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The influence of disturbance and habitat on the presence of non-native plant species along transport corridors

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Abstract

The impact from transportation corridors on surrounding habitat often reaches far beyond the edge of the corridor. The altered disturbance regime in plant communities along corridor edges and vehicle traffic facilitate the spread and establishment of invasive non-native plant species. We compared the frequency of non-native plant species along highways and railways and the ability of these species to invade grasslands and dense forests along these corridors. We measured the frequency of several non-native plant species along transects 0–150 m from the edge of highways and railways in grasslands and forests, as well as at control sites away from corridors. Both transportation corridors had higher frequency of non-native species than respective control sites. Grasslands had higher frequency of non-native species than forested habitats, but the frequency did not differ between the highways and the railways. The frequency of non-native species in grasslands along highways and railways was higher than at grassland control sites up to 150 m from the corridor edge, whereas the frequency in forested habitats along corridors was higher than at forested control sites up to only 10 m from the corridor edge. There was a significant decrease in the frequency of non-native species with increasing distance from both corridors in the forest, while grasslands showed no significant change in non-native species frequency with distance from corridors. This suggests that corridor edges and grassland habitats act as microhabitats for non-native species and are more prone to invasion than forests, especially if disturbed. Our results emphasize the importance of minimizing the disturbance of adjacent plant communities along highways and railways during construction and maintenance, particularly in grassland habitats and in areas sensitive to additional fragmentation and habitat loss.

Keywords: Transportation corridors; Road ecology; Non-native plant invasions; Habitat effect; Disturbance; Edge effect

1. Introduction

Biological invasion by non-native species is a worldwide environmental concern and a focus of current ecological research (Alpert et al., 2000). As many landscapes undergo extensive and rapid change because of human activities (Hansson and Angelstam, 1991; Houghton, 1994), plant communities become more susceptible to invasion by non-native plant species and the eradication of non-native plant species in native plant communities can be challenging (Bugg et al., 1997; Benefield et al., 1999; Myers et al., 2001). One of the major changes associated with landscape modification is the fragmentation of habitat (Bennett, 1999). Fragmented habitat has more edges than continuous habitat (Tabarelli et al., 1999) and therefore is thought to be more vulnerable to invasion by non-native species (Vitousek et al., 1997; Lindenmayer and McCarthy, 2001; Watkins et al., 2003) and to loss of native species (Turner, 1996; Tomimatsu and Ohara, 2004; but see Spooner et al., 2004; Spooner, 2005).

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Less conspicuous than other forms of habitat disturbance, fragmentation by transportation corridors such as highways, railways and other linear developments frequently disturb and alter natural disturbance regimes of ecosystems in many areas of the world (Reed et al., 1996; Auerbach et al., 1997; Goosem, 1997; Forman and Alexander, 1998; Saunders et al., 2002). There has been a growing interest in the effects of transportation corridors on plant species composition (Angold, 1997; Trombulak and Frissell, 2000; Safford and Harrison, 2001; Gelbard and Belnap, 2003; Godefroid and Koedam, 2004), particularly the spread and establishment of invasive non-native plant species (Tyser and Worley, 1992; Greenberg et al., 1997; Ullmann et al., 1998; Parendes and Jones, 2000; Williamson and Harrison, 2002). An important question is what determines the susceptibility of a plant community to the spread and establishment of invasive species (Angold, 1997; Alpert et al., 2000; Williamson and Harrison, 2002). Habitats where many barriers to invasion have been removed due to anthropogenic disturbance tend to be more vulnerable than intact habitats (Johnstone, 1986). Obstacles in the landscape such as dense forest edges and closed forest canopy can act as physical barriers and affect dispersal and thus the pathway along which invasions travel (Parendes and Jones, 2000; Cadenasso and Pickett, 2001). Environment conditions such as light availability and soil moisture act as environment barriers and affect the establishment of non-native plants (Newsome and Noble, 1986; Parendes and Jones, 2000).

Transportation corridors may encourage the invasion by non-native plant species by removing barriers in several ways. First, transportation corridors alters disturbance regimes in adjacent plant communities, both directly by creating gaps and by changing the plant composition (Sousa, 1984), and indirectly by altering environmental conditions such as light and soil moisture (Newsome and Noble, 1986; Parendes and Jones, 2000). Secondly, vehicle traffic on roads aids in the dispersal of non-native species into surrounding habitat by causing air turbulence and by acting as vectors for spread of seeds and vegetative plant parts (Ross, 1986; Schmidt, 1989; Panetta and Hopkins, 1991; Tyser and Worley, 1992; Lonsdale and Lane, 1994).

High concentrations of non-native species have been observed near transportation corridors in various habitat types (Forcella and Harvey, 1983; Tyser and Worley, 1992; Angold, 1997), suggesting that corridor edges act as microhabitats for many non-native species. The impact of non-native species on habitats adjacent to these corridors may, however, extend far beyond the corridor edge (Tyser and Worley, 1992; Forman and Deblinger, 2000; Watkins et al., 2003). Many studies addressing the impact by non-native plants along transportation corridors have taken place in open, semi-arid habitats, often already disturbed, which offer suitable conditions for survival and spread of non-natives (Gelbard and Belnap, 2003). Few studies have, however, compared the presence of non-native species along transportation corridors in grassland with the presence along corridors in dense forest (Forcella and Harvey, 1983; Williamson and Harrison, 2002).

Several studies have documented roads as corridors for non-native plant dispersal (Tyser and Worley, 1992; Forman et al., 2002; Gelbard and Belnap, 2003), however, most have focused on roads that are characterized by low traffic volumes. Also, few studies have explored the relationship between non-native plants and railway corridors (Zika, 1990; Warwick and Wall, 1998). Descriptive and anecdotal information on the plant communities associated with railways have been documented (Thomson, 1940; Messenger, 1968; Niemi, 1969; Borowske and Heitlinger, 1980). Yet, we are unaware of any study that has assessed the impacts of railways on plant species composition or compared the invasibility of plant communities by non-native plant species along high traffic volume roads and railway corridors.

