AN ABSTRACT OF THE DISSERTATION OF

Laurie Anne Parendes for the degree of Doctor of Philosophy in Geography presented on June 27, 1997. Title: Spatial Patterns of Invasion by Exotic Plants in a Forested Landscape.

Abstract approved: _____

Julia Allen Jones

Few landscapes are immune to invasion by exotic plant species. The forested landscape in the western Cascade Range of Oregon appears to have some barriers to invasion, but the extensive road network provides a corridor and habitat for a suite of exotic species to enter and become established. This study examined how biological factors and physical factors interact to produce the observed spatial pattern of invasion in the forested landscape, particularly along roads and streams. Results from a seed bank study indicated that dispersal barriers may be preventing movement of some exotics from the road into mature forest. Exotics that were found in the seed bank within mature forest have a high potential for dispersal, especially by wind. However, no exotic plants were found in the existing vegetation within the mature stands, suggesting that environmental barriers were preventing their establishment.

Surveys at 1-km and 100-km scales showed that the most frequent species also had a high potential for dispersal. However, dispersal potential did not explain all of the

observed spatial patterns. Confounding factors such as time since introduction, length of the "lag phase" after introduction, and various biological factors may have a strong influence on the spatial patterns of invasion.

Exotic plant distribution at the 1-km scale varied among four habitat types that represent different levels of disturbance. The number and frequency of exotic species were much higher along high-use and low-use roads than along abandoned roads or streams. This pattern may reflect the more favorable light conditions along currently used roads, and the lower light levels along abandoned roads and streams may be barriers to invasion for many exotics. However, confounding factors such as competitive exclusion by natives and opportunities for dispersal may also be operating. Spatial patterns of exotics along the 100-km road network provide additional evidence that environmental barriers influence the pattern of invasion. Spatial analysis results provided evidence of patchiness and spatial gradients for some target species along some roads. The heterogeneous arrangement of patches on the landscape suggests that the process of invasion is generating multiple, discrete "foci" from which further invasion can occur.

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Spatial Patterns of Invasion by Exotic Plants in a Forested Landscape

by

Laurie Anne Parendes

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APPROVED:

Major Professor, representing Geography

Chair of Department of Geosciences

Dean of Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Laurie Anne Parendes, Author

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DEDICATION

This dissertation is dedicated to

Nancy Bartley Parendes,

Mark Allen Wickenheiser,

and

Owen Parendes Wickenheiser

in honor of

past, present, and future.

Spatial Patterns of Invasion by Exotic Plants in a Forested Landscape

Chapter 1

Introduction

Among the many global effects of human activity has been the introduction (either accidental or deliberate) of plant species into areas in which they are not native (Baker 1986; Mooney and Drake 1989). Once introduced, some species are able to greatly expand their distribution in this new environment by successfully invading areas in which they previously did not occur.

Exotic plant species are important in an ecological context because their successful invasion may seriously disrupt the functional and structural properties of an ecosystem. Examples of potential impacts include alteration of water and mineral cycling, reduced ecosystem productivity, alteration of natural fire regimes, and replacement of native species (Mooney and Drake 1989). Invasive exotic species are also important in a management context, such as in nature reserves or managed forests. If the impacts are significant enough to disrupt the management goals, measures to control or eradicate the exotic plants may be necessary and may be costly (Usher 1988).

Researchers have approached the topic of biological invasions from two main points of view. One approach has been to focus on the biological characteristics of invading exotic species (e.g., Baker 1986; Bazzaz 1986; Newsome and Noble 1986; Heywood 1989; di Castri 1990; Kornas 1990). A generalized "ideal" invasive plant species is one with 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. However, possession of certain characteristics does not always correlate well with successful invasion.

A second approach has been to focus on the physical characteristics that promote invasibility of communities or ecosystems. Generalizations tend to concentrate on the important role of disturbance in facilitating invasion (Fox and Fox 1986; Swincer 1986; Crawley 1987; Hobbs 1989; Rejmanek 1989; Lepart and Debussche 1991), although disturbance may not always be required (Ewel 1986).

As noted by DeFerrari and Naiman (1994), few studies of the process of invasion by exotic species have been conducted at the landscape scale. The relatively recent interest in landscape ecology has focused attention on temporal and spatial scales in relation to pattern-process interactions. Hierarchy theory has been invoked to provide guidelines for understanding the relationships between different scales; in general, at a given scale of observation, smaller-scale factors interact to generate observed phenomena at higher levels and larger-scale factors exert control over those at lower levels (Urban et al. 1987). Factors at the scale of individual plants, populations, communities, or ecosystems (such as life history characteristics, competition, succession, disturbance) interact to produce patterns at the higher landscape scale; factors at the regional scale (such as climate) control patterns at the lower landscape scale.

Examining the pattern of distribution of exotic species at the landscape scale may yield some additional insight about the process of invasion. Johnstone (1986) proposed a generalized explanation of invasion: it is caused by removing all barriers that previously excluded a plant species from a site. Figure 1.1 presents a conceptual model of the process

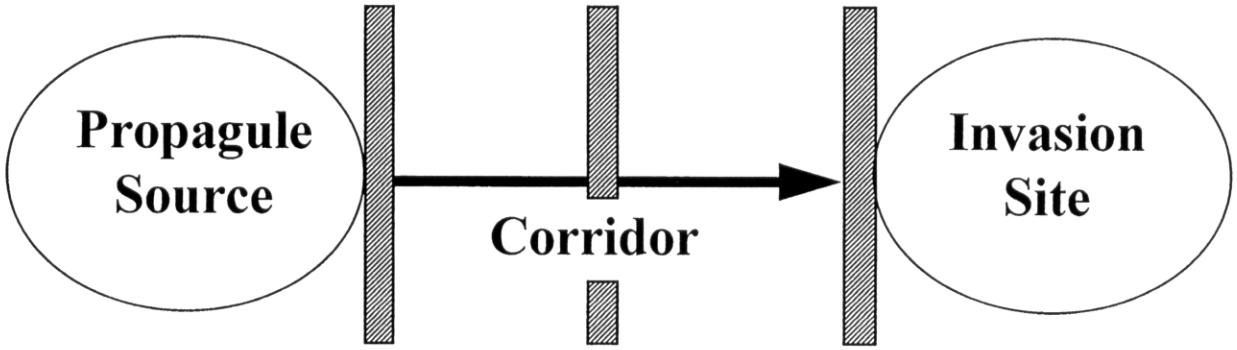

Figure 1.1. Conceptual model of exotic plant invasion. Vertical bars represent biological, physical, or environmental barriers. Invasion can only occur when all barriers are removed.

of invasion in which invasion occurs in a landscape when all biological, physical, and ecological barriers are removed at all scales and propagules are able to move along a corridor to an invasion site. For example, a biological barrier that may influence invasion is dispersal limitation; within the same landscape, exotic plants with wind dispersal mechanisms may have a different pattern of distribution than plants that rely on animals or gravity for dispersal. Even if a propagule reaches a site, physical barriers, such as light levels, may prohibit successful invasion. Exotic plants that require high light levels may not be able to germinate in a closed canopy forest; disturbances that create light gaps may promote invasion if there is a corridor from the propagule source to the gap.

The patterns in the occurrence of exotic plants in a forested landscape present a good opportunity to examine the process of invasion. This landscape is composed of a mosaic of disturbed versus undisturbed patches as well as networks of forest roads and streams. Disturbances include natural events such as fire, windthrow, landslides, and floods as well as human-induced perturbations such as timber harvest and road construction. The linear road network is of particular interest in studying invasions because it may provide habitat for invaders as well as a corridor by which exotic plants gain access to previously unoccupied areas. Some species may be able to further spread into the surrounding landscape if suitable habitat is present. Riparian areas along stream networks are also of interest in this context because they are subject to frequent disturbance (Tabacchi et al. 1994, unpublished manuscript) and may provide an alternate corridor for invasive species in a forested landscape. Comparisons of the road versus stream network may provide some insight on invasion in this landscape.

The research presented in this dissertation was conducted at the H.J. Andrews Experimental Forest (HJA), located about 80 km (50 miles) east of Eugene, Oregon, in the Cascade Range. This forest is part of the network of Long-Term Ecological Research sites, and reliable records exist regarding the history of both human-induced and natural disturbances (such as road construction, timber harvest, floods, landslides). Road construction and timber harvest began in the late 1940s, and little additional harvest or road construction occurred after the 1970s. Approximately 10% of the 480 plant species found in the HJA are not native [based on a checklist prepared by Franklin and Dyrness (1971)]. Some of these species, such as *Dactylis glomerata*, *Holcus lanatus*, *Lotus corniculatus*, *Trifolium pratense*, and *Trifolium repens*, were introduced in seed mixes that were planted to stabilize slopes after road construction (Dyrness 1967, 1970, 1975), although it is impossible to know if these seed mixes were the primary means by which these species were introduced into the HJA. Most of the exotic plants at the HJA were probably introduced accidentally, and their present distribution reflects their ability to invade the forested landscape.

The central question of this research is how do exotic species characteristics (i.e., biological factors such as dispersal mechanisms) and invasibility of landscape features (i.e., physical factors such as disturbance that increases light availability) interact to produce the observed patterns of invasion by exotic plants at the landscape scale? Chapter 2 presents the results of a seed bank study in which soil samples were taken along the road, 5 m from the road, and 50 m from the road into mature forest in order to determine whether dispersal or environment is limiting the observed distribution of exotic species in the forested landscape. Chapter 3 presents a spatial pattern analysis of exotic plant distribution

along four habitat types (high-use roads, low-use roads, abandoned roads, and streams) in order to examine the interaction between dispersal characteristics and environmental factors. Chapter 4 presents the spatial patterns of distribution of eight target exotic species along the entire road network in the HJA in relation to seven environmental attributes: elevation, precipitation, aspect, solar radiation, age of adjacent cut unit, road age, and road-use level.

Chapter 2

Seed Bank Patterns of Exotic Plants in a Forested Landscape in the Western Cascade Range, Oregon

Laurie A. Parendes

in preparation for journal submission

2.1 Introduction

Soil seed banks have been studied in a variety of habitats (Leck et al. 1989) and their role in succession has been discussed in the literature (Livingston and Allessio 1968; Kellman 1974; Thompson 1978; Donelan and Thompson 1980; Ebersole 1989). After a disturbance, a site may become revegetated by successful germination and establishment of plant species that were already present in the form of buried viable seeds. Other pathways for recolonization are vegetative sprouting from remnant plant material, incoming seed rain from adjacent portions of the site, or transport of propagules from off-site by a dispersal agent or gravity. Seed bank densities tend to be higher under higher levels of disturbance and under lower levels of stress [factors that limit productivity (*sensu* Grime 1979)] (Thompson 1978). Thus, seed densities are predicted to decline during succession, during which the vegetation composition changes from species that are disturbance-adapted to species that are stress-tolerant (Donelan and Thompson 1980).

Seed banks may play an important role in exotic plant invasion, which often involves some type of disturbance. The term invasion is used here to describe a process by which exotic plants are introduced and become established in an area where they previously did not occur. At any given time, the invasion process may be characterized, in part, by the distribution pattern of exotic species. Chambers and MacMahon (1994) suggested that it is essential to understand seed movements and fates in order to control exotic species. The initial dispersal of seeds (or other propagules) to a new site is a crucial step in exotic plant invasion. If seeds of exotic species are already present in the soil, then they may be readily available to recolonize a site after a disturbance. Understanding the

spatial and temporal patterns of seed sources and seed banks may provide additional insight on the process of invasion.

Most seed bank studies have focused on the dynamics and composition within particular communities. An approach that examined different habitat types within a landscape could consider interactions among different landscape features. Such an approach may be especially important when considering the process of exotic plant invasion, because it may help disentangle whether exotic species are limited by dispersal (i.e., their seeds do not reach a potential invasion site) or environment (i.e., seeds are present in the seed bank, but the species is not in the existing vegetation). As with any component of a seed bank, sources of exotic species may be local or distant. Hume and Archibold (1986), for example, found that a weedy pasture provided an important source of seeds to an adjacent cultivated field, although the effect was greatest up to 7 m from the pasture/field edge and then declined with increasing distance from the pasture; however, two weedy species were found in small numbers at 45 m and 100 m from the pasture. Poiani and Dixon (1995) studied the potential contribution of vegetation in the surrounding landscape to the seed bank composition of Carolina bays. They found significantly more upland weedy species in bays near clearcuts (20 m) than in bays farther from clearcuts (100 m). Most of the weedy species were dispersed by wind, which provides a potentially effective mechanism for seeds to travel some distance from a parent plant and invade a new site (Poiani and Dixon 1995).

Temporal patterns are also important. Since seeds of some species can remain viable in the soil over time (Cook 1980; Kivilaan and Bandurski 1981), presence of exotic species in a soil seed bank can have long-term implications for invasion at a site.

Observations in a forested landscape in western Oregon suggest that many of the exotic plants are restricted to disturbed areas, such as roadsides or recently cut forest patches. Populations of exotics along roads or at other disturbed sites could, theoretically, serve as seed sources for undisturbed features of the landscape, but it is unclear whether exotics are absent from undisturbed mature forest because they are not dispersed there or because the environment is not suitable. Data from a seed bank study can be used to more accurately characterize the invasion potential by different exotic species across this forested landscape. Exotic species that are present in local seed banks have already dispersed and are potential invaders if conditions become appropriate (e.g., after a disturbance).

This study was undertaken to examine the seed bank patterns along forest roads (assumed source of seeds of exotic plants) and known distances into mature forest (where exotics are typically not present in the existing vegetation). Specifically, this research aimed to address several hypotheses: (1) Seeds of exotic species are expected to be concentrated along the road and decrease in abundance away from the road. (2) Dispersal barriers, environment barriers, or both are expected to limit the distribution of some exotic species in this landscape. (3) Exotic species with higher potential for long-distance dispersal (such as wind-dispersed species) are expected to be more widely distributed than other species.

2.2 Methods

2.2.1 Study site

Seed bank samples were collected from the H.J. Andrews Experimental Forest (hereafter, HJA), a National Science Foundation-sponsored Long-Term Ecological Research site located along the western slope of the Cascade Range, about 80 km (50 miles) east of Eugene, Oregon. HJA occupies about 6400 ha (15,800 acres), and elevations range from 410 to 1630 m (1350 to 5340 ft). The maritime climate of the region includes warm, dry summers and mild, wet winters.

The forest vegetation is primarily composed of conifers in the *Tsuga heterophylla* (western hemlock) zone at lower elevations and in the *Abies amabilis* (Pacific silver fir) zone at higher elevations (Franklin and Dyrness 1988). A species list prepared in the early 1970s for the HJA (Franklin and Dyrness 1971) included 480 taxa, about 10% of which are not native to Oregon. Some of the exotic species were deliberately introduced as part of seeding mixes to stabilize cut slopes during road construction (Dyrness 1967, 1970, 1975); these were primarily grasses and legumes. Other exotic plants were probably introduced when seeds or vegetative material were brought in accidentally by various sources, including soil imported during road construction; vehicles or clothing of timber harvest crews, researchers, and other visitors to HJA; livestock that was seasonally grazed in high-elevation meadows; wind or other natural forces from adjacent areas.

HJA was established as a research forest in the late 1940s. Most of the 100-km road network was constructed in the 1950s and 1960s, with some additional construction

in the 1970s and 1980s. Most of the timber harvest also took place in the 1950s and 1960s, with some additional units harvested in the 1970s and 1980s. The main types of disturbance along the road network are vehicle traffic and maintenance activity; landslides and blowdown also affect discrete segments of the network.

2.2.2 Field sampling

Three similar sites (A, B, and C) with a road/forest interface were selected for sampling (Figure 2.1A). Criteria for site selection included the following: the road was used regularly by vehicular traffic, the forest patch was a stand of mature or old-growth trees, and the site was near road transects that had been surveyed for another part of this study. Elevations ranged from 490 to 610 m (1600 to 2000 ft).

Twenty soil samples were collected from three locations (0 m, 5 m, and 50 m from the road edge) at each of the three sites (A, B, and C), for a total of 180 samples. At each location, samples were taken randomly from within a 10 m by 2 m plot that had its long axis oriented parallel to the road (Figure 2.1B). Each soil sample was 50 cm^2 by 5 cm deep (below the litter layer). The 20 samples at each location represented an area of 0.1 m^2. A total of 0.9 m^2 was sampled in this study.

Soil samples were collected in late March 1995, after snowmelt, and placed in individual plastic bags. The bagged samples were placed in cold storage (6 °C; 43 °F) for no more than 1 week in order to prevent early germination and were then transferred to the greenhouse for the remainder of the study.

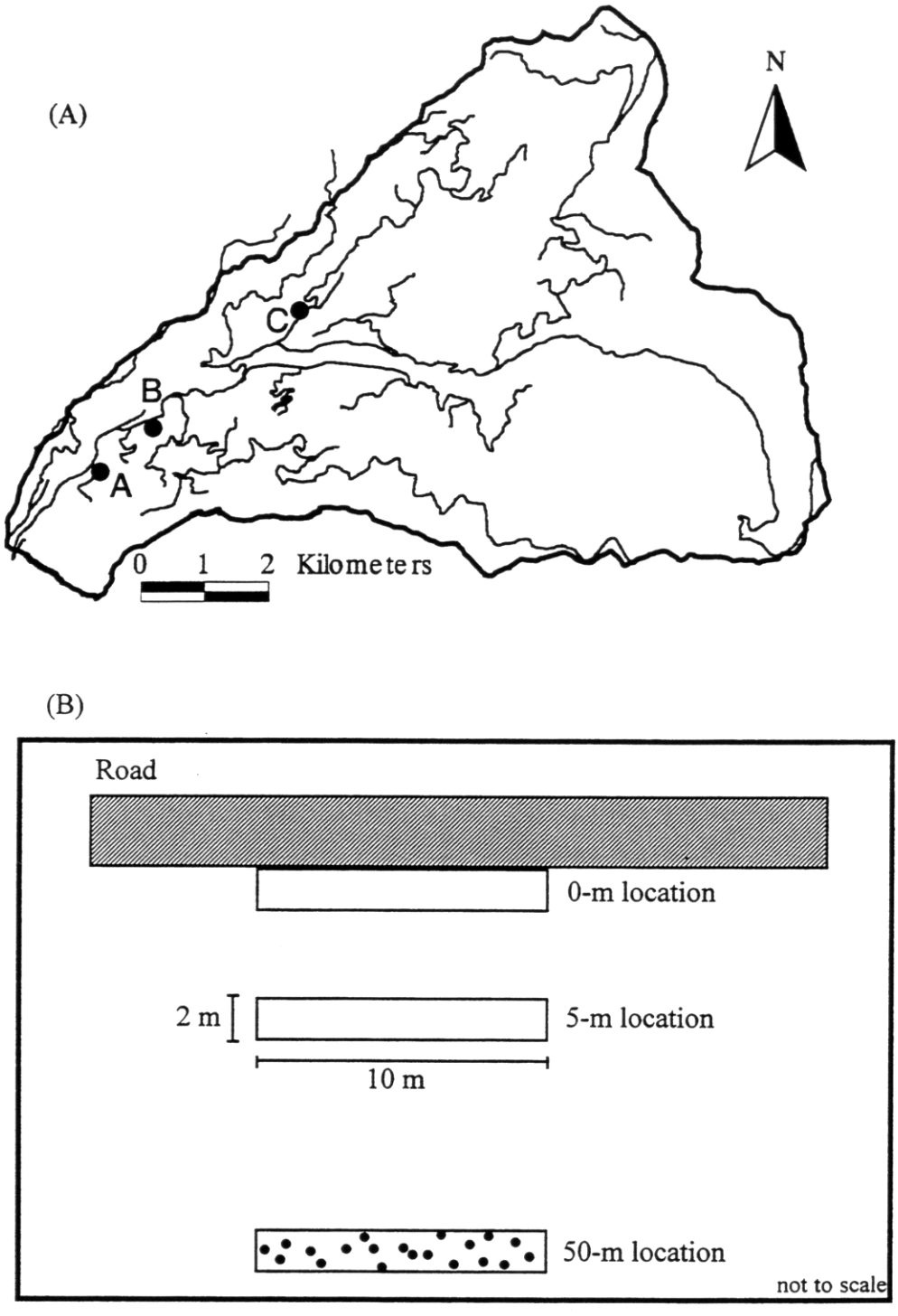

Figure 2.1. Seed bank study: (A) location of three study sites [A, B, and C] and (B) sampling design at each site [dot symbols represent soil samples (20 per sampling location)].

Each location at each site was revisited in June or July 1995. Plants within the sampling plots were listed, and the list was used to compare species observed in the field with species found in the soil seed bank.

2.2.3 Greenhouse work

Greenhouse facilities were at Oregon State University. After the soil samples were removed from cold storage, each was coarsely sifted in order to remove large rock particles and live plant material that could have sprouted. Each sample was then placed in a germination flat in the greenhouse. Small (25 × 25 cm) and large (25 × 50 cm) germination flats were divided into halves and quarters, respectively, so that each could hold either two or four soil samples. The flats were filled with vermiculite to a depth of about 4 cm and the soil samples were spread out on top to a depth of about 1 cm. Two control flats were filled with vermiculite only and were intended to capture any seeds that may have been introduced within the greenhouse.

No special lighting or heating was provided during the course of this study. The samples were watered as needed and fertilized every few weeks with Peters 20-20-20 in order to promote germination and growth. Flats were checked every 1 to 2 weeks and new germinants were marked with a toothpick. Once seedlings were identified, they were removed and either pressed to save the specimen or discarded (if specimens had already been saved). Seedling emergence was monitored from early April to mid-October 1995.

2.2.4 Data analysis

Descriptive summaries were used to examine how the distribution of exotic germinants relates to distance from the road; whether the data indicate if a particular exotic species is limited by dispersal, environment, or both; and how dispersal mechanism influences the pattern of germinants. Jaccard index (Ludwig and Reynolds 1988) was used to compare the similarity of the species composition in the seed bank with that of the existing vegetation.

Logistic regression was used to test hypotheses regarding the probability of a germinant being an exotic, depending on the distance from the road. Because the response variables were based on binary data, the more commonly used linear or multiple regression methods are not appropriate because of their assumptions of linearity and normal errors (Trexler and Travis 1993). Logistic regression is an appropriate analysis tool for the current study, because it examines the functional relationship between a binomial response variable and explanatory variables that are either continuous or categorical (Trexler and Travis 1993). The explanatory variables in this study were categorical (three sites and three sampling locations).

Logistic regression models were computed with SAS (version 6.10), and drop-in-deviance tests (Ramsey and Schafer 1993) were used to evaluate the significance of individual explanatory variables. Final models were evaluated based on χ^2 values. Statistically significant models were defined as those with p-values <0.05. Odds ratios, which represent the probability of the occurrence of the response variable in association with the explanatory variable, provide a useful way of interpreting the logistic regression

models. The odds ratios were calculated from the coefficient estimates (Hosmer and Lemeshow 1989; Ramsey and Schafer 1993) and are interpreted relative to a reference category (50-m sampling location).

2.3 Results

2.3.1 Patterns at site and location scales

A total of 1955 seedlings (representing 2172 germinants per m^2) were found in the soil samples (Table 2.1). Of these, 85% were in soil samples taken at the 0-m locations, 10% were from the 5-m locations, and 5% were from the 50-m locations. Table 2.2 summarizes the density of germinants (number per m^2) at each sampling location. (See Appendix A for information regarding the complete data set.)

Most of the germinants were herbaceous species. None were canopy tree species and only three species were shrub species (*Berberis nervosa*, *Gaultheria shallon*, and *Rubus ursinus*). Over half (53%) of the germinants were monocots, but a large proportion (63% of the monocots) could not be identified beyond genus and therefore could not be designated at exotic or native. One exotic grass (*Festuca arundinacea*) was positively identified at the 0-m location. The rest of the monocots were either native (four species) or unknown (at least eight species) (Table 2.1).

The distribution of monocots was strongly concentrated along the road. Of the 1028 monocots that emerged, 89% were found in samples from the 0-m locations (Table

Table 2.1. Number of seedlings and number of species that germinated in the seed bank study.

Exotic versus native species	Sampling location (distance from road) 0 m	5 m	50 m	Total [a]
	Number of germinant seedlings			
Dicots				
Exotic	466	23	20	509
Native	247	55	68	370
Unknown	36	8	4	48
Total	**749**	**86**	**92**	**927**
Monocots				
Exotic	3	0	0	3
Native	372	0	5	377
Unknown	543	104	1	647
Total	**918**	**104**	**6**	**1028**
Grand total	**1667**	**190**	**98**	**1955**
	Number of species			
Dicots				
Exotic	8	6	5	10
Native	12	10	9	17
Unknown	≥5	≥2	≥3	≥5
Monocots				
Exotic	1	0	0	1
Native	4	0	1	4
Unknown	≥7	≥5	1	≥8
Total	**≥37**	**≥23**	**≥19**	**≥45**

[a] Total number of species across rows are not sums; some species occurred at more than one location.

Table 2.2. Density of germinants (number per m^2), summarized by sampling location. SD = standard deviation; CV = coefficient of variation; N/A = not applicable. Mean calculated from totals for each site (n = 3).

	0-m locations			5-m locations			50-m locations		
Species	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
Exotic Dicots									
Cerastium vulgatum	10	17.3	1.73	0	0	N/A	0	0	N/A
Chrysanthemum leucanthemum	1177	2012.1	1.71	0	0	N/A	0	0	N/A
Cirsium arvense	0	0	N/A	0	0	N/A	3	5.8	1.73
Cirsium vulgare	77	115.9	1.51	10	17.3	1.73	3	5.8	1.73
Hypericum perforatum	217	212.2	0.98	3	5.8	1.73	0	0	N/A
Hypochaeris radicata	3	5.8	1.73	3	5.8	1.73	0	0	N/A
Lactuca muralis	33	25.2	0.75	7	5.8	0.87	3	5.8	1.73
Lactuca serriola	0	0	N/A	3	5.8	1.73	0	0	N/A
Lotus corniculatus	13	23.1	1.73	0	0	N/A	3	5.8	1.73
Senecio sylvaticus	23	15.3	0.65	50	10.0	0.20	53	32.1	0.60
Total exotic dicots	**1553**	**2370.9**	**1.53**	**77**	**20.8**	**0.27**	**67**	**37.9**	**0.57**
Native Dicots									
Anaphalis margaritacea	73	127.0	1.73	10	10.0	1.00	3	5.8	1.73
Berberis nervosa	0	0	N/A	0	0	N/A	3	5.8	1.73
Boykinia occidentalis	297	406.5	1.37	3	5.8	1.73	23	40.4	1.73
Conyza candensis	93	92.9	1.00	0	0	N/A	0	0	N/A
Epilobium angustifolium	0	0	N/A	7	5.8	0.87	0	0	N/A
Epilobium minutum	3	5.8	1.73	0	0	N/A	0	0	N/A
Epilobium watsonii var. *occidentale*	100	70.0	0.70	90	52.9	0.59	127	167.7	1.32
Fragaria vesca	0	0	N/A	7	11.5	1.73	3	5.8	1.73

Table 2.2, Continued.

Species	0-m locations			5-m locations			50-m locations		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
Galium triflorum	30	26.5	0.88	10	17.3	1.73	0	0	N/A
Gaultheria shallon	0	0	N/A	37	63.5	1.73	33	41.6	1.25
Gnaphalium canescens ssp. *thermale*	7	5.8	0.87	0	0	N/A	23	25.2	1.08
Lotus purshianus	0	0	N/A	0	0	N/A	3	5.8	1.73
Prunella vulgaris	97	100.2	1.04	0	0	N/A	0	0	N/A
Ranunculus uncinatus	113	179.3	1.58	0	0	N/A	0	0	N/A
Rubus ursinus	3	5.8	1.73	13	15.3	1.15	0	0	N/A
Vancouveria hexandra	3	5.8	1.73	3	5.8	1.73	0	0	N/A
Viola sempervirens	3	5.8	1.73	3	5.8	1.73	7	11.5	1.73
Total native dicots	**823**	**570.5**	**0.69**	**183**	**96.1**	**0.52**	**227**	**238.6**	**1.05**
Unknown Dicots									
Cirsium sp.	3	5.8	1.73	0	0	N/A	3	5.8	1.73
Erigeron sp.	27	37.9	1.42	3	5.8	1.73	3	5.8	1.73
Gnaphalium sp.	3	5.8	1.73	0	0	N/A	0	0	N/A
Trifolium sp.	3	5.8	1.73	0	0	N/A	0	0	N/A
Unknown dicot - various	83	37.9	0.45	23	15.3	0.65	7	11.5	1.73
Total unknown dicots	**120**	**65.6**	**0.55**	**27**	**20.8**	**0.78**	**13**	**15.3**	**1.15**
Exotic monocots									
Festuca arundinacea	10	10.0	1.00	0	0	N/A	0	0	N/A
Total exotic monocots	**10**	**10.0**	**1.00**	**0**	**0**	**N/A**	**0**	**0**	**N/A**

Table 2.2, Continued.

