSP, and BOGR). Each is named for its climax dominant vegetation and abbreviated with initial letters from its generic and specific epithets.

^bTemperatures (Weaver 1980, 1990) include average January minimum, growing season mean, and average July maximum.

^cWater data include annual precipitation, drought months, and annual water deficit (Weaver 1980, 1990, 1994), and water-holding capacity of the rooted zone (Weaver 1978), all in mm.

^dGrowing season months are defined as those with moist soils and average air temperature above 0°C (Weaver 1994).

sites in the ET). Potential dominance on those sites is indicated by cover (the average cover on sites which are occupied); and current realized success is found by multiplying these entries. Presence in undisturbed vegetation is reported nonquantitatively from plots of the same size and shape. The material in cells having constancies >30% is in boldface because a higher constancy indicates that the plant has established more or less regularly in that environmental type.

The 29 exotic plants occurring in >10% of the sites in at least one environmental type are listed (Table 3, vertically). Ten species have a narrow amplitude; i.e., they have a high constancy in only 1 or 2 types. Ten species have a moderate amplitude, that is, range over 4–8 environmental types, as arranged in Table 3. Four species have a broad amplitude, ranging over 10–14 ETs. The ranges of 5 species of moderate to broad distribution are interrupted; that is, they occupy low and higher sites, but not the intervening environments. Two types of occurrence deserve further comment. First, plants with low constancy in a single ET are ignored because they may occupy microsites in an environmental type; that is, they do not actually occupy the environmental type discussed. Alternatively, they could either be new to the region (Forcella and Harvey 1981) or be the vanguard of a newly adapted ecotype. Second, 7 environmental types contain a species which occurs on undisturbed, but not on non-competitive disturbed, sites. Such species could possibly require a stability not found at roadsides, e.g., lack of erosion or frost action. More likely, these species are “accidentals”; other-

wise this pattern would repeat in similar types, as it does for *Taraxacum*.

On disturbed sites the number of high-constancy (>30%) exotics (Fig. 1, Table 3) was 10–11 in grasslands, 9–12 in dry forests, and 8–10 in warm moist forests and 7–11 in cool forests. Numbers were lower in shrublands (5–7), mountain meadows (5), and alpine (1). Numbers of low-constancy exotics were 3–6 in grasslands, 5–11 in dry forests, 3–6 in warm moist forests, and 2–6 in cool forests. Low-constancy richness was similar in mountain shrublands (2–5) and mountain meadows (7), and low in alpine (2).

The number of exotics entering undisturbed sites (Fig. 1, Table 3) decreased from grasslands (9–13) through aspen forests (8) and shrublands (5–7) to conifer forests (0). It increased again in mountain meadows (7) and alpine tundra (2). While the richness (average number of species per sample) on undisturbed sites is always lower than on disturbed sites, most grassland ETs are occupied by at least one species not found on disturbed sites in it.

DISCUSSION

Exotics in the Northern Rocky Mountains

We found only 29 exotic species (Table 3) in our sample of major upland environmental types of Glacier National Park, Grand Teton National Park, and little disturbed intervening areas including parts of Yellowstone National Park. Our list does not include species that have invaded since 1986, which occupy heavily grazed areas or uncommon substrates. To

TABLE 3. Presence of major exotic species in major environmental types^a of the northern Rocky Mountains. Code digits^b indicate constancy and cover on disturbed sites and tendency to invade undisturbed vegetation. Constancies >30% are in boldface to emphasize environments where the species is common.