Our aim was to compare the frequency of non-native plant species along highways and railways in grassland and dense forest. We specifically addressed three questions: (1) To what extent do transportation corridors influence the frequency of non-native species? (2) Are non-native species more abundant in grasslands adjacent to transportation corridors than in dense forest? (3) Do the frequency of non-native decrease with distance from the transportation corridor in both of these habitats? Understanding the impact from transportation corridors on different habitat types will provide critical information for decision makers who asses the threat of non-native species and for land managers responsible for managing invasive plant species and maintaining the integrity of biological communities in fragmentated habitats.

2. Methods

2.1. Study area

The study was carried out in the Bow River Valley in Banff National Park (BNP), Alberta, Canada (Fig. 1). BNP was established in 1887 in southwestern Alberta about 120 km west of Calgary. With over 5 million visitors per year, Banff is the most heavily visited national park in North America.

The Bow River Valley is situated within the front and main ranges of the Canadian Rocky Mountains. Topography is regarded as mountainous with elevations from 1300 m to over 3400 m, and a valley floor width from 2 to 5 km. The climate is continental and characterized by relatively long winters and short summers (Holland

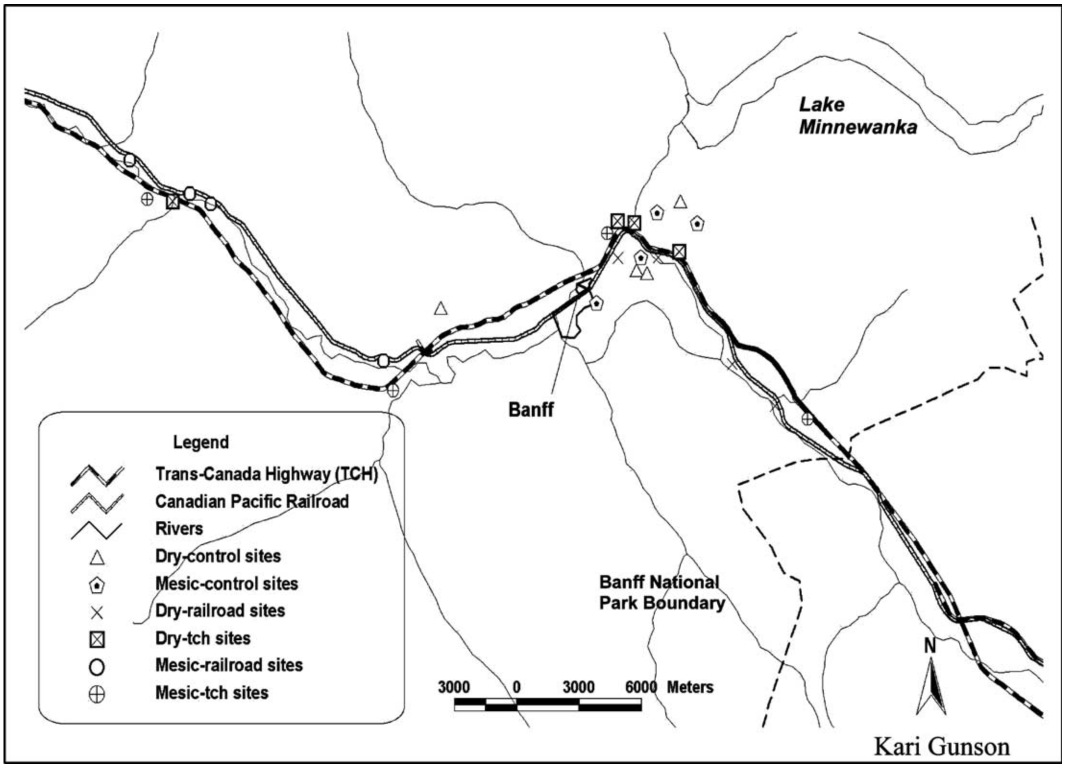

Fig. 1. Map of the study area in Banff National Park, Alberta, Canada and transportation corridors used to investigate non-native plant invasions.

and Coen, 1982). Vegetation in the park encompasses montane, subalpine and alpine ecoregions. Montane habitats are found in low elevation valley bottoms and are characterized by Douglas fir, *Pseudotsuga menziesii* (Mirbel) Franco; white spruce, *Picea glauca* (Moench) Voss; lodgepole pine, *Pinus contorta* Dougl. ex Loud.; aspen, *Populus tremuloides* Michx., and natural grasslands (Achuff and Corns, 1983).

Most visitors arrive by private vehicles or motor coaches along the Trans-Canada Highway (TCH; Fig. 1), which is the major transportation corridor through the national park and the Rocky Mountains. The TCH runs along the floor of the Bow Valley sharing the valley bottom with the Bow River and the Canadian Pacific Railway (CPR; Fig. 1). In 2000, annual average daily traffic volume at the park east entrance was 15,270 vehicles per day and summer annual average traffic volume was 22,220 vehicles per day (Parks Canada Highway Service Center, unpublished data). We chose BNP as the study area for our research because of the concurrence of the two transportation corridors and their recognized impact on native plant communities in the sensitive valley-bottom, montane habitat of this World Heritage site (Parks Canada, 1996; United Nations Environment Programme/World Conservation Monitoring Centre, 2000).

The current route of the TCH was completed in 1956. Upgrading the TCH from two to four lanes progressed in three highway expansion phases between 1982 and 1997 (McGuire and Morrall, 2000). Seed mixes containing up to 100% non-native grass species (Hammer, O., personal communication) and topsoil from outside the park were used to landscape roadsides during the first two expansion projects between 1982 and 1988 (Pengelly, I., personal communication). Topsoil from within the park was used for landscaping the sides of the highway during the most recent highway phase in 1997 and seed mixes used in the revegetation contained mostly native species (Parks Canada, 1995).

The CPR was constructed through the Bow Valley in 1883. Local topsoil was used to landscape the railway ballast. We were, however, unable to obtain information regarding the use of seed mixes for railway projects, but assume that railway ballasts were allowed to revegetate naturally. In 1998 there were on average 28 trains passing through the park per day (Canadian Pacific Railway, unpublished data).

