Role of Light Availability and Dispersal in Exotic Plant Invasion along Roads and Streams in the H. J. Andrews Experimental Forest, Oregon

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Abstract: *We examined the roles of dispersal mechanism, a biological barrier; light availability, an environmental barrier; and level of disturbance, a physical barrier, in explaining the spatial patterns of exotic plant species along road and stream segments in a forest landscape in the western Cascade Range of Oregon (U.S.A.). The presence or absence of 21 selected exotic plant species and light levels were observed along 0.3- to 1.0-km transects within four habitat types. Each habitat represented a different level of disturbance: high-use roads, low-use roads, abandoned roads, and streams in the H. J. Andrews Experimental Forest. Nearly 300 50 × 2-m sampling units were surveyed along five transects in each habitat type. We used ordination (nonmetric multidimensional scaling) and logistic regression to analyze data. All of the nearly 200 sampling units along roads with high and low levels of vehicle traffic contained at least one exotic plant species, and some contained as many as 14. Streams that were most recently disturbed by floods 20–30 years ago and abandoned spur roads with no traffic for 20–40 years also had numerous exotic species. Roads and streams apparently serve multiple functions that enhance exotic species invasion in this landscape: they act as corridors or agents for dispersal, provide suitable habitat, and contain reservoirs of propagules for future episodes of invasion. Species-specific dispersal mechanisms, habitat characteristics, and disturbance history each explain some, but not all, of the patterns of exotic species invasion observed in this study.*

Disponibilidad de Luz y Mecanismos de Dispersión e Invasión de Plantas Exóticas a lo Largo de Caminos y Arroyos en el Bosque Experimental H. J. Andrews, Oregon

Resumen: *Para explicarnos los patrones espaciales de plantas exóticas a lo largo de segmentos de caminos y de arroyos en un paisaje boscoso del Cascade Range, Oregon, examinamos el papel de los mecanismos de dispersión (una barrera biológica), de la luz (una barrera ambiental) y del nivel de perturbación (una barrera física). Se observaron la presencia o ausencia de 21 especies de plantas exóticas y los niveles lumínicos a lo largo de transectos de 0.3 a 1.0 km en cuatro tipos de hábitat. Cada hábitat presentaba diferentes niveles de perturbación: caminos de uso frecuente, caminos de uso no frecuente, caminos abandonados y arroys en el Bosque Experimental H. J. Andrews. Se trabajó en cerca de 300 unidades de muestreo de 50 × 2 m, a lo largo de cinco transectos en cada tipo de hábitat. Para el análisis de datos utilizamos ordenamiento (escala multidimensional no-numérica) y regresión logística. Las cerca de 200 unidades de muestreo a lo largo de caminos con uso frecuente y no frecuente presentaron por lo menos una especie de planta exótica y algunas presentaron hasta 14. Los arroyas recientemente perturbados por inundaciones (20–30 años) y los caminos abandonados hace 20 - 40 años también presentaron numerosas especies exóticas. Aparentemente, los caminos y arroyos realizan varias funciones que acrecientan la invasión de especies exóticas en este paisaje. Actúan como corredores o agentes dispersores, proporcionan hábitats adecuados y contienen reservorios de propágulos para futuras invasiones. Los mecanismos específicos de dispersión, las características del hábitat y los antecedentes de perturbación permiten explicar algunos, pero no todos, los patrones de invasión de especies exóticas observados en este estudio.*

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Introduction

Research on exotic plant invasions traditionally has focused on two aspects: biological characteristics of invading species and habitat characteristics of the invaded site. Few research efforts have focused on the spatial aspect of invasion in landscapes, although the process is inherently spatial. The conceptual framework underlying our study is inherently spatial and combines traditional approaches to invasion research with the concept that invasion occurs when all "barriers" that previously excluded a plant species from a site are removed (Johnstone 1986). In our model (Fig. 1), exotic plant invasion can occur when propagules move from their parent population (the source) to colonize an invasion site (the sink). Barriers may be biological, physical, and/or environmental (Fig. 1). Low seed production or viability or dispersal limitations (biological barriers) may affect the spread of exotic species. Distance or obstacles in the landscape such as oceans, mountains, or closed-canopy forest (physical barriers) may affect the pathway along which invaders travel. Unsuitable light, soil, or moisture conditions (environmental barriers) also affect invasion.

Disturbance facilitates plant invasion by overcoming physical and environmental barriers (Fox & Fox 1986; Hobbs 1991; Lepart & Debussche 1991). For example, physically disturbed habitat and an increased ratio of forest edge to interior in fragmented old-growth forests in Indiana may have facilitated invasion by exotic species (Brothers & Spingarn 1992). Changes in the historical disturbance regime may create opportunities for invasion, and interactions between different disturbances may have synergistic effects (Hobbs & Huenneke 1992).

Roads and streams may facilitate invasion both by providing corridors in a landscape and by creating or channeling disturbance. Roads are especially well-documented sites for exotic plant invasion (Tyser & Worley 1992; Wilson et al. 1992; Lonsdale & Lane 1994) and represent obvious dispersal corridors in a landscape. Riparian zones along streams, too, may serve as corridors for dispersal of plants (Gregory et al. 1991), including exotic

species (Pysek & Prach 1993; Pyle 1995; Tabacchi et al., unpublished manuscript). Perhaps less obvious but also important are the disturbances that occur along roads and streams, notably road construction, traffic, maintenance activities, and flooding. These disturbances may facilitate some biological processes such as dispersal (via vehicle tires or streamflow), remove some biological barriers such as competitors, overcome physical barriers such as impenetrable closed-canopy forest, and modify environmental characteristics such as light levels in potential invasion sites.

Roads and streams may be arrayed along a gradient of disturbance regimes (sensu Sousa 1984) and hence may illustrate the relationship between disturbance and invasion. Roads with heavy traffic and regular maintenance experience higher frequency and severity of disturbance than roads with less traffic and maintenance. Abandoned roads and streams may experience infrequent but severe disturbances.