Species	0-m locations			5-m locations			50-m locations		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
Native Monocots									
Agrostis exarata	1167	1106.0	0.95	0	0	N/A	17	28.9	1.73
Deschampsia elongata	63	92.9	1.47	0	0	N/A	0	0	N/A
Juncus bufonius	7	11.5	1.73	0	0	N/A	0	0	N/A
Juncus ensifolius	3	5.8	1.73	0	0	N/A	0	0	N/A
Total native monocots	**1240**	**1182.0**	**0.95**	**0**	**0**	**N/A**	**17**	**28.9**	**1.73**
Unknown Monocots									
Agrostis sp.	843	1460.7	1.73	323	560.0	1.73	0	0	N/A
Carex sp.	153	265.6	1.73	3	5.8	1.73	0	0	N/A
Juncus sp.	770	1333.7	1.73	13	23.1	1.73	0	0	N/A
Unknown Grass A	10	17.3	1.73	0	0	N/A	0	0	N/A
Unknown Grass B	23	23.1	0.99	3	5.8	1.73	3	5.8	1.73
Unknown Grass C	3	5.8	1.73	0	0	N/A	0	0	N/A
Unknown Cyperaceae	7	11.5	1.73	0	0	N/A	0	0	N/A
Unknown Monocot	0	0	N/A	3	5.8	1.73	0	0	N/A
Total unknown monocots	**1810**	**1537.2**	**0.85**	**347**	**540.0**	**1.56**	**3**	**5.8**	**1.73**
Grand total	**5557**	**2239.7**	**0.40**	**633**	**491.2**	**0.78**	**327**	**256.6**	**0.79**

2.1). The three most abundant monocots were *Agrostis exarata*, an unknown *Agrostis* species, and an unknown *Juncus* species (Table 2.3). Because a large proportion of monocots could not be identified to species, most of the subsequent analyses of the seed bank data focused on the dicots.

As with the monocots, the distribution of dicots was also concentrated along the road. Of the 927 dicots that emerged, 81% were found in samples from the 0-m locations (Table 2.1). Species richness was progressively lower from the 0-m to the 50-m locations, but the difference was not as dramatic as for monocots (Table 2.1). At least two exotic dicot species were found at each sampling site, regardless of distance from the road.

When the data were pooled across sites, the proportion of exotic dicots was highest at the 0-m locations (Figure 2.2A). Although the variability within and between sites was quite high, the dicots in the seed bank samples contained at least 10% exotic species at all sites and sampling locations (except the 50-m location at Site C) (Figure 2.2B).

The most abundant dicot was *Chrysanthemum leucanthemum*, an exotic herb that was only found at the 0-m locations. The seed bank samples contained 353 germinants of this species, most of which were found at site A at the 0-m location (Table 2.3). *Boykinia occidentalis* and *Epilobium watsonii* var. *occidentale*, both native herbs, were the next most abundant dicots (Table 2.3). Their distributions were quite different. *Boykinia occidentalis* was found in at least one site at all three locations, but was most abundant at the 0-m locations. *Epilobium watsonii* var. *occidentale* was found at all sites and all locations, and was more evenly distributed across locations. *Hypericum perforatum*, an

Table 2.3. Total number of germinants in seed bank samples, summarized by site (A, B, C) and sampling location (distance from road).

Species	0-m locations				5-m locations				50-m locations				Grand
	A	B	C	**Total**	A	B	C	**Total**	A	B	C	**Total**	**total**
Exotic Dicots													
Cerastium vulgatum	3	0	0	**3**	0	0	0	**0**	0	0	0	**0**	**3**
Chrysanthemum leucanthemum	350	3	0	**353**	0	0	0	**0**	0	0	0	**0**	**353**
Cirsium arvense	0	0	0	**0**	0	0	0	**0**	0	1	0	**1**	**1**
Cirsium vulgare	21	2	0	**23**	3	0	0	**3**	1	0	0	**1**	**27**
Hypericum perforatum	46	12	7	**65**	0	1	0	**1**	0	0	0	**0**	**66**
Hypochaeris radicata	0	0	1	**1**	1	0	0	**1**	0	0	0	**0**	**2**
Lactuca muralis	1	6	3	**10**	1	0	1	**2**	1	0	0	**1**	**13**
Lactuca serriola	0	0	0	**0**	1	0	0	**1**	0	0	0	**0**	**1**
Lotus corniculatus	4	0	0	**4**	0	0	0	**0**	0	0	1	**1**	**5**
Senecio sylvaticus	4	2	1	**7**	4	5	6	**15**	9	4	3	**16**	**38**
Total exotic dicots	**429**	**25**	**12**	**466**	**10**	**6**	**7**	**23**	**11**	**5**	**4**	**20**	**509**
Native Dicots													
Anaphalis margaritacea	22	0	0	**22**	1	2	0	**3**	0	0	1	**1**	**26**
Berberis nervosa	0	0	0	**0**	0	0	0	**0**	0	0	1	**1**	**1**
Boykinia occidentalis	0	76	13	**89**	0	0	1	**1**	0	0	7	**7**	**97**
Conyza candensis	5	3	20	**28**	0	0	0	**0**	0	0	0	**0**	**28**
Epilobium angustifolium	0	0	0	**0**	1	0	1	**2**	0	0	0	**0**	**2**
Epilobium minutum	0	0	1	**1**	0	0	0	**0**	0	0	0	**0**	**1**
Epilobium watsonii var. *occidentale*	13	15	2	**30**	3	11	13	**27**	2	4	32	**38**	**95**
Fragaria vesca	0	0	0	**0**	0	0	2	**2**	0	0	1	**1**	**3**

Table 2.3, Continued.

Species	0-m locations				5-m locations				50-m locations				Grand
	A	B	C	**Total**	A	B	C	**Total**	A	B	C	**Total**	**total**
Galium triflorum	2	1	6	**9**	0	0	3	**3**	0	0	0	**0**	**12**
Gaultheria shallon	0	0	0	**0**	0	11	0	**11**	8	0	2	**10**	**21**
Gnaphalium canescens ssp. *thermale*	1	0	1	**2**	0	0	0	**0**	0	2	5	**7**	**9**
Lotus purshianus	0	0	0	**0**	0	0	0	**0**	0	0	1	**1**	**1**
Prunella vulgaris	9	20	0	**29**	0	0	0	**0**	0	0	0	**0**	**29**
Ranunculus uncinatus	0	32	2	**34**	0	0	0	**0**	0	0	0	**0**	**34**
Rubus ursinus	0	1	0	**1**	1	3	0	**4**	0	0	0	**0**	**5**
Vancouveria hexandra	1	0	0	**1**	1	0	0	**1**	0	0	0	**0**	**2**
Viola sempervirens	1	0	0	**1**	1	0	0	**1**	2	0	0	**2**	**4**
Total native dicots	**54**	**148**	**45**	**247**	**8**	**27**	**20**	**55**	**12**	**6**	**50**	**68**	**370**
Unknown Dicots													
Cirsium sp.	1	0	0	**1**	0	0	0	**0**	1	0	0	**1**	**2**
Erigeron sp.	0	1	7	**8**	1	0	0	**1**	0	0	1	**1**	**10**
Gnaphalium sp.	1	0	0	**1**	0	0	0	**0**	0	0	0	**0**	**1**
Trifolium sp.	0	0	1	**1**	0	0	0	**0**	0	0	0	**0**	**1**
Unknown dicot - various	11	4	10	**25**	4	2	1	**7**	2	0	0	**2**	**34**
Total unknown dicots	**13**	**5**	**18**	**36**	**5**	**2**	**1**	**8**	**3**	**0**	**1**	**4**	**48**
Exotic Monocots													
Festuca arundinacea	2	1	0	**3**	0	0	0	**0**	0	0	0	**0**	**3**
Total exotic monocots	**2**	**1**	**0**	**3**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**3**

Table 2.3, Continued.

Species	0-m locations				5-m locations				50-m locations				Grand total
	A	B	C	**Total**	A	B	C	**Total**	A	B	C	**Total**	
Native Monocots													
Agrostis exarata	0	130	220	**350**	0	0	0	**0**	0	0	5	**5**	**355**
Deschampsia elongata	0	2	17	**19**	0	0	0	**0**	0	0	0	**0**	**19**
Juncus bufonius	2	0	0	**2**	0	0	0	**0**	0	0	0	**0**	**2**
Juncus ensifolius	0	0	1	**1**	0	0	0	**0**	0	0	0	**0**	**1**
Total native monocots	**2**	**132**	**238**	**372**	**0**	**0**	**0**	**0**	**0**	**0**	**5**	**5**	**377**
Unknown Monocots													
Agrostis sp.	253	0	0	**253**	97	0	0	**97**	0	0	0	**0**	**350**
Carex sp.	0	0	46	**46**	0	0	1	**1**	0	0	0	**0**	**47**
Juncus sp.	0	0	231	**231**	0	0	4	**4**	0	0	0	**0**	**235**
Unknown monocot - various	5	4	4	**13**	0	2	0	**2**	0	0	1	**1**	**16**
Total unknown monocots	**258**	**4**	**281**	**543**	**97**	**2**	**5**	**104**	**0**	**0**	**1**	**1**	**648**
Grand total	**758**	**315**	**594**	**1667**	**120**	**37**	**33**	**190**	**26**	**11**	**61**	**98**	**1955**

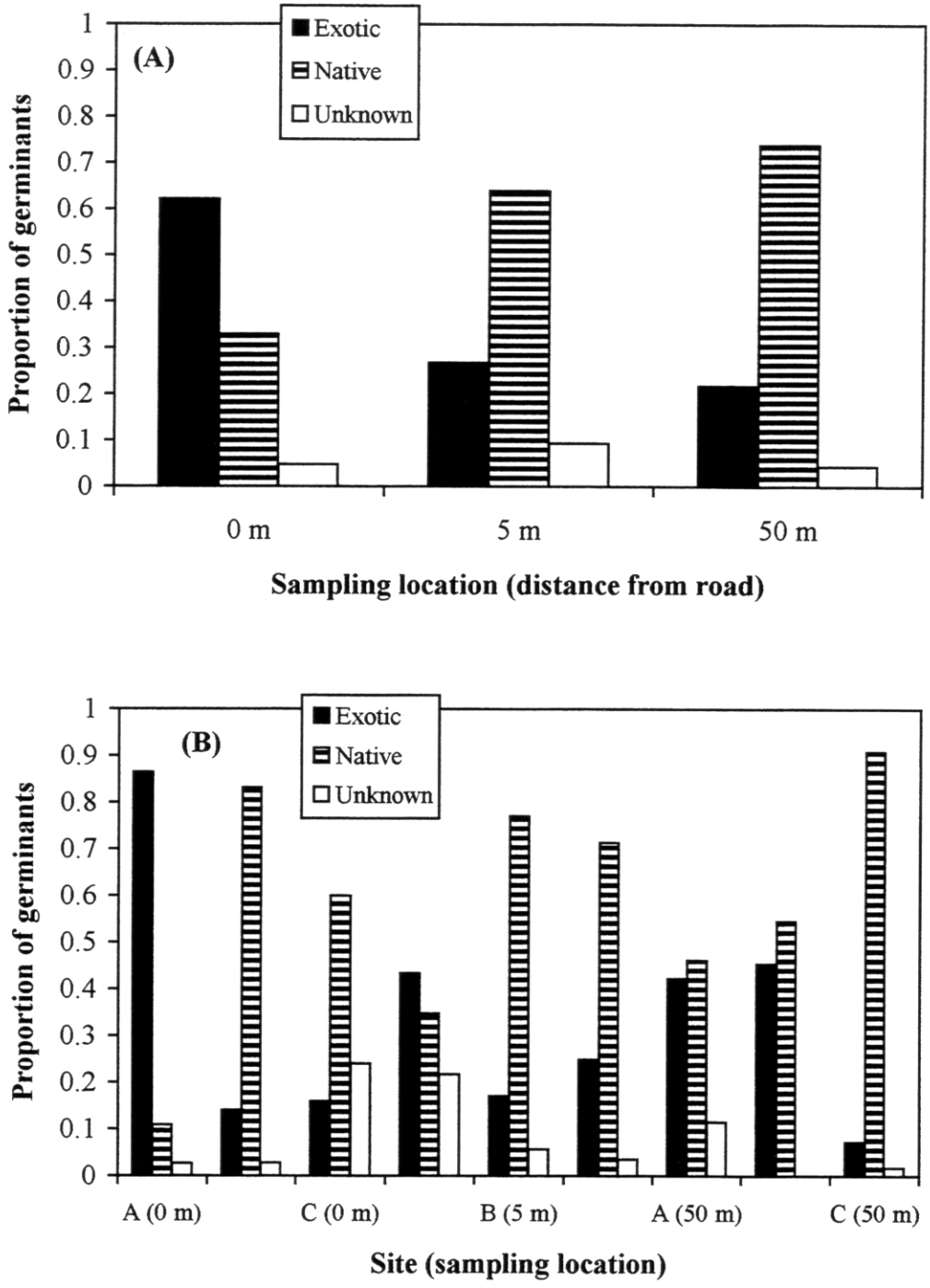

Figure 2.2. Proportion of exotic and native dicot germinants in seed bank samples (A) pooled across sites, and (B) by site and sampling location.

exotic herb, was the next most abundant dicot; most of the germinants were in samples from the 0-m locations (Table 2.3).

The frequency distributions of native and exotic dicots were fairly similar. *Epilobium watsonii* var. *occidentale* (a native) and *Senecio sylvaticus* (an exotic) occurred in 50 and 33 samples, respectively, (of 180 total) and had fairly even distributions between the 0-m, 5-m and 50-m sampling locations (Figures 2.3A and 2.3B). The other native and exotic species occurred in fewer than about 20 of the 180 samples and, for most species, the distributions were concentrated in the 0-m sampling locations (Figures 2.3A and 2.3B).

Of the exotic dicots, only *Cerastium vulgatum* and *Chrysanthemum leucanthemum* were restricted to samples from the 0-m locations (Table 2.3; Figure 2.3B). *Cirsium vulgare*, *Lactuca muralis*, and *Senecio sylvaticus* were found in at least one site at all three locations. In fact, *Senecio sylvaticus* was the most widely distributed exotic dicot. This species was found at all three locations at all three sites, and, as noted above, its distribution was fairly even across locations. *Cirsium arvense* and *Lactuca serriola* were the least abundant exotic dicots; each was only found at one location (50 m and 5 m, respectively) at one site (Table 2.3).

2.3.2 Logistic regression analysis

Three logistic regression models were developed to test hypotheses regarding exotic dicot species in the seed bank samples. The dependent variables in the models

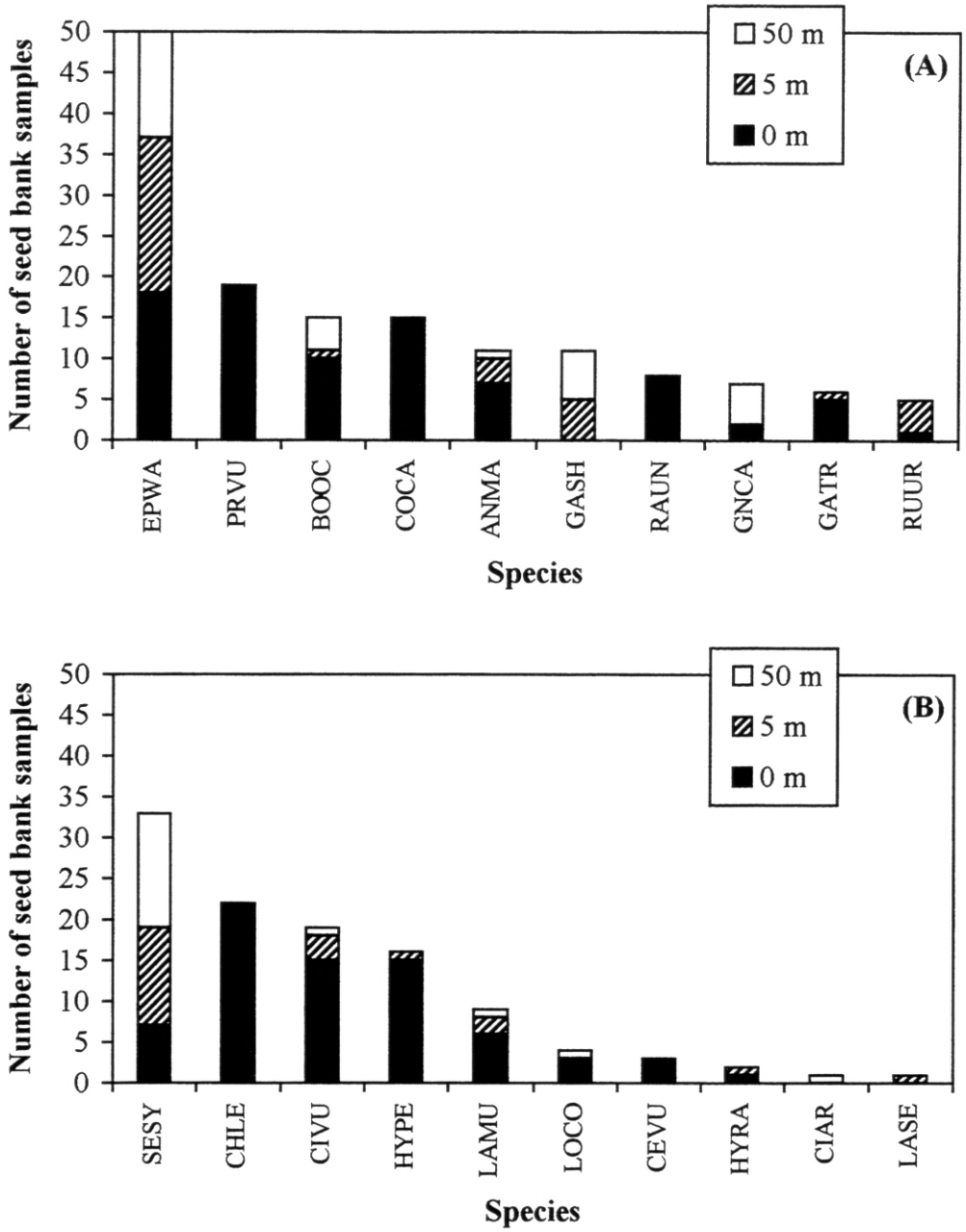

Figure 2.3. Frequency of (A) most common native dicots and (B) exotic dicots in seed bank samples. (EPWA = *Epilobium watsonii* var. *occidentale*; PRVU = *Prunella vulgaris*; BOOC = *Boykinia occidentalis*; COCA = *Conyza canadensis*; ANMA = *Anaphalis margaritacea*; GASH = *Gaultheria shallon*; RAUN = *Ranunculus uncinatus*; GNCA = *Gnaphalium canescens* ssp. *thermale;* GATR = *Galium triflorum*; RUUR = *Rubus ursinus*; SESY = *Senecio sylvaticus*; CHLE = *Chrysanthemum leucanthemum*; CIVU = *Cirsium vulgare*; HYPE = *Hypericum perforatum*; LAMU = *Lactuca muralis*; LOCO = *Lotus corniculatus*; CEVU = *Cerastium vulgatum*; HYRA = *Hypochaeris radicata*; CIAR = *Cirsium arvense*; LASE = *Lactuca serriola)*

varied depending on the hypothesis being tested (as described below). The following two explanatory variables were used to develop the final models:

SITE = sampling site (A, B, or C); and

LOC = sampling location (0, 5, or 50 m from the road).

An interaction term (SITE*LOC) was also tested for significance.

One null hypothesis is that the proportion of germinant dicots that are exotic is not related to distance from the road. The dependent variable in used to test this hypothesis is NUMEX/TOTEMERG, where

NUMEX = number of exotic dicots that germinated in a given seed bank sample;

TOTEMERG = total number of dicot germinants in a given seed bank sample.

The final logistic regression model included the variables SITE, LOC, and an interaction term, SITE*LOC (Table 2.4). The results indicate that the variability among sites is an important factor. At Site A, the odds ratio (which expressed the probability of a germinant being an exotic) was 9 for the 0-m sampling location relative to the 50-m location. The odds ratio was about equal for the 5-m location relative to the 50-m location (Table 2.4). At Site B, the odds ratio was 0.2 for both the 0-m and 5-m locations relative to the 50-m location, indicating that there was lower probability of a germinant being an exotic at the sampling locations closer to the road (Table 2.4). At Site C, the odds ratio was higher for the 5-m location than for the 0-m location (both relative to the 50-m location) (Table 2.4).

Table 2.4. Logistic regression results for dependent variable EXIND/TOTEMERG. Odds ratios are calculated with the 50-m sampling location as the reference class; the other odds ratios are with respect to that location. (Note: 49 of the 180 soil samples had no germinants; these were omitted from this analysis, so n=131)

Final model:

Variable	n	DF	χ^2	Pr>Chi
SITE	131	2	23.26	0.0001
LOC	131	2	1.66	0.44
SITE*LOC	131	4	15.99	0.0030

Odds ratios:

		Sampling location (distance from road)		
Site	Statistic	0 m	5 m	50 m
A	β	2.17	0.05	0
	SE	0.63	0.88	
	odds ratio	9	1	1
	95% CI [a]	3-30	0.2-6	
B	β	-1.63	-1.39	0
	SE	0.97	1.14	
	odds ratio	0.2	0.2	1
	95% CI	0.03-1	0.03-2	
C	β	0.89	1.45	0
	SE	0.92	1.03	
	odds ratio	2	4	1
	95% CI	0.4-15	0.6-32	

[a] CI = Confidence Interval for odds ratio.

A second null hypothesis was that the probability of a seed bank sample having an exotic species is not related to sampling location (distance from the road). The dependent variable in this case was EXYES/N, where

EXYES = 1 if the seed bank sample contained an exotic dicot, 0 otherwise; and

N = 1 (to represent each of the 180 samples).

The final logistic regression model included the variables SITE, LOC, and SITE*LOC (Table 2.5). The results reject the null hypothesis and indicate that the probability of a sample containing an exotic decreased away from the road, although the patterns varied among sites. For all sites, samples from the 0-m location were more likely to have an exotic than were samples from the 50-m location (the reference category). The odds ratio (which expressed the probability that a sample had an exotic) for the 0-m location at Site A was extremely large (Table 2.5) and reflects the fact that all samples at this location had an exotic dicot. The value of this odds ratio is therefore not meaningful, but, clearly, samples from the 0-m location were more likely to have an exotic were than those from the 50-m location. For Sites B and C, samples from the 0-m locations were 4 and 2 times more likely, respectively, to have an exotic than were samples from the 50-m locations (Table 2.5).

The odds ratios of exotics in samples from the 5-m locations relative to the 50-m locations were 0.6 and 1 for Sites A and B, respectively (Table 2.5), suggesting little difference in probability of exotics at these distances from the road. At Site C, the odds

Table 2.5. Logistic regression results for dependent variable EXYES/N. Odds ratios are calculated with the 50-m sampling location as the reference class; the other odds ratios are with respect to that location.

Final model:

Variable	n	DF	χ^2	Pr>Chi
SITE	180	2	18.53	0.0001
LOC	180	2	21.74	0.0001
SITE*LOC	180	4	16.06	0.0029

Odds ratios:

		Sampling location (distance from road)		
Site	Statistic	0 m	5 m	50 m
A	β	25.77	-0.44	0
	SE	75341.04	0.70	
	odds ratio	$1x10^{11}$ [a]	0.6	1
	95% CI [b]		0.2-3	
B	β	1.50	0	0
	SE	0.72	0.76	
	odds ratio	4	1	1
	95% CI	1-18	0.2-4	
C	β	0.64	0.89	0
	SE	0.85	0.83	
	odds ratio	2	2	1
	95% CI	0.4-10	0.5-12	

[a] All samples at this site and sampling location had an exotic dicot. Therefore, this odds ratio is not meaningful and 95% CI was not calculated.
[b] CI = Confidence Interval for odds ratio.

ratio for the 5-m location (relative to the 50-m location) was 2, slightly higher than for the other two sites (Table 2.5).

A third null hypothesis is that the probability of a sample having a native species is not related to distance from the road. The dependent variable in this case is NATYES/N, where

NATYES = 1 if the seed bank sample contained a native dicot, 0 otherwise.

The final logistic regression model included only the variable LOC (Table 2.6). The results do not support the null hypothesis. Rather, they indicate that samples from the 0-m location were about 4 times more likely to have a native species than were samples from the 50-m location. Samples from the 5-m location were about equally likely to have a native as were samples from the 50-m location (Table 2.6). Differences among sites were not significant in this model.

2.3.3 Field surveys

Field surveys revealed fairly low overlap in the species found in the seed bank and the species growing at the sampling sites. Overall, 87 species were found in either the field survey or in the seed bank study (Table 2.7). (Unknown dicots and unknown monocots were lumped and counted as one species each.) Only 16 of these species were found in both the field and in the seed bank in one or more site/location combination; 7 of these are

Table 2.6. Logistic regression results for dependent variable NATYES/N. Odds ratios are calculated with the 50-m sampling location as the reference class; the other odds ratios are with respect to that location.

Final model:

Variable	n	DF	χ^2	Pr>Chi
LOC	180	2	10.92	0.0043

Odds ratios:

	Sampling location (distance from road)		
Statistic	0 m	5 m	50 m
β	1.42	0.33	0
SE	0.46	0.42	
odds ratio	4	1	1
95% CI [a]	2–10	0.6–3	

[a] CI = Confidence Interval for odds ratio.

Table 2.7. Species present in seed bank and in field survey of sites from which soil samples were taken.
O = present in seed bank only; X = present in field survey only; [X] = present in field survey and seed bank.

	0 m from the road			5 m from the road			50 m from the road		
Species	Site A	Site B	Site C	Site A	Site B	Site C	Site A	Site B	Site C
Exotic Dicots									
Cerastium vulgatum	O								
Chrysanthemum leucanthemum	[X]	[X]	X						
Cirsium arvense								O	
Cirsium vulgare	[X]	[X]	X	O			O		
Daucus carota			X						
Hypericum perforatum	[X]	[X]	[X]		O				
Hypochaeris radicata	X		[X]	O					
Lactuca muralis	[X]	[X]	[X]	O		O	O		
Lactuca serriola				O					
Lotus corniculatus	[X]								O
Plantago major	X		X						
Senecio jacobaea	X								
Senecio sylvaticus	O	O	O	O	O	O	O	O	O
Trifolium repens	X	X	X						
Native/Unknown Dicots									
Achlys triphylla	X	X					X		
Anaphalis margaritacea	[X]	X	X	O	O				O
Antennaria racemosa	X		X						
Aralia californica			X						
Berberis nervosa				X	X	X	X	X	[X]
Boykinia occidentalis		[X]	O	X		O			O

Table 2.7, Continued.

Species	0 m from the road			5 m from the road			50 m from the road		
	Site A	Site B	Site C	Site A	Site B	Site C	Site A	Site B	Site C
Chimaphila menziesii					X	X	X	X	X
Cirsium sp.		X							
Clintonia uniflora						X			
Collomia heterophylla			X						
Conyza candensis	O	O	O						
Coptis laciniata			X	X			X	X	X
Cornus canadensis				X		X			
Epilobium angustifolium			X	O		O			
Epilobium minutum			O						
Epilobium watsonii var. *occidentalis*	O	O	O	O	O	O	O	O	O
Erigeron sp.		O	O	O					O
Fragaria sp.			X						
Fragaria vesca						O			O
Fragaria virginiana	X								
Galium aparine	X	X	X	X					X
Galium triflorum	O	O	O			O			
Gaultheria shallon		X			[X]	X	[X]	X	[X]
Gnaphalium canescens ssp. *thermale*	O		O					O	O
Gnaphalium sp.	O		X						
Goodyera oblongifolia							X	X	X
Habenaria sp.		X							
Hieracium albiflorum		X	X	X		X			
Linnaea borealis		X		X	X			X	
Lotus purshianus		X	X						O
Madia sp.			X						

Table 2.7, Continued.