2.2. Study design

We surveyed non-native plant species along two types of transportation corridors in two different habitats using a factorial design. Corridors included the TCH (hereafter referred to as the highway) and the CPR (hereafter referred to as the railway). Habitats consisted of grasslands (dry open areas dominated by grass and forbs with as low disturbance as possible) and forest

Table 1
Surveyed non-native plant species in Banff National Park, including their duration, mode of introduction and origin

Target species	Duration	Introduction	Origin
Agropyron cristatum	Perennial	Unintentional	Southern Russia
Bromus inermis	Perennial	Used for restoration of roadsides and pastures	Europe
Cirsium arvense	Perennial	Unintentional	Europe
Festuca rubra	Perennial	Used for restoration of roadsides	Europe
Leucanthemum vulgare	Perennial	Unintentional	Europe
Linaria vulgaris	Perennial	Unintentional	Europe and Asia
Medicago sativa	Annual/perennial	Unintentional	Europe
Melilotus officinalis	Perennial	Unintentional	Europe
Phleum pratense	Perennial	Used for restoration of roadsides and pastures	Europe
Poa pratensis/*Poa communis*	Perennial	Used for restoration of roadsides	Europe
Sonchus arvensis	Perennial	Unintentional	Europe
Tanecetum vulgare	Perennial	Unintentional	Europe
Taraxacum officinale	Perennial	Unintentional	Europe
Trifolium hybridum	Perennial	Unintentional	Europe
Trifolium repens	Perennial	Unintentional	Europe

(dense forest dominated by *Picea glauca* and *Pinus contorta*).

We surveyed 15 non-native plant species between May and September 2000 (Table 1). The choice of species was made after studying the park records of non-native plant species in the area, consulting local plant ecologists, and based on our own field observations prior to field data collection. All identified non-native species at each study site were recorded and used in the analysis. The taxonomy follows the Flora of Alberta (Moss, 1959) and Plants of the Rocky Mountains (Kershaw et al., 1998).

We selected 24 study sites (>1 km apart; Fig. 1) including four replicates of each corridor type-habitat combination and eight control sites. Eight study sites were selected along the highway (= 4 grassland, 4 forest) and eight along the railway (= 4 grassland, 4 forest). Eight control sites were selected in undisturbed grassland and forest habitats, situated in the Bow Valley at similar elevation as the highway and railway, and at least 200 m from any non-natural linear feature (road, railway, trail or power line). Control sites were, therefore, comparable with sites along the highway and railway in terms of microclimate, drainage, dispersal, and overall native plant community.

Our sampling scheme was based on a series of transects, each 25 m long, parallel to the highway or railway. The first transect was placed at the highway shoulder or railway ballast (corridor edge). The following six transects were placed at distances of 5, 10, 25, 50, 100 and 150 m from the corridor edge. Some sites were not large enough to allow for the complete sampling scheme. The same sampling design was used at the control sites. Each transect included eight study plots located 3 m apart. Each plot measured $0.5 \times 0.5\ m^2$ and was divided into $10 \times 10\ cm^2$ sections in which we recorded non-native plant species as present or absent.

2.3. Data analysis

Percent frequency of non-native species (percentage of plot sections in which the species was present) was determined for each species and transect. Total frequency of non-native species was also determined for each transect by calculating the total percentage of plot sections in which non-native species were present. Differences in the frequency ($p < 0.05$) of non-native species (individual and total) between corridor types and habitats were analyzed using analysis of variance (ANOVA). An ANOVA with contrast was used to analyze the interaction between the frequency of non-native species at different distances from the corridors in grassland and forest habitats with respective control sites. Regression analysis was performed to test for relationships between the frequency of total non-native species and distance from corridors. Data were log-transformed to reduce for heterogeneity of variance among sites and distances. Four of the selected target species (*Leucanthemum vulgare*, *Tanecetum vulgare*, *Agropyron cristatum*, and *Medicago sativa*) had low sample sizes (present only at one transect at one study site or absent) and were therefore not included in the analysis. Analyses were performed in JMP statistical package (version 3.1.5; SAS Institute, 1994, Cary, NC, USA).

3. Results

3.1. Transportation corridor effect

Non-native species were more frequent along corridors than at control sites in both grasslands (highway: $F_{1,53} = 58.90$, $p < 0.0001$; railway; $F_{1,54} = 68.01$, $p < 0.0001$) and forests (highway: $F_{1,54} = 16.73$, $p < 0.0001$; railway; $F_{1,54} = 27.29$, $p < 0.0001$). There was no significant difference in the total frequency of non-native species between the highway and the railroad ($F_{1,110} = 0.26$; $p = 0.6094$). *Festuca rubra* and *Sonchus arvensis*, however, were significantly more frequent along the highway than the railway (*F. rubra*: $F_{1,110} = 18.51$, $p < 0.0001$; *S. arvensis*: $F_{1,110} = 5.76$, $p = 0.0182$), and *Linaria vulgaris* was significantly more frequent along the railway ($F_{1,110} = 7.20$, $p = 0.0085$). Other studied species were equally frequent along the highway and railway.

3.2. Habitat effect

In general, non-native species were more frequent in grasslands along corridors than in forests ($F_{1,110} = 79.32$; $p < 0.0001$). *Bromus inermis* ($F_{1,110} = 12.83$, $p = 0.0005$), *Trifolium repens* ($F_{1,110} = 4.78$, $p = 0.031$) and *Poa* sp. ($F_{1,110} = 42.86$, $p < 0.0001$) were more frequent in grasslands along corridors. *Trifolium hybridum*, on the other hand, was more frequent in forests along corridors ($F_{1,110} = 8.14$, $p = 0.0052$). Other studied species were equally frequent in both habitats.

3.3. Distance effect

In grasslands, the total frequency of non-native species was higher adjacent to corridors than at control sites up to 150 m from the corridor edge (Table 2). On the other hand, in forests, the total frequency of non-native species was higher up to 10 m from the corridor edge only (Table 2). The frequency of individual non-native species such as *Festuca rubra* and *Cirsium arvense* declined with distance from the corridor, especially from the highway, in both grassland and forest habitats, and were absent from control sites (Table 3). *Linaria vulgaris* and *Phleum pratense* declined with distance from the railway in both grasslands and forest, but where absent along highways. *L. vulgaris* was present at control sites in grasslands, but not in forest (Table 3). *P. pratense* was absent at control sites. *Melilotus officinalis* and *Sonchus arvensis* were present close to the corridor edges in both habitats, but did not seem to spread from edges. *Bromus inermis*, *Taraxacum officinale*, *Trifolium repens* and *Poa* sp. were common through-out grassland habitats along corridors and at grassland control sites, while they declined with distance from the corridors in forest habitats and were absent from forest control sites (*T. officinale* was present at one transect at one forest control site). *Trifolium hybridum* was frequent along the corridor edges and up to 25 m from the corridor edge in forest habitats, while absent in grasslands and at control sites (Table 3).