"Ideal" invasive plants are well equipped to overcome barriers and respond to disturbance. Although species possessing these characteristics are not always successful invaders (Newsome & Noble 1986), the biological characteristics of a generalized, ideal invasive plant include broad germination requirements, a short life cycle, self-compatibility, early flowering, high seed production, good long- and short-distance dispersal mechanisms, and the capacity to reproduce vegetatively (Baker 1965; Bazzaz 1986; Rejmanek & Richardson 1996). Dispersal mechanisms in particular have a powerful influence on species distribution (Howe & Smallwood 1982; Green 1983; Primack & Miao 1992), including patterns of invasion by exotic plants (McEvoy & Cox 1987; Chambers & MacMahon 1994; Higgins et al. 1996). If biological barriers prevent dispersal away from the parent population, then invasion of a new site cannot occur. For example, species with heavy seeds confront a biological barrier to invasion if there is no dispersal agent to transport seeds away from the source.

We expect that roads and streams have spatial distributions of exotic plant species which reflect the removal of biological, physical, and environmental barriers. We examined the roles of dispersal mechanism, a biological barrier; light availability, an environmental barrier; and level of disturbance, a physical barrier, in explaining the spatial patterns of exotic plant species along road and stream segments in a forest landscape in the western Cascade Range of Oregon (U.S.A).
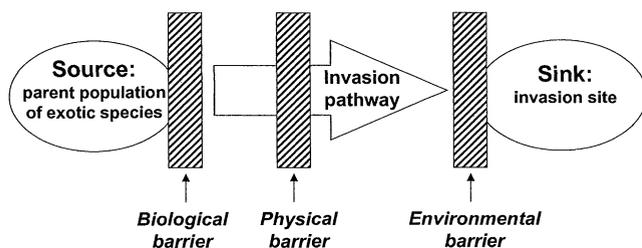

Figure 1. Conceptual model of exotic plant invasion as it is affected by biological, physical, or environmental barriers. Invasion can occur only when all barriers are removed.

Methods

Study Site

We collected field data at the H. J. Andrews Experimental Forest (hereafter, HJA), a Long-Term Ecological Re-

search site sponsored by the National Science Foundation and located along the western slope of the Cascade Range about 80 km east of Eugene, Oregon. The HJA occupies about 64 km^2, and elevations range from 410 to 1630 m. The maritime climate of the region includes warm, dry summers and mild, wet winters.

Native vegetation is dominated by conifers in the *Tsuga heterophylla* (western hemlock) zone at lower elevations and in the *Abies amabilis* (Pacific silver fir) zone at higher elevations (Franklin & Dyrness 1988). Exotic plants (species not native to Oregon) represented about 10% of the 480 taxa found in the HJA in the early 1970s (Franklin & Dyrness 1971). Some of these, primarily grasses and legumes, were introduced deliberately as part of the seeding mixes used to stabilize cut slopes during road construction (Dyrness 1967, 1970, 1975). Others were probably introduced accidentally as seeds or vegetative material.

Most of the 119-km road network in HJA was established in the 1950s and 1960s, but some additional roads were constructed at higher elevations in the 1970s and 1980s (Wemple et al. 1996). All roads are gravel, except for a 3-km paved stretch near the entrance to HJA, and are bordered by 16 km^2 of clearcuts created from 1948 to 1990 (Jones & Grant 1996). Disturbance along the roads is primarily by vehicle traffic and maintenance activity, including road grading, ditch clearing, and trimming of overhanging vegetation. Landslides and blowdowns also affect discrete segments of the road network.

The 138-km stream network is a fifth-order mountain stream. The road network crosses first- to fifth-order segments of the stream network at hundreds of points in the HJA (Wemple et al. 1996). Disturbance along streams is primarily by floods (Jones & Grant 1996; Perkins 1997) and debris flows (Swanson & Dyrness 1975) and associated transport of sediment (Grant & Wolff 1990) and wood (Nakamura & Swanson 1994).

Target Species

We chose 21 exotic species (hereafter, target species) for our study (Table 1) that had been previously recorded at HJA (personal observation; Franklin & Dyrness 1971). The species represent 9 plant families and 17 genera, are native to Europe and Asia and have a range of dispersal ability. We classified target species using a modified version of a classification scheme created by Dansereau and Lems (1957) for dispersal types (Table 1). Each target species was classified according to its morphological appendages that affect the seeds' ability to be carried by wind or a vector such as an animal, bird, or vehicle. Target species also were classified by logarithmically scaled seed-weight classes defined by Baker (1972), because lighter seeds may be more easily transported by wind or some other vector than heavier seeds.

Field Sampling

We identified four habitat types: high-use roads, low-use roads, abandoned roads, and streams. All transect locations were chosen arbitrarily without preconceived bias (B. McCune, Oregon State University, unpublished course packet), except that approximately 10% of the basin above 1200 m was not sampled. Because the distribution of some species may be limited by elevation, transects were placed in locations below 1200 m to minimize bias of this factor. Road-use categories were based on a subjective evaluation of the frequency of vehicle traffic (A. McKee and F. Swanson, personal communication): high-use roads, daily to weekly use, and low-use roads, less than biweekly use. Categories also represented the relative frequency and intensity of road maintenance activities. Abandoned roads were considered no longer passable by vehicles. Abandonment of roads occurred in the 1950s and 1960s in four of the transects. In a fifth transect the road may have been used for access into the Blue River basin in the late 1970s (A. Levno, personal communication), but it is no longer accessible. The stream transects represented one third-order, two fourth-order, and two fifth-order reaches. At the time of our survey (1994), the stream network had been recovering for 20–30 years from record floods, although smaller floods continued to create small light gaps associated with bank scour and individual treefall.

Five belt transects 0.3–1.0 km long were established in each of the four habitat types (20 total; Fig. 2). Transect lengths varied as follows: 950–1000 m for high-use roads; 800–1000 m for low-use roads; 300–500 m for abandoned roads; and 500 m for streams. The lower limits on transect length were dictated by the actual length of each road segment. The maximum length of 500 m in abandoned roads and streams was dictated by time constraints. To determine whether the varying transect length may have influenced results, we analyzed a subset of the data from the longer transects along high-use and low-use roads, but the results were not substantially different. The full data set is reported here.