	STCO	AGSP	ARAR	ARTR	FESC	PSME	PSME	POTR	TSHE	ABLA	ABLA	ABLA	ABLA	ABLA	ABLA	FEID	DECA
	BOGR	BOGR	FEID	FEID	FEID	SYAL	PHMA	CARU	CLUN	CLUN	XETE	ARGO	VACC	AGCA	CARX		
SPECIES WITH NARROW AMPLITUDE																	
Agropyron cristatum	7CX ^b	X		1A													
Alyssum alyssoides	8AX	9BX			1AX		1A										
Camelina microcarpa	4AX	5AX				1A	X		1C								
Bromus japonicus	8BX	6AX				1A										2CX	
Descurainia pinnata	5AX	5AX															0A
Rumex acetosa			9DX	9D		1A				1A							
Dactylis glomerata			2B	3B		2BX	5EX		1A	1A		1B	2B				
Festuca pratensis						1A	5A										
Verbascum thapsus	2AX	1AX			2B		5B	1A									
Chrysanthemum leucanthemum									5B								
SPECIES WITH MODERATE AMPLITUDE																	
Tragopogon dubius	4AX	8AX	1AX	5BX	4AX	2A	5BX	1A	1A	2B		1B	1A				
Centaurea maculosa	4BX	3AX	1D		7EX	2A		7C	2B								
Melilotus officinalis	8BX	8BX			6BX	3B	5A	9CX	2A	1B	1A		3E	1BX			
Cirsium arvense		1A			3CX	4A	1A	8CX				1A					
Poa compressa	1A	1A			6CX	1AX	1A	8C	1A	1A	3A	1A		1A			X
Trifolium procumbens					4BX			7BX	7C	5D	3B						
Trifolium pratense									7D	1C							
Trifolium repens									8C	4B	8B	1B	4B	1C			
Agrostis alba									6C	4A	5B	2B	4B				
Trifolium hybridum					2A	1AX		2C	9D	8D	6D	8E	8E	6C			
SPECIES WITH BROAD AMPLITUDE																	
Bromus inermis	2B	5E	2B		5D	5DX	8B	2AX	5E	8E	6B	7D	4D				
Poa pratensis	4EX	5EX	9EX	9EX	8DX	7CX	6CX	7BX	4B	6C	7B	5C	4C				
Taraxacum officinale	X	2AX	X	5BX	3B	8CX	8BX	8BX	9C	8C	5C	9E	8D	9CX	3BX		
Phleum pratense			1AX		9DX	7CX	8DX	9EX	9D	9C	9C	8B	8C	7BX	0A		
SPECIES WITH INTERRUPTED RANGES																	
Lactuca serriola	5AX	2BX		2A		1A	5A										
Bromus tectorum	9BX	7DX				X	3BX										
Polygonum aviculare		1AX		4BX													X
Madia glomerata			7AX	5CX		1A		3B				3A	5B	2BX			
Medicago lupulina			1A			4C	6C					3C	4D	3A			

^aEnvironmental types are listed from dry to moist, as in Table 1; grasslands (1, 2, 5), shrublands (3, 4), dry forests (6, 7), aspen (8), warm moist forests (9-11), cool forests (12, 13), mountain meadows (14), and alpine (15).
^bCodes indicate constancy in roadside sites, cover in occupied roadside sites, and invasiveness. Constancy (= the probability of occurring in a stand in the environment): 0 = 0-9, 1 = 10-19, 2 = 20-29, . . . , 9 = 90-100%. Cover classes are: A = +, B = 0-1%, C = 1-2%, D = 2-5%, E = 5-25%, F = >25%. Invasion of undisturbed areas in an environmental type is indicated by X.