In forests, there was a significant decrease in the frequency of total non-native species with increasing distance from corridors both along the highway ($R^2 = 0.41$, $F = 18.42$, $p = 0.0002$, df = 27; Fig. 2) and the railway ($R^2 = 0.35$, $F = 14.18$, $p = 0.0009$, df = 27; Fig. 2). In contrast, grasslands showed no significant change in total non-native species frequency with distance from corridors (highway: $R^2 = 0.08$, $F = 2.09$ $p = 0.1607$, df = 26; railway: $R^2 = 0.0014$, $F = 0.04$, $p = 0.8501$, df = 27; Fig. 2).

4. Discussion

4.1. To what extent do transportation corridors influence the frequency of non-native species?

Habitats along highways and railways had equal frequencies of total non-native plant species, but had significantly higher frequencies than respective control sites. Our results agree with results from previous studies, where transportation corridors had high abundance of non-native plant species (Forcella and Harvey, 1983; Tyser and Worley, 1992; Angold, 1997).

The main reasons for the presence of non-native species along transportation corridors are often altered disturbance regimes at the edges, such as physical disturbance of soil and vegetation during construction (Trombulak and Frissell, 2000), altered light conditions

Table 2
Results (F-values) from ANOVA with contrast comparing total frequency of non-native species in grasslands and forests along corridors with respective control sites. Transects were located parallel to the corridors at 0–150 m away from the corridor edge

Transect	Grassland highway vs. control	Grassland railway vs. control	Forest highway vs. control	Forest railway vs. control
Corridor edge	6.03*	5.26*	171.62***	38.31***
5	4.21*	7.68**	171.95***	35.39***
10	7.06*	4.41*	11.54**	18.07**
25	11.31**	9.17**	2.71	3.02
50	9.09**	8.91**	0.18	0.29
100	14.45**	24.49***	0.05	0.51
150	4.84*	13.37**	0.0007	0.903

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.0001$.

Table 3

Results (F-values) from ANOVA with contrast comparing the frequency of individual non-native species in grasslands and forests along corridors with respective control sites. Transects were located parallel to the corridors at 0–150 m away from the corridor edge

Habitat	Corridor	Transect	brin	ciar	feru	livu	meof	phpr	poa	soar	taof	trhy	trre
Grassland	Highway	Corridor edge	5.35* (p)	9.80** (a)	2.62 (a)	x	x	x	0.45 (p)	x	0.14 (p)	x	0.13 (p)
		5	0.02 (p)	4.44* (a)	10.19** (a)	x	6.83* (a)	x	0.50 (p)	19.41*** (a)	0.71 (p)	x	0.18 (p)
		10	2.30 (p)	2.72 (a)	0.56 (a)	x	x	x	1.41 (p)	x	2.12 (p)	x	2.34 (p)
		25	3.80 (a)	x	1.42 (a)	x	x	x	4.81* (p)	x	2.32 (p)	x	1.42 (a)
		50	0.14 (p)	x	1.31 (a)	x	x	x	6.18* (p)	x	0.08 (p)	x	0.11 (p)
		100	1.40 (p)	x	1.47 (a)	x	x	x	5.03* (a)	x	0.95 (p)	x	0.99 (p)
		150	x	x	1.77 (a)	x	x	x	0.72 (p)	x	0.63 (p)	x	2.97 (p)
	Railway	Corridor edge	0.02 (p)	16.23** (a)	2.27 (a)	2.86 (p)	x	1.75 (a)	0.04 (p)	x	0.75 (p)	x	1.46 (p)
		5	3.43 (p)	2.06 (a)	x	9.69** (p)	x	5.25* (a)	4.45* (p)	x	0.38 (p)	x	0.96 (p)
		10	1.56 (p)	x	1.91 (a)	0.01(a)	x	x	<0.01 (p)	x	2.68 (p)	x	2.33 (p)
		25	2.34 (a)	x	2.27 (a)	x	x	x	1.29 (p)	x	2.96 (p)	x	0.75 (a)
		50	3.12 (p)	x	0.91 (a)	x	x	x	1.93 (p)	x	1.94 (p)	x	0.02 (p)
		100	14.41** (p)	x	1.15 (a)	x	x	x	5.37* (a)	x	2.97 (p)	x	1.13 (p)
		150	7.35** (a)	x	0.91 (a)	x	x	x	2.11 (p)	x	2.76 (p)	x	0.01 (p)
Forest	Highway	Corridor edge	19.85*** (a)	12.23** (a)	25.70*** (a)	x	x	x	11.13** (a)	x	27.93*** (a)	17.72** (a)	5.77* (a)
		5	19.80*** (a)	4.52* (a)	21.19*** (a)	x	13.33** (a)	x	3.34 (a)	31.35*** (a)	52.54*** (a)	8.18** (a)	4.22* (a)
		10	0.08 (a)	x	1.23 (a)	x	x	x	0.52 (a)	x	0.61 (a)	x	x
		25	0.09 (a)	x	0.01 (a)	x	x	x	x	x	0.43 (p)	x	x
		50	x	x	x	x	x	x	x	x	0.18 (a)	x	x
		100	0.04 (a)	x	x	x	x	x	x	x	x	x	x
		150	x	x	x	x	x	x	x	x	x	x	x
	Railway	Corridor edge	16.92** (a)	2.25 (a)	7.00*** (a)	7.00* (a)	0.09 (a)	7.00* (a)	4.59* (a)	x	45.38*** (a)	5.08* (a)	1.79 (a)
		5	2.25 (a)	4.75* (a)	x	x	6.91* (a)	x	18.19*** (a)	x	20.00*** (a)	x	x
		10	9.45** (a)	x	x	x	x	x	x	x	24.06*** (a)	x	0.30 (a)
		25	x	x	x	x	x	x	x	x	3.08 (p)	1.29 (a)	5.38* (a)
		50	x	x	x	x	x	x	x	x	0.32 (a)	0.55 (a)	x
		100	x	x	x	x	x	x	x	x	1.10 (a)	0.08 (a)	x
		150	x	x	x	x	x	x	x	x	2.37 (a)	x	x

brin = *Bromus inermis*, ciar = *Cirsium arvense*, feru = *Festuca rubra*, livu = *Linaria vulgaris*, meof = *Melilotus officinalis*, phpr = *Phleum pratense*, poa = *Poa pratensis*/*Poa communis*, soar = *Sonchus arvensis*, taof = *Taraxacum officinale*, trhy = *Trifolium hybridum*, and trre = *Trifoliumrepens*. x = species absent at corridor sites, a/p = species absent/present at control sites.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.0001$.