Each transect was subdivided into sampling units 50 m long that were parallel to the road or stream; the width of each sampling unit was about 2 m from both sides of the road or stream edge. Data on light levels and the presence or absence of all target species were collected in each sampling unit in the summer of 1994. Light levels were classified into one of three categories based on ocular estimates of the approximate percentage of overstory canopy cover: high light (0–30% cover), medium light (31–70% cover), and low light (71–100% cover).

Data Analysis

We analyzed data with descriptive summaries, ordination, and logistic regression. Descriptive summaries

Table 1. Dispersal classification scheme and frequency of occurrence of target exotic species at H. J. Andrews Experimental Forest.

Morphological characters[a]	Species	Mean seed weight[b] (mg)	Seed weight class[c]	Frequency of occurrence (species group[d])
Diaspore has obvious morphological appendages that may aid dispersal appendages are thin, light, flexible	Cirsium arvense	1.57	7	2
	Cirsium vulgare	2.85[e]	7	1
	Hypochaeris radicata	0.81[e]	6	1
	Lactuca muralis	0.43[e,f]	6	1
	Senecio jacobaea	0.28	5	2
	Taraxacum officinale	0.86	6	3
appendages are short, stiff, spiny or glandular	Daucus carota	1.50[e]	7	2
Diaspore has no obvious morphological appendages diaspore has juicy or fleshy outer layers	Rubus discolor	5.24[e]	8	3
diaspore has hard outer layer	Chrysanthemum leucanthemum	0.22	5	1
	Cytisus scoparius	7.60	8	3
	Dactylis glomerata	0.90	6	2
	Digitalis purpurea	0.09	4	3
	Holcus lanatus	0.22[e]	5	2
	Hypericum perforatum	0.13	5	1
	Lotus corniculatus	1.20	7	3
	Plantago lanceolata	1.55	7	2
	Plantago major	0.20	5	2
	Rumex acetosella	0.41	6	3
	Trifolium hybridum	0.88	6	3
	Trifolium pratense	1.90	7	3
	Trifolium repens	0.64	6	1

[a] Adapted from Dansereau and Lems (1957).

[b] Salisbury (1942) is source, except as noted.

[c] Based on seed-weight classes in Baker (1972): class 4, 0.032–0.099 mg; class 5, 0.100–0.315 mg; class 6, 0.316–0.999 mg; class 7, 1.000–3.161 mg; class 8, 3.162–9.999 mg.

[d] Group 1, most frequent; group 2, moderately frequent; group 3, least frequent.

[e] Source is H. and I. Baker, unpublished data curated in The Baker Seed Herbarium, The Berry Botanic Garden, Portland, Oregon. Summaries of the seed-weight data were published in Baker (1972).

[f] Seed weight for Lactuca muralis was not available. Value listed is an average of mean seed weights for L. saligna and L. serriola.

were frequencies (i.e., proportion of sampling units with target species) and frequency distributions by target species and habitat type.

Ordination (nonmetric multidimensional scaling, or NMS) was used to examine general patterns of target species along the transects. The NMS is a nonparametric multivariate ordination technique that is well suited to ecological data sets (Minchin 1987) because it can be used for data that are nonnormal or on arbitrary or discontinuous scales (McCune & Mefford 1995). With NMS the p-dimensional space of the original data set is reduced such that "stress" (inverse measure of fit) is minimized in the k-dimensional ordination space.

Input data were arcsin–square root–transformed proportions of each species in each transect, and the analysis was run by means of the Sorenson distance measure, following McCune (Oregon State University, unpublished course packet) and McCune and Mefford (1995).

The NMS analysis was run with data for 14 species; rarely occurring species (average proportion based on frequency of <0.05 per transect) had insufficient data and were excluded. One species (*Cytisus scoparius*) was an outlier (SD of mean distance >2) and was also excluded from this portion of the analysis. Significance of the outcome was determined by means of a Monte Carlo simulation for the appropriate number of dimensions ($p < 0.05$) and the coefficient of determination (r^2), which describes the proportion of variance explained by each axis in the ordination solution (B. McCune, Oregon State University, unpublished course packet).

We used logistic regression to test hypotheses regarding the probability of a target species occurring in a particular habitat type and under particular light levels. Two logistic regression models were run for each of 13 species with a mean frequency of >15% in at least one
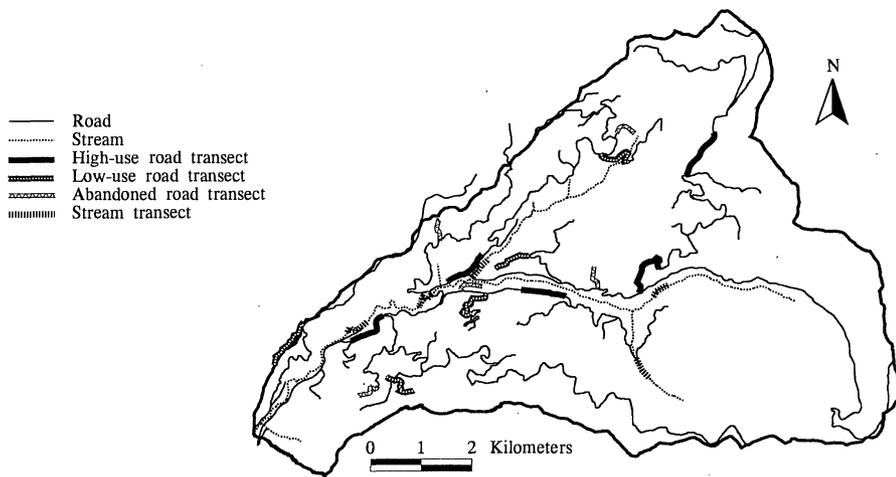
Road
Stream
High-use road transect
Low-use road transect
Abandoned road transect
Stream transect