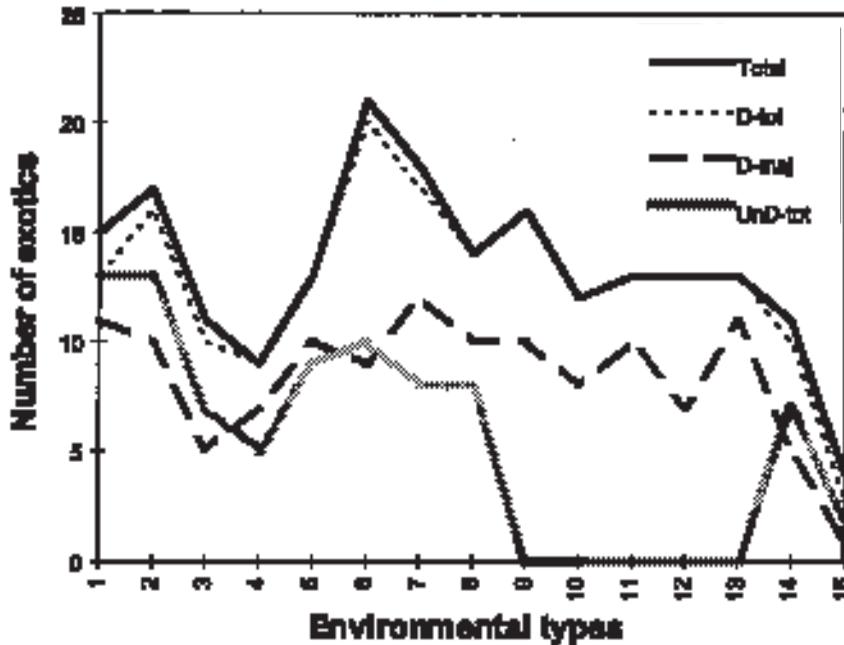


Fig. 1. Number of exotics (richness) by class and environmental type. Classes are total exotics of undisturbed sites (UnD-tot), common exotics of disturbed sites (D-maj), all exotics of disturbed sites (D-tot), and all exotics of disturbed and undisturbed sites (Total). Environmental types are as listed in Tables 1 and 3, that is, grasslands (1, 2, 5), shrublands (3, 4), dry forest (6, 7), aspen (8), warm moist forests (9, 10, 11), cool forests (12, 13), mountain meadows (14), and alpine (15).

illustrate this qualifying statement, we give *Chrysanthemum leucanthemum* as a species underrepresented because its range is expanding, *Centaurea maculosa* as less common than expected because it expands with grazing absent on the sites we studied, and *Euphorbia esula* as a species that is most important in areas moister than we sampled, e.g., riparian sites. Since volcanic materials are uncommon in the region, extrapolation to volcanic parts of Yellowstone National Park must be made with caution.

Exotic Richness Across Environmental Types

The presence of an exotic in an environmental type depends on at least 3 factors. First, the environment must be within the physiologic niche of the species. A species range on disturbed sites across the broad altitudinal gradient suggests the breadth of the physiologic niche. Second, the environment/vegetation must be within the realized niche of the species. Presence in undisturbed vegetation of an environmental type demonstrates presence in the realized niche, with respect to climax

(= late seral) vegetation. And third, presence in either disturbed or undisturbed sites demonstrates that the species has dispersed to the site. While proximity to a highway maximized the exotic's likelihood of arrival at the sites we studied, sites in environmental types in the agricultural zone had far more exposure to invading propagules than did sites in the high mountains.

On disturbed sites the exotic richness (species number) across the environmental gradient seems remarkably constant (Fig. 1), despite changes in its composition (Table 3). Regulars (constancy >30%) were 8–12 except in shrublands (5–7), one conifer forest (7), mountain meadows (5), and tundra (1). While one might argue that incidentals (constancy <30%) indicate microsite effects, numbers of incidentals were also rather constant (2–6), except in the *Pseudotsuga/Symphoricarpos* environment (11). Thus, disturbed sites seem to have a more or less constant "richness capacity," but filled with species differing among environments. Shrubland environments are slightly species deficient, for no obvious reason. *Pseudotsuga* environments have a small

excess, possibly due to their location at elevations supporting floras from Mediterranean/steppe environments and northern coniferous environments. While we see no corresponding break in environmental rigor (Table 2), the tundra environment is notably exotic poor.

In contrast, numbers of species invading undisturbed vegetation of different environmental types vary greatly (Table 3): grasslands (7–13), aspen (8), dry *Pseudotsuga* forests (8–10), other conifer forests (0), and alpine (2). This suggests that the undisturbed vegetation of major environmental types differs greatly in competitiveness. In grasslands and dry forests, exotics occupying disturbed sites, i.e., tolerating the physical environments, also colonize adjacent undisturbed vegetation. The open structure of these vegetation types apparently provides non-competitive microsites for these exotics. The exotic deficiency seen in the shrub zone was also seen on disturbed sites and is most likely induced by the physical environment. In contrast, exotics known to tolerate physical conditions in the conifer zone (i.e., disturbed sites) rarely invade adjacent forest. These exotics are probably excluded from forests by heavy competition for water/nutrients (Watt and Fraser 1933) or light. Thus, removal of forest communities, by fire or harvest, should allow plants capable of occupying noncompetitive disturbed sites to colonize more widely in the forest environment, where they may inhibit forest establishment but will finally yield when they are overtopped by tree species.