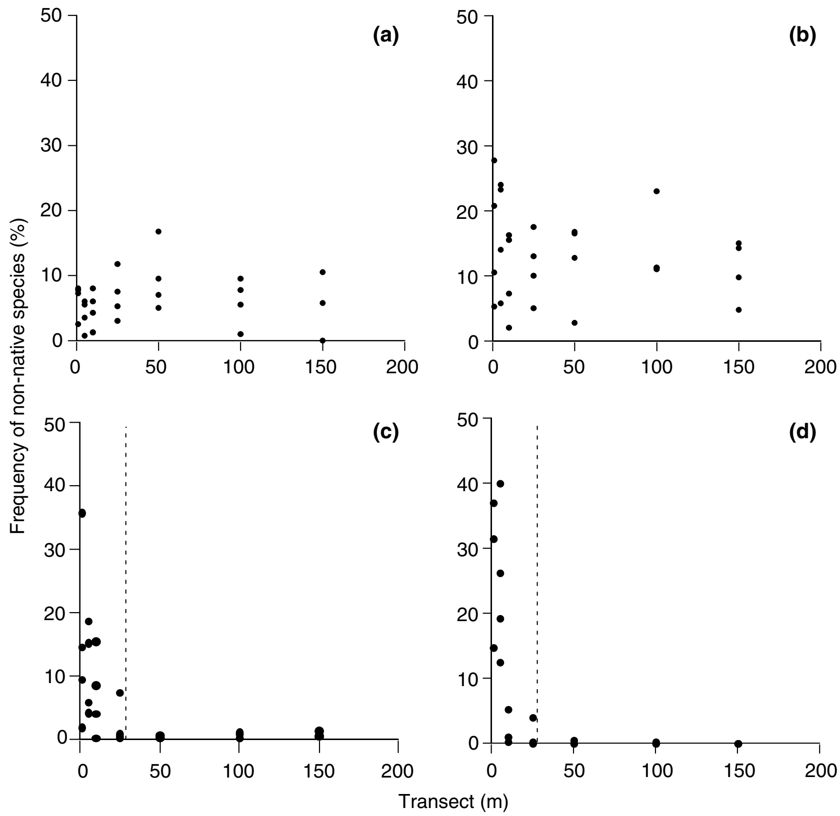

Fig. 2. Frequency (average) of non-native plant species (%) at seven transects (corridor edge, 5, 10, 25, 50, 100, and 150 m from corridor edge) along: (a) highway in grassland habitat, (b) railway in grassland habitat, (c) highway in forest habitat, and (d) railway in forest habitat. There was a significant decrease in the frequency of non-native plant species with the distance from the corridor edge in forest habitats along the highway and railway, and vegetation did not differ significantly from forest control sites beyond 25 m from the corridor edge (indicated by the dashed line). There was no decrease in the frequency of non-native plant species with the distance from the corridor edge in grassland habitats.

(Parendes and Jones, 2000), as well as intentionally introduced plants on corridor edges (Tyser and Worley, 1992). The potential of non-native species to spread from disturbed edges into native plant communities increases the effect of fragmentation by these corridors (Forman and Deblinger, 2000). Physical disturbance, such as, removal of soil and vegetation have shown to encourage establishment of non-native species (Hobbs and Huenneke, 1992), since it often causes changes in the species composition of plant communities (Wilson and Tilman, 2002) and creates gaps (Sousa, 1984). In addition, many non-native species are ruderals and establishes well in disturbed habitats (Newsome and Noble, 1986). Areas along both the highway and railway have been subjected to disturbance, but sites along the highway were more recently and more frequently disturbed than sites along the railway. Frequent disturbance has shown to encourage establishment by non-native species (Hobbs and Huenneke, 1992; Parendes and Jones, 2000; Gelbard and Belnap, 2003). Our results, however, indicate that sites along the highway and railway have equal frequency of non-native species regardless of time and frequency of disturbance.

Altered light conditions are likely to arise along forest edges (Gehlhausen et al., 2000) including transportation corridors (Parendes and Jones, 2000). A change in solar radiation often influences the temperature (Brothers and Spingarn, 1992) and soil moisture (Gehlhausen et al., 2000). This edge effect affects species composition (Brothers and Spingarn, 1992; Gehlhausen et al., 2000) due to altered germination and survival rates of species present or in the seed bank (Witkowski and Wilson, 2001). Our results show a high frequency of non-native species up to 25 m from the edges of both corridors in forest habitats. This suggests that the edge effect in forest habitats due highway and railway corridors is equal and it affects the frequency of non-native species up to 25 m from the corridor edge.