0   1   2 Kilometers

Figure 2. Location of transects in the H. J. Andrews Experimental Forest.

habitat type. The response variable was frequency of a target species in both models; the categorical explanatory variable was habitat type (high-use road, low-use road, abandoned road, and stream) in one model and light level (high, medium, and low) in the other. A multiple logistic regression approach was precluded because habitat type and light level were correlated. Logistic regression models were run with SAS (version 6.10), and model significance was evaluated based on chi-squared values with $p < 0.05$. Models were interpreted by means of odds ratios calculated from the coefficient estimates (Hosmer & Lemeshow 1989). The odds ratio represents the relative probability of occurrence of the response variable (presence of target species) in a given category of the explanatory variable (e.g., high-use roads or high light levels) relative to a reference category (e.g., streams, low light).

sampling units had no target species at all. A modal value of 1 target species occurred per sampling unit in both habitat types, and over 60% of the sampling units had only 1-3 target species. The maximum number of target species per sampling unit was 8 and 7 for abandoned roads and streams, respectively.

Ordination results indicated that transects along high-use and low-use roads were floristically similar. In contrast, transects along abandoned roads and streams were highly variable and floristically dissimilar to high-use and low-use roads (Fig. 5). The final solution for the NMS ordination analysis was two-dimensional and statistically significant ($p < 0.05$, cumulative $r^2 = 0.93$). The r^2 values for axes 1 and 2 were 0.28 and 0.65, respectively. Unlike other ordination techniques, axis numbers in an

Results

Habitat type was strongly related to light level in this survey (Fig. 3). The 50-m sampling units along high-use and low-use roads had predominantly medium and high light levels, whereas sampling units along abandoned roads and streams had predominantly low light levels.

Exotic species were more frequent along high-use and low-use roads than on abandoned roads or streams (Fig. 4). Target species were frequent and normally distributed along high-use and low-use roads (Fig. 4a & 4b). At least one target species occurred in each of the 195 sampling units. A modal value of 6 and 7 target species occurred per sampling unit along high-use and low-use roads, and over 60% of the sampling units had 4-7 target species. As many as 13 or 14 target species occurred in some sampling units. In contrast, target species were less frequent and distributions were skewed along abandoned roads and streams (Fig. 4c & 4d). Some of the 95
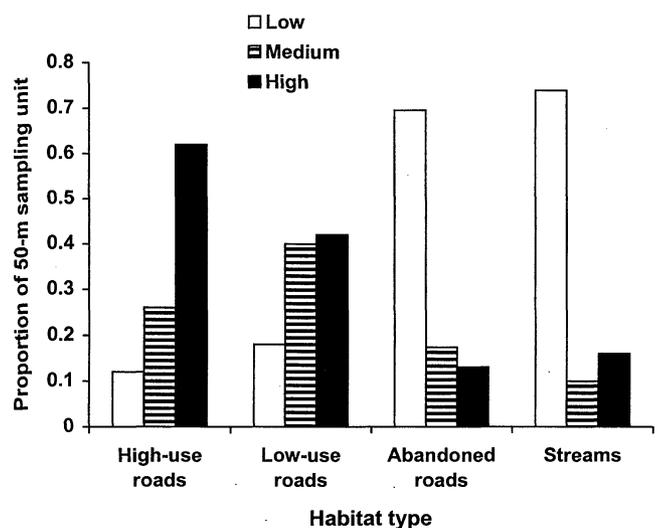

Figure 3. Distribution of light classes (low, medium, and high) along each habitat type surveyed in the H. J. Andrews Experimental Forest.
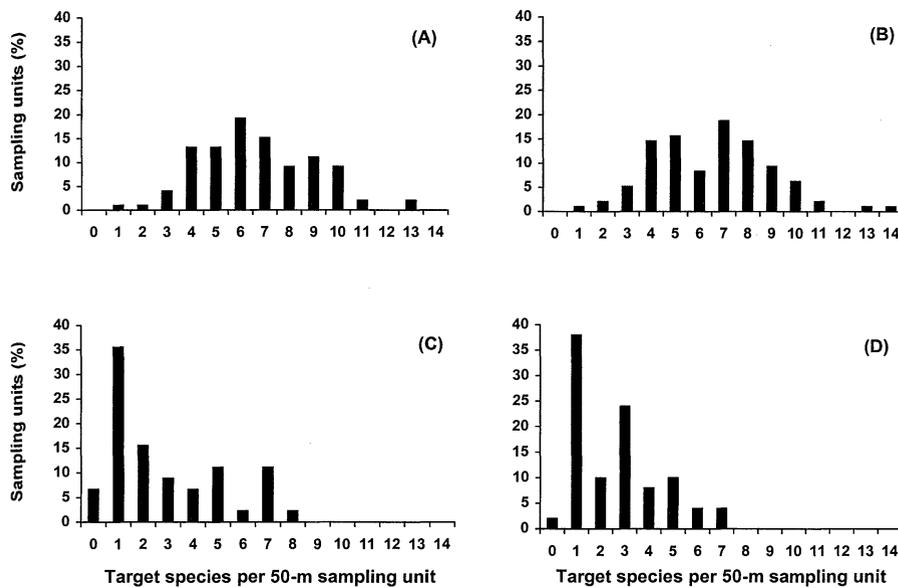
Figure 4. Frequency distribution of target exotic species in 50-m sampling units along (a) high-use roads (b) low-use roads (c) abandoned roads, and (d) streams.

NMS analysis are arbitrary (McCune & Mefford 1995), so the lower r^2 value for axis 1 is not unusual.

Because the transects were clustered to the left along axis 1 (Fig. 5), it was difficult to interpret what underlying factor(s) may explain the relationships on this axis. Axis 2 of the ordination is suggestive of a gradient of disturbance intensity and light levels, which generally increase from low to high along this axis (Fig. 5). Six species (*Chrysanthemum leucanthemum, Cirsium vulgare, Daucus carota, Hypericum perforatum, Hypochaeris radicata,* and *Plantago lanceolata*) had strong positive correlations with axis 2 ($r > 0.75$). All other target species were also positively correlated with this axis, except *Lactuca muralis,* which was negatively correlated ($r = -0.35$).