The low exotic richness of the alpine is probably due in part to environments too rigorous for establishment of opportunists (Billings and Mooney 1968), but this does not explain the sharp decline from the forest and meadows below. It is likely that failure of dispersal also contributes. To illustrate, we contrast the exotic presence in alpine and mountain meadow vegetation. (1) First, while plants adapted to disturbed Old World alpine environments may exist, vectors—crops, animals, machinery—rarely pass directly from these areas to high-altitude areas in the Rockies. Thus, the transfer of potential weeds has been slight. We conservatively suggest that as recreational use grows, managers should minimize introductions (exchanges) of exotics by increasing both quarantine and efforts to detect and eradicate unwanted establishment. (The presumed need for this caution might be tested by showing

that alpine opportunists are available in the Old World [Alps, Himalayas, Southeast Asia] flora and that the grazing disturbance has been sufficient and environmental rigor slight enough to induce the evolution of opportunistic species.) (2) In contrast, while mountain meadows seem almost equally isolated, our culture has provided a stepping stone for exotics to them. The exotics have been introduced to environmentally similar foothill sites through commercial and agricultural activity, have established, and are being transported upward, especially as motorized backcountry use increases. For example, while an experimentally bared portion of a remote mountain meadow (Weaver and Collins 1977) was not infected by *Cirsium arvense* in the preceding 2 decades, thistle appeared soon after loggers entered nearby forests.

Distribution of Individual Species

Knowledge of the tolerance range of a species tells us where to look for established stands and where to expect establishment. Both are useful in planning control. It may also help us estimate a species' ability to cross stressful—dry or cold—zones without assistance. The importance of the latter is declining as human transport becomes the dominant dispersal mechanism.

DISTRIBUTION AMONG DISTURBED SITES.—The physiologic niche of a species is suggested by its presence in disturbed sites because open spacing reduces competition. We recognize 4 distribution types (niche types).

First, species with narrow distributions are most important in lower, warmer environments (Table 3). Some occupy dry grasslands (*Agropyron cristatum*, *Alyssum alyssoides*, *Camelina microcarpa*, and *Bromus japonicus*), shrublands (*Rumex acetosa*), and warm forests (*Dactylis glomerata*, *Festuca pratensis*, *Verbascum thapsus*). None are important in the moist conifer zone, cool conifer zone, or mountain grasslands/tundra. In our data *Chrysanthemum leucanthemum* seems to have narrow tolerances, but it is spreading rapidly into drier environmental types including those dominated by *Pseudotsuga menziesii* and *Festuca idahoensis*.

Second, plants with broader tolerances populate wider zones in the altitudinal gradient (Table 3). Low-site plants (*Tragopogon dubius*, *Centaurea maculosa*, and *Melilotus officinalis*)

may prefer grasslands over shrublands. Exotics dominating near the lower forest margin plants include *Cirsium arvense*, *Poa compressa*, and the most drought tolerant (?) of the clovers (*Trifolium procumbens*). *Trifolium pratense* occurs throughout the low/warm conifer zone. *Trifolium repens*, *T. hybridum*, and *Agrostis alba* occur in the moist conifer zone, both low/warm and high/cool.

Third, 2 plants (*Poa pratensis* and *Taraxacum officinale*) have remarkably wide distributions, extending from low grasslands through forests to mountain meadows and even tundra (Table 3). Two others (*Bromus inermis* and *Phleum pratense*) range from moister grassland environments through forest environments to mountain meadow environments. All of these species cover 2–5% (D in Table 3) or 5–25% (E) of the ground surface on disturbed sites in some environments they occupy.

Fourth, 5–6 species representing 2 subgroups have interrupted or bimodal distributions (Table 3). First, *Lactuca serriola* and *Bromus tectorum* were found in dry grasslands (*Bouteloua* and *Agropyron*), were absent from moister grassland environments, and reappeared in dry forests (*Pseudotsuga*). One might speculate that these species tolerate arid environments, cannot compete in moister grassland environments, and become competitive again where precipitation evaporates from treetops before it becomes available to plants in the ground layer. This hypothesis would be more convincing if the interruption occurred in the undisturbed zone, but not in the disturbed zone. The same interruption was reported for 2 native grasses (*Stipa viridula* and *Koeleria nitida*) and 5–10 exotic species (including *Bromus inermis*, *B. tectorum*, *B. japonicus*, 3 annual mustards, and *Kochia scoparia*) that are present in the dry plains of eastern Montana, disappear in the foothills and grasslands, and reappear in the *Pseudotsuga* zone to the west (Weaver and Meier 1997). Second, 3–4 species have modes in both a lower-elevation zone and in the *Abies*/mountain meadow zone. *Descurania* (listed as unimodal) appears in dry grasslands and has a weak high mode. *Polygonum* and *Madia* appear first in moister grasslands and have solid high modes. *Medicago* appears first in the dry forest zone (*Pseudotsuga*) and reappears in the *Abies*/mountain meadow zone. We speculate (hypothesize) that plants of the lower mode occupy a site dry due

to lack of precipitation and those of the high mode occupy sites dry due to the high wind flows near mountain ridges (cf. Weaver 2001).