Due to disturbance and altered environment conditions, corridor edges frequently act as microhabitats for many non-native species (Matlack, 1994; Parendes and Jones, 2000). This edge effect is often more pronounced in forested habitats (Meekins and McCarthy, 2001), which does not provide a suitable habitat for many invasive non-native species. Grassland habitats, however, may not show a pronounced edge effect (Tyser and Worley, 1992) since this habitat type, especially if disturbed, may act as a refuge for many common non-native species that are abundant in the species pool. The high frequency of unintentionally introduced non-native plant species along both transport corridors may, therefore, be explained by the high persistence and overall commonness of these species in the area (Table 1). Several of the studied species, such as *Bromus inermis* and *Phleum pratense* were used for hay and were probably planted in some areas in the park to improve pastures in the past. All studied species were perennials and may, therefore persist in the area for a long time once they are established even if conditions are not suitable for new colonization. Grassland habitats that are disturbed during construction of transportation corridors may, therefore, provide suitable habitats for many non-native species long after the disturbance. Time and frequency of disturbance may not be an important factor when predicting invasions, especially not in grassland habitats. Similar results have been found in previous studies where high-use roads were compared with low-use backcountry trails (Tyser and Worley, 1992). The frequency of use was shown not to be an important factor, instead several non-native plant species were present >100 m from roads and trails regardless of use (Tyser and Worley, 1992). *Festuca rubra* and *Sonchus arvensis* were the only non-native species that were significantly more common along the highway than along the railway, while *Linaria vulgaris* was significantly more frequent adjacent to railways than along highways (Table 3). The high frequency of *Festuca rubra* along highways, while absent at control sites, can be explained by its high contribution (40%) to the seed-mix used to revegetate one segment of the highway during early 1980s (Hammer, O., personal communication). This suggests that non-native species used to revegetate roadsides may persist within the native plant community for a long time, which also agrees with earlier studies (Tyser and Worley, 1992).

The role of road corridors in landscape fragmentation and disturbance, and as a reservoir of non-native plant species has been widely studied (Angold, 1997; Forman and Alexander, 1998; Saunders et al., 2002; Gelbard and Belnap, 2003), while no studies have documented the impact contributed by railways. The results from this study suggest that transportation corridors such as highways and railways contribute equally as a reservoir of non-native species and that the disturbance contributed by these two types of transportation corridors are comparable.

4.2. Are non-native species more abundant in grasslands than in forests?

Non-native species present in this area were most frequent in grassland habitats. Accordingly, habitat type is the most important factor when describing the frequency of non-native plant species along transportation corridors. Sites with open canopies have shown to have an increased risk of becoming invaded by non-native species in previous studies (Parendes and Jones, 2000), suggesting that the lack of trees facilitates both dispersal (Cadenasso and Pickett, 2001) and establishment. The establishment of many non-native species is promoted by high light levels associated with grassland habitats, open forest canopies and forest edges (Cousens and Mortimer, 1995; Parendes and Jones, 2000; Meekins and McCarthy, 2001). These findings agree with our results: many of the non-native species present in this area were well established in high concentrations through-out grassland habitats along corridors, whereas a lower frequency of non-native species were found in forests, particularly >25 m from the corridors (Tables 2 and 3). Some non-native species, such as *Bromus inermis*, *Taraxacum officinale*, *Trifolium repens* and *Poa* sp. were even common through-out grassland control sites.

The characters and origin of non-native plant species may explain their high abundance in grasslands and disturbed areas. Many invasive non-native plants in North America have their origin in Asia, Europe and the Mediterranean Basin (Mooney and Drake, 1986; Pons et al., 1990; Cousens and Mortimer, 1995) (Table 1). Cousens and Mortimer (1995) suggest that long history of cultivation in these areas could have allowed plants species to evolve adaptation to human activities and, therefore, higher tolerance to disturbance, drought, and high light levels. As a result, such species when introduced to North America may displace native grassland species, especially in areas subjected to disturbance (Tyser and Worley, 1992; McIntyre and Lavorel, 1994). Grasslands along the highway and railway in the Bow Valley may have been frequently disturbed in the past. Much of the grassland along the highway, for example, have been used as gravel and topsoil depots during construction in the 1960s and were therefore disturbed (Hammer, O., personal communication).

Forests, on the other hand, had lower frequency of non-native species, suggesting that few non-native species were able to disperse far from the transportation corridors (Cadenasso and Pickett, 2001) and colonize forest interiors. Also, few non-native plants common in this area are adapted to the environmental conditions that characterize the interior of this montane forest, such as low light, little disturbance (Parendes and Jones, 2000; Watkins et al., 2003) and competition from native species (Simberloff et al., 2002). *Bromus inermis*, *Trifolium hybridum* and *Taraxacum officinale* were the only non-native species recorded >50 m from the corridor edge in forest habitats, while *Taraxacum officinale* was the only non-native species that was recorded at forest control sites (Table 3).

4.3. Do the frequency of non-native species decrease with distance from the transportation corridor in both habitats?

Many non-native species were present throughout grasslands along both the highway and railway (Tables 2 and 3), suggesting that grassland habitats are especially vulnerable to invasion by non-native species, especially if disturbed. Our results support earlier studies that suggest that non-native species disperse far from corridor edges in grassland habitats, where they also easily establish (Tyser and Worley, 1992). The area affected along transportation corridors, i.e. the ''road-effect zone'' has previously shown to be asymmetric depending on habitat characteristics and terrain features (Forman and Deblinger, 2000). Tyser and Worley (1992) found that several non-native forbs invaded >100 m into grasslands along roads in Glacier National Park in Montana (USA). They suggest that the replacement of native forbs by non-native species mainly was caused by the introduction of non-native grass species on the roadsides (Tyser and Worley, 1992).

In contrast, in forest habitats the frequency of non-native species declined drastically about 10 m from the corridor edge, while some species occurred infrequently beyond that distance (Table 2 and Fig. 2), suggesting that this forest habitat is less vulnerable to invasion. Similar results have been observed in earlier studies (Brothers and Spingarn, 1992; Forman and Deblinger, 2000; Watkins et al., 2003). Watkins et al. (2003) reported abundant non-native species within 15 m of unpaved forest roads in a northern hardwood forest in Wisconsin (USA). High frequencies of non-native species is associated with disturbance (Watkins et al., 2003) as well as high light levels and temperature (Brothers and Spingarn, 1992) along the road, while low frequencies in the interior forest is associated with low light levels and several decades or more without severe disturbance (Watkins et al., 2003). Forests may, however, become heavily invaded by non-native species if disturbed (Williamson and Harrison, 2002). Also, Forman and Deblinger (2000) found that the zone affected by woody non-native species planted on road sides was 20–120 m into forested areas, but did not include forbs or grasslands.