Species	0 m from the road			5 m from the road			50 m from the road		
	Site A	Site B	Site C	Site A	Site B	Site C	Site A	Site B	Site C
Medicago lupulina	X		X						
Petasites frigidus var. *palmatus*		X	X						
Prunella vulgaris	[X]	[X]	X						
Ranunculus uncinatus		[X]	O						
Rhododendron macrophyllum					X			X	X
Rosa gymnocarpa						X			
Rubus parviflorus						X			
Rubus ursinus	X	[X]	X	[X]	[X]	X	X	X	X
Salix sp.		X							
Symphoricarpos albus var. *laevigatus*			X	X					
Tiarella trifoliata var. *unifoliata*									X
Trientalis latifolia		X	X	X		X			
Trifolium sp.			O						
Trillium ovatum	X			X			X		X
Vaccinium parvifolium		X			X	X	X	X	X
Valeriana sp.		X							
Vancouveria hexandra	[X]		X	[X]			X		X
Viola sempervirens	O			O			O		
Viola sp.			X	X		X	X		X
Whipplea modesta	X		X	X		X			
Various unknown dicots	O	O	O	O	O	O	O		
Native/Unknown Monocots									
Agrostis exarata		O	O						O
Agrostis sp.	O			O					

Table 2.7, Continued.

Species	0 m from the road			5 m from the road			50 m from the road		
	Site A	Site B	Site C	Site A	Site B	Site C	Site A	Site B	Site C
Carex sp.			O			O			
Deschampsia elongata		O	[X]						
Elymus glaucus		X							
Festuca occidentalis		X							
Juncus bufonius	O								
Juncus ensifolius			O						
Juncus sp.			O			O			
Melica smithii			X						
Various unknown monocots	O	O	O	X	O		X		O
Exotic Monocots									
Agrostis stolonifera	X		X						
Festuca arundinacea	[X]	O		X					
Poa pratensis	X			X					
Tree Seedlings/Saplings									
Acer circinatum							X		X
Acer macrophyllum			X			X	X		
Alnus rubra		X							
Pseudotsuga menziesii	X	X	X				X		
Taxus brevifolia									X
Thuja plicata	X	X	X						X
Tsuga heterophylla	X	X		X	X	X	X		X

exotics (Table 2.7). Among the exotic dicots, four species (*Cerastium vulgatum, Cirsium arvense, Lactuca serriola,* and *Senecio sylvaticus*) were found only in the seed bank samples. Two species (*Hypericum perforatum* and *Lactuca muralis*) were found in both the field and in the seed bank at the 0-m location at all three sites (Table 2.7). Only three exotic monocot species (*Agrostis stolonifera, Festuca arundinacea,* and *Poa pratensis*) were positively identified in the field survey. Only *Festuca arundinacea* was also found in the seed bank (Table 2.7).

The percentage of species found in the seed bank only, field survey only, or both varied among exotic dicots, native dicots, monocots, and trees (Figure 2.4). The Jaccard index of similarity (Ludwig and Reynolds 1988) was calculated to compare the seed bank "community" with the existing vegetation "community" for each of these groups of species at each sampling location (Table 2.8). Nearly one-third of the 14 exotic species found in this study was present in both the seed bank and existing vegetation at the 0-m locations (Figure 2.4A), which is reflected in the moderately high Jaccard index (Table 2.8). The "communities" of exotics in the seed bank and in the existing vegetation along the roads were more similar than were any other species group/sampling location combination (Table 2.8). No exotic species were found in the field survey at either the 5-m or 50-m locations (Figure 2.4A) and therefore the Jaccard index was 0 for both sampling locations (Table 2.8).

Among the native dicots, a very low percentage of species was found in both the seed bank and field survey (Figure 2.4B), which is reflected in the low Jaccard indices at all three sampling locations (Table 2.8). Monocots were present in either the seed bank or the existing vegetation at all sampling locations, but only at the 0-m locations were species

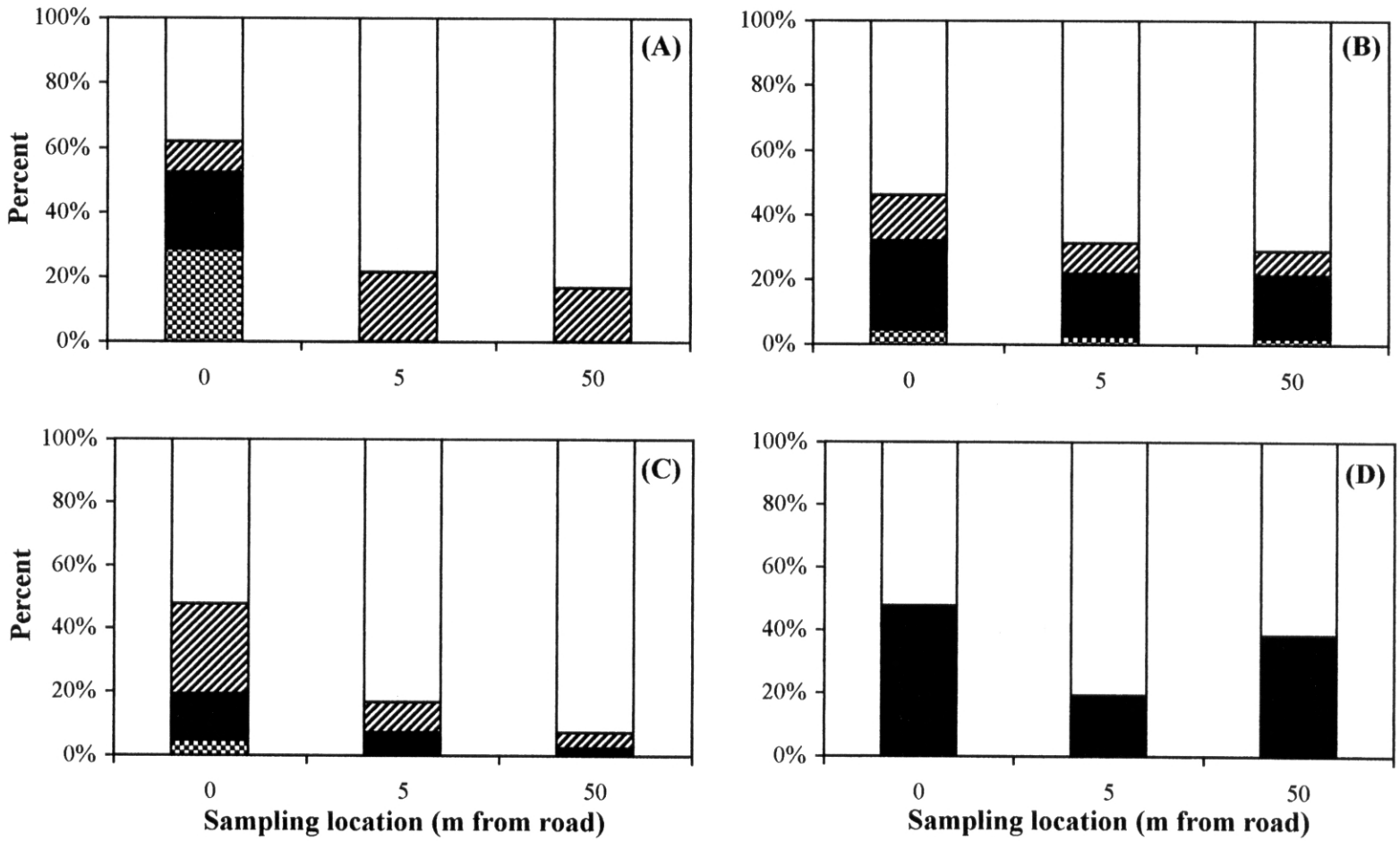

Figure 2.4. Presence of species in seed bank samples and field surveys: (A) exotic dicots (n=14); (B) native dicots (n=52); (C) monocots (n=14); and (D) trees (n=7).

Table 2.8. Jaccard index[a] of similarity between species found in the seed bank and those present in the existing vegetation.

Species	Sampling location (distance from road) 0 m	5 m	50 m	Pooled over all distances
Exotic dicots	0.46	0	0	0.28
Native dicots	0.10	0.08	0.07	0.08
Monocots	0.10	0	0	0.07
Trees	0	0	0	0

[a] Jaccard index = $a/(a + b + c)$, where a = number of species present in both seed bank and existing vegetation; b = number of species present only in seed bank; c = number of species present only in existing vegetation. Jaccard index = 0, no similarity; Jaccard index = 1, maximum similarity (Ludwig and Reynolds 1988).

found in both the seed bank and field survey (Figure 2.4C). The percentage was low, as is reflected in the low Jaccard index (Table 2.8). Tree species were only found in the field survey (Figure 2.4D) and therefore the Jaccard index was 0 for all sampling locations (Table 2.8).

2.4 Discussion

2.4.1 Critique of methods

The seedling emergence method that was used to estimate the composition of the seed banks in this study is the most frequently used method in seed bank studies (Brown 1992), although it probably underestimates the total seed bank because germination requirements may not have been met for some species. Ingersoll and Wilson (1990) also gathered soil samples at HJA and experimented with various types of disturbance treatments that could stimulate germination, but found that density of germinants was actually highest in their control (unmanipulated greenhouse conditions). They attributed these results, in part, to the spreading of soil over a larger area in the controls (12.5 × 12.5 × 10 cm samples spread out over sand/vermiculite in a 25 × 25 cm flat) compared with the experimental treatments (samples placed intact in a plastic pot) (Ingersoll and Wilson 1990). In the current study, the samples received no special treatments other than water and fertilizer, but they were spread to about 1 cm depth, which may have helped promote germination.

Sample sizes used in seed bank studies have varied tremendously. Whipple (1978) argued that sample sizes in most seed bank studies are inadequate and that results should be used to estimate species presence rather than seed densities. Forcella (1984) constructed a species-area curve for a seed bank in a pasture and recommended that a minimum of 1000 cm^2 be sampled for any given treatment. This sampling intensity was achieved in the current study, where the 20 samples at each site/location represented 50 cm^2 in surface area each.

Sampling depth also varied in previous seed bank studies. However, most results indicate that seed density decreases with increasing soil depth, with most seeds occurring within the top 5 cm (Kellman 1970; Pratt et al. 1984; Kramer and Johnson 1987). Sampling depth in the current study was 5 cm. Therefore, it is reasonable to assume that a large proportion of the seed bank was captured.

Although the results of the current study probably underestimate the total number of species and viable seeds in the soil at the study sites (Poiani and Johnson 1988; Brown 1992), the seedling emergence method probably provides a good estimate of the weedy component of the seed bank because the germination requirements of these species are usually relatively general (Grime et al. 1981). Brown (1992) compared the seedling emergence method with the seed extraction method (which may overestimate seed bank composition because unviable seeds may be counted) and concluded that both methods were able to distinguish between different conditions and therefore are suitable for comparative studies. The results of the current study should not be taken as an absolute estimate of the seed bank composition, but the data do provide valuable comparisons of the different sampling locations.

2.4.2 Comparisons with other studies

The mean density of seeds across all sampling locations in the current study was 2171/m^2 (5557/m^2, 633/m^2, and 327/m^2 for the 0-m, 5-m, and 50-m sampling locations, respectively), which is within the range reported for other temperate conifer forests (e.g., Kellman 1970, 1974; Pratt et al. 1984; Kramer and Johnson 1987; Archibold 1989). The high variability among samples, sampling locations, and sites in the current study reflects the clumped spatial distribution of species in the seed bank, which probably indicates that both biological and environmental factors influenced the spatial patterns in the seed bank (Bigwood and Inouye 1988).

Several researchers have noted the presence of exotic species in soil seed banks. Kellman (1974), for example, found *Senecio sylvaticus* in the soil of both an old-growth and secondary forest in coastal British Columbia. The secondary forest also contained seeds of *Hypochaeris radicata*, *Lactuca muralis*, *Holcus lanatus*, and *Rumex acetosella*.

Pratt et al. (1984), in a seed bank study in a *Pinus ponderosa-Symphoricarpos albus* stand in east-central Washington, found 57 species in their soil samples, 24 of which were exotic. Three exotic species, *Poa pratensis, Stellaria media*, and *Cerastium vulgatum*, accounted for over half of the seed bank germinants. Kramer and Johnson (1987) found 8 exotic species among the 80 species in the seed banks of three mature conifer forests in central Idaho. The exotics comprised only 3% of the total seed bank, but they were fairly widespread and were found in over half of the 48 stands sampled.

Exotic species were also found in three seed bank studies conducted at HJA. Ingersoll and Wilson (1990) found seedlings of *Senecio sylvaticus* and *Hypochaeris*

radicata in soil samples from an old-growth forest. Clark (1991) examined seed banks in an old-growth and a disturbed forest, both of which contained seeds of *Senecio sylvaticus.* Harmon and Franklin (1995) examined the seed bank in the riparian zone along third- and fifth-order streams at HJA and found several exotic species, including *Chrysanthemum leucanthemum, Cirsium arvense, Cirsium vulgare, Hypericum perforatum, Hypochaeris radicata, Lactuca muralis, Senecio sylvaticus, Taraxacum officinale,* and *Trifolium repens.* All but the latter two species were also found in the seed bank in the current study.

2.4.3 Field survey vs. seed bank results

The current study had low overlap between the species found in the seed bank and those found in the field survey. Also, no conifers were found in the seed bank samples, although they are overstory dominants. Such poor correspondence between existing vegetation and seed bank composition has been reported in a number of other studies (e.g., Livingston and Allessio 1968; Kellman 1974; Whipple 1978; Thompson and Grime 1979; Pratt et al. 1984; Gilfedder and Kirkpatrick 1993; McGee and Feller 1993; Sem and Enright 1996). The lack of conifers apparently reflects their low persistence in seed banks (Frank and Safford 1970; Gashwiler 1970).

Archibold (1989) suggested that seed banks may be the mechanism by which short-lived, early successional species are maintained in a disturbance-prone area. In the current study, several of the native dicots are considered weedy and were found more

often in the seed bank than in the existing vegetation (including *Anaphalis margaritacea*, *Conyza canadensis*, *Epilobium angustifolium*, *Epilobium watsonii* var. *occidentalis*, and *Gnaphalium canescens* ssp. *thermale*). The pattern for exotic dicots was a bit different. There was actually fairly good correspondence between the seed bank and existing vegetation along the roadside (0-m sampling locations) for some species (*Chrysanthemum leucanthemum, Cirsium vulgare, Hypericum perforatum, Lactuca muralis*). However, none of the exotic dicots were found during the field survey at any of the sampling locations at 5 or 50 m away from the road, although quite a few were present in the seed bank.

2.4.4 Landscape implications

The presence of exotics in the seed bank of a mature forest has implications about invasion in this landscape. In a conceptual model, the process of invasion can occur if there is a source of propagules, if those propagules can disperse to an invasion site, and if the invasion site has suitable conditions for germination and establishment. If any of these criteria are not met, then a barrier to invasion exists. Part of the goal of the current study was to disentangle whether exotic species are not typically found in mature forests because of dispersal barriers or because of environmental barriers.

It is reasonable to assume that the roadside is the one of the primary sources of propagules for many of the exotics found at HJA. In the current study, several exotic species were found in both the seed bank and the existing vegetation at the roadside (0-m

sampling locations) (Table 2.7), and the exotic seed bank at the roadside was much larger than in the mature forest (either 5-m or 50-m sampling locations) (Tables 2.1 and 2.2). (The pattern for *Senecio sylvaticus* was different from that of the other species and will be discussed below.) The exotic species that were found in the seed bank within the mature forest included *Cirsium arvense, Cirsium vulgare, Hypericum perforatum, Hypochaeris radicata, Lactuca muralis, Lactuca serriola, Lotus corniculatus,* and *Senecio sylvaticus.* In terms of the conceptual model of invasion, it may be concluded that these species do not have a barrier to dispersal.

2.4.4.1 Dispersal of exotics

It was surprising that there was such a dramatic decline in the number of exotic germinants in the 5-m compared with the 0-m sampling locations. These results could reflect a kind of edge effect at the 5-m sampling locations, which had a lot of woody debris on the forest floor that was probably left from earlier road construction. This debris may have altered the soil conditions in a way that inhibited seed viability.

The difference between the 0-m and 5-m sampling locations could also reflect the process of dispersal. Chambers and MacMahon (1994) distinguished between two phases of dispersal. During Phase I, seeds move from the parent plant to a surface. The resulting seed distributions typically represent either a negative exponential curve or a leptokurtic distribution (characterized by a curve that peaks a short distance away from the parent plant and then decreases in a negative exponential fashion). In either case, seeds typically

only move short distances from their parents during this phase (Chambers and MacMahon 1994). McEvoy and Cox (1987), for example, measured dispersal distances of *Senecio jacobaea* (an exotic species found at HJA, although not present in the seed bank samples). None of the achenes they monitored traveled farther than 14 m; most traveled <5 m from the parent plant during Phase I dispersal. In a study of *Cytisus scoparius* (another exotic species found at HJA), Smith and Harlen (1991) found that most seeds dispersed within 1 m of the parent plant. The maximum dispersal distance they observed was 5 m.

Phase II dispersal includes all subsequent movements of seeds: horizontal movements (i.e., to a new location) and vertical movements (i.e., into the soil). Dispersal agents (e.g., wind, water, animals) would be responsible for the horizontal movements. Soil disturbance or other processes that bury seeds would be responsible for the vertical movements. Chambers and MacMahon (1994) argued that Phase II dispersal has more influence on the pattern of plant distribution in communities and ecosystems than does Phase I.

This conceptual model of dispersal may explain the pattern of exotics found in the current study. Exotic species were only found in the existing vegetation along the roadside. Therefore, it is likely that most seeds were still concentrated along the roads after Phase I dispersal. The higher densities of exotic seeds in the seed bank at the 0-m locations suggest a couple of scenarios during Phase II dispersal: (1) Seed movement was primarily vertical, and most seeds entered the seed bank near their parent plants. (2) Seed movement was both horizontal and vertical, but the horizontal movement was concentrated along the road corridor. This is a reasonable scenario for seeds that are moved by wind and water during Phase II dispersal. The road corridor functions as a

drainage network that redirects water movement in this landscape (Wemple et al. 1996). The open road corridor may also serve as a wind tunnel in which wind speeds are higher and more concentrated than in the adjacent forest patch, because there are no physical features (i.e., trees or other vegetation) that offer resistance (Wales 1967 and Ranney et al. 1981, both cited in Brothers and Springarn 1992). Water or wind that flows preferentially along the road corridor could easily transport seeds along the way. Furthermore, vehicles could also disperse seeds along the roadway (Schmidt 1989; Lonsdale and Lane 1994).

The low densities of exotic species in the seed bank within the mature forest, even at the relatively close 5-m sampling locations, suggest that horizontal movement away from the road is a less common event for most species than is movement along the road. The overall density of exotics in the seed bank at the farthest distance from the road (50 m) was surprisingly similar to that at the 5-m sampling locations. This suggests that dispersal barriers are not preventing invasion by some species, even some distance away from the purported source of propagules. Most of the exotic species that were found in the seed bank at either the 5-m or the 50-m sampling locations are composites that have plumed achenes, which facilitate wind dispersal (e.g., *Cirsium arvense, Cirsium vulgare, Hypochaeris radicata, Lactuca muralis, Lactuca serriola, Senecio sylvaticus*). The other two species found at sampling locations away from the road, *Hypericum perforatum* and *Lotus corniculatus*, do not have special appendages for wind dispersal. *Hypericum perforatum* has fairly small seeds that could easily be carried some distance by a breeze (Ridley 1930). *Lotus corniculatus* has heavier seeds, and it is not clear what mode of dispersal was used. Certainly animals could serve as dispersal agents for the *Lotus* as well

as the other species. Seeds of normally wind-dispersed plants can easily adhere to the fur of animals, especially when the vegetation is wet. Some of the plumes of Compositae, for example, are mucilaginous when wet (Ridley 1930), a characteristic aiding dispersal.

2.4.4.2 Environmental barriers

Since some exotics were found in the seed bank but none were in the existing vegetation within the mature forest, there must be some environmental barrier that prevents successful invasion at these sites. One of the controlling factors could be light levels. Roadside locations were definitely more open than either location within the mature forest. Differences in light levels between the 5-m and 50-m sampling locations were not measured, but both locations at all sites had fairly closed canopies, thus permitting less light penetration than along the road. Also, differences in disturbance type and frequency could also be involved. Roadside locations would be disturbed by vehicle traffic and road maintenance activity, whereas sampling locations in the mature forest were relatively undisturbed.

The seed bank patterns for *Senecio sylvaticus* were different from those of the other exotics and deserve special consideration. This species was found in the seed bank at all sites and all locations (Table 2.3), although it was not found in the existing vegetation at any site. *Senecio sylvaticus* is an early successional species that is often a short-term dominant in recent clearcuts, especially those that have been burned (West and Chilcote 1968; Halpern and Spies 1995). This species apparently has high nutrient requirements and

poor competitive ability (Halpern 1989) that preclude it from persisting at a site more than 2 to 3 years after a disturbance. Other studies at HJA also found this species in the seed banks of old-growth forest (Ingersoll and Wilson 1990; Clark 1991), disturbed forest (Clark 1991), and riparian areas (Harmon and Franklin 1995). Thus, in terms of invasion in the forested landscape, *Senecio sylvaticus* does not seem to have major barriers to dispersal, but is limited by local environmental conditions. It may be that this species is fairly prevalent throughout this landscape, but exists primarily as dormant seeds in the soil in a variety of habitats. Once a disturbance occurs, the seeds are readily available to germinate and occupy to the site.

2.4.4.3 Seed viability

The issue of seed longevity is also important. Seeds of an exotic species that disperse to a site at which current environmental conditions are unsuitable would only be available to colonize the site if they can remain viable in the soil seed bank until conditions change some time in the future. Although buried seeds of some weed species are known to remain viable for over 50 years (Thompson and Grime 1979; Kivilaan and Bandurski 1981), the literature is fairly limited regarding specific data on the exotic species found in the seed bank in the current study. Kellman (1974) found that the densities of buried viable seed was several times that of trapped seeds for most species, suggesting that the buried seed represented an accumulation over several years. *Lactuca muralis* was an exception to this pattern, which suggests that seeds of this species may have short-term viability. In an

interesting study on *Cirsium vulgare*, Doucet and Cavers (1996) found that local site conditions had a strong influence on how persistent this species was in the seed bank. Seeds placed at shallow depths in a fairly open site with arable sandy soil did not persist longer than 6 months. In contrast, some seeds placed in shallow depths in a partly shaded site with clay loam soil persisted for 30 months. The authors noted that previous studies had concluded that *Cirsium vulgare* does not form a persistent seed bank at shallow depths. However, all of those studies had been conducted in a sand dune habitat. Based on the results of Doucet and Cavers (1996), it is reasonable to conclude that seeds of *Cirsium vulgare* that reach a mature forest in a landscape (such as at HJA) may persist in the seed bank for a few years.

2.5 Conclusions

This study indicates that, for both exotics and natives, the overall density of the seed bank was higher along the road than in the mature forest. Logistic regression models indicated that distance from the road was a significant predictor of whether a sample contained an exotic and what proportion of germinants in each sample was exotic. Variability among sites was also a significant factor in the logistic regression models for exotic dicots, but not for native dicots.

The exotic dicots in the existing vegetation and in the seed bank along the roads were more similar in composition than were any other species group at any sampling location. The similarity between native dicots in the existing vegetation and in the seed

bank was low but fairly equal for all sampling locations, whereas there was no similarity for exotic dicots at the 5-m or 50-m locations.

The patterns revealed in this study suggest that dispersal barriers prevent some, but not all, exotic species from dispersing away from the road. The exotics that were in the seed bank within the mature forest either had special morphological features (plumes on the achenes) or lightweight seeds, both of which would promote wind dispersal. Environmental barriers appear to preclude establishment of all exotics that were able to disperse into the mature forest but, depending on the longevity of the seeds, several species may be immediately available to occupy the site in the event of a disturbance that changes the environmental conditions.

The overall results of this study support the opportunistic habit of weedy exotic species, especially in suitable sites such as roadsides. Populations of exotics along roads appear to be one of the primary sources of seeds for most species, although *Senecio sylvaticus* may be more prevalent in seed banks throughout this forested landscape than are other exotic species. Finally, these results support the general model of invasion, which holds that species can expand their occurrence over a landscape if both dispersal barriers and environmental barriers are removed.

Chapter 3

Patterns of Exotic Plant Invasion along Roads and Streams in a Forested Landscape in the Western Cascade Range, Oregon

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in preparation for journal submission

3.1 Introduction

Johnstone (1986) proposed a generalized explanation of invasion: it is caused by removing all barriers that previously excluded a plant species from a site. Mooney and Drake (1989) suggested that the rate at which exotic plants successfully spread into new territory after their initial introduction is a complex function of habitat characteristics (degree of heterogeneity; size and distribution of patches; distance between suitable patches) and species characteristics (population growth rates and dispersal ability).

These generalizations underlie a conceptual model of invasion, which suggests that invasion occurs when propagules are able to move along a corridor (either actual or conceptual) to colonize an invasion site. The term invasion is used here to describe a process by which exotic plants are introduced and become established in an area where they previously did not occur. At any given time, the invasion process may be characterized, in part, by the distribution pattern of exotic species (also called invasion pattern). A number of barriers may prevent invasion (Figure 1.1). Biological and genetic barriers (such as dispersal limitations) may affect the propagule source; physical barriers (such as oceans, mountains, or closed-canopy forest) may affect the corridor; and environmental barriers (such as unsuitable light, soil, or moisture conditions) may affect the invasion site. In order for an exotic plant species to successfully colonize an invasion site, all barriers must be removed. This conceptual model could represent either the initial introduction of an exotic species or its subsequent spread outside its native range.

Biological characteristics that may promote invasion have been discussed by numerous authors (e.g., Baker 1965; Bazzaz 1986; Heywood 1989; di Castri 1990;

Kornas 1990; Primack and Miao 1992; Mack 1996; Rejmanek 1996; Rejmanek and Richardson 1996; Williamson and Fitter 1996a; Reichard and Hamilton 1997). A generalized "ideal" invasive plant is one with 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. However, lists of traits of an "ideal" invasive plant are simply checklists of potential attributes rather than hard and fast rules, because possession of certain characteristics does not always correlate well with successful invasion (Newsome and Noble 1986).

Dispersal is one of the most important biological processes that affects species distribution (Howe and Smallwood 1982; Green 1983; Primack and Miao 1992), including the patterns of invasion by exotic plants (McEvoy and Cox 1987; Chambers and MacMahon 1994; Lavorel et al. 1995; Higgins et al. 1996; Kot 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 very heavy seeds would have a biological barrier to invasion if there were no dispersal agent to transport seeds away from the parent plants.

Generalizations about the physical factors that promote invasibility of communities or ecosystems tend to emphasize the important role of disturbance in facilitating invasion (Elton 1958; Fox and Fox 1986; Swincer 1986; Crawley 1987; Heywood 1989; Hobbs 1989; Rejmanek 1989; Bossard 1991; Hobbs 1991; Lepart and Debussche 1991; D'Antonio 1993). Hobbs and Huenneke (1992) suggested that changes in the historical disturbance regime may create opportunities for invasion and that interactions between different disturbances may have synergistic effects. Brothers and Spingarn (1992) discussed the role of habitat fragmentation in promoting invasion. Based on their study of

old-growth forests in Indiana, they suggested that disturbed habitat and an increased ratio of forest-edge-to-interior may create conditions suitable for invasion by exotic species.

Few studies of the process of invasion have been conducted at the landscape scale, although the emerging principles of landscape ecology (Forman and Godron 1986; Urban et al. 1987; Turner 1989) may offer some insights on what the patterns of exotic plant distribution reveal about the process of invasion. DeFerrari and Naiman (1994) focused their multi-scale study on landscape patches (clearcuts, young and mature forests, and patches in the riparian zone), but concluded that both stream and road networks play important roles as corridors for invasion in the forested landscape. Various other studies have also documented the association of roads and exotic plants (Frenkel 1970; Forcella and Harvey 1983a; Wester and Juvik 1983; Reznicek and Catling 1987; Schmidt 1989; Ullmann and Heindl 1989; Heindl and Ullmann 1991; Tyser and Worley 1992; Wilson et al. 1992; Lonsdale and Lane 1994; Forman and Hersperger 1996). The road may be the initial point of entry into a new landscape, and it may serve both as habitat as well as a corridor by which a plant species is able to invade other parts of the landscape (Wace 1979 in Wester and Juvik 1983). Riparian zones along streams, too, may serve as corridors for plant dispersal (Gregory et al. 1991), including exotic plants (Pysek and Prach 1993; Tabacchi et al. 1994, unpublished manuscript; Pyle 1995).