Each altitudinal zone contains species of both narrow and broad environmental amplitudes. This is demonstrated by listing the species within an amplitude group according to their locations on the altitudinal gradient (Table 3). Thus, among species with narrow distribution, *Agropyron cristatum*, important only in the driest environments, appears first. And among species with broad distribution, *Poa pratensis* appears before *Taraxacum officinale* because it becomes important at lower altitudes.

DISTRIBUTION AMONG UNDISTURBED SITES.—The tendency of exotics to escape from distribution corridors is inversely related to the penetrability of adjacent vegetation. Thus, while establishment on disturbed sites provides an indication of the physiologic niche, invasion of natural vegetation provides an indication of the realized niche, i.e., performance under competition from natural vegetation.

The escape of species of all amplitudes and gradient segments is proportional to the openness of the adjacent native vegetation. Species of narrow to moderate altitudinal ranges often escape into relatively open grassland or Douglas-fir (*Pseudotsuga*) vegetation, but they are unlikely to escape into denser subalpine fir forests (*Abies*; Table 3). Similarly, species with broad ranges tend to escape into grassland and low forests but are unlikely to escape into dense forest environments (Table 3). Given these observations, we expect bimodal species to escape in their lower, drought-stressed environments, but to be competitively constrained in their upper, moister environments. This is true except where the environment in the upper arm is sufficiently wind-dried to create competitive conditions (and escape) similar to that in the low-elevation mode (Table 3). *Polygonum aviculare* and *Madia glomerata* are bimodal plants illustrating the last point.

While undisturbed vegetation in the center of the forest zone may be impenetrable, segments of the forest zone that have been logged or burned are probably more penetrable, either because competition for light or water/nutrients (Watt and Fraser 1933) is reduced or because wind dispersal is facilitated. Analysis of comparable samples (existing data) will eventually test this hypothesis.

TABLE 4. Median constancy of both invading species and noninvading species on disturbed sites. The lower constancy of noninvading species may indicate poorer adaptation or a smaller seed supply.

Environmental type (HT)	BOGR STCO	AGSP BOGR	FEID ARAR	FEID ARTR	FESC FEID	PSME SYAL	PSME PHMA	POTR CARU	FEID AGCA	DECA CARX	Overall
Invaders	5.0	5.0	7.0	5.0	6.0	5.0	5.0	7.5	2.0	1.0	5.0
Noninvaders	1.5	1.0	1.5	2.5	2.5	1.0	5.0	2.5	2.0	0.0	1.0
$P = 0.0005^a$		0.07	0.23	0.08	0.16	0.06	0.06	0.61	0.06	—	0.57

^aKruskal-Wallis test (Gibbons 1985)

We expect the dominance of a species on disturbed sites of an environmental type to indicate its capacity to invade undisturbed sites in that environmental type, both because a species thriving on the disturbed site must be well adapted to the physical environment it occupies and because, as a well-adapted species, it will produce more seed. Our hypothesis is, then, that invading species will be more dominant on adjacent disturbed sites than noninvaders. In fact, the median constancy of invaders usually does exceed the median constancy of noninvaders, and the difference is significant in 70% of the cases (Table 4). When data are pooled across all except the moist conifer types, which show no escape, the difference is significant ($P < 0.0005$). The moist conifer types, PSME/PHMA, TSHE, and ABLA forests are reasonably excluded from this analysis because no exotic species have moved from roadside to forested environments.

Evaluating Exotics

If public forest and park vegetation is to be managed for “pre-Columbian” condition (cf. U.S. Congress 1872), exotics should be excluded. If this is impossible, managers should strive to prevent exotics from dominating the vegetation because dominants are most likely to affect the success of native plant associates and, through their influence on vegetation composition, animal associates as well (cf. Clinton 1999). In evaluating species, we minimize “breadth of distribution” as a criterion on the assumption that conservationists should equally emphasize preservation of all vegetation types important in the region. Vegetation types rare in the region deserve special attention if they are endemic to it, but they are less critical if they are well represented in other regions. Because our project was designed for generality, we studied no rare types.