Some species (Table 3), such as *Sonchus arvensis*, *Cirsium arvense*, *Melilotus officinalis* and *Phleum pratense* were more common close to the corridor than further out at grasslands (Table 3), indicating that these species were dispersed from the transportation corridor. Other species, such as *Bromus inermis* and *Poa* sp., *Festuca rubra*, *Trifolium repens* and *Taraxacum officinale* were common through-out grasslands along the corridor edge and were present at control sites, indicating that they were not dispersed from the corridor. Instead, these species have either been used in revegetation of corridor edges, pastures and other disturbed areas, and are thus part of the local species pool and common in disturbed grassland habitats in the area.

5. Conclusions

Our findings are consistent with the idea that the influence of transportation corridors on the frequency of non-native plant largely is due to factors associated with habitat characteristics. Habitat type, altered disturbance regimes, and intentionally introduced non-native species are, therefore, essential to consider when describing the impact of non-native species on native plant communities along all types of transportation corridors. Disturbance frequency and the type of transportation corridor, however, were less important factors and may not be associated with the frequency of non-native plant species. Our results also confirm that the impact from transportation corridors on adjacent habitats extends far beyond the corridor edge, which explains why these corridors often contribute to such severe habitat fragmentation and species loss. Our results emphasize the importance of minimizing the disturbance of adjacent plant communities along highways and railways during construction and maintenance. Native plant species should be used when revegetating roadsides, particularly in grassland habitats and in areas sensitive to additional fragmentation.

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References

Achuff, P.L., Corns, I.G.W. 1983. Vegetation. In: Holland, W.D., Coen, G.M., (Eds.), Ecological Land Classification of Banff and Jasper National Parks, vol. 1: Summary, Publication M-83-2. Alberta Institute of Pedology, Edmonton, Canada, pp. 71–156.

Alpert, P., Bone, E., Holzapfel, C., 2000. Invasiveness, invisibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant, Ecology Evolution and Systematics 3, 52–66.

Angold, P.G., 1997. The impact of a road upon adjacent heathland vegetation: effects on plant species composition. Journal of Applied Ecology 34, 409–417.

Auerbach, N.A., Walker, M.D., Walker, D.A., 1997. Effects of roadside disturbance on substrate and vegetation properties in arctic tundra. Ecological Applications 7, 218–235.

Benefield, C.B., DiTomaso, J.M., Kyser, G.B., Orloff, S.B., Churches, K.R., Marcum, D.B., Nader, G.A., 1999. Success of mowing to control yellow starthistle depends on timing and plant's branching form. California Agriculture 53, 17–21.

Bennett, A.F., 1999. Linkages in the landscape: the role of corridors and connectivity in wildlife conservation. IUCN (International Union for the Conservation of Nature), Gland, Switzerland.

Borowske, J.R., Heitlinger, M.E., 1980. Survey of native prairie on railroad rights-of-way in Minnesota. In: Kucera, C.L. (Ed.), Proceedings of the Seventh North American Prairie Conference. Southwest Missouri State University, Springfield, USA.

Brothers, T.S., Spingarn, A., 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forest. Conservation Biology 6, 91–100.

Bugg, R.L., Brown, C.S., Anderson, J.H., 1997. Restoring native perennial grasses to rural roadsides in the Sacramento Valley of California: establishment and evaluation. Restoration Ecology 5, 214–228.

Cadenasso, M.L., Pickett, S.T.A., 2001. Effect of edge structure on the flux of species into forest interiors. Conservation Biology 15, 91–97.

Cousens, R., Mortimer, M., 1995. Dynamics of Weed Populations. Cambridge University Press, Cambridge, UK.

Forcella, F., Harvey, S.J., 1983. Eurasian weed infestation in western Montana in relation to vegetation and disturbance. Madrono 30, 102–109.

Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29, 207–231.

Forman, R.T.T., Deblinger, R.D., 2000. The ecological road-effect zone of a Massachusetts (USA) suburban highway. Conservation Biology 14, 36–46.

Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T., Winter, T.C., 2002. Road Ecology: Science and Solutions. Island Press, Washington, DC, USA.

Gehlhausen, S.M., Schwartz, M.W., Augspurger, C.K., 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. Plant Ecology 147, 21–35.

Gelbard, J.L., Belnap, J., 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology 17, 420–432.

Godefroid, S., Koedam, N., 2004. The impact of forest paths upon adjacent vegetation: effects of the path surfacing material on the species composition and soil compaction. Biological Conservation 119, 405–419.

Goosem, M., 1997. Internal fragmentation: the effects of roads, highways, and powerline clearings on movements and mortality of rainforest vertebrates. In: Laurance, W.F., Bierregaard, J.R.O. (Eds.), Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago, USA, pp. 241–255.

Greenberg, C.H., Crownover, S.H., Gordon, D.R., 1997. Roadside soil: a corridor for invasion of xeric scrub by nonindigenous plants. Natural Areas Journal 17, 99–109.

Hansson, L., Angelstam, P., 1991. Landscape ecology as a theoretical basis for nature conservation. Landscape Ecology 5, 191–201.

Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implication for conservation. Conservation Biology 6, 324–337.

Holland, W.D., Coen, G.M., 1982. Ecological Land Classification of Banff and Jasper National Parks. vol. II: Soil and Vegetation Resources. Alberta Institute of Pedology Publication, Edmonton, Canada.

Houghton, R.A., 1994. The worldwide extent of land-use change. Bioscience 44, 305–313.

Johnstone, I.M., 1986. Plant invasion windows: a time-based classification of invasion potential. Biological Review 61, 369–394.

Kershaw, L., Mackinnon, A., Pojar, J., 1998. Plants of the Rocky Mountains. Lone Pine, Edmonton, Canada.

Lindenmayer, D.B., McCarthy, M.A., 2001. The spatial distribution of non-native plant invaders in a pine–eucalypt landscape mosaic in south-eastern Australia. Biological Conservation 102, 77–87.

Lonsdale, W.M., Lane, L.A., 1994. Tourist vehicles as vectors of weed seeds in Kakadu National Park, northern Australia. Biological Conservation 69, 277–283.

Matlack, G.R., 1994. Vegetation dynamics of the forest edge – trends in space and succesional time. Journal of Ecology 82, 113–123.

McGuire, T.M., Morrall, J.F., 2000. Strategic highway improvements to minimize environmental impacts within the Canadian Rocky Mountain national parks. Canadian Journal of Civil Engineering 27, 523–532.