The underlying question of the current study is how biological and physical factors interact to produce the patterns of invasion in four "habitat types" along two networks (roads and streams) in a forested landscape: (1) high-use roads, (2) low-use roads, (3) abandoned roads, and (4) third- to fifth-order streams. Roads-use levels were assumed to represent relative amounts of human disturbance (specifically, vehicle traffic and

maintenance activity), with high-use and abandoned roads having the most and least disturbance, respectively. Streams were included to represent a natural network system that may have different patterns of invasion because of different disturbance regimes. Field sampling was conducted to test the following hypotheses: (1) exotic plants are more frequent along the most disturbed habitat type, which also have more available light, than along the less disturbed types, which have more canopy cover; (2) species that are wind-dispersed are the most widely distributed; and (3) different processes control the patterns of invasion at different spatial and temporal scales.

3.2 Methods

3.2.1 Study site

Field data for this study were collected at the H.J. Andrews Experimental Forest (hereafter, HJA), a National Science Foundation-sponsored Long-Term Ecological Research site located along the western slope of the Cascade Range, about 80 km (50 miles) east of Eugene, Oregon. HJA occupies about 6400 ha (15,800 acres), and elevations range from 410 to 1630 m (1350 to 5340 ft). The maritime climate of the region includes warm, dry summers and mild, wet winters.

The forest vegetation is primarily composed of conifers in the *Tsuga heterophylla* (western hemlock) zone at lower elevations and in the *Abies amabilis* (Pacific silver fir) zone at higher elevations (Franklin and Dyrness 1988). A species list prepared for the HJA

in the early 1970s (Franklin and Dyrness 1971) included 480 taxa, about 10% of which are not native to Oregon. Some of the exotic species were deliberately introduced as part of seeding mixes to stabilize cut slopes during road construction (Dyrness 1967, 1970, 1975); these were primarily grasses and legumes. Other exotic plants were probably introduced when seeds or vegetative material were brought in accidentally by various sources, including soil imported during road construction; vehicles, clothing, or tools of timber harvest crews, researchers, and other visitors to HJA; livestock that was seasonally grazed in high-elevation meadows at the turn of the century; wind or other natural forces from adjacent areas.

HJA was established as a research forest in the late 1940s. Most of the road construction and timber harvest took place in the 1950s and 1960s, with some additional roads being constructed at higher elevations in the 1970s and 1980s (Wemple et al. 1996). Except for a short paved stretch (about 3 km long) near the entrance to HJA, most of the roads in the approximately 100-km network are gravel. The main types of disturbance along the roads are vehicle traffic and maintenance activity; landslides and blowdown also affect discrete segments of the road network. Vehicle use at HJA has varied, with some segments having fairly regular traffic throughout the snow-free period (and especially during the summer field season). Other road segments were constructed to access a particular logging unit and subsequently have had very little regular vehicle traffic. A few roads were abandoned after the unit was logged or after a slide or treefall blocked the road, and these are not accessible by vehicles at all now. Road maintenance schedules have also varied, with the higher use roads receiving more frequent activity (including road grading, ditch clearing, trimming of overhanging vegetation).

The stream network includes first- to fifth-order reaches that intersect the road network in a variety of configurations. The main types of large-scale disturbance along streams include debris flows and floods. The two largest floods in recent history occurred in December 1964 and February 1996. The latter occurred after the field surveys were conducted for the current study. Many of the gravel bars and streamside habitats that had been revegetated since the 1964 flood were heavily scoured during the 1996 event. Annual flooding, however, creates small areas that are open to establishment every year.

3.2.2 Target species

A group of 21 exotic species (hereafter, target species) that have been recorded at HJA [based either on personal observation or on the species list compiled by Franklin and Dyrness (1971)] were chosen for this study. The species represent 9 plant families and 17 genera that are native to Europe and Asia, and they have varying life forms and potential dispersal modes (Appendices B, C, and D).

3.2.3 Field sampling

Five transects were established in each of the four "habitat types": high-use roads, low-use roads, abandoned roads, and streams (Figure 3.1). Road-use categories are somewhat subjective, but reflect (approximately) the following frequency of vehicle

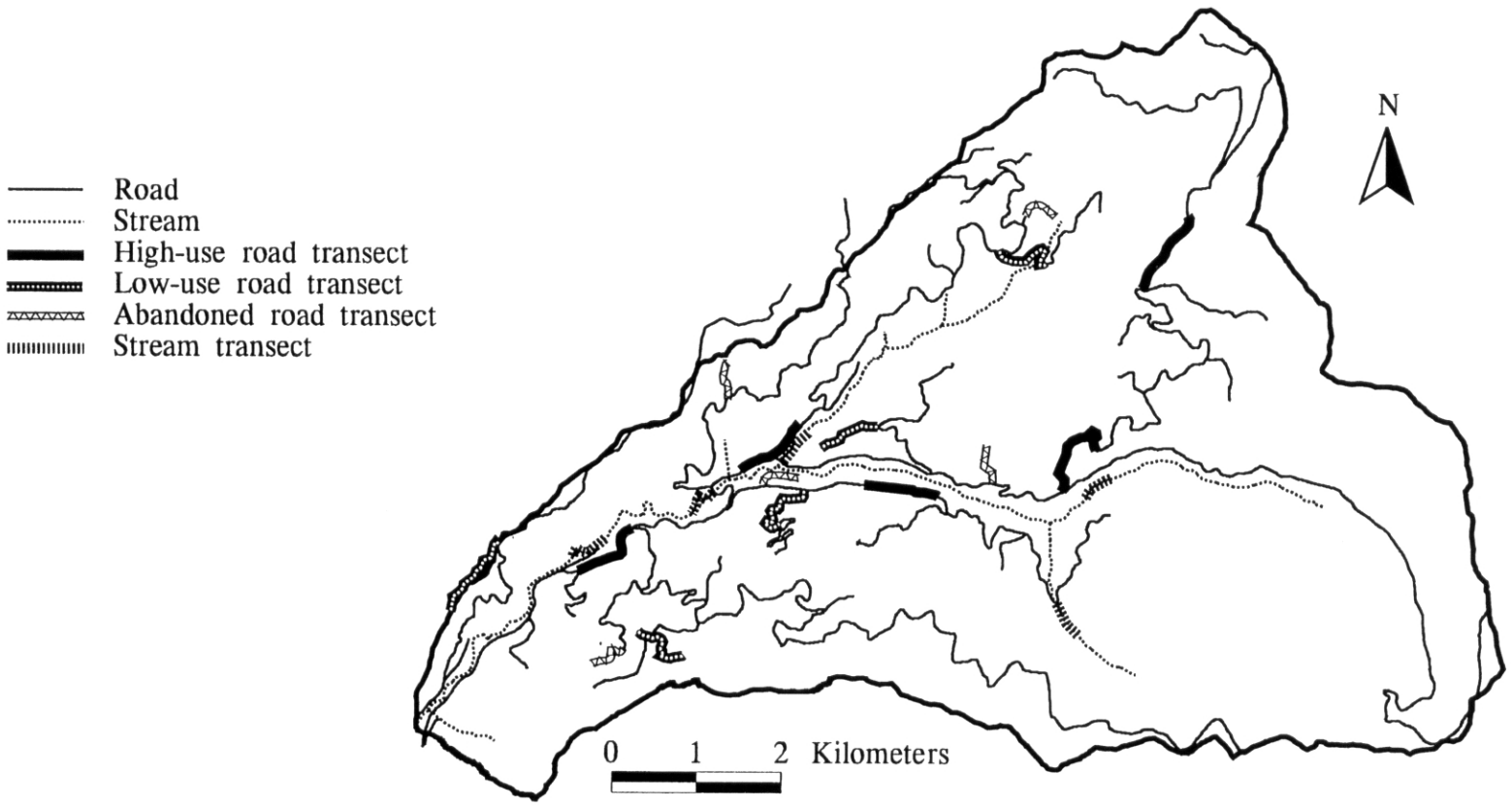


Figure 3.1. Location of transects at the H.J. Andrews Experimental Forest.

traffic: high-use roads = regular daily to weekly; and low-use roads = less than biweekly. In general, road-use categories also represent relative frequency and intensity of road maintenance activities. Abandoned roads are no longer passable by vehicles. Abandonment occurred in the 1950s and 1960s for four of the transects; the fifth 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 represent one third-order, two fourth-order, and two-fifth order reaches. All transect locations were chosen arbitrarily without preconceived bias (McCune 1995), except that higher elevations were not sampled. Because the distribution of some species may be limited by elevation, transects were placed in locations <1200 m (4000 ft) in order to minimize bias of this factor in the results. Elevation ranges were estimated from a 1:24,000 map of HJA (Table 3.1).

Data on the occurrence of target species were collected at coarse and fine scales within each of the transects. At the coarse scale, transects were divided into 50-m-long sampling units that were parallel to the road/stream (Figure 3.2A). The width of each sampling unit was about 2 m from both sides of the road/stream edge (Figure 3.2B). Transect lengths varied as follows: 950 to 1000 m for high-use roads, 800 to 1000 m for low-use roads, 300 to 500 m for abandoned roads, and 500 m for streams. Presence/absence and abundance data were collected for all target species at the coarse scale along all four habitat types in 1994. Presence/absence data were also collected in 1993 along high-use and low-use roads only. Abundance of each target species was based on an estimate of the number of individuals present in each sampling unit and was classified on an approximate logarithmic scale: rare (+/-10 plants), common (+/-100 plants), abundant (+/-1000 plants).

Table 3.1. Elevation of transects sampled along each habitat type.

Habitat type	Range (m)	Average (m)
High-use roads	520 - 1170	730
Low-use roads	650 - 860	740
Abandoned roads	560 - 895	725
Streams	470 - 785	615

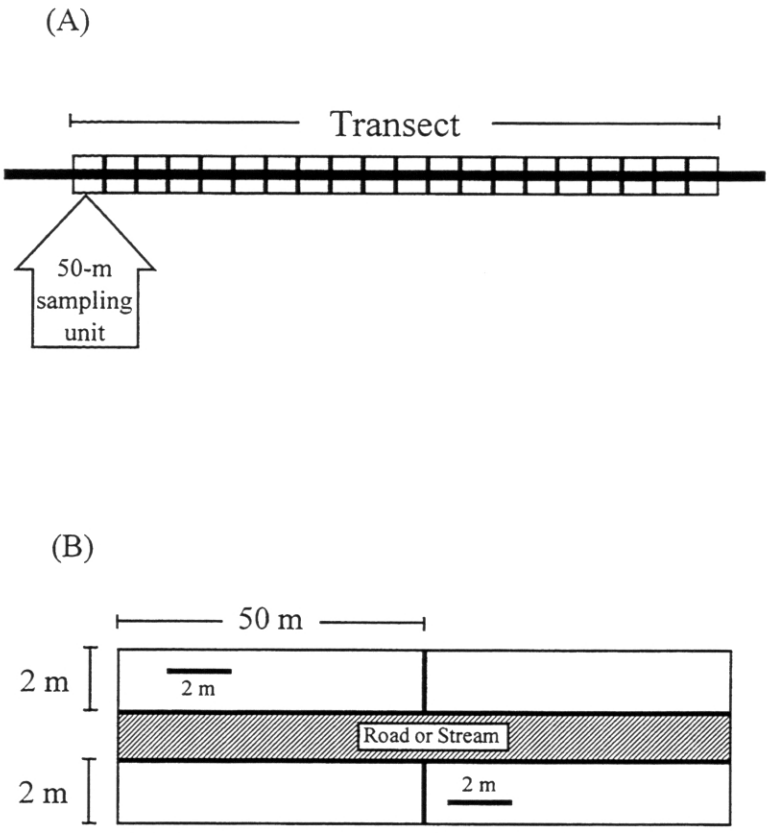


Figure 3.2. Sampling design for transects along each habitat type: (A) coarse-scale transect layout along road or stream and (B) sampling units for coarse and fine scales. Drawing is not to scale.

At the fine scale, the sampling unit was 2 m. One fine-scale sampling unit was established within each of the first ten 50-m segments of the coarse-scale transects described above. Each fine-scale sampling unit was placed approximately 1 to 2 m away from the road edge at a random number of paces from the beginning of the 50-m segment (Figure 3.2B); upslope and downslope locations were alternated regularly. Data collected at the fine scale were presence/absence and percent cover (based on line intercept with the 2-m sampling unit) of the target species. All data at the fine scale were collected in 1994.

The physical parameters examined in this study were general light levels and aspect. Data for both of these parameters were collected in 1994 at 50-m intervals (up to 500 m) along each of the coarse-scale transects. Light levels were classified into one of five categories in the field, based on approximate percent canopy cover: very high light ($\leq$10% cover), high light (11%–30% cover), medium light (31%–70% cover), low light (71%–90% cover), and very low light (>90% cover). Aspect was measured in degrees to indicate the exposure of the slope at each sampling location along the transects. Aspect was only recorded along the three habitat types along roads; it was not relevant for the streams because they are always positioned at the bottom of a hillslope.

3.2.4 Data analysis

Four general analytic tools were employed to examine the data: descriptive summaries, ordination, classification, and logistic regression. Coarse-scale data (collected in the 50-m sampling units) were analyzed unless otherwise noted. Descriptive summaries

were used to examine how the distribution of target species varied by habitat type, by scale (fine versus coarse), by year (1993 versus 1994), and by species. Presence/absence data were used to calculate frequencies (i.e., proportion of sampling units with target species). An index was calculated from the abundance data, and the relative difference between frequency and the abundance index indicated how common a particular species was. The three abundance classes, "rare," "common," and "abundant," were assigned values of 1, 2, and 3, respectively. Thus, if a particular target species was always "rare," its abundance index would equal its frequency. If the species was always "common," its abundance index would equal 2 times its occurrence proportion.

The light and aspect data collected in the field were reclassified for descriptive summaries and other analyses. The five classes of light level that were recorded in the field were collapsed to three classes for analysis: "very high" and "high" light levels were combined into a single "high" class; likewise, "very low" and "low" light levels were combined into a single "low" class; the "medium" light levels were retained as a separate class. Aspect measurements in degrees were reclassified into four cardinal directions for analysis: north (0°–45° and 316°–360°); east (46°–135°); south (136°–225°); and west (226°–315°).

Nonmetric multidimensional scaling (NMS) was used to examine general patterns of target species along the transects. NMS is a nonparametric multivariate ordination technique that is well suited to ecological data sets, because it can be used for data that are nonnormal or on questionable scales (McCune 1995). Minchin (1987) evaluated several ordination techniques and concluded that NMS is a robust technique that is appropriate for ecological analyses. The basic approach with NMS is to reduce the p-dimensional

space of the original data set in such a way that "stress" is minimized in the *k*-dimensional ordination space. Stress, which is an inverse measure of the fit of the data, measures the departure from a monotonic relationship between the dissimilarity distance in the original *p*-dimensional space and distance in the *k*-dimensional ordination space (McCune 1995). One of the most important initial steps when using NMS is to choose an appropriate number of dimensions for the solution. NMS differs from other ordination techniques in that, as the number of dimensions (axes) is added to solution, the configuration of the other dimensions changes. Thus, the solution for a given axis is unique to that *k*-dimensional ordination; axis 1 of a 3-d solution is not equivalent to axis 1 of a 2-d solution (McCune 1995).

The procedures for NMS outlined in McCune (1995) and in the PC-ORD program (McCune and Mefford 1995) were followed for this analysis, which was based on the proportion (transformed to arcsin square root values) of each transect that each species was present. Species were eliminated from this part of the analysis if they were either rare [defined as species with an average proportion (based on frequency) of <0.05 per transect] or outliers [defined as species with standard deviation (of mean distance) >2]. The Sorenson distance measure was specified in the NMS analysis. Once the number of dimensions was chosen, a Monte Carlo simulation was run to compare the results with those that would be expected by chance alone.

The data for each species along each transect were also subjected to a classification analysis, which employed a hierarchical, agglomerative, polythetic cluster technique [using Ward's Method for group linkage (McCune and Mefford 1995)]. Species that were either rare or outliers (as defined above) were not included in this analysis. The

classification results were compared with the general groupings suggested by the ordination results from NMS.

Logistic regression was used to test hypotheses regarding the probability of a target species occurring in a particular habitat type and under particular light levels (based on coarse-scale data). Because the response variable was based on binary data (i.e., species present = 1; species absent = 0), the more commonly used linear or multiple regression methods are not appropriate because of their assumptions of linearity and normal errors (Trexler and Travis 1993). Logistic regression is an appropriate analysis tool for the current study, because it examines the functional relationship between a binomial response variable and explanatory variables that are either continuous or categorical (Trexler and Travis 1993). The explanatory variables in this study (habitat type and light level) were categorical.

Logistic regression models were run for the 13 species that had sufficient data (>15% mean frequency in at least one habitat type). Two simple models were developed in which species presence was the response variable. Habitat type (high-use road, low-use road, abandoned road, and stream) was the explanatory variable in one model; light level (high, medium, and low) was the explanatory variable in the other model. Multiple logistic regression models were not attempted with this data because several categories of the response variables were not well represented (i.e., abandoned roads had a low proportion of high light levels; high-use roads had a low proportion of low light levels).

Computations for the logistic regression models were made with SAS (version 6.10), and models were evaluated based on χ^2 values. Statistically significant models were defined as those with p-values <0.05. Odds ratios were calculated from the coefficient

estimates (Hosmer and Lemeshow 1989; Ramsey and Schafer 1993) and provide a useful way of interpreting the logistic regression models. The odds ratios represent the probability of the occurrence of the response variable (presence of target species) in association with the explanatory variable (habitat type or light level) relative to a reference category. Streams were the reference category for the logistic regression models with habitat type as the explanatory variable; low light was the reference category for the models with light level as the explanatory variable.

3.3 Results

3.3.1 General/overall patterns

The ordination and classification analyses were based on frequency data for 14 target species (listed in Table 3.2) along each of the 20 transects (5 transects × 4 habitat types). Most of the species that were omitted were rare (i.e., average proportion was <0.05 per transect). *Cytisus scoparius* was omitted because it was an outlier (i.e., standard deviation of mean distance was >2). The final solution for the NMS ordination analysis was 2-dimensional. A Monte Carlo simulation indicated that this solution had significantly lower stress (i.e., data had more structure) than would be expected by chance ($p < 0.05$). The coefficient of determination (r^2) provides the proportion of variance explained by each axis in the ordination solution and is based on the correlations between distances in the 2-d

Table 3.2. Pearson correlations (r) between individual target species and ordination axes. (r-values $\geq |0.75|$ are in bold)

Species	Axis 1	Axis 2
Chrysanthemum leucanthemum	-0.52	**0.79**
Cirsium arvense	-0.25	0.48
Cirsium vulgare	-0.44	**0.84**
Dactylis glomerata	-0.12	0.48
Daucus carota	-0.47	**0.77**
Holcus lanatus	-0.44	0.45
Hypericum perforatum	**-0.81**	**0.89**
Hypochaeris radicata	-0.44	**0.93**
Lactuca muralis	0.22	-0.35
Plantago lanceolata	-0.27	**0.75**
Plantago major	-0.40	0.64
Senecio jacobaea	-0.39	0.48
Trifolium pratense	-0.25	0.63
Trifolium repens	-0.51	**0.77**

ordination space and distances in the original space. The r^2 values for axes 1 and 2 were 0.28 and 0.65, respectively; cumulative r^2 was 0.93 for this 2-d solution.

Figure 3.3 presents a plot of the ordination results. Because the transects are clustered to the left along axis 1, it is difficult to interpret what underlying factor(s) may explain the relationships along this axis. Along axis 2, however, the transects are spread over a relatively wider range, and this pattern may reflect a gradient of disturbance intensity along the habitat types (Figure 3.3A) or a gradient of average light levels along the transects (Figure 3.3B) or both. As shown in Figure 3.3A, transects along high-use and low-use roads were floristically very similar. In contrast, transects along abandoned roads and streams were floristically dissimilar to high-use and low-use roads, but also dissimilar to each other. There was much more variation among abandoned road and stream transects, especially along axis 2, than among high-use and low-use roads (Figure 3.3A). As will be discussed below, the numbers and frequencies of target species were higher along high-use and low-use roads than along abandoned roads and streams.

Another possible interpretation of axis 2 in the ordination plot is that it reflects a gradient of average light levels along the transects. As shown in Figure 3.3B, light levels generally increase from low to high along axis 2.

The individual target species had a negative correlation (r) with axis 1 and a positive correlation with axis 2, except *Lactuca muralis*, which will be discussed below. All species had stronger correlations with axis 2 than with axis 1 (Table 3.2). *Hypericum perforatum* had the strongest correlation with axis 1 ($r = -0.81$); all other species had r-values $< |0.52|$. Six species (*Chrysanthemum leucanthemum, Cirsium vulgare, Daucus carota, Hypericum perforatum, Hypochaeris radicata*, and *Plantago lanceolata*) had

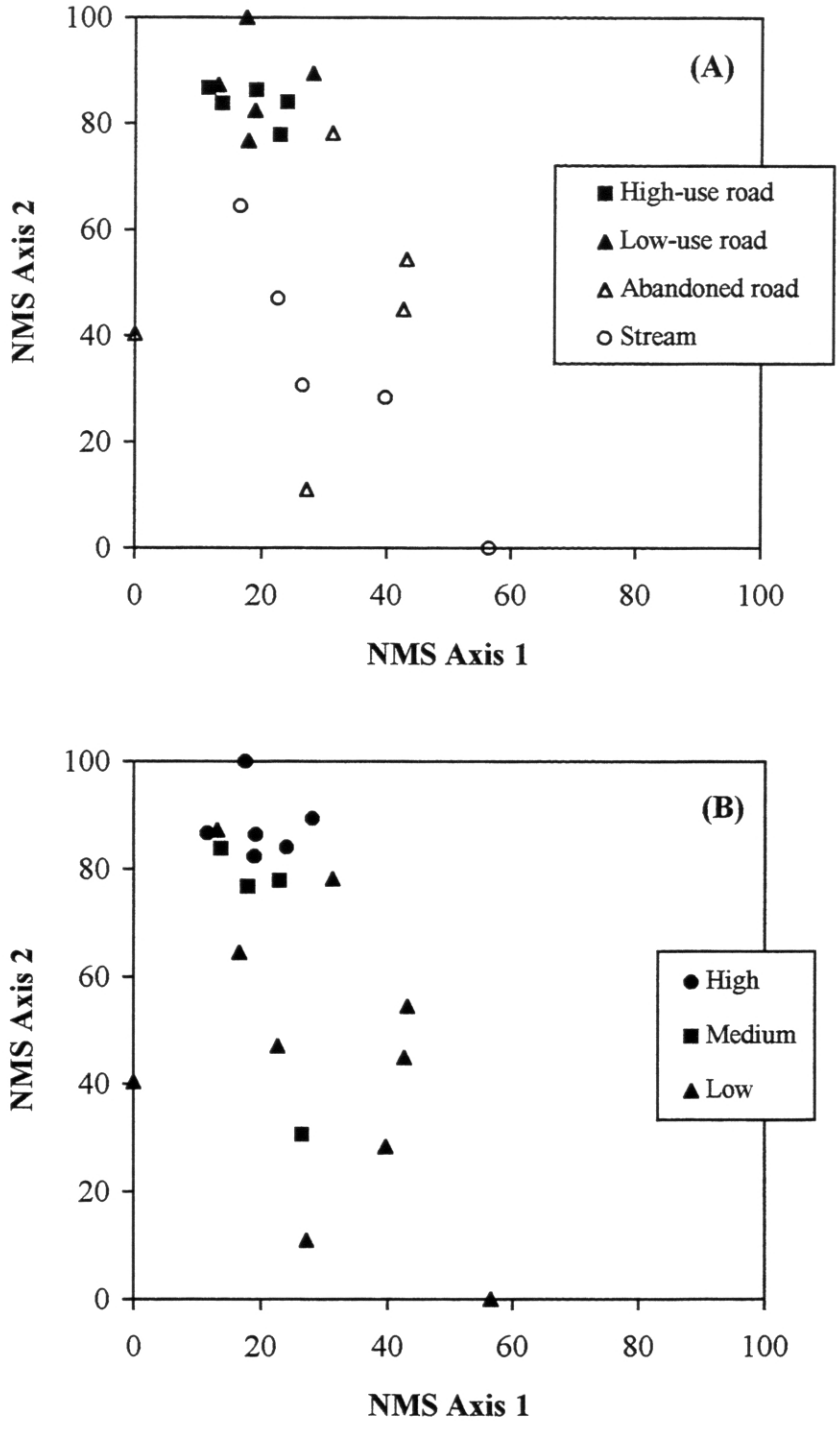


Figure 3.3. Nonmetric multidimensional scaling (NMS) ordination results overlayed with (A) habitat type and (B) light level.

strong positive correlations ($r > 0.75$) with axis 2 values (Table 3.2). *Lactuca muralis* was an anomaly among target species with regard to correlations with ordination axes: the sign was positive for axis 1 and negative for axis 2, opposite that for all other species. However, the *r*-values were low for both axes (Table 3.2).

The general groupings by habitat type suggested in the ordination results are similar to those provided in cluster analysis classification. The high-use and low-use roads (and one abandoned road) clustered into one large group at the highest level, and the abandoned roads and streams clustered in another (Figure 3.4). No clear relationships are evident at other levels of the classification.

3.3.2 Transect patterns -- species

3.3.2.1 Coarse-scale patterns

The frequency distribution of target species along each habitat type support the groupings suggested by the ordination and classification. Along high-use and low-use roads, the data were normally distributed (Figures 3.5A and 3.5B). All of the 50-m sampling units had at least one target species. The maximum number of target species per sampling unit was 13 and 14 for the high-use and low-use roads, respectively. The mode was 6 and 7 target species per sampling unit for the high-use and low-use roads, respectively (Figures 3.5A and 3.5B). Over 60% of the sampling units had 4 to 7 target species per sampling unit.