Sites undergoing primary succession are rare in the forest and grassland zones (e.g.,

river deposits or landslides) and more common in ridge sites of the alpine (e.g., undecomposed rock). Although slopes of our roadside sites may be steeper than the average disturbed site, our data (Table 3, cover classes D and E) probably identify the most problematic species of upland sites undergoing primary succession. On disturbed grassland sites (including mountain meadows) the only exotic with 5–25% cover (E) was *Poa pratensis* and exotics having 2–5% cover (D) were *Bromus inermis*, *B. tectorum*, *Phleum pratense*, and *Rumex acetosa*. In dry forests exotics with cover 5–25% (E) were *Dactylis glomerata* and *Phleum pratense*, while those with cover 2–5% (D) were *Agrostis alba*, *Bromus inermis*, and *Trifolium repens*. In moister conifer forests, those with cover 5–25% (E) were *Bromus inermis*, *Melilotus officinalis*, *Taraxacum officinale*, and *Trifolium hybridum*; and 2–5% (D) were *Medicago lupulina*, *Phleum pratense*, *Trifolium pratense*, and *T. procumbens*. No exotic covered as much as 5% of either disturbed or undisturbed sites in the alpine. Ironically, the most aggressive exotics are rarely discussed as problematic, and none of the exotics designated as noxious seem to dominate in the wide range of environments we studied.

Secondary secession sites—such as recent burns, logged areas, or old fields—are more common on public lands than are primary succession sites. Here, the performance of exotics may be similar to their performance on primary succession sites. This expectation may overstate the problem since exotics, mostly dispersing laterally through space, must compete with natives colonizing both from the propagule bank and dispersing laterally. Thus, we expect the grasses (*Agrostis*, *Bromus*, *Dactylis*, *Phleum*, and *Poa*), legumes (*Melilotus*, *Medicago*, and *Trifolium*), and dandelion, listed above, to be among the most important exotic invaders.

Late seral sites may be as common as or more common than secondary succession sites in national forests and parks. Later seral vegetation of moister forests is impenetrable, but grasslands, shrublands, and dry forests are invaded by many species (Table 3). However, because dominance of all species falls from disturbed to undisturbed sites, we discount most of the species not listed as invaders of secondary succession sites. This position may understate the effects of robust (e.g., *Agropyron cristatum* or *Melilotus officinalis*) or very numerous (e.g., *Bromus tectorum*, *B. japonicus*, or *Alyssum alyssoides*) plants of the driest environmental types.

CONCLUSIONS

The number of exotics currently common in vegetation of the northern Rocky Mountains is relatively few, approximately 29 (Table 3). The altitudinal (temperature/moisture) amplitude of each of these species is described by presence in environmental types (HTs) representing segments of the environmental gradient (Table 3). Knowledge of species amplitudes will enable managers to estimate and even map potential distributions of exotics, both in disturbed (primary succession) and undisturbed (late seral) vegetation.

The overall invasibility of major environmental types—in both disturbed and undisturbed conditions—is indexed by tabulating exotic species richness across a broad altitudinal gradient of types. Grasslands and dry forest environments harbor the most exotic species, both in disturbed and undisturbed sites. Moist conifer forests have similar species richness on disturbed sites, but no exotics appear on undisturbed sites. Tundra environments support few exotics on either disturbed or undisturbed sites.

Dominance in vegetation in at least one environmental type is our criterion for recognizing an exotic of special concern, because a dominant is most likely to affect the success of plant associates and, through its influence on vegetation composition, the success of animal associates as well. We minimize breadth of distribution as a criterion on the assumption that conservationists should emphasize equally the preservation of all regionally common and internationally unique ecosystems. Seven species exhibited cover of 5–25% on disturbed

sites they occupied in at least one type (Table 3); they include grasses (*Agrostis*, *Bromus*, *Dactylis*, *Phleum*, and *Poa*), legumes (*Melilotus*, *Medicago*, and *Trifolium*), *Rumex* and *Taraxacum* species. An additional seven species exhibited cover of 2–5% on disturbed sites in at least one environmental type (HT). Most of these plants were introduced intentionally and none of these stealth plants is normally considered a noxious weed.

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