Frequently occurring exotic species showed clear trends with habitat type or light level but rather complex relationships with dispersal ability (Fig. 6a). Six species (*Hypericum perforatum, Chrysanthemum leucanthemum, Cirsium vulgare, Hypochaeris radicata, Trifolium repens,* and *Lactuca muralis*) were most frequent, occurring in >50% of the 50-m sampling units for at least two of the habitat types. All of these species except *Cirsium vulgare* have relatively light seeds (classes 5 and 6, 0.13–0.81 mg), and three of the species (*Lactuca muralis, Hypochaeris radicata,* and *Cirsium vulgare*) have thin, light appendages that may aid in dispersal (Table 1). *Cirsium vulgare* seeds are the heaviest of this group, but their large plumed achenes compensate for the extra weight, and they fly well in light breezes. Not all of the species with light-weight seeds or with wind-dispersal abilities were frequent, however (Table 1).

The six most frequent species were significantly more frequent with increasing disturbance and light levels, ex-

cept for *Lactuca muralis,* which was most frequent at both the highest and lowest disturbance and light levels (Table 2; Fig. 6a). Odds ratios indicated that these species were 9–61 times more likely to occur on high-use roads than on streams, 6–47 times more likely to occur on low-use roads than on streams, and 1–4 times more likely to occur on abandoned roads than on streams (Table 2). They also were 3–25 times more likely to occur in high than low light levels, and 3–9 times more likely to occur in medium than low light levels (Table 3). In contrast, *Lactuca muralis* was 25–50 times *less* likely to occur on roads than streams (Table 2) and 2.5–5 times less likely to occur in high or medium than low light levels (Table 3).

Moderately frequent exotic species showed muted but detectable trends with habitat type and light level and complex relationships with dispersal ability (Fig. 6b). Seven species (*Daucus carota, Plantago major, Plantago lanceolata, Dactylis glomerata, Holcus lanatus, Cirsium arvense,* and *Senecio jacobaea*) were moderately frequent, occurring in 10–49% of the 50-m sampling units for at least two of the habitat types. Seed weights for these species ranged from light (class 5, 0.20 mg) to moderately heavy (class 7, 1.57 mg), and only two of the species (*Senecio jacobaea, Cirsium arvense*) have thin, light appendages, whereas one species (*Daucus carota*) has other appendages that may aid in dispersal (Table 1). These species were more frequent (although significance level was weak) on sites with greater disturbance and high light levels (i.e., on high- and low-use roads vs. abandoned roads and streams), except for *Holcus lanatus* and *Cirsium arvense* (Tables 2 & 3; Fig. 6b). Although odds ratios were not statistically significant, these species were 2–16 times more frequent on high-use roads than streams, 2–31 times more
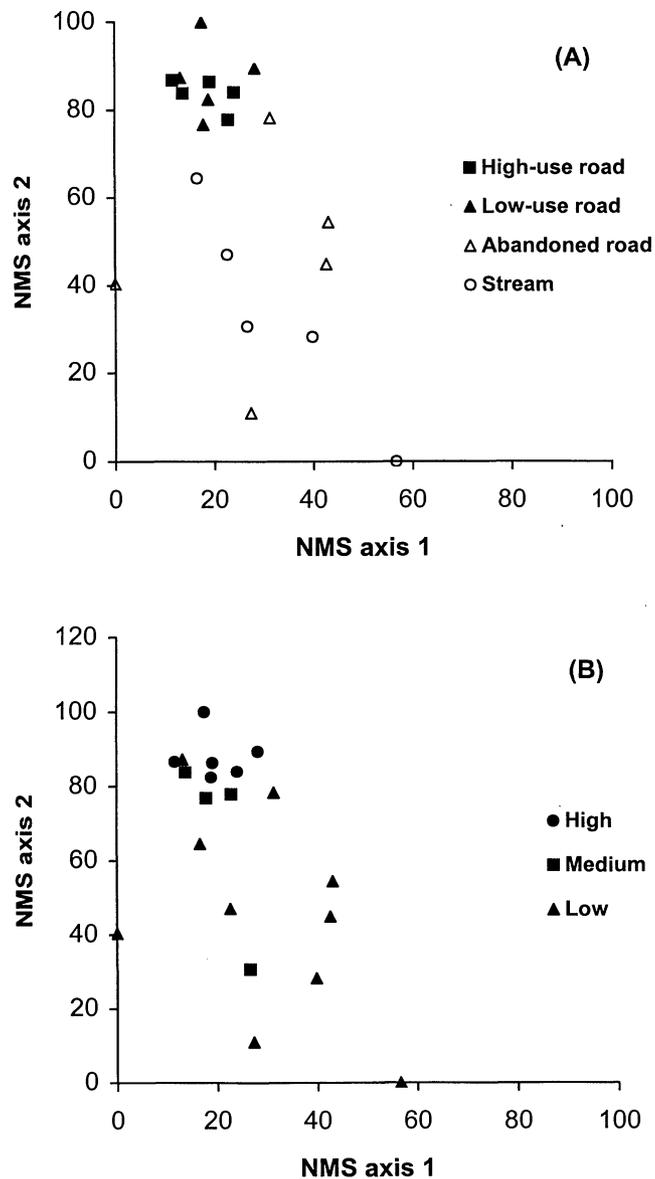
Seed weights for these species ranged from very light (class 4, 0.09 mg) to very heavy (class 8, 7.60 mg), and all but one of these species lacked morphological appendages (Table 1). The frequency of occurrence of these species showed no clear trends with disturbance or light levels, although they were less likely to be present along streams than along roads (Fig. 6c).