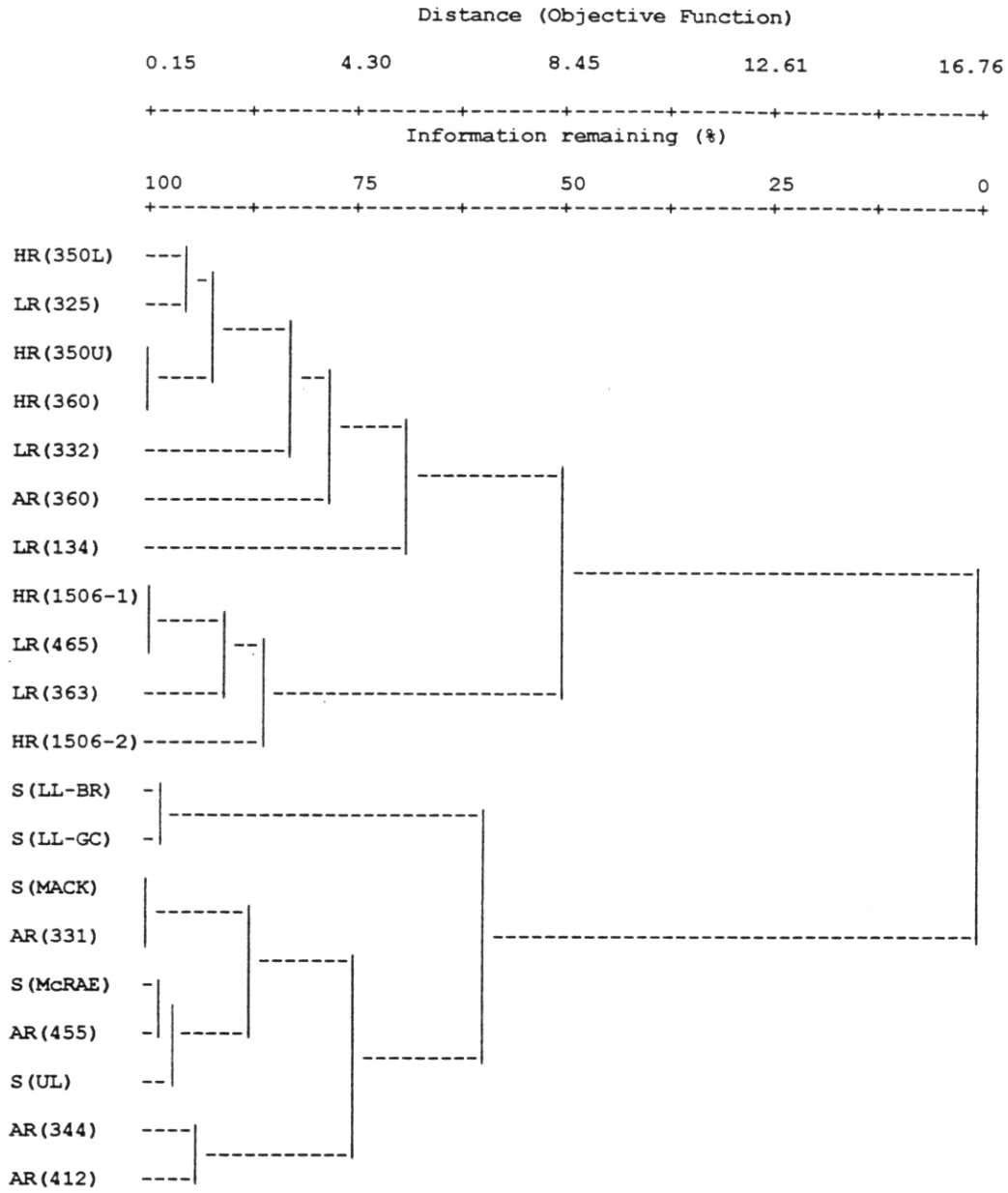


Figure 3.4. Cluster analysis results: classification of habitat type. HR = high-use roads; LR = low-use roads; AR = abandoned roads; S = streams. Road number or stream name/abbreviation is in parentheses.

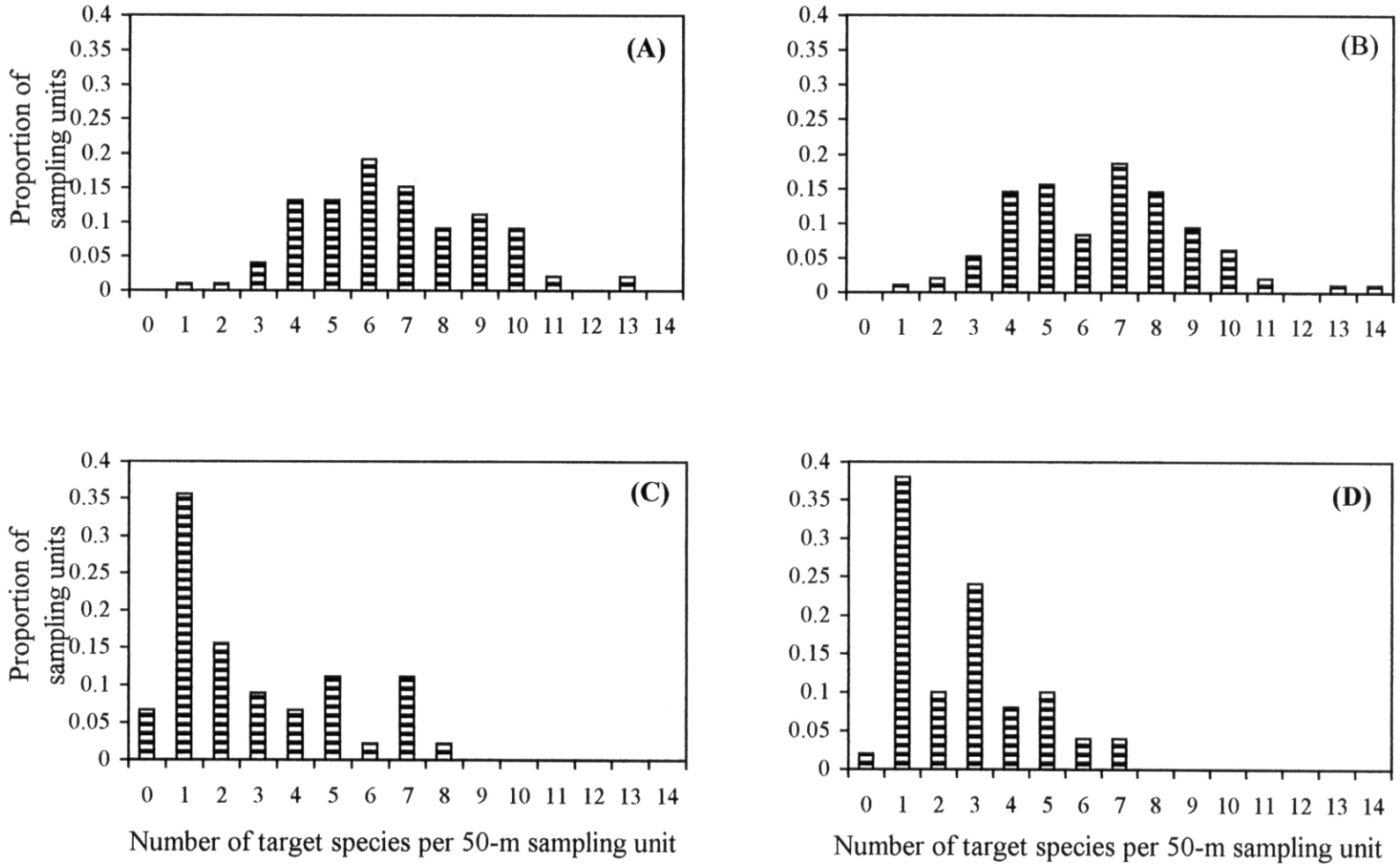


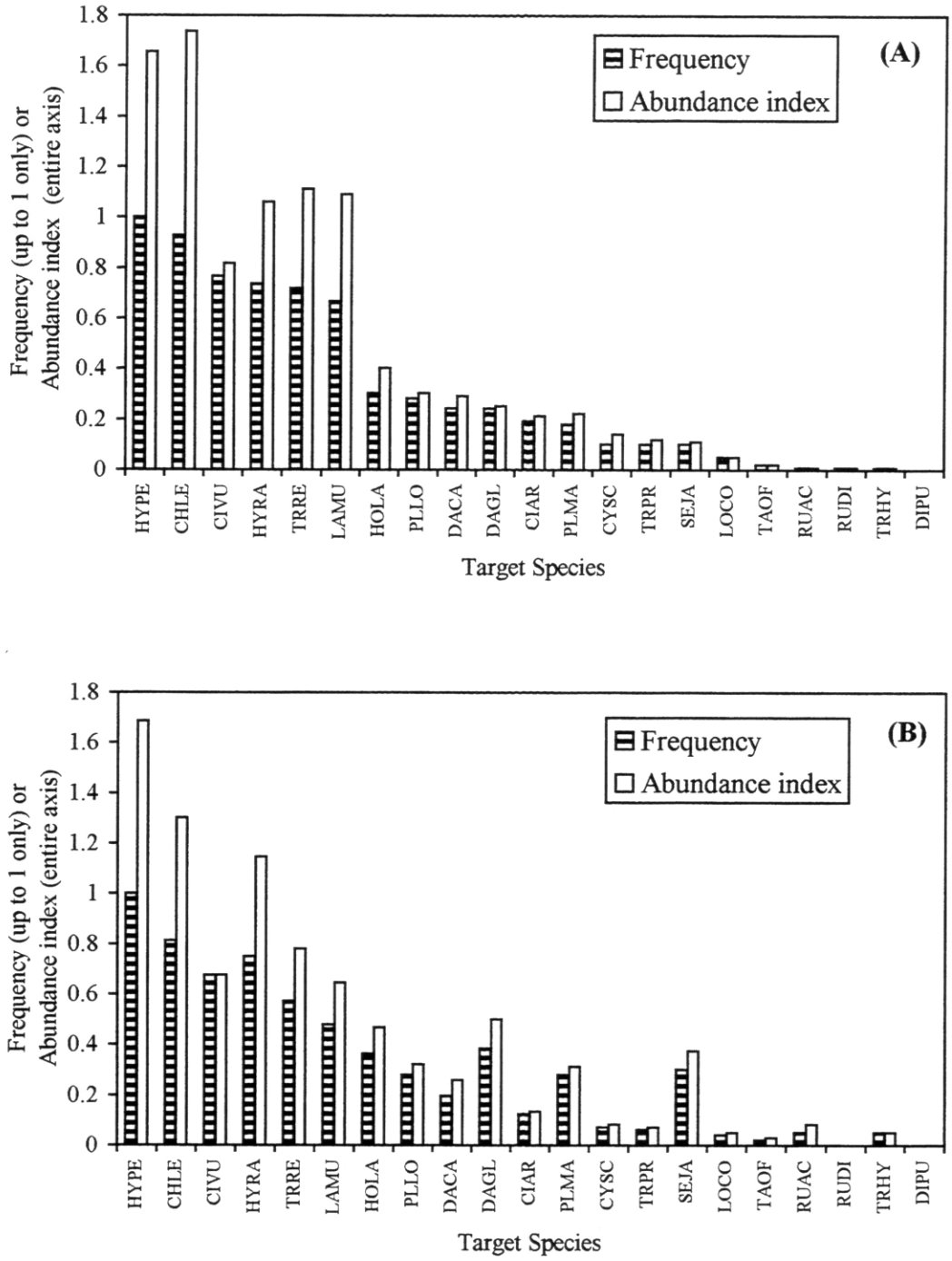
Figure 3.5. Frequency distribution of target species in 50-m sampling units along (A) high-use roads, (B) low-use roads, (C) abandoned roads, and (D) streams.

The frequency distribution of target species along abandoned roads and streams, in contrast, was highly skewed (Figures 3.5C and 3.5D). A low proportion of sampling units had no target species at all. The maximum number per sampling unit was 8 and 7 for the abandoned roads and streams, respectively. The mode was 1 target species per sampling unit for both habitat types. Over 60% of the sampling units had only 1 to 3 target species per sampling unit.

The frequency and abundance data of individual target species along each habitat type provide additional evidence that high-use and low-use roads are similar to each other and different than abandoned roads and streams. Figure 3.6 illustrates the frequency and an abundance index for all 21 target species. (See Appendix A for information regarding the complete data set.) Frequency (= occurrence) is expressed as the proportion of the 50-m sampling units in which a given species was present. Although abundance may confound other measures such as density, cover, and frequency (Castro and Cain 1959), the abundance index calculated in the current study simply provides a basis of comparison: the relative difference between frequency and the abundance index indicates how common a particular species was (Figure 3.6). If a particular target species was always "rare," its abundance index would equal its frequency. If the species was always "common," its abundance index would equal 2 times its frequency.

Along high-use roads, six species occurred in >50% of the sampling units: *Hypericum perforatum, Chrysanthemum leucanthemum, Cirsium vulgare, Hypochaeris radicata, Trifolium repens,* and *Lactuca muralis* (Figure 3.6A). All had abundance indices greater than occurrence proportions, indicating that they were classified as "common" or "abundant" in some of the sampling units. *Cirsium vulgare* was the least abundant of the

Figure 3.6. Frequency and abundance index of individual target species in 50-m sampling units along (A) high-use roads, (B) low-use roads, (C) abandoned roads, and (D) streams. Frequency represents the proportion of the 50-m sampling units in which the species occurred; only values up to 1 on the y-axis apply to the frequency data. The relative difference between frequency and abundance index indicates how common a particular species was. The three abundance classes, "rare," "common," and "abundant," were assigned values of 1, 2, and 3, respectively. Thus, if a particular target species was always "rare," its abundance index would equal its frequency. If the species was always "common," its abundance index would equal 2 times its frequency. Target species: HYPE = *Hypericum perforatum*; CHLE = *Chrysanthemum leucanthemum*; CIVU = *Cirsium vulgare*; HYRA = *Hypochaeris radicata*; TRRE = *Trifolium repens*; LAMU = *Lactuca muralis*; HOLA = *Holcus lanatus*; PLLO = *Plantago lanceolata*; DACA = *Daucus carota*; DAGL = *Dactylis glomerata*; CIAR = *Cirsium arvense*; PLMA = *Plantago major*; CYSC = *Cytisus scoparius*; TRPR = *Trifolium pratense*; SEJA = *Senecio jacobaea*; LOCO = *Lotus corniculatus*; TAOF = *Taraxacum officinale*; RUAC = *Rumex acetosella*; RUDI = *Rubus discolor*; TRHY = *Trifolium hybridum*; DIPU = *Digitalis purpurea*.


(A)
Frequency
Abundance index
Frequency (up to 1 only) or
Abundance index (entire axis)
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
HYPE
CHLE
CIVU
HYRA
TRRE
LAMU
HOLA
PLLO
DACA
DAGL
CIAR
PLMA
CYSC
TRPR
SEJA
LOCO
TAOF
RUAC
RUDI
TRHY
DIPU
Target Species
(B)
Frequency
Abundance index
Frequency (up to 1 only) or
Abundance index (entire axis)
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
HYPE
CHLE
CIVU
HYRA
TRRE
LAMU
HOLA
PLLO
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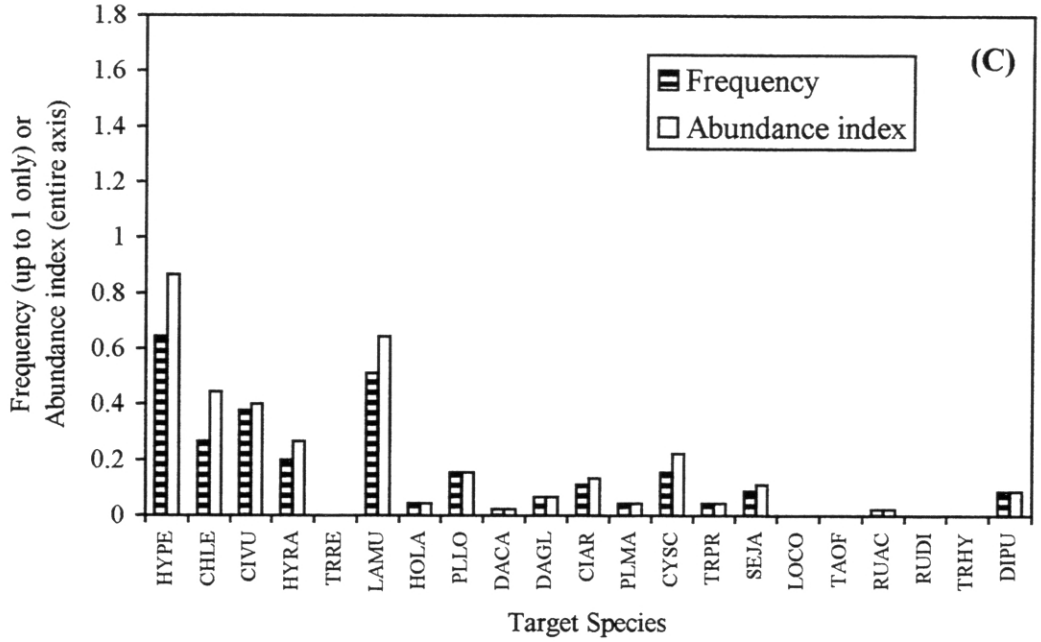
Target Species

Figure 3.6.



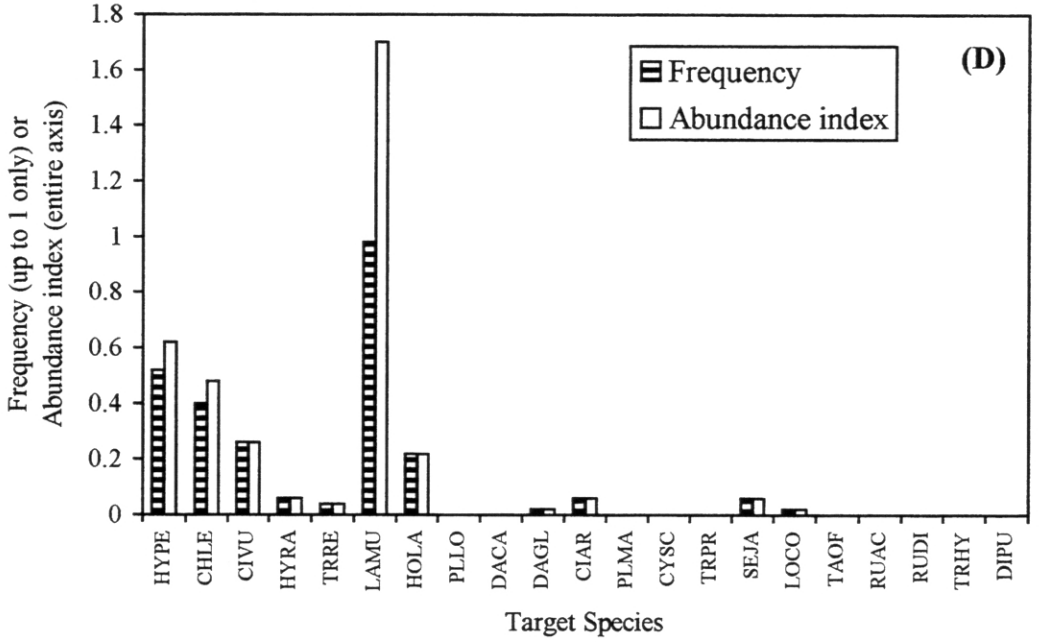


Figure 3.6, Continued.

most frequent species; *Hypericum perforatum* and *Chrysanthemum leucanthemum* were the most abundant. Of the 21 target species, 20 were found in at least one sampling unit along high-use roads; 12 of these occurred in >20% of the sampling units. Only *Digitalis purpurea* was not present in any of the sampling units along high-use roads.

Patterns were similar along low-use road transects. The same six species were the most frequent. Five of them occurred in >50% of the sampling units; only *Lactuca muralis* was slightly less frequent and occurred in 48% of the sampling units (Figure 3.6B). Compared with that along high-use roads, relative abundance was a little lower for *Chrysanthemum leucanthemum*, *Trifolium repens*, and *Lactuca muralis*. Only *Cirsium vulgare* and *Trifolium hybridum* were always classified as "rare." A few species occurred more frequently in low-use roads than along high-use roads (e.g., *Dactylis glomerata* and *Senecio jacobaea*). Of the 21 target species, 19 were found in at least one sampling unit along low-use roads; 12 of these occurred in >20% of the sampling units. Only *Digitalis purpurea* and *Rubus discolor* were not present in low-use road transects.

Along abandoned roads, only *Hypericum perforatum* and *Lactuca muralis* occurred in >50% of the sampling units (Figure 3.6C). All target species were generally less frequent and less abundant in this habitat type than along low-use and high-use roads. Of the 21 target species, 16 were found in at least one sampling unit along abandoned roads; only 5 of these occurred in >20% of the sampling units (Figure 3.6C).

As in the abandoned road transects, only *Hypericum perforatum* and *Lactuca muralis* occurred in >50% of the sampling units along streams (Figure 3.6D). Only these two species and *Chrysanthemum leucanthemum* were more abundant than "rare" in some of the sampling units. The pattern for *Lactuca muralis* was especially distinct; this species

was much more frequent and abundant along streams than along the other habitat types. Of the 21 target species, 11 were found in at least one sampling unit along streams; only 5 of these occurred in >20% of the sampling units (Figure 3.6D).

3.3.2.2 Fine-scale patterns

Data collected at the fine scale (2-m sampling units) revealed that the pattern of distribution is affected by the scale of observation. Fewer target species were detected along each of the four habitat types at the finer scale than at the coarser scale (Table 3.3). Percent cover of most target species at the fine scale was fairly low. Only two species (*Chrysanthemum leucanthemum* along high-use roads and *Lactuca muralis* along streams) had an average cover over 5% for a given habitat type, and the standard deviations were fairly high (Table 3.4). The frequency distribution of target species at the fine scale was different than that for the coarse scale (50-m sampling units) discussed above. The shape of the distribution for the high-use roads was still approximately normal, but the maximum number of target species per 2-m sampling unit was 5 and the mode was 3 (Figure 3.7A). About 10% of the 2-m sampling units had no target species. The shape of the distribution for low-use roads was more skewed (Figure 3.7B). The maximum number of target species was 4, and the mode was 1. Over 25% of the sampling units had no target species. The distribution for abandoned roads was highly skewed; over 75% of the 2-m sampling units had no target species (Figure 3.7C). The maximum was 2. The frequency distribution

Table 3.3. Number of target species (out of 21) detected within each sampling unit size.

	Sampling unit size	
Habitat type	50 m	2 m
High-use roads	20	13
Low-use roads	19	10
Abandoned roads	16	6
Streams	11	3
Total	21	15
Present in all 4 habitat types	9	3

Table 3.4. Average percent cover of target species at 2-m sampling sites. Standard deviations are in parentheses. Cover values ≥1% are in bold.

Species	Habitat type			
	High-use roads	Low-use roads	Abandoned roads	Streams
Chrysanthemum leucanthemum	**5.2** (2.9)	0.6 (0.3)	0.7 (1.3)	0.4 (0.6)
Cirsium arvense	0.02 (0.04)	0	0	0
Cirsium vulgare	0.6 (1.3)	0.1 (0.2)	0	0
Dactylis glomerata	0	0.5 (0.9)	0	0
Daucus carota	0.8 (1.0)	0.1 (0.2)	0	0
Holcus lanatus	0.1 (0.2)	0.1 (0.2)	0	0
Hypericum perforatum	**1.0** (0.7)	**1.5** (1.3)	0.3 (0.7)	0.6 (0.8)
Hypochaeris radicata	**3.0** (3.0)	**3.4** (5.5)	0.1 (0.3)	0
Lactuca muralis	**1.6** (1.3)	**1.4** (1.2)	0.2 (0.3)	**7.3** (7.0)
Plantago lanceolata	0.2 (0.3)	0	0.1 (0.2)	0
Plantago major	0.2 (0.4)	0	0	0
Senecio jacobaea	0	0.3 (0.6)	0	0
Trifolium pratense	0.2 (0.3)	0	0	0
Trifolium repens	**1.5** (1.6)	**1.8** (2.4)	0	0

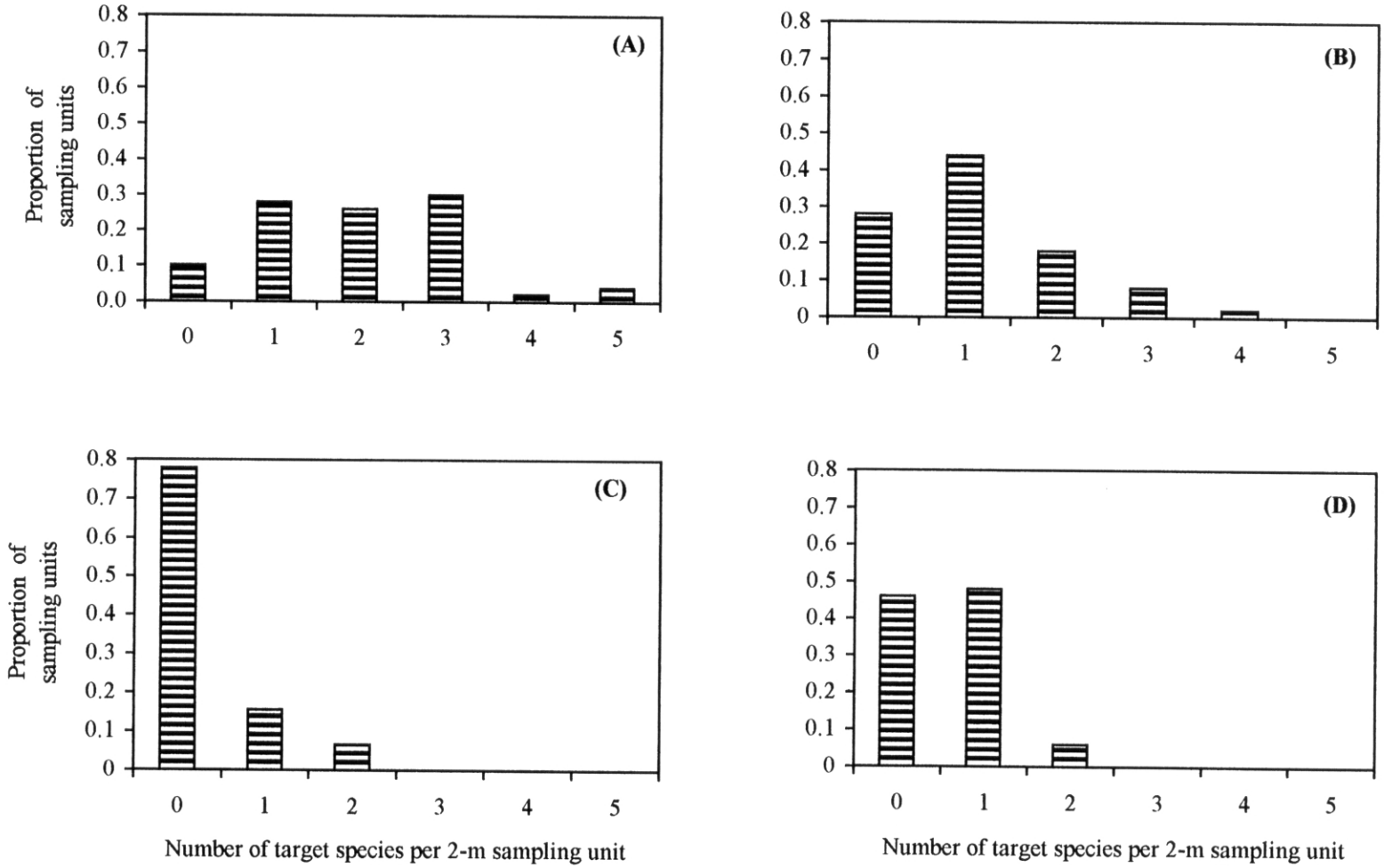


Figure 3.7. Frequency distribution of target species in 2-m sampling units along (A) high-use roads, (B) low-use roads, (C) abandoned roads, and (D) streams.

along streams was also skewed, although a relatively equal proportion of sampling units had either 0 or 1 target species (Figure 3.7D). The maximum was 2.

The frequency of individual species was also different at the fine scale than at the coarser scale. None of the target species occurred in over 50% of the 2-m sampling units (Figure 3.8). Along high-use roads, 13 target species were sampled in the fine-scale sampling units, but only 4 of these occurred in >20% of these sampling units (Figure 3.8A). Along low-use roads, only 2 of the 10 target species found were present in >20% of the fine-scale sampling units (Figure 3.8B). Only 6 target species were found at the fine scale along abandoned roads, and none were present in >10% of these sampling units (Figure 3.8C). Three target species were sampled at the fine scale along streams. One of them, *Lactuca muralis*, was present in 50% of the fine-scale sampling units; the other two were found in <10% of these sampling units (Figure 3.8D).

3.3.2.3 Temporal patterns

There is some evidence of interannual change in the distribution of target species along the high-use and low-use roads from 1993 to 1994, although the patterns were not consistent by species (Figure 3.9). At least two target species along all five high-use roads had ≥20% change in frequency (Figure 3.9A). In most cases, the change reflected an increase in frequency from 1993 to 1994, but frequencies decreased along one high-use road. Fewer target species changed in frequency along low-use roads (Figure 3.9A). Of all

Figure 3.8. Frequency of individual target species in 2-m sampling units along (A) high-use roads, (B) low-use roads, (C) abandoned roads, and (D) streams. Species are listed in the order in which they are presented in Figure 3.6 (frequency in the 50-m sampling units). Target species: HYPE = *Hypericum perforatum*; CHLE = *Chrysanthemum leucanthemum*; CIVU = *Cirsium vulgare*; HYRA = *Hypochaeris radicata*; TRRE = *Trifolium repens*; LAMU = *Lactuca muralis*; HOLA = *Holcus lanatus*; PLLO = *Plantago lanceolata*; DACA = *Daucus carota*; DAGL = *Dactylis glomerata*; CIAR = *Cirsium arvense*; PLMA = *Plantago major*; CYSC = *Cytisus scoparius*; TRPR = *Trifolium pratense*; SEJA = *Senecio jacobaea*. The following target species were not found in any of the 2-m sampling units: *Lotus corniculatus*, *Taraxacum officinale*, *Rumex acetosella*, *Rubus discolor*, *Trifolium hybridum*, and *Digitalis purpurea*.