McIntyre, S., Lavorel, S., 1994. Predicting species richness of native, rare, and exotic plants in response to habitat and disturbance variables across a variegated landscape. Conservation Biology 8, 521–531.

Meekins, J.F., McCarthy, B.C., 2001. Effect of environmental variation on the invasive success of a non-indigenous forest herb. Ecological Applications 11, 1336–1348.

Messenger, K.G., 1968. A railway flora of Rutland. Proceedings of the Botanical Society of the British Isles 7, 325–344.

Mooney, H.A., Drake, J.A., 1986. Ecology of Biological Invasions of North America and Hawaii. Springer Verlag, New York, USA.

Moss, E.H., 1959. Flora of Alberta. University of Toronto Press, Toronto, Canada.

Myers, J.H., Simberloff, D., Kuris, A.M., Carey, J.R., 2001. Eradication revisited: dealing with exotic species. Trends in Ecology and Evolution 15, 316–320.

Newsome, A.E., Noble, I.R., 1986. Ecological and physiological characters of invading species. In: Groves, R.H., Burdon, J.J. (Eds.), Ecology of Biological Invasions. Cambridge University Press, Cambridge, UK, pp. 1–20.

Niemi, A., 1969. On the railway vegetation and flora between Esbo and Inga, southern Finland. Acta Botanica Fennica 83, 1–28.

Panetta, F.D., Hopkins, A.J.M., 1991. Weeds in corridors: invasion and management. In: Saunders, D.A., Hobbs, R.J. (Eds.), Nature Conservation 2: The Role of Corridors. Surrey Beatty, Chipping Norton, Australia, pp. 341–351.

Parendes, L., Jones, J.A., 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H.J. Andrews Experimental Forest, Oregon. Conservation Biology 14, 64–75.

Parks Canada, 1995. Trans-Canada Highway Phase IIIA. Initial Assessment Determination. Department of Canadian Heritage, Ottawa, Canada.

Parks Canada, 1996. Banff-Bow Valley: At the Crossroads – Summary Report for the Banff-Bow Valley Task Force. Department of Canadian Heritage, Ottawa, Canada.

Pons, A., Couteaux, M., de Beaulieu, J.L., Reille, M., 1990. Plant invasions in southern Europe from the paleoecological point of view. In: di Castri, F., Hansen, A.J., Debussche, M. (Eds.), Biological Invasions in Europe and the Mediterranean Basin. Kluwer Academic Publishers, Dordrecht, Netherlands, pp. 169–177.

Reed, R., Johnson-Barnard, J., Baker, W., 1996. Contribution of roads to forest fragmentation in the Rocky Mountains. Conservation Biology 10, 1098–1106.

Ross, S.M., 1986. Vegetation change on highway verges in south-east Scotland. Journal of Biogeographic 13, 109–113.

Safford, H.D., Harrison, S.P., 2001. Grazing and substrate interact to affect native vs. exotic diversity in roadside grasslands. Ecological Applications 11, 1112–1122.

Saunders, S.C., Mislivets, M.R., Chen, J., Cleland, D.T., 2002. Effects of roads on landscape structure within nested ecological units of

the Northern Great Lakes Region, USA. Biological Conservation 103, 209–225.
Schmidt, W., 1989. Plant dispersal by motor cars. Vegetation 80, 147–152.
Simberloff, D., Relva, M.A., Nuñez, M., 2002. Gringos En El Bosque: introduced tree invasion in a native *Nothofagus/Austrocedrus* forest. Biological Invasions 4, 35–53.
Sousa, W.P., 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15, 353–391.
Spooner, P.G., 2005. Response of *Acacia* species to disturbance by roadworks in roadside environments in southern New South Wales, Australia. Biological Conservation 122, 231–242.
Spooner, P.G., Lunt, I.D., Briggs, S.V., Freudenberger, D., 2004. Effects of soil disturbance from roadworks on roadside shrubs in a fragmented agricultural landscape. Biological Conservation 117, 393–406.
Tabarelli, M., Mantovani, W., Peres, C.A., 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. Biological Conservation 91, 119–127.
Thomson, J.W.J., 1940. Relic prairie areas in central Wisconsin. Ecological Monographs 10, 685–717.
Tomimatsu, H., Ohara, H., 2004. Edge effects on recruitment of *Trillium camschatcense* in small forest fragments. Biological Conservation 117, 509–519.
Trombulak, S.C., Frissell, C.A., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14, 18–30.
Turner, I.M., 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of Applied Ecology 33, 200–209.
Tyser, R.W., Worley, C.A., 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (USA). Conservation Biology 6, 253–262.
Ullmann, I., Bannister, P., Wilson, J.B., 1998. Lateral differentiation and the role of exotic species in roadside vegetation in southern New Zealand. Flora 193, 149–164.
United Nations Environment Programme/World Conservation Monitoring Centre, 2000. A global overview of protected areas on the World Heritage list of particular importance for biodiversity, UNEP/World Conservation Monitoring Centre, Cambridge, UK.
Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Reimanke, M., Westbrooks, R., 1997. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21, 1–16.
Warwick, S.I., Wall, D.A., 1998. The biology of Canadian weeds. 108. *Erucastrum gallicum* (Willd.) O.E. Schulz. Canadian Journal of Plant Science 78, 155–165.
Watkins, R.Z., Chen, J., Pickens, J., Brosofske, K.D., 2003. Effects of forest roads on understory plants in a managed hardwood landscape. Conservation Biology 17, 411–419.
Williamson, J., Harrison, S., 2002. Biotic and abiotic limits to the spread of exotic revegetation species. Ecological Applications 12, 40–51.
Wilson, S.D., Tilman, D., 2002. Quadratic variation in old-field species richness along gradients of disturbance and nitrogen. Ecology 83, 492–504.
Witkowski, E.T.F., Wilson, M., 2001. Changes in density, biomass, seed production and soil seed banks of the non-native invasive plant, *Chromolaena odorata*, along a 15 year chronosequence. Plant Ecology 152, 13–27.
Zika, P.F., 1990. Range expansions of some grasses in Vermont, USA. Rhodora 92, 80–89.