Discussion

Exotic plant species are widely distributed in the HJA, but they are almost completely restricted to roadsides, streams, and recent clearcuts. Exotic species occur in clearcuts adjacent to roads, but they are rare in canopy gaps or on recent landslides, and they are almost absent from the soil seedbank under mature or old-growth forest (Miles & Swanson 1986; Halpern 1989; Halpern & Spies 1995; Parendes 1997; London 1999). In contrast, all of the nearly 200 50 × 2-m sampling units along high- and low-use roads contained at least one exotic species, and some contained as many as 14 different exotic plant species. Six exotic species occurred in more than half of the 50-m sampling units in the 10 roughly 1-km transects sampled along high- and low-use roads. Streams that were most recently disturbed by floods 20–30 years ago and abandoned spur roads that have had no traffic for 20–40 years also had numerous exotic species. Exotic species apparently have overcome barriers to invasion along road and stream networks in the HJA, consistent with the findings of other studies (Forcella & Harvey 1983; DeFerrari & Naiman 1994).

Roads and streams enhance exotic species invasion in this landscape by acting as corridors or agents for dispersal, providing suitable habitats, and containing reservoirs of propagules for future episodes of invasion. Species-specific dispersal mechanisms, habitat characteristics, and disturbance history each explain some but not all of the patterns of exotic species observed in this study.

Some authors (e.g., Reichard & Hamilton 1997) have suggested that invasion success depends more on species characteristics than species–environment interactions. In our study, potential for dispersal based on seed morphology was only partially related to invasion success. The most frequently occurring species had seed morphological characteristics (special appendages or fairly light seeds) that suggest a high potential for dispersal by wind or by adhesion of wetted, plumed seeds to animals (Ridley 1930), whereas less frequently occurring species tended to have heavier seeds. Two of the least-frequent target species (*Cytisus scoparius* and *Rubus discolor*, both shrubs) had the heaviest seeds. On the other hand, *Digitalis purpurea* has the lightest seeds of the target species and was one of the least fre-

Figure 5. Nonmetric multidimensional scaling (NMS) ordination results overlayed with (a) habitat type and (b) light level.

frequent on low-use roads than streams, and roughly as frequent on abandoned roads as streams (Table 2). They also were 1–8 times more frequent in high than low light levels and 1–4 times more frequent in medium than low light levels (Table 3).

The least frequent species showed no detectable trends with habitat type and light levels, and they had complex relationships with dispersal ability (Fig. 6c). Eight species (*Cytisus scoparius, Trifolium pratense, Rumex acetosella, Lotus corniculatus, Taraxacum officinale, Rubus discolor, Trifolium hybridum*, and *Digitalis purpurea*) were present in <10% of the 50-m sampling units for at least three of the habitat types (Fig. 6c).
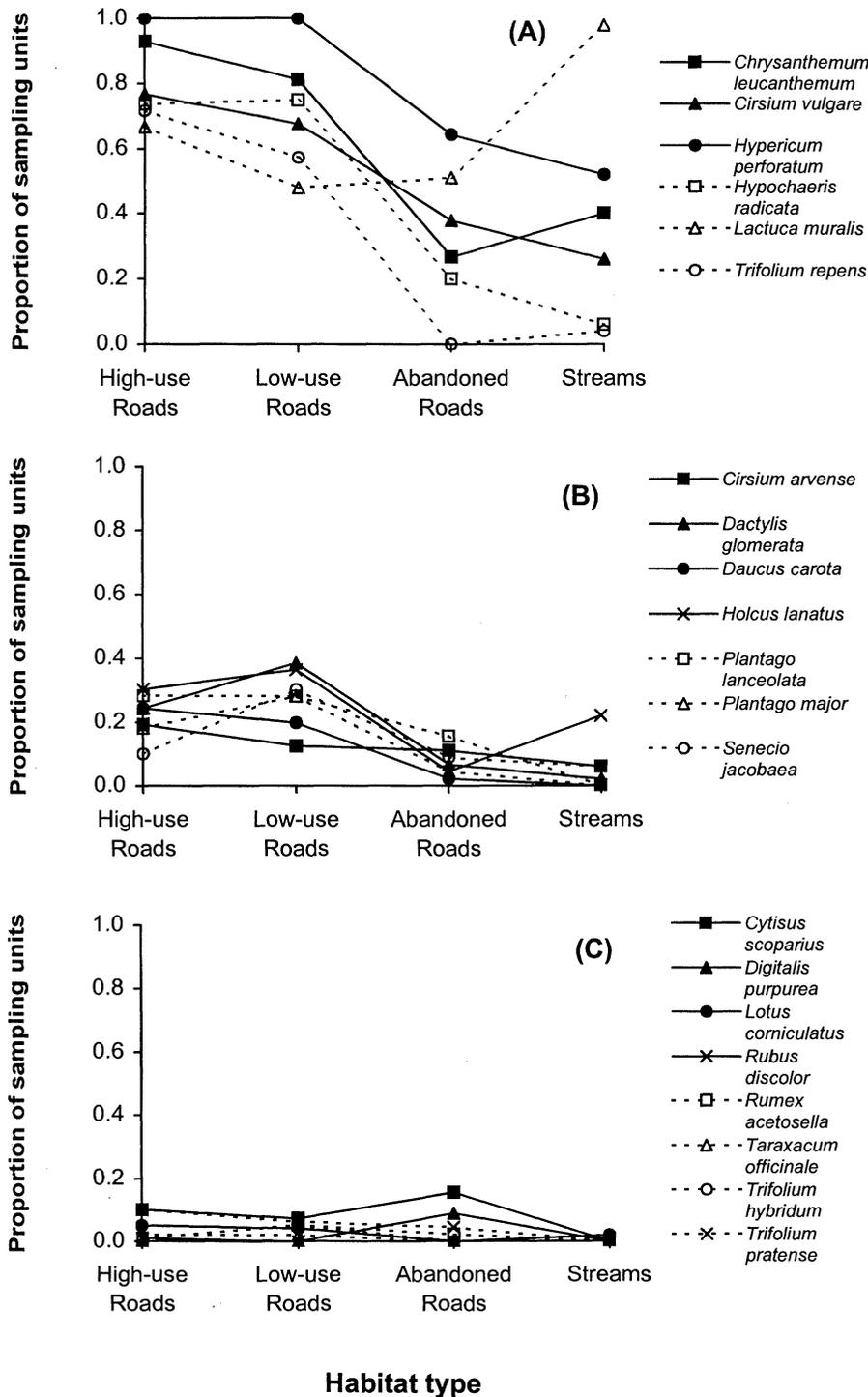
Figure 6. Frequency distribution of target exotic species in 50-m sampling units along each habitat type: (a) most frequent (≥0.5 in at least two habitat types); (b) moderately frequent (>0.1 and <0.5 in at least two habitat types); and (c) least frequent (≤0.1 in at least three habitat types).