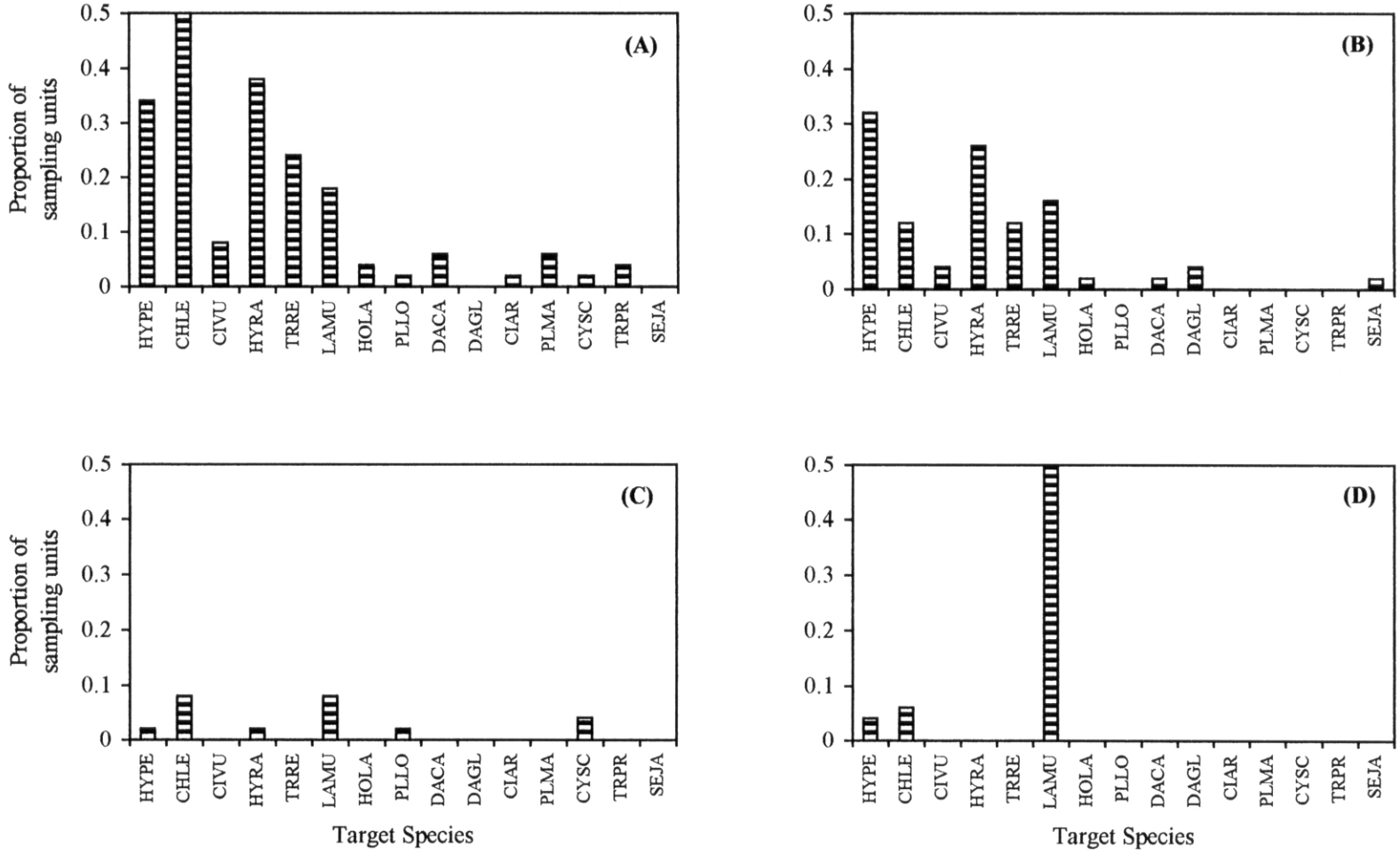

(A)
(B)
(C)
(D)
Proportion of sampling units
Target Species
0.5
0.4
0.3
0.2
0.1
0
HYPE
CHLE
CIVU
HYRA
TRRE
LAMU
HOLA
PLLO
DACA
DAGL
CIAR
PLMA
CYSC
TRPR
SEJA

Figure 3.8.

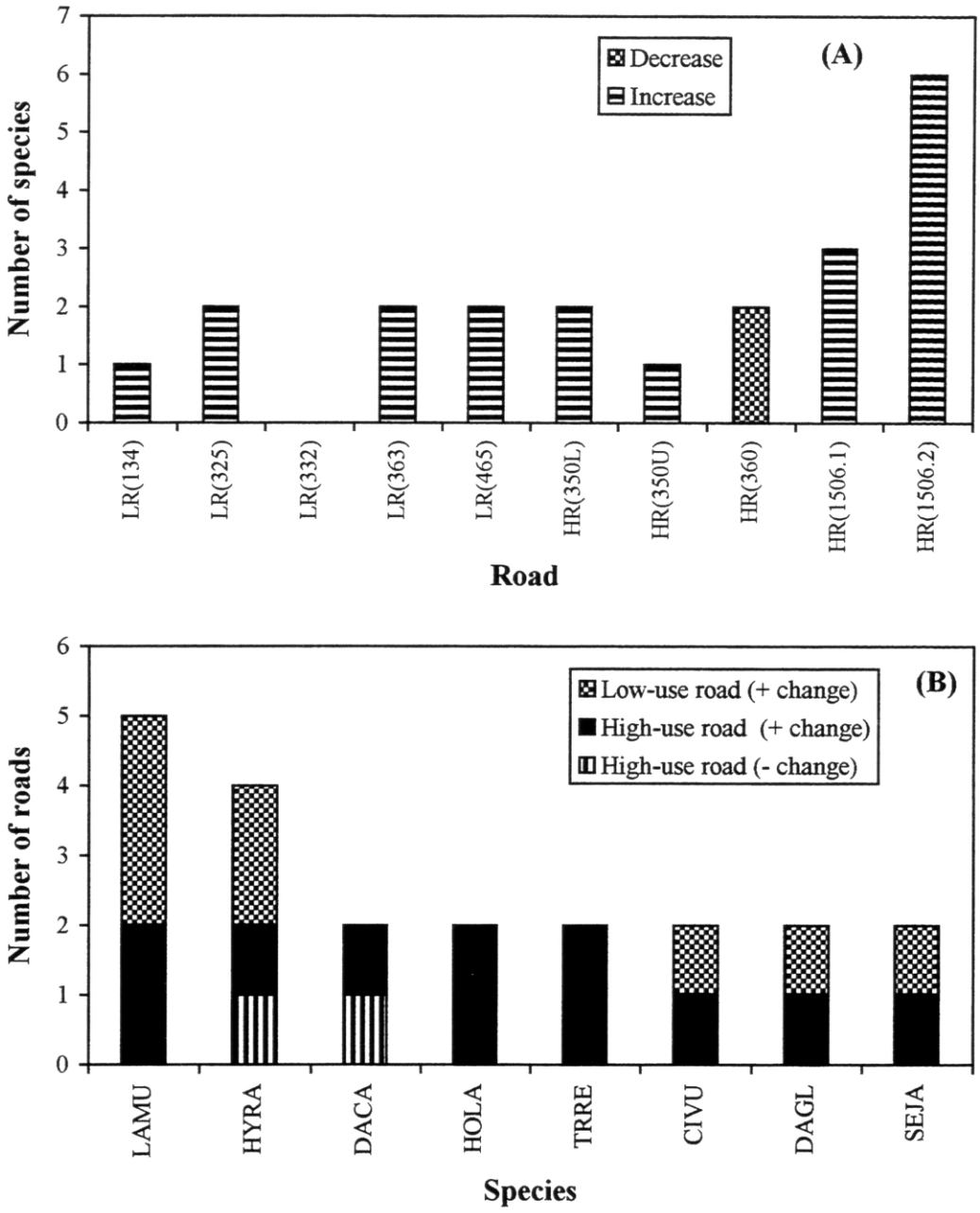


Figure 3.9. Interannual changes in target species distribution along high-use and low-use roads from 1993 to 1994: (A) number of species with >20% change and (B) number of roads with >20% change. (LR = low-use road; HR = high-use road; road number is in parentheses) (LAMU = *Lactuca muralis*; HYRA = *Hypochaeris radicata*; SEJA = *Senecio jacobaea*; DACA = *Daucus carota*; HOLA = *Holcus lanatus*; TRRE = *Trifolium repens*; CIVU = *Cirsium vulgare*; DAGL = *Dactylis glomerata*)

the target species, *Lactuca muralis* changed the most across all transects; its frequency increased at least 20% along three high-use roads and along two low-use roads (Figure 3.9B).

3.3.3 Transect patterns -- environment

The two physical parameters examined in this study were aspect and general light levels. The distribution of aspect in the three road habitat types was similar to the distribution for the whole road network at HJA, except for a higher frequency of west-facing sampling units along high-use road transects (Figure 3.10). The overall similarities suggest that the sampling was not biased with regard to aspect.

The distribution of the three light classes (high, medium, and low levels) along the habitat types is shown in Figure 3.11. Clearly, high-use and low-use roads are similar in the frequency of medium and high light levels. In contrast, abandoned roads and streams are similar to each other and have a very high proportion of samples with low light levels.

3.3.4 Species patterns

The target species were placed into one of three groups, according to their frequency distribution. Species in Group 1 were most frequent and occurred in ≥50% of the 50-m sampling units for at least two of the habitat types (Figure 3.12A). Species in

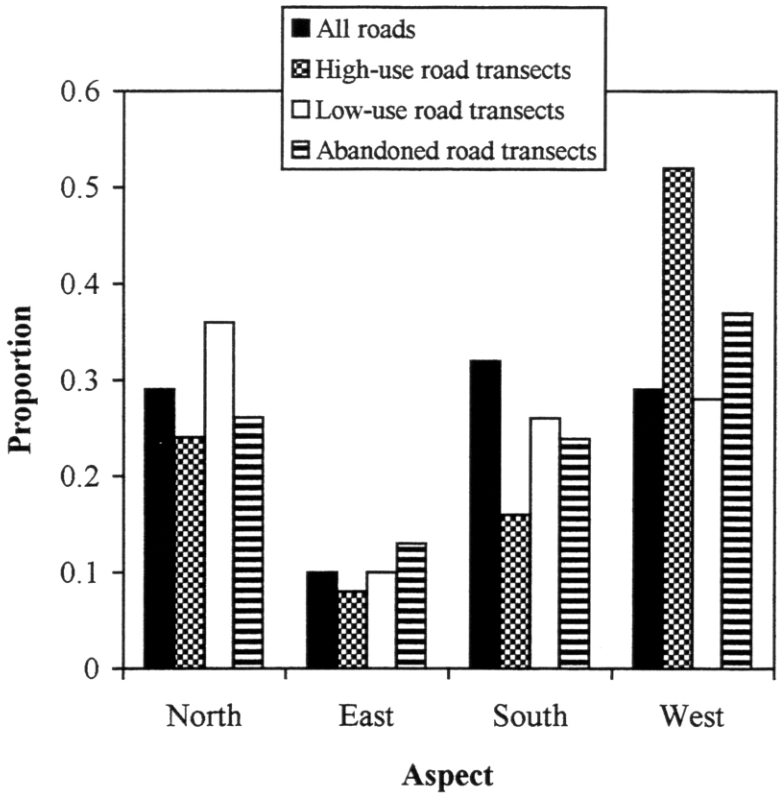


Figure 3.10. Distribution of aspect classes along all roads in the H.J. Andrews Experimental Forest and along road transects sampled in the current study.

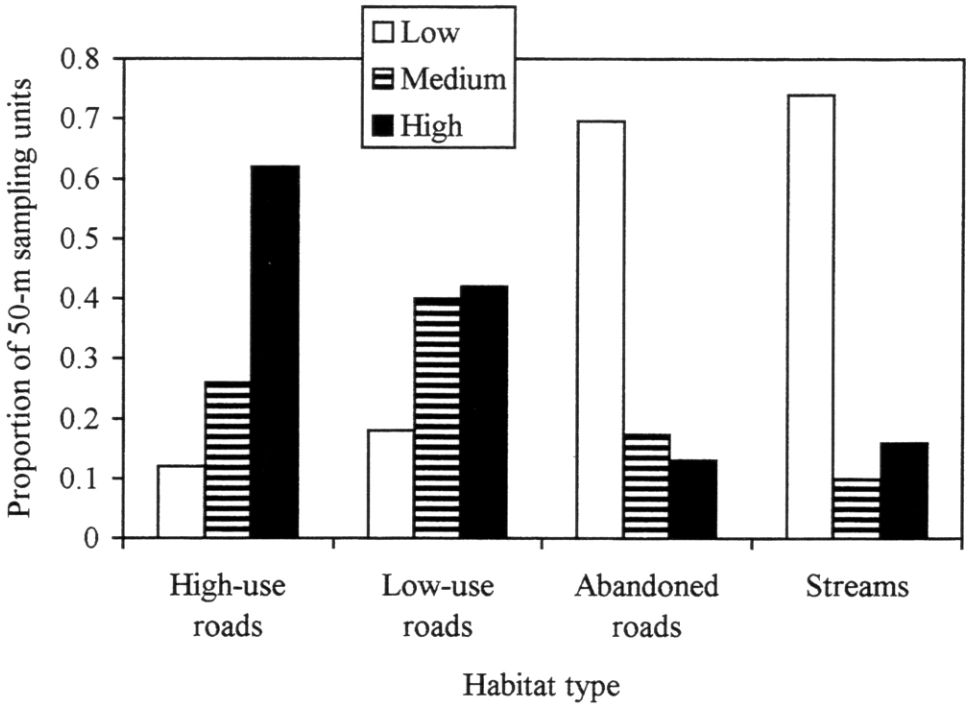


Figure 3.11. Distribution of light classes along each habitat type.

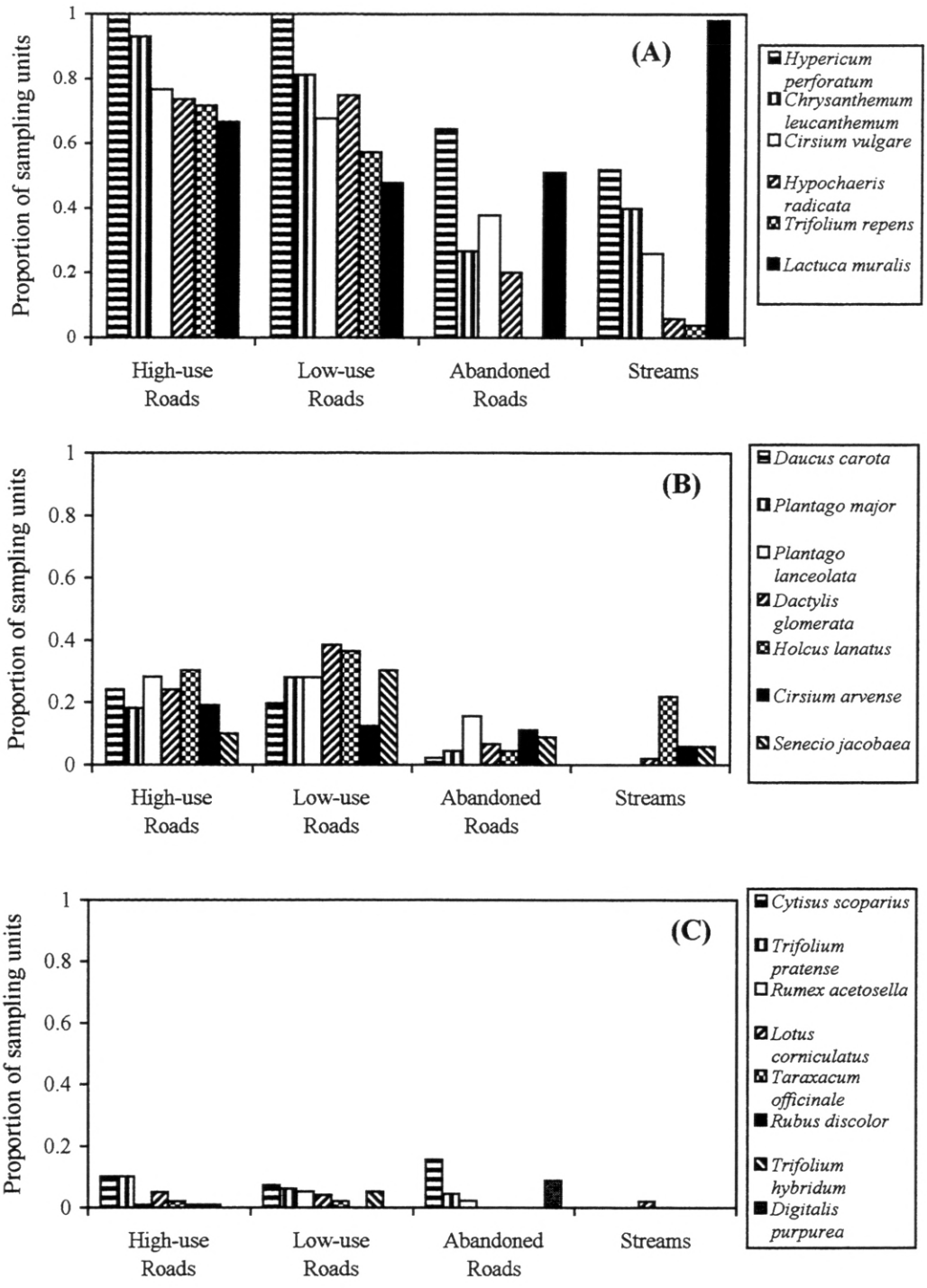


Figure 3.12. Frequency distribution of target species in 50-m sampling units along each habitat type: (A) Group 1 (most frequent), (B) Group 2 (moderately frequent), and (C) Group 3 (least frequent). Group assignments were based on proportion of species occurrence: Group 1, ≥ 0.5 in at least two habitat types; Group 2, >0.1 and <0.5 in at least two habitat types; Group 3, ≤ 0.1 in at least three habitat types.

Group 2 were moderately frequent; these occurred in about 10% to 49% of the 50-m sampling units for at least two of the habitat types (Figure 3.12B). Species in Group 3 were the least frequent and were present in <10% of the 50-m sampling units for at least three of the habitat types (Figure 3.12C).

All species in Group 1, except *Trifolium repens*, occurred in all four habitat types (Figure 3.12A). The spatial patterns for most species in this group were similar: frequencies along high-use and low-use roads were similar to each other and higher than along abandoned roads and streams. The pattern for *Lactuca muralis* was a notable exception. This species was more frequent along streams than was any other species, although it was fairly frequent in other habitat types as well (Figure 3.12A).

The species in Group 2 occurred in all three types of roads (high-use, low-use, and abandoned); four of the species also occurred along streams (Figure 3.12B). Although the general spatial patterns for Group 2 species were similar to that described for Group 1, the patterns showed more variation among species. For example, *Senecio jacobaea* was most frequent along low-use roads; frequencies along the other three habitat types were similar to each other. *Cirsium arvense* was most frequent along high-use roads; frequencies were similar along low-use and abandoned roads, and lowest along streams (Figure 3.12B).

The species in Group 3 were the least frequent and no regular patterns could be discerned (Figure 3.12C). Only one species in this group, *Lotus corniculatus,* was found along streams. *Digitalis purpurea* was only found along abandoned roads.

Logistic regression models were significant for all of the most frequent (Group 1) species, indicating that habitat type and light levels are useful for predicting the presence of these target species. Some, but not all, of the models were significant for the

moderately frequent (Group 2) species (Tables 3.5 and 3.6). None of the least frequent (Group 3) species had sufficient data for this portion of the analysis. Odds ratios generally indicate that the target species were significantly more likely to occur on high-use or low-use roads (relative to streams, the reference category) and under high or medium light levels (relative to low light, the reference category). None of the target species were significantly more likely on abandoned roads than on streams. For example, the odds ratios for *Cirsium vulgare* indicate that this species was 9 and 6 times more likely to be present on high-use roads ($p = 0.0001$) and low-use roads ($p = 0.0015$), respectively, than on streams; the difference between abandoned roads and streams was not statistically significant ($p = 0.40$) (Table 3.5).

Lactuca muralis was an exception to the general pattern. The odds ratios were <1 for both explanatory variables, which indicates that this species was less likely to occur along a particular habitat type or under a particular light level, compared with the reference category. For the logistic regression model with habitat type, the odds ratios indicate that *Lactuca muralis* was 1/50 as likely (or 50 times *less* likely) to be present on low-use roads ($p = 0.059$) or abandoned roads ($p = 0.074$) compared with streams; however, the difference between high-use roads and streams was not statistically significantly different ($p = 0.13$) (Table 3.5). For the logistic regression model with light levels, the odds ratios indicate that *Lactuca muralis* was 5 and 2.5 times *less* likely under high light ($p = 0.0004$) and medium light ($p = 0.025$), respectively, than under low light (Table 3.6).

Table 3.5. Results of logistic regression models with target species presence as the response variable and habitat type as the explanatory variable. Separate models were run for each species.

Species	Chi Sq	Pr>Chi	Habitat type comparison[a]	Estimate	SE	Pr>Chi	Odds ratio
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
Hypericum perforatum[b]	33.40	0.0001	AR vs. S				2
Trifolium repens[c]	30.64	0.0001	HR vs. S				61
			LR vs. S				32
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
Daucus carota[d]	14.98	0.0018					
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

Table 3.5. Continued.

Species	Chi Sq	Pr>Chi	Habitat type comparison[a]	Estimate	SE	Pr>Chi	Odds ratio
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 major[d]	8.65	0.034					
Plantago lanceolata[d]	8.50	0.037					
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
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
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
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

Table 3.5. Continued.

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[a] HR = high-use road; LR = low-use road; AR = abandoned road; S = stream.

[b] *Hypericum perforatum* was present in all 50-m sampling units along all HR and LR transects. Therefore, neither estimates of logistic regression coefficients nor comparisons between HR vs. S or LR vs. S are meaningful. Odds ratio for AR vs. S was calculated from raw data.

[c] Estimates of logistic regression coefficients are not meaningful because of insufficient data in AR and S habitat types. *Trifolium repens* was not present in AR. Therefore, AR vs. S comparison and odds ratios are not meaningful. Odds ratios for HR vs. S and LR vs. S were calculated from raw data.

[d] Estimates of logistic regression coefficients are not meaningful because of insufficient data in AR and S habitat types. *Daucus carota, Plantago major*, and *Plantago lanceolata* were not present in S. Therefore, habitat type comparisons and odds ratios are not meaningful.

Table 3.6. Results of logistic regression models with target species presence as the response variable and light level as the explanatory variable. Separate models were run for each species.

Species	Chi Sq	Pr>Chi	Light level comparison	Estimate	SE	Pr>Chi	Odds ratio
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
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
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
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
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
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
Chrysanthemum 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

Table 3.6. Continued.

Species	Chi Sq	Pr>Chi	Light level comparison	Estimate	SE	Pr>Chi	Odds ratio
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
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
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
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
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

3.4 Discussion

3.4.1 Physical factors

The similarity between invasion patterns along high-use and low-use roads at the 1-km scale suggests that the current disturbance level is not an important factor for determining the distribution of target species at this scale. Perhaps the initial disturbance during road construction, which would likely be similar for all roads, or early use levels are more important than are current differences in vehicle use and frequency/intensity of maintenance. The data along high-use and low-use roads were normally distributed (Figures 3.5A and 3.5B), which suggests that these habitat types have suitable environmental conditions for quite a few target species and that these conditions were well-distributed along these roads.

The distribution of exotics along abandoned roads was significantly different; target species were less frequent and less abundant than along the high-use and low-use roads. Also, the frequency distribution was skewed (Figure 3.5C), which suggests that suitable environmental conditions were more restricted than along high-use and low-use roads and that they were only suitable for a few target species. It is impossible to determine from this retrospective study whether abandoned roads had similar invasion patterns when they were accessible to vehicles, but results suggest that current environmental conditions along abandoned roads are barriers to invasion. The differences in light levels support this hypothesis. Abandoned roads had much lower light levels than

did high-use or low-use roads, and the logistic regression models with light as an explanatory variable were significant for many of the target species.

These results have implications for management of forested landscapes on which roads have been constructed. The road network may be considered a linear light gap that, at the coarser scale, provides fairly continuous environmental conditions that are suitable for a variety of exotic plant species. Relative to the conceptual model of invasion, the roads remove physical and ecological barriers to invasion (Johnstone 1986) by providing both a corridor along which species may move and a suitable invasion site for establishment of the species.

When a road is abandoned, disturbance associated with vehicle traffic and maintenance activities ceases, and natural successional processes take over. The roadbed had not been removed from any of the abandoned roads surveyed in the current study, so the compacted gravel was still present. However, all had been abandoned long enough that vegetation was encroaching on the roadbed. The most common understory species was *Rubus ursinus*, a trailing vine. Common tree species included *Alnus rubra* and *Pseudotsuga menziesii*. The physical conditions change in an abandoned road as the adjacent vegetation grows over the roadbed and the canopy closes, thus providing less light at the ground level. The lower light levels along abandoned roads appear to negatively influence invasion. Thus, management strategies that include road closure may be an indirect way of controlling invasion by exotic plants.

The similarity between current invasion patterns along abandoned roads and streams appears to be related to the similar light levels observed at the time of the field survey. As in the abandoned roads, the frequency distribution along streams was skewed

(Figure 3.5D), which suggests that suitable environmental conditions were fairly restricted. Both abandoned roads and streams had mostly low light levels, and the logistic regression models with habitat type as the explanatory variable indicated that the odds of finding a target species was not significantly different between abandoned roads and streams.

However, light conditions along streams probably "reset" more frequently than they do along abandoned roads. The field survey for this study was conducted in 1994, 30 years after an intense flooding event that scoured much of the riparian zone at the study site. Although there had been other large floods between 1964 and 1994, none of those events was severe enough to extensively remove stands of *Alnus rubra*, *Salix* spp., and other shade-providing trees and shrubs that had established after the 1964 flood. Thus, the canopy vegetation along the streams during the 1994 survey was probably at least 30 years old (or nearly so) and provided a significant amount of shade. Another large flood occurred in 1996 and affected much of riparian zone of stream segments that were surveyed in 1994. Several streams were revisited after the 1996 flood to informally assess any changes. In general, the most frequent target species were still present (although their frequency was not formally evaluated). The most dramatic difference was that light levels were generally much higher in 1996 than they were in 1994. Thus, patterns of invasion along streams may be quite different in another few years, after plants have had an opportunity to become established on the newly created light gaps. A similar large-scale disturbance is unlikely along abandoned roads, unless they are reopened for vehicle traffic.

Although this study focused on light levels based on canopy cover, roads and streams differ in a number of other respects that may have an influence on exotic plant

distribution. The topographic position of streams is always at the bottom of a hillslope, whereas roads may be in various hillslope positions. This position has a strong influence on the available light, with streams being especially affected by topographic shading. The soils along streams generally have a wide range of particle sizes, from very fine to large rocks or boulders, and they have a high moisture content or are saturated. Along roads, soils are much drier and are composed of compacted gravel material that has been imported. Competition with natives may be more important along abandoned roads and streams than along high-use and low-use roads. As natural succession proceeds along abandoned roads without any disturbance from vehicles or maintenance activity, natives that reoccupy the roadside and roadbed may be able to exclude the exotics through competitive interactions over time. Vegetation along streams includes a suite of native species that are adapted to the disturbance regime, and they may also be able to exclude exotics through competition. Finally, wind dispersal may be less likely along abandoned roads compared with the other three habitat types examined in this study. As the vegetation recolonizes the abandoned roadbed, the closed canopy may offer more wind resistance than along roads that are still actively used. Streams always have a continuous flow of water, which may aid in the dispersal of some species.

This study demonstrates that the observed patterns of invasion are clearly influenced by the scale at which data were collected. Although the main focus of this study was the coarse (1-km) scale, observations along the 2-m sampling units have implications for detectability and the scale of species patterns. Fewer target species were detected at the finer scale of observation (Table 3.3), and these tended to be the species that were more frequent at the coarser scale. Patterns among the habitat types observed at the finer

scale reveal some differences that were not evident at the coarser scale. High-use roads generally had more target species per 2-m sampling unit than did any other habitat type. Low-use roads had more 2-m sampling units with no target species than did high-use roads; over 75% of the 2-m sampling units along abandoned roads had no target species, much higher than along streams (about 45%). For the roads, perhaps the differences in vehicle use and frequency of maintenance along high-use versus low-use roads have more influence on the patterns of invasion observed at the finer scale than at the coarser scale. For all habitat types, perhaps the different patterns observed at the finer scale reflect differences in size and frequency of suitable patches for establishment, such as light gaps, that were not evident at the coarser scale.

General interannual patterns along high-use and low-use roads suggest that the frequency of some target species increased from 1993 to 1994. However, one year is probably insufficient to evaluate whether the observed changes reflect a significant increase in invasion sites occupied by the species, or fluctuation in populations related to climatic conditions or some other factor. Temperature and precipitation records from HJA climate stations, for example, indicate that 1993 was generally wetter and cooler than 1994 (Appendix E), which may have influenced the observed species patterns.

3.4.2 Biological factors

Ridley (1930) compiled a thorough, descriptive summary of plant dispersal based on observations by a wide variety of researchers across a broad geographic range. Most

species included in the current study were listed in Ridley's work, and his information on dispersal mechanisms and agents for each is summarized in Appendix C. Van der Pijl (1982) developed a complex dispersal classification system that was based on presumed dispersal agents. However, an approach that focused on dispersal agents was not used for evaluating the potential for dispersal of the target species in the current study, because most species are likely have more than one potential dispersal agent (for example, wind and adhesion on animals) and it was difficult to determine the relative importance of each agent. Also, most target species are capable of being dispersed at least some distance by wind, but that information alone does not help discriminate among the species. Thus, neither the observations presented in Ridley (1930) nor the classification scheme discussed by van der Pijl (1982) were used to objectively evaluate dispersal for this study.

Dansereau and Lems (1957) took a different approach and developed a classification of dispersal types that was based primarily on morphological characters. One primary division of the dispersal classes was based on whether the diaspore (unit of dispersal) has any obvious morphological feature that may aid in dispersal. Another general division was based on diaspore weight. This approach is more objective and only indirectly invokes potential dispersal agents.

A modified version of the Dansereau and Lems (1957) scheme was developed for the current study in order to evaluate dispersal potential of the target species. The main factors included were presence/absence of morphological appendages and seed weight. Since the primary interest in this study was invasion at the landscape scale, special mechanisms that promote Phase I dispersal [movement of the diaspore from the parent plant to a surface (Chambers and MacMahon 1994)] were ignored. *Cytisus scoparius*, for

example, has ballistic dispersal [fruits are equipped to explosively release seeds from the parent plant when the fruits are mature (Bossard 1991)], but this mechanism would not explain dispersal farther than a few meters (Smith and Harlen 1991). Phase II dispersal (which includes all vertical and horizontal movement of the diaspore after it has left the parent plant during Phase I dispersal) is of greater interest in the current study because it has more influence on the pattern of plant distributions in communities and ecosystems (Chambers and MacMahon 1994).

Seed weight was included in the scheme for evaluating dispersal potential, because lighter seeds may be more easily transported by wind or some other force than are heavier seeds. Logarithmically scaled seed weight classes defined by Baker (1972) were adopted for the current study.

Table 3.7 presents a classification of dispersal types, with each of the target species listed under the appropriate category in order of increasing mean seed weight. The species group number from the current study is also included in Table 3.7 in order to compare observed frequency patterns of target species with an objective assessment of dispersal potential. The species included in Group 1 have biological characteristics that may help explain why they are among the most frequent: either they have special, lightweight appendages (pappus attached to the achenes) that may aid in dispersal, or the seeds themselves are fairly light (Table 3.7). The general biological characteristics of Group 1 species suggest a high potential for dispersal, particularly by wind, although other forces are possible as well. Adhesion of plumed seeds to animals, for example, is especially common when the vegetation is wet (Ridley 1930). *Cirsium vulgare* seeds are the heaviest

3.7. Dispersal classification scheme (based on morphological characters and seed weight) and species group (based on frequency of occurrence in the current study).

Morphological characters[a]	Species	Mean seed weight[b] (mg)	Seed weight class[c]	Species group[d]
Diaspore has obvious morphological appendages that may aid dispersal				
Appendages are thin, light, flexible	*Senecio jacobaea*	0.28	5	2
	Lactuca muralis	0.43[e,f]	6	1
	Hypochaeris radicata	0.81[e]	6	1
	Taraxacum officinale	0.86	6	3
	Cirsium arvense	1.57	7	2
	Cirsium vulgare	2.85[e]	7	1
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	*Digitalis purpurea*	0.09	4	3
	Hypericum perforatum	0.13	5	1
	Plantago major	0.20	5	2
	Holcus lanatus	0.22[e]	5	2
	Chrysanthemum leucanthemum	0.22	5	1
	Rumex acetosella	0.41	6	3
	Trifolium repens	0.64	6	1
	Trifolium hybridum	0.88	6	3
	Dactylis glomerata	0.90	6	2
	Lotus corniculatus	1.20	7	3
	Plantago lanceolata	1.55	7	2
	Trifolium pratense	1.90	7	3
	Cytisus scoparius	7.60	8	3

[a] Adapted from Dansereau and Lems (1957).
[b] Source: Salisbury (1942) except as noted.

Table 3.7, Continued.

[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] Based on frequency of occurrence in the current study. Group 1 = most frequent; Group 2 = moderately frequent; Group 3 = least frequent.
[e] Source: Herbert and Irene 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*.

of the species in Group 1, but their large plumed achene clearly compensates for the extra weight as they fly well in light breezes.

The species with heavier seeds tended to be in Groups 2 and 3 (moderately and least frequent species, respectively) (Table 3.7). Seed weight might be a barrier to long-distance dispersal, and species with heavier seeds might have a lower potential for dispersal than do species with lighter seeds. The heaviest seeds belong to the only two shrubs among the target species, *Cytisus scoparius* and *Rubus discolor*, which were in Group 3, the least frequent species. However, the lightest seeds belong to *Digitalis purpurea*, which was also in Group 3. Thus potential for dispersal alone does not explain the patterns of invasion.

A number of confounding factors need to be considered. A number of biological factors, for example, may confound the ability of dispersal potential alone to predict invasion patterns. These include germination requirements, competitive ability, predation, and seed longevity. Even if a seed can disperse to an invasion site, it may not be able to germinate and become established. Even among the most frequent species (those assigned to Group 1 in this study), differences were observed among the different habitat types. Group 1 species were generally most frequent along high-use and low-use roads, and present but less frequent along abandoned roads and streams. In contrast, *Lactuca muralis* was most frequent and abundant along streams, which suggests that it has different environmental tolerances than do the other target species. More specifically, *Lactuca muralis* appears to be more tolerant of shade, although it may also require more soil moisture or be more tolerant of saturated soils than any other species in this study.

Time since the initial introduction may also be a confounding factor. There are numerous examples in the literature of an initial lag phase during the process of invasion (Forcella and Harvey 1983b, Forcella 1985; Moody and Mack 1988; Perrins et al. 1993; Pysek and Prach 1993; U.S. Office of Technology Assessment 1993; Asher 1995). After a species has been introduced, it often is maintained in small populations of low frequency for some period of time before it begins its expansion phase, which is often quite rapid and is typically characterized by a logistic growth curve. It may be that several of the target species that were infrequent in the current study are still in the initial lag phase of invasion and will expand their range with time.

The "tens rule" (Williamson and Fitter 1996b) may also help explain the patterns in this study. After an exotic species has been imported (either accidentally or deliberately) from its native range, the process of invasion involves the transition through three main phases: initial introduction, establishment, and pest. The tens rule suggests that each transition has a probability of about 10%: about 1 in 10 imported species escape into the wild; of those, about 1 in 10 become established; and of those, 1 in 10 become pests (Williamson and Fitter 1996b). For a variety of reasons, including the confounding factors discussed above, only some of the exotics that are introduced to a new area such as HJA are likely to become established, and only some of those are likely to become widespread. Also, at any given time of observation, various exotics may be at different stages of the invasion process.

3.5 Conclusions

The underlying research question in this study was how physical and biological factors interact to produce the observed patterns of invasion. The results showed that, despite differences in disturbance frequency (particularly vehicle use and maintenance activity), high-use and low-use roads had fairly similar current invasion patterns at the 1-km scale (although more target species were detected along the high-use roads at the finer (2-m) scale). Perhaps the large-scale disturbance during initial road construction was more important, in terms of creating a suitable invasion site, than were any subsequent activities. Abandoned roads had much lower frequencies of the target species, and the difference appeared to be related to the lower light levels on this road type, although it could also be due to competitive exclusion by natives, fewer opportunities for dispersal, or lack of disturbance required to promote germination. Streams also had low light levels during the survey, and the invasion patterns were similar to that of abandoned roads. The disturbance regime along streams is different, however, and some of the target species may become more frequent in riparian areas that were affected by the 1996 flood and now have more available light.

A dispersal classification scheme based on morphological characters revealed that the most frequent species in this study share some biological traits: either they have special, lightweight appendages that may aid in dispersal, or the seeds themselves are fairly light. Although the general trend was that species with lighter seeds tended to be more frequent, this pattern did not hold for all species and a number of confounding factors are likely involved.

The interaction between physical and biological factors was most apparent for the most frequent species. Most of the Group 1 species were present along all four habitat types, which indicates that they did not have dispersal barriers that prevented invasion. However, the frequency patterns varied among habitat types, with Group 1 species generally most frequent along high-use and low-use roads, and present but less frequent along abandoned roads and streams. *Lactuca muralis*, which was more frequent along streams, was an exception. This species appears to be more tolerant of shade than is any other species in this study.

Chapter 4

Landscape-Scale Patterns of Exotic Plant Invasion along Road Networks in Conifer Forests of the Western Cascade Range, Oregon

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in preparation for journal submission

4.1 Introduction

Landscape studies focus on how pattern-process interactions vary with temporal and spatial scale (Turner et al. 1989b). Landscape ecology provides a framework for addressing research questions at scales larger than have traditionally been studied by ecologists (Forman and Godron 1986; Franklin and Forman 1987; Turner 1989; Zonneveld and Forman 1990). Hierarchy theory has been invoked to provide guidelines for understanding the relationship between phenomena at different scales (Allen and Starr 1982; O'Neill et al. 1986; Urban et al. 1987). In general, hierarchy theory addresses how, at a given scale of observation, smaller scale factors may interact to generate observed phenomena at higher levels and larger scale factors may exert control over those at lower levels (Meentemeyer and Box 1987; Urban et al. 1987; di Castri and Hadley 1988; Pickett et al. 1989; Levin 1992). Factors at the scale of individual plants, populations, communities, or ecosystems (such as life history characteristics, competition, succession, disturbance) interact to produce patterns at the higher landscape scale; factors at the regional scale (such as climate) control patterns at the lower landscape level.

Most previous studies of the process of invasion by exotic plants have examined spatial scales that are finer than the landscape scale (DeFerrari and Naiman 1994). However, disturbance can facilitate invasion (Fox and Fox 1986; Swincer 1986; Crawley 1987; Hobbs 1989; Rejmanek 1989; Hobbs 1991), and landscapes are composed of mosaics of patches and networks that are subject to a variety of disturbance types (Pickett and White 1985; Forman and Godron 1986; Turner 1989). Therefore, a study of exotic

plant invasion at the landscape scale may provide insight about the susceptibility of that landscape to invasion (Lee et al. 1992).

The structure of a forested landscape may be described in terms of patches (polygons of various sizes and shapes that were created by a suite of disturbances such as fire, windthrow, mass wasting, timber harvest) and networks (linear features that are interconnected, such as streams and roads). The road network in a forested landscape may be the initial point of entry for many exotic plants. The role of roads in facilitating invasion has been discussed by numerous researchers (e.g., Frenkel 1970; Forcella and Harvey 1983a; Wester and Juvik 1983; Reznicek and Catling 1987; Schmidt 1989; Ullmann and Heindl 1989; Heindl and Ullmann 1991; Tyser and Worley 1992; Wilson et al. 1992; Lonsdale and Lane 1994; Forman and Hersperger 1996). The road and roadside may serve both as habitat as well as a corridor by which a plant species is able to invade other parts of the landscape (Wace 1979 in Wester and Juvik 1983).

The objective of this study was to examine how physical and biological factors affect the process of invasion. The term invasion is used here to describe a process by which exotic plants are introduced and become established in an area where they previously did not occur. At any given time, the invasion process may be characterized, in part, by the distribution pattern of exotic species (also called invasion pattern). The process of invasion can occur if there is a source of propagules, if those propagules can disperse to an invasion site, and if the invasion site has suitable conditions for germination and establishment. If any of these criteria are not met, then a barrier to invasion exists.

In this study, a conceptual model of the invasion process in a landscape is evaluated in the light of observed landscape-scale patterns of exotic species. The results

may be useful for predicting invasion patterns in other similar landscapes, while also contributing to a general susceptibility model for invasion in a forested landscape.

4.2 Methods

4.2.1 Conceptual model

This study proposes a conceptual model of the process of invasion by exotic plants in a landscape over time and space. After an exotic species is introduced, the area that it occupies typically increases over time, and the expansion may be characterized by a logistic growth curve (Forcella and Harvey 1983b; Forcella 1985; Moody and Mack 1988; Hengeveld 1989; Perrins et al. 1993; Pysek and Prach 1993; U.S. Office of Technology Assessment 1993; Asher 1995; Luken and Thieret 1996). Such a curve has three phases (Figure 4.1A): (1) lag phase with slow expansion, (2) a period of rapid expansion, and (3) a state of dynamic equilibrium with no net expansion.

This general curve may take different forms depending upon the specific characteristics of the landscape, the time period, or the species involved (Figure 4.1B). For example, two species introduced at the same time may reach different equilibrium levels in the same landscape (e.g., species A and B in Figure 4.1B). Such an outcome implies that the two species have different dispersal capabilities or are sensitive to different environmental barriers in that landscape. On the other hand, two species introduced at the same time to the same landscape may reach the same equilibrium level at different rates

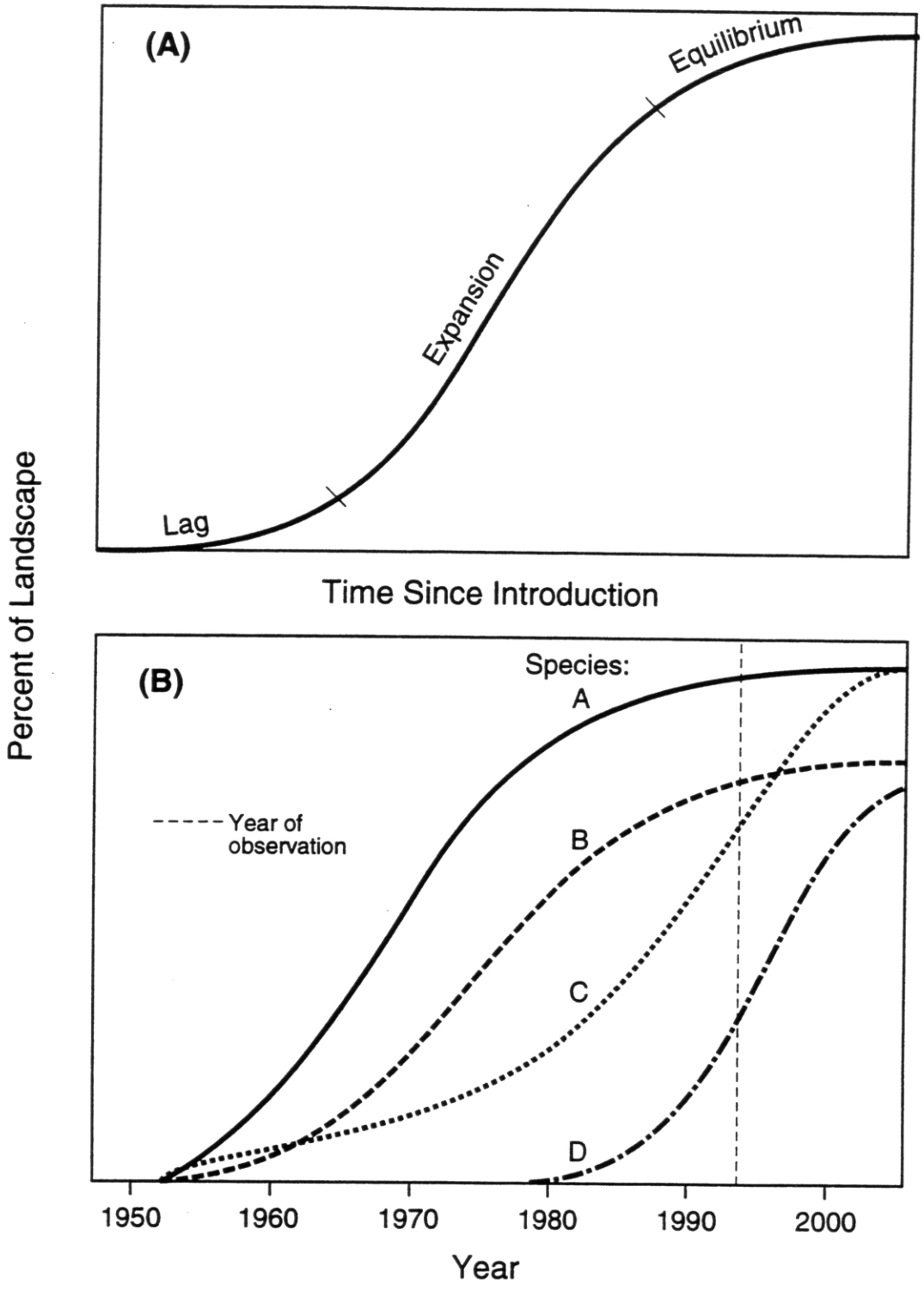

Figure 4.1. Conceptual model of the process of invasion in a landscape over time: (A) typical invasion curve and (B) invasion curve for several species over a specific time period.

(e.g., species A and C in Figure 4.1B). This implies that the two species have different biological characteristics, such as different life forms, rates of seed production, competitive abilities, or susceptibility to herbivory; it could also mean that one species is sensitive to a temporary environmental barrier (e.g., a period of cold or dry years). Another scenario is that two species may have similar rates of expansion yet are displaced by different times of introduction (e.g., species A and D in Figure 4.1B). A key implication of this conceptual model is that at a specific time of observation, species may be at various points along their respective invasion curves (Figure 4.1B). Hence, a single date or short-term description of invasion pattern is severely limited in its ability to discriminate among contrasting invasion trajectories over time.

Invasion over space may be conceptualized in two ways. Assuming a single point of introduction, an exotic species may invade a landscape in an advancing wavefront, with complete occupation behind the wavefront (Figure 4.2A, simplified to display invasion along a road network only). This model assumes that there are no dispersal or environmental barriers to invasion for that species in that landscape. It is similar to a simple reaction-diffusion model in which the rate of invasion is a function of the species' local density and its intrinsic rate of increase (Levin 1992; Hastings 1996a, 1996b; Higgins et al. 1996).

A second conceptual model assumes the presence of invasion barriers and is similar to theoretical modeling approaches that combine biological characteristics of the species with spatially explicit characteristics of the environment (Andow et al. 1990; Hastings 1996b; Higgins et al. 1996). After introduction (again, assuming a single point of entry), the initial pattern of distribution of the species may appear random, but over time the

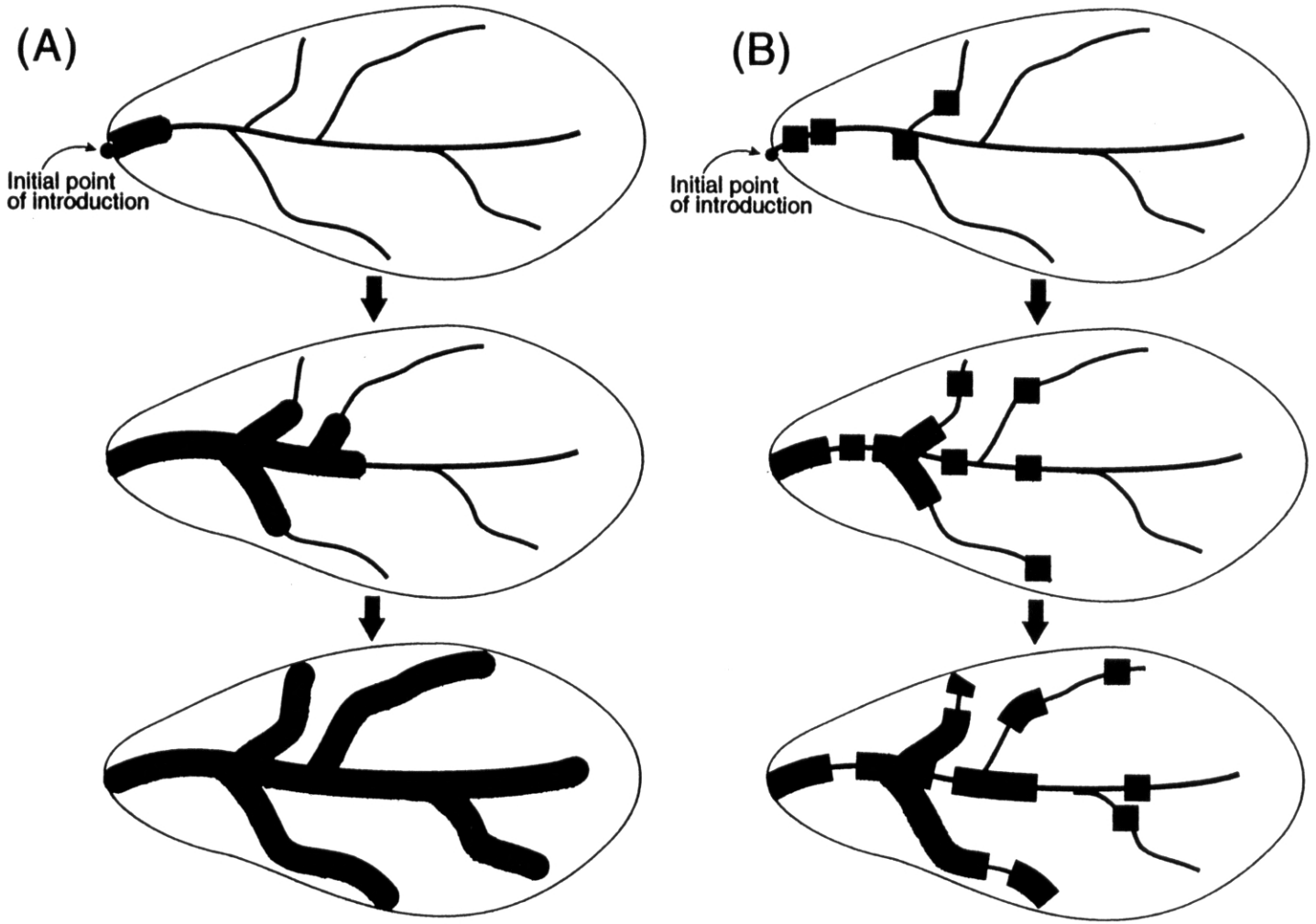

Figure 4.2. Conceptual models of the process of invasion over space in a landscape: (A) advancing wavefront, without barriers; and (B) coalescing patches, with biological/physical barriers.

populations expand into discrete patches (Figure 4.2B, again simplified to a road network only). If the patches continue to coalesce over time, eventually the pattern may be characterized by a spatial gradient. The spatial pattern of distribution in the landscape reflects the biological (e.g., dispersal) and environmental barriers to invasion.

These conceptual models may be combined with tenets from landscape ecology to study the process of invasion. Significant spatial structure may provide some evidence about how invasion is proceeding and whether barriers to invasion exist but, as Figure 4.1 shows, there will always be several plausible interpretations for a given pattern at any point in time. In particular, no pattern type is uniquely attributable to environmental versus biological factors. Nevertheless, it may be possible to discriminate among competing hypothetical factors by (1) examining the spatial structures of groups of biologically similar species, and (2) comparing the spatial patterns of groups of biologically similar species to selected mapped environmental factors.

In this study, mapped patterns of exotic species were compared to mapped environmental attributes that represent physical/climatic factors and human disturbance on the landscape. Physical/climatic factors included in this study were elevation, precipitation, aspect, and solar radiation. Previous studies of the relationship between various physical/climatic factors and invasion by exotic plants (e.g., Lindsay 1953; Frenkel 1974; Forcella and Harvey 1983a; Wester and Juvik 1983; Brothers and Spingarn 1992; Wilson et al. 1992) suggest that, in general, exotic plants would be expected to be more frequent at lower elevations, where conditions are milder than they are at higher elevations. Also, higher frequencies would be expected along sites with higher light levels (south and west aspects and sites with higher solar radiation).

Environmental attributes related to human disturbance on the landscape included in this study were age of adjacent cut units, road age, and road-use levels. Previous studies of the relationship between disturbance and invasion (e.g., Frenkel 1970, 1974; Crawley 1987; Hobbs 1989, 1991; Lepart and Debussche 1991; Hobbs and Huenneke 1992; DeFerrari and Naiman 1994) suggest that higher frequencies of exotic plants would be expected near recent or more intense disturbances than near older or low intensity disturbances. However, some species take time to get established and may have higher frequencies near older disturbances.

The species distribution patterns were also interpreted with regard to a biological factor: potential for dispersal. Dispersal is one the most important biological processes that affects the distribution of plant species (Howe and Smallwood 1982; Green 1983; Primack and Miao 1992), including exotic plants (Frenkel 1970, 1974; McEvoy and Cox 1987; Chambers and MacMahon 1994; Higgins et al. 1996; Kot et al. 1996). Exotic species with higher dispersal potential (i.e., with seeds that are easily dispersed, especially by wind) are expected to be more widely distributed than species with lower dispersal potential (i.e., with heavier seeds, not easily dispersed over long distances).

4.2.2 Study site

Field data for this study were collected at the H.J. Andrews Experimental Forest (hereafter, HJA), a National Science Foundation-sponsored Long-Term Ecological Research site located along the western slope of the Cascade Range, about 80 km (50

miles) east of Eugene, Oregon. HJA occupies about 6400 ha (15,800 acres), and elevations range from 410 to 1630 m (1350 to 5340 ft). The maritime climate of the region includes warm, dry summers and mild, wet winters.

The forest vegetation is primarily composed of conifers in the *Tsuga heterophylla* (western hemlock) zone at lower elevations and in the *Abies amabilis* (Pacific silver fir) zone at higher elevations (Franklin and Dyrness 1988). A species list prepared in the early 1970s (Franklin and Dyrness 1971) included 480 taxa, about 10% of which are not native to Oregon. Some of the exotic species were deliberately introduced as part of seeding mixes to stabilize cut slopes during road construction (Dyrness 1967, 1970, 1975); these were primarily grasses and legumes. Other exotic plants were probably introduced when seeds or vegetative material were brought in accidentally by various sources, including soil imported during road construction; vehicles, clothing, or tools of timber harvest crews, researchers, and other visitors to HJA; livestock that was seasonally grazed in high-elevation meadows; wind or other natural forces from adjacent areas; or some combination of these sources.

HJA was established as a research forest in the late 1940s. Most of the roads construction and timber harvest took place in the 1950s and 1960s; some additional road segments were constructed in the 1970s and 1980s (Wemple et al. 1996). Except for a short paved stretch near the entrance to HJA (about 3 km long), most of the roads in the approximately 100-km network are gravel. The main types of disturbance along the roads are vehicle traffic and maintenance activity; ditch erosion, sedimentation, landslides, and blowdown also affect discrete segments of the road network. Vehicle use at HJA has varied, with some segments having fairly regular traffic throughout the year (and

especially during the summer field season). Other road segments were constructed to access a particular cut unit and subsequently have had very little regular vehicle traffic. A few roads were abandoned after the adjacent cut unit was harvested or after a slide or treefall blocked the road, and these are not accessible by vehicles at all now. Road maintenance schedules have also varied, with the higher use roads receiving more frequent activity (including road grading, ditch clearing, trimming of overhanging vegetation).

4.2.3 Field sampling

Eight exotic species (hereafter, target species) were chosen for study: *Chrysanthemum leucanthemum*, *Cirsium arvense*, *Cirsium vulgare*, *Cytisus scoparius*, *Digitalis purpurea*, *Hypericum perforatum*, *Rubus discolor*, and *Senecio jacobaea*. These species were known to occur at HJA, represent a variety of plant families and dispersal mechanisms (Appendices B and C), and have phenological or morphological traits that allowed easy identification from a vehicle during the survey. Data on the occurrence of each species were collected by driving the entire 100-km road network at HJA and recording presence/absence at 0.1-mile (0.16-km) increments (measured with the vehicle's odometer). Species were recorded as present if they occurred along either side of the road, within approximately 2 m of the road edge. This survey was conducted in 1993 and again in 1994 in order to examine both spatial and interannual patterns.

4.2.4 Environmental attributes

Existing data sets were used for the following environmental attributes: elevation, precipitation, aspect, age of the adjacent cut unit (if present), and road age (data source: Forest Science Data Bank, Department of Forest Science at Oregon State University and USDA Forest Service Pacific Northwest Research Station; see Appendix A). Data on solar radiation was based on output of a model created by Harmon and Marks (1995); the variable used for this analysis was average daily total solar radiation during the growing season (April to September). The attribute road-use level was created specifically for this analysis. Three categories of road use were defined, based on estimated frequency of vehicle travel (A. McKee and F. Swanson, personal communication). High, medium, and low road-use categories are somewhat subjective, but reflect (approximately) the following frequency of vehicle traffic: high-use = regular daily to weekly; medium-use = weekly to biweekly; low-use = less than biweekly. In general, the road-use categories also represent relative frequency and intensity of road maintenance activities.

4.2.5 Data analysis

Descriptive summaries were used to compare the 1993 and 1994 survey results and to determine if the species patterns varied temporally. All subsequent analyses were conducted with the 1994 data.

Understanding the spatial structure of ecological phenomena may yield some insight on the relationship between pattern and process (Turner et al. 1990). The spatial pattern may be characterized in terms of its patchiness (i.e., size and distribution of discrete phenomena) or its gradient (i.e., how the spatial structure varies over distance) (Forman and Godron 1986; Legendre and Fortin 1989; Turner et al. 1990). A variety of tools are now available for conducting spatial analyses (e.g., Wierenga et al. 1987; Boots and Getis 1988; Palmer 1988; Fortin et al. 1989; Legendre and Fortin 1989; Turner et al. 1989a; Milne 1990; Stamp and Lucas 1990; Turner et al. 1990; Bradshaw and Spies 1992; Rossi et al. 1992), and goals of the study can help guide the choice of method(s) (Fortin et al. 1989).

The objectives in the current study were to test for spatial autocorrelation and, if present, to describe the spatial structure. Correlograms and semivariograms are appropriate tools to meet these objectives (Legendre and Fortin 1989). Rossi et al. (1992) recommended constructing both correlograms and semivariograms, because each presents a slightly different perspective on the spatial pattern being examined.

The correlogram is a plot of a spatial autocorrelation coefficient versus lag distance (the distance between pairs of observations), and it can provide information about the patchiness of the spatial structure of each of the target species along each of the roads. The spatial autocorrelation coefficient Moran's I (following Legendre and Fortin 1989) was used in the current study; 95% confidence intervals were also calculated following Sokal and Oden (1978). Statistically significant ($p < 0.05$) positive values of Moran's I provide information about the patch size and interpatch spacing; significant negative values provide evidence for patch–interpatch distance. The semivariogram is a plot of

semivariance (following Rossi et al. 1992) versus lag distance. Because both Moran's I and semivariance are computed for pairs of points at increasing lag distances, the number of pairs decreases with increasing distance (Legendre and Fortin 1989). Therefore, only the first third of the correlograms and semivariograms was analyzed for spatial structure.

Separate correlograms and semivariograms were plotted for each target species along each road that was at least 3.6 miles (5.8 km) long (so that there were a sufficient number of observations). The correlograms were examined for evidence of patchiness in the spatial pattern of species' occurrence (following Legendre and Fortin 1989). If patches were evident, the correlograms were further analyzed to determine patch size and spacing. The semivariograms were examined for evidence of a spatial gradient (following Legendre et al. 1989).

A Geographic Information System (GIS) data layer was created for the survey results for all eight target species along the entire road network. ArcInfo (version 7) and ArcView (version 2.1) were used to spatially relate this survey data with other environmental attributes of the HJA. Each environmental attribute examined in this study was classified into categories for analysis and included as a separate GIS data layer. Maps of each attribute were generated in ArcView for the whole HJA landscape. Then, the HJA road network was added as a separate data layer, and the "spatial join" function within ArcView was used to assign a value of each environmental attribute to each 0.1-mile increment along each road. The results included the percentage of the HJA road network within each class of each environmental attribute and the percentage of each attribute class in which each target species was present.

4.3 Results

4.3.1 General invasion patterns

The eight target species surveyed in this study varied in their distribution patterns along the road network. Table 4.1 summarizes the overall frequency of each species in 1993 and 1994. (See Appendix A for information regarding the complete data set.) The total odometer mileage was slightly higher in 1994 than in 1993, which reflects two factors: (1) a few extra road segments were surveyed in 1994 (0.95 miles in total), and (2) the trip odometer readings varied slightly because a different vehicle was used each year. In order to compare the temporal patterns for the two years, the extra road segments surveyed in 1994 were omitted and a correction factor was applied to the 1993 odometer miles to yield the corrected miles and corrected percentages (Table 4.1).

The interannual patterns show that five of the target species were more frequent along the roads at HJA in 1994 than in 1993, although the percent change was generally low (Table 4.1). *Chrysanthemum leucanthemum* and *Senecio jacobaea* had the highest increase, with about +7% and +8% change, respectively. Only *Hypericum perforatum* was less frequent in 1994 than in 1993, but the difference was low (−1%) (Table 4.1).

The 1994 data suggest that the overall frequency and spatial arrangement of the target species represent three general spatial patterns. One pattern is represented by *Hypericum perforatum*, *Chrysanthemum leucanthemum*, and *Cirsium vulgare*, which were present on >70% of the road network (Table 4.1). The spatial pattern of these species was generally continuous at 0.1-mile intervals along the road network, except

Table 4.1. Summary of presence of eight target species along the H.J. Andrews Experimental Forest road network.

	Odometer miles		Corrected miles		Corrected percent		
Species	1993	1994	1993	1994	1993	1994	Change
Hypericum perforatum	59.39	60.22	60.32	59.47	94	93	-1
Chrysanthemum leucanthemum	45.59	50.49	46.30	50.14	72	79	7
Cirsium vulgare	44.12	46.59	44.81	45.89	70	72	2
Senecio jacobaea	13.7	19.53	13.91	19.43	22	30	8
Cirsium arvense	7.9	10.42	8.02	10.42	13	16	3
Cytisus scoparius	6.1	7.27	6.20	7.07	10	11	1
Digitalis purpurea	0.8	0.5	0.81	0.5	1	1	0
Rubus discolor	0.3	0.3	0.30	0.3	0.5	0.5	0
Total miles	62.89	64.82	63.87	63.87			

toward the ends of the individual roads (Figure 4.3). A second pattern is represented by *Senecio jacobaea*, *Cirsium arvense*, and *Cytisus scoparius*, which were present on 10% to 30% of the road network (Table 4.1). These species occurred in scattered locations throughout much of the road network, but the spatial arrangement was generally discontinuous (Figure 4.4). A third pattern is represented by *Digitalis purpurea* and *Rubus discolor*, which were present in only a few isolated locations that covered ≤1% of the road network (Table 4.1, Figure 4.5).

4.3.2 Spatial analysis

Only six of the eight target species and only data from the 1994 survey were included in this portion of the analysis. *Digitalis purpurea* and *Rubus discolor* were excluded because they were rare, and the spatial analysis would not be meaningful. Also, only roads longer than about 3.6 miles (5.8 km) could be used, because the statistical tools required a sufficient number of data points to detect spatial pattern (Fortin et al. 1989). Seven individual roads (representing approximately 70% of the total miles along the HJA road network) were long enough to be included in the spatial analysis (Figure 4.6).

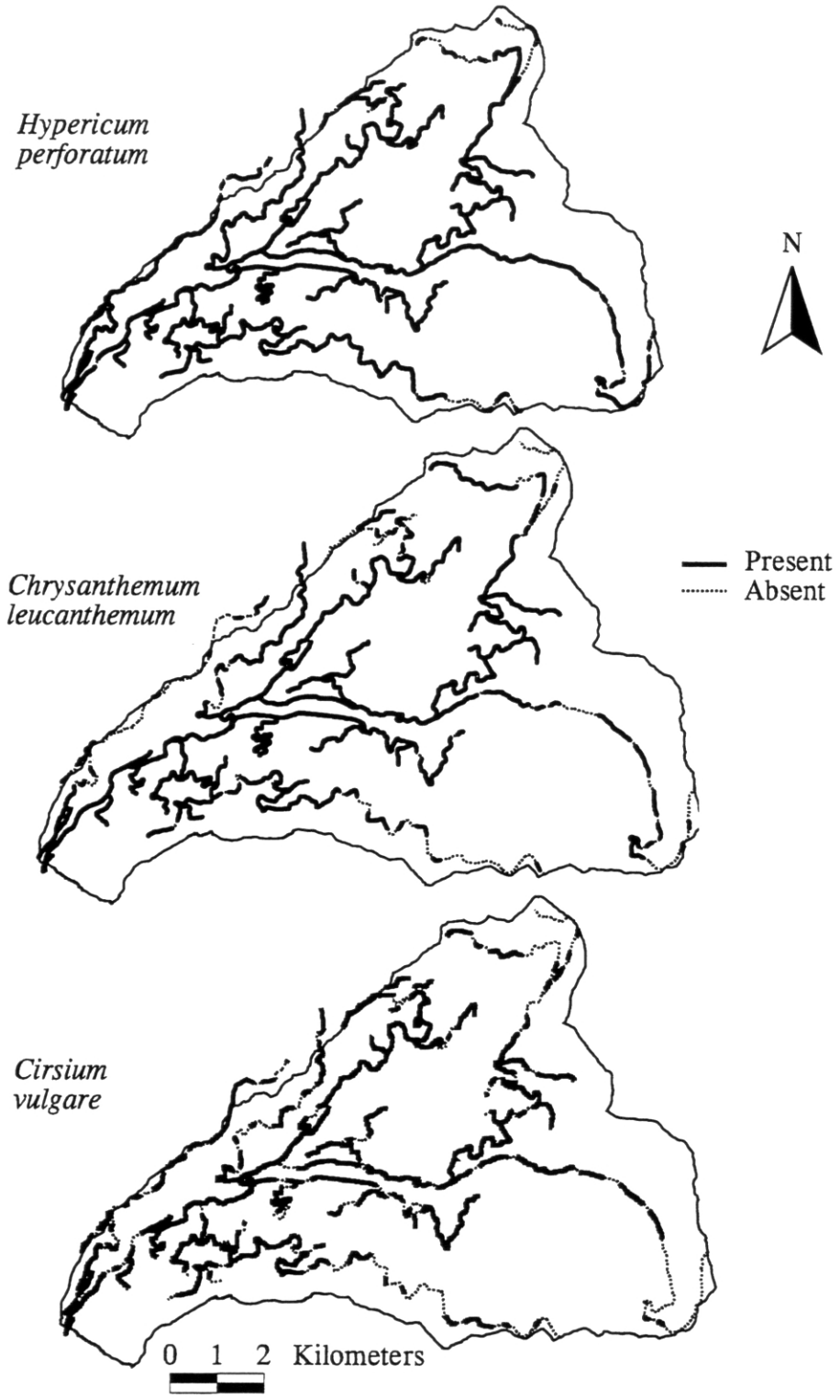

Figure 4.3. Distribution of the three most frequent target species along the road network at the H.J. Andrews Experimental Forest. Data were collected in 1994 at 0.1-mile increments.

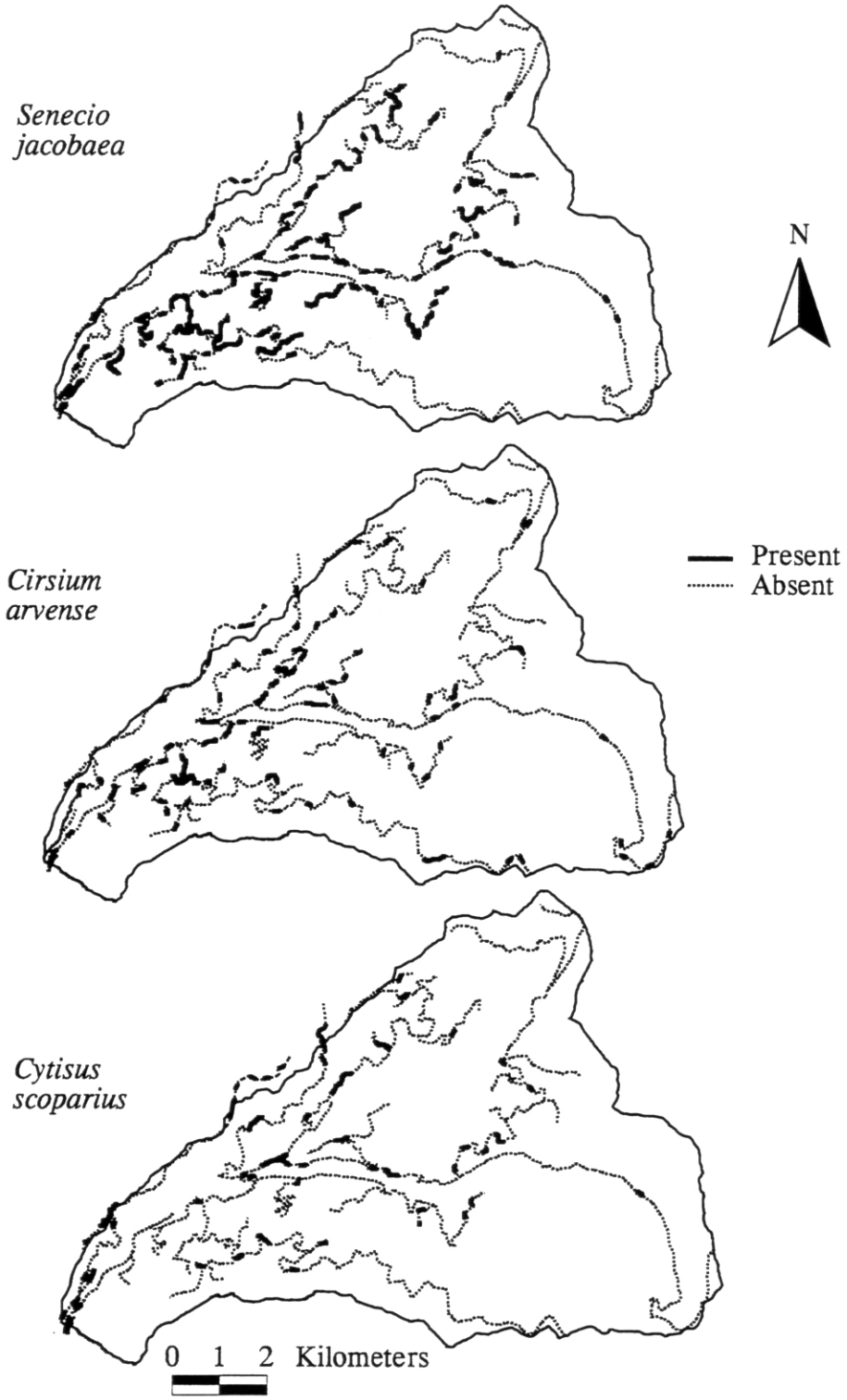

Figure 4.4. Distribution of the three moderately frequent target species along the road network at the H.J. Andrews Experimental Forest. Data were collected in 1994 at 0.1-mile increments.

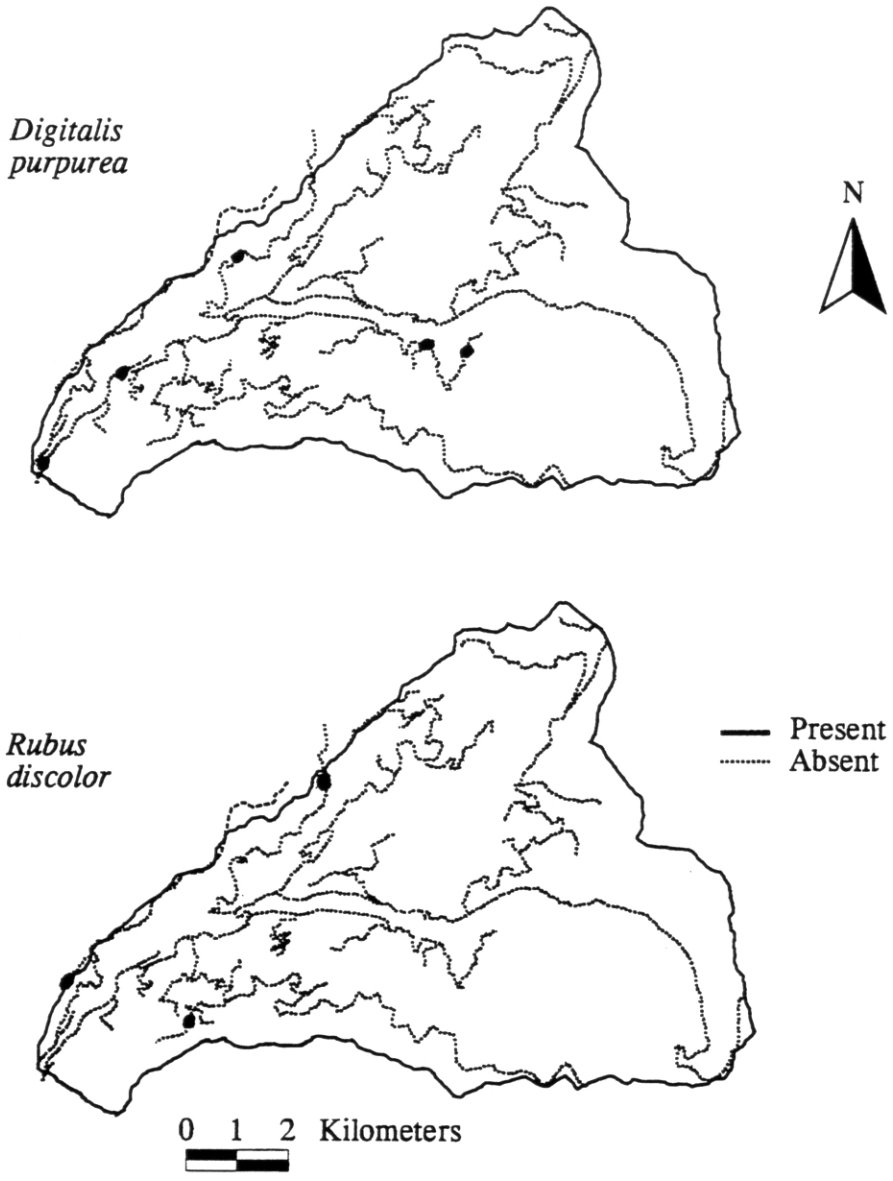

Figure 4.5. Distribution of the least frequent target species along the road network at the H.J. Andrews Experimental Forest. Data were collected in 1994 at 0.1-mile increments.

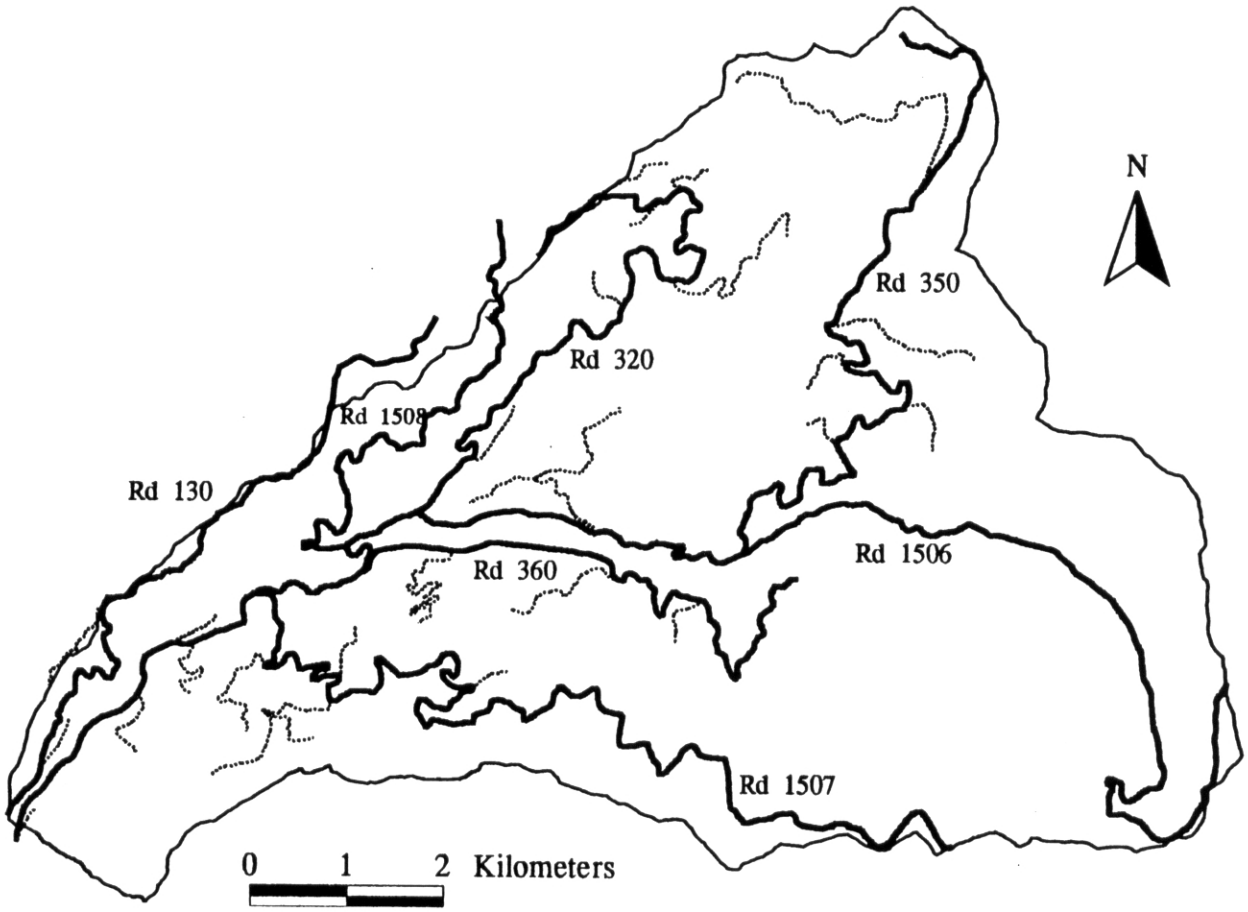

Figure 4.6. Roads in the H.J. Andrews Experimental Forest that were used in the spatial analysis. Bold indicates roads that were used in this analysis; dotted lines indicate roads that were surveyed, but not used in the spatial analysis.

4.3.2.1 Patchiness

There was evidence of a patchy spatial structure in the species distribution patterns [i.e., Moran's I values, either positive or negative, were statistically significant ($p < 0.05$)] for at least one road for all six target species included in this analysis (Table 4.2). The three species that were generally more frequent over the entire road network (*Hypericum perforatum*, *Chrysanthemum leucanthemum*, and *Cirsium vulgare*) showed patchiness on more individual roads than did the other three target species. For example, *Chrysanthemum leucanthemum* had significant Moran's I values along five of the seven roads used in this analysis, whereas *Cirsium arvense* had significant values along only one road (Table 4.2).

The lag distance and sign (positive or negative) of the significant Moran's I values provide evidence about patch size, interpatch spacing, and patch–interpatch distance (Figure 4.7). For example, along Road 320 at HJA, *Chrysanthemum leucanthemum* had significant positive Moran's I values at lag distances of 0.2 to 0.3 miles (interpreted as patch size) and 0.7 miles (interpreted as interpatch spacing), and significant negative Moran's I values at about 1.5 miles (interpreted as patch–interpatch distance) (Figure 4.8A, Table 4.2). Some species had evidence of spatial structure, but only some attributes of patches could be inferred. For example, along Road 360 at HJA, *Cytisus scoparius* had a significant positive Moran's I value at a lag distance of 0.2 miles (interpreted as patch size) and a significant negative value at 1 mile (interpreted as patch–interpatch distance); however, there was no evidence for a significant interpatch spacing (Figure 4.8B, Table 4.2).

Table 4.2. Summary of spatial analysis results.[a]

Species	Road	Evidence of patchiness?	Patch size (mi)	Interpatch spacing (mi)	Patch-Inter distance (mi)	Evidence of gradient?
Chrysanthemum leucanthemum	130	No	--	--	--	Yes
	320	Yes	0.2-0.3	0.7	1.5	Yes - slight
	350	Yes	varying	varying	1.7	Yes
	360	Yes	NS	1.1	1.4	No
	1506	Yes	varying	varying	NS	No
	1507	Yes	0.1-0.3	0.4-0.6, 1.5	2.7	Yes - slight
	1508	No	--	--	--	No
Cirsium arvense	130	No	--	--	--	No
	320	No	--	--	--	No
	350	No	--	--	--	Yes - slight
	360	No	--	--	--	No
	1506	No	--	--	--	No
	1507	Yes	0.1	NS	NS	Yes - slight
	1508	No	--	--	--	No
Cirsium vulgare	130	No	--	--	--	Yes - slight
	320	Yes	0.1	NS	NS	No
	350	Yes	0.2-0.3	1.2	NS	Yes
	360	No	--	--	--	Yes - slight
	1506	Yes	0.1-0.5	0.9-1.5	NS	Yes
	1507	Yes	0.1	NS	NS	Yes
	1508	No	--	--	--	Yes - slight

Table 4.2, Continued.

Species	Road	Evidence of patchiness?	Patch size (mi)	Interpatch spacing (mi)	Patch-Inter distance (mi)	Evidence of gradient?
Cytisus scoparius	130	No	--	--	--	Yes - slight
	320	No	--	--	--	No
	350	No	--	--	--	No
	360	Yes	0.2	NS	1	No
	1506	Yes	0.2	NS	NS	No
	1507	Yes	NS	1.7	NS	No
	1508	No	--	--	--	Yes
Hypericum perforatum	130	Yes	0.2	NS	1.2	No
	320	Yes	NS	NS	1.1	No
	350	Yes	0.1-0.2	0.7-1	1.2	Yes
	360	No	--	--	--	No
	1506	Yes	NS	1.5	3.6	No
	1507	Yes	0.1-0.3	0.6-1	2	Yes - slight
	1508	Spatial analysis not meaningful; species in all 0.1-mile increments				
Senecio jacobaea	130	No	--	--	--	No
	320	No	--	--	--	No
	350	No	--	--	--	No
	360	No	--	--	--	No
	1506	No	--	--	--	No
	1507	Yes	0.1-0.3	0.5-1	NS	Yes - slight
	1508	No	--	--	--	No

[a] Symbol "--" means not applicable. "NS" means not significant.

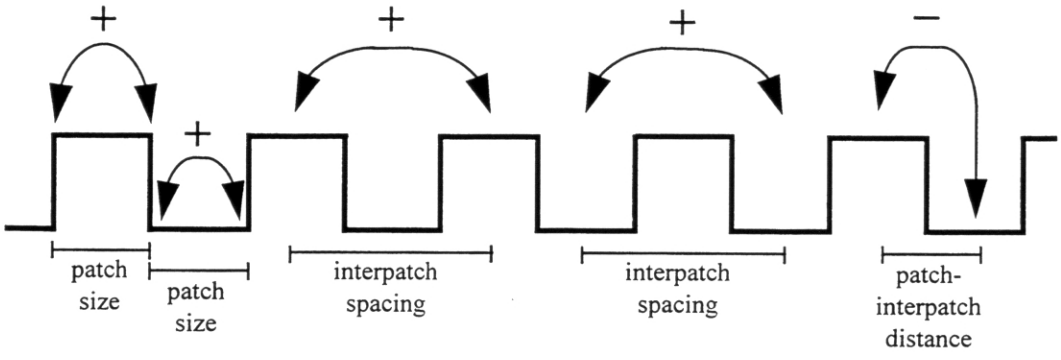

Figure 4.7. Diagram of spatial structure that contributes to significant values of Moran's I. The first positive significant values reflect patch size. The next positive significant values reflect interpatch spacing. The first negative significant values reflect patch-interpatch spacing.