quently occurring species. Although our approach to classifying dispersal potential (Dansereau & Lems 1957) worked well for us, other measures of dispersal, such as more complex classification schemes or observations of dispersal (e.g., Ridley 1930; van der Pijl 1982), might produce different outcomes. Other life-history traits such as production, longevity, and germination requirements of seeds, or species interactions such as competi-

tion and predation, also may explain exotic-species distributions. Dispersal along roads may be confounded by vehicle traffic that transports propagules on tires. Additional work may be needed to sort out biological effects (dispersal ability) and disturbance effects (vehicle transport) on the observed patterns.

Ecosystem properties, notably light and moisture limitations, explained part of exotic-species distributions.

Table 2.　Results of logistic regression models, with target species presence as the response variable and habitat type as the explanatory variable.[a]

Species	χ^2	$p > \chi^2$	Habitat type comparison[b]	Estimate	SE	$p > \chi^2$	Odds ratio
Chrysanthemum leucanthemum	12.27	0.0065	HR vs. S	2.98	1.34	0.026	20
			LR vs. S	1.87	1.07	0.081	6
			AR vs. S	−0.61	1.22	0.62	1
Cirsium arvense	2.09	0.55	HR vs. S	1.31	1.07	0.22	4
			LR vs. S	0.81	1.11	0.47	2
			AR vs. S	0.67	1.26	0.59	2
Cirsium vulgare	22.70	0.0001	HR vs. S	2.24	0.58	0.0001	9
			LR vs. S	1.79	0.56	0.0015	6
			AR vs. S	0.55	0.64	0.40	2
Dactylis glomerata	6.91	0.075	HR vs. S	2.75	2.47	0.26	16
			LR vs. S	3.43	2.45	0.16	31
			AR vs. S	1.25	2.79	0.65	3
Daucus carota[c]	14.98	0.0018					
Holcus lanatus	2.42	0.49	HR vs. S	0.43	1.20	0.72	2
			LR vs. S	0.71	1.19	0.55	2
			AR vs. S	−1.80	2.37	0.45	0.2
Hypericum perforatum[d]	33.40	0.0001	AR vs. S				2
Hypochaeris radicata	53.44	0.0001	HR vs. S	3.78	0.92	0.0001	44
			LR vs. S	3.85	0.92	0.0001	47
			AR vs. S	1.37	1.01	0.18	4
Lactuca muralis	11.87	0.0079	HR vs. S	−3.20	2.11	0.13	0.04
			LR vs. S	−3.98	2.11	0.059	0.02
			AR vs. S	−3.85	2.15	0.074	0.02
Plantago lanceolata[c]	8.50	0.037					
Plantago major[c]	8.65	0.034					
Senecio jacobaea	7.92	0.048	HR vs. S	0.57	1.13	0.62	2
			LR vs. S	1.91	1.05	0.068	7
			AR vs. S	0.42	1.31	0.75	2
Trifolium repens[e]	30.64	0.0001	HR vs. S				61
			LR vs. S				32

[a] *Separate models were run for each species.*
[b] *HR, high-use road; LR, low-use road; AR, abandoned road; S, stream.*
[c] *Estimates of logistic regression coefficients are not meaningful because of insufficient data in abandoned road and stream habitat types. Species was not present in streams so comparisons of habitat type and odds ratios are not meaningful.*
[d] *Present in all 50-m sampling units along all high- and low-use road transects, so neither estimates of logistic regression coefficients nor comparisons between high-use road vs. stream or low-use road vs. stream are meaningful. Odds ratio for abandoned road vs. stream was calculated from raw data.*
[e] *Estimates of logistic regression coefficients are not meaningful because of insufficient data for abandoned road and stream habitat types. Species was not present in abandoned road. Therefore, abandoned road vs. stream comparison and odds ratios are not meaningful. Odds ratios for high-use road vs. stream and low-use road vs. stream were calculated from raw data.*

Exotic species were most numerous and most diverse in areas with high light and were least numerous and relatively depauperate in areas with low light. In contrast to the other 20 target species in this study, *Lactuca muralis* was most frequent and abundant along streams, which suggests that it may be more tolerant of shade or saturated soils or may require more soil moisture than other species. A record flood in February 1996, after our survey, created high light levels along streams at HJA; post-flood monitoring in these locations might reveal important aspects of light and moisture controls on exotic plant frequencies.

The gradient of disturbance (from high- to low-use roads, to abandoned roads, to streams) is correlated with light levels and also explains part of present-day patterns of exotic species. High frequencies of all but one of the 21 target exotic plant species were significantly associated with high light levels and frequent, severe disturbance resulting from high road traffic and road-maintenance activities such as grading. In contrast, low frequencies of exotic plants were associated with low light levels and two or more decades without severe disturbance: abandoned roads had had no traffic since the 1950s or 1970s, and streams had not been affected by a severe flood since the 1970s. The strong inverse relationship between frequency and disturbance level was most clearly expressed for exotic species that appeared to have overcome all barriers (i.e., they reached nearly 100% frequency in some portion of the study area), but a relationship with disturbance was muted for exotic species with frequencies <30% and indistinguishable for species with frequencies <10%.

The history of disturbance in the HJA also may explain some aspects of current distributions of exotic plant spe-

Table 3.   Results of logistic regression models, with target species presence as the response variable and light level as the explanatory variable.*

Species	χ^2	$p > \chi^2$	Light level comparison	Estimate	SE	$p > \chi^2$	Odds ratio
Chrysantemum leucanthemum	12.17	0.0023	high vs. low	1.17	0.40	0.0033	3
			medium vs. low	1.20	0.45	0.0081	3
Cirsium arvense	0.86	0.65	high vs. low	−0.051	0.46	0.91	1
			medium vs. low	0.38	0.47	0.42	1
Cirsium vulgare	25.63	0.0001	high vs. low	1.89	0.41	0.0001	7
			medium vs. low	1.34	0.43	0.0019	4
Dactylis glomerata	7.12	0.028	high vs. low	1.11	0.44	0.012	3
			medium vs. low	0.86	0.50	0.082	2
Daucus carota	20.57	0.0001	high vs. low	2.07	0.56	0.0002	8
			medium vs. low	1.91	0.60	0.0014	7
Holcus lanatus	3.41	0.18	high vs. low	−0.16	0.44	0.71	1
			medium vs. low	0.65	0.43	0.13	2
Hypericum perforatum	38.58	0.0001	high vs. low	2.31	0.52	0.0001	10
			medium vs. low	2.20	0.59	0.0002	9
Hypochaeris radicata	69.58	0.0001	high vs. low	3.20	0.44	0.0001	25
			medium vs. low	1.75	0.44	0.0001	6
Lactuca muralis	14.11	0.0009	high vs. low	−1.47	0.41	0.0004	0.2
			medium vs. low	−1.03	0.46	0.025	0.4
Plantago lanceolata	10.48	0.0053	high vs. low	1.17	0.46	0.011	3
			medium vs. low	1.39	0.49	0.0047	4
Plantago major	7.30	0.026	high vs. low	0.50	0.45	0.26	2
			medium vs. low	1.21	0.45	0.0075	3
Senecio jacobaea	0.34	0.84	high vs. low	−0.09	0.44	0.84	1
			medium vs. low	0.20	0.47	0.67	1
Trifolium repens	42.04	0.0001	high vs. low	2.49	0.45	0.0001	12
			medium vs. low	2.08	0.48	0.0001	8

**Separate models were run for each species.*

cies, and it suggests a potential for future expansion. Building on ideas from other studies (e.g., Forcella 1985; Pysek & Prach 1993; U.S. Office of Technology Assessment 1993), we speculate that species introduced to the HJA some decades ago may have persisted at a low frequency for varying periods of time before beginning an expansion phase, in this case initiated by disturbances. In HJA, patches of bare substrate created by natural disturbance processes, such as treefall, landslides, or floods, are small and often isolated. In contrast, road construction and road grading are "exotic disturbances" that create long, connected bare areas on hillslopes and may possibly increase the magnitude of disturbance patches in streams by enhancing the severity of flood and landslide disturbances (Jones & Grant 1996; Swanson et al. 1998). Major disturbances in HJA over the 50 years preceding this study consisted of construction of the road network (<2% of area) and patch clearcut logging (20% of area) during the 1950s and 1960s, and extreme floods in 1964, 1972, and 1977 (Jones & Grant 1996; Wemple et al. 1996). The exact dates of introduction of the 21 target exotic species in HJA are unknown. All but three species (*Dactylis glomerata, Plantago lanceolata*, and *Trifolium hybridum*), however, were included in a 1971 checklist of plants at HJA, whereas only one (*Holcus lanatus*) was described as "widespread" (Franklin &

Dyrness 1971). *Digitalis purpurea* was reported in small patches in the HJA in the 1970s (J. Franklin, personal communication), is still rare throughout the Cascade Range, but it is widespread in the Oregon Coast Range. *Chrysanthemum leucanthemum* was described as "occasional" in 1971 (Franklin & Dyrness 1971) but was among the most frequently encountered species in our study. Some exotic species presently at low frequency at HJA may be triggered to expand in the future, perhaps in conjunction with some disturbance or change in the environment.

Our study revealed how some aspects of space (i.e., barriers) might influence exotic plant invasion in several types of road and stream segments. But these findings do not address the broader question of how the arrangement of road and stream segments in a landscape might influence broad-scale patterns of exotic plant invasion. Parendes (1997) and Parendes and Jones (unpublished data) take a broader view of this problem, examining the entire road network in a landscape and addressing how connectivity and arrangement of networks might have contributed to landscape-scale patterns of exotic plant invasion. The spread of exotic plants along discrete invasion pathways, such as road and stream corridors, is an important aspect of the invasion process and warrants further investigation.

Our study provides only limited species-specific recommendations for management of exotic plants. Some species, such as *Hypericum perforatum*, which is toxic to some animals and has been the target of biological control efforts elsewhere, may be too widespread at HJA for complete eradication. *Cytisus scoparius* and *Rubus discolor* were relatively infrequent in our study, but given that they both have become serious pests in other similar habitats, proactive control measures may be appropriate before their populations expand much farther.

In a general sense, our study provides support for the idea that disturbance and light level may be useful for managing exotic plant invasion along road networks in conifer forest landscapes of the Pacific Northwest. In our study, exotic species were most prevalent in areas that had high light levels and high road use, although they also occurred in shaded areas that were disturbed (streams) and in undisturbed areas that were somewhat less shaded than mature or old-growth forest (abandoned roads). Forest succession after disturbance, canopy closure, and declining light levels were associated with declines in all but one of the target exotic species. As natural resource management goals on public lands change from an emphasis on resource (i.e., timber) extraction to an emphasis on watershed restoration with concomitant reductions in budgets for management activities, more road closures may occur. Management activities such as road closures (but other measures as well) that promote canopy closure (such as over an old road bed) are likely to reduce the numbers of exotic species in the existing vegetation. On the other hand, the prevalence of exotic species in streams and abandoned roads after two decades of relatively low disturbance suggests that complete eradication of exotic plant species in forest landscapes of the Pacific Northwest is unlikely to be achieved.

Acknowledgments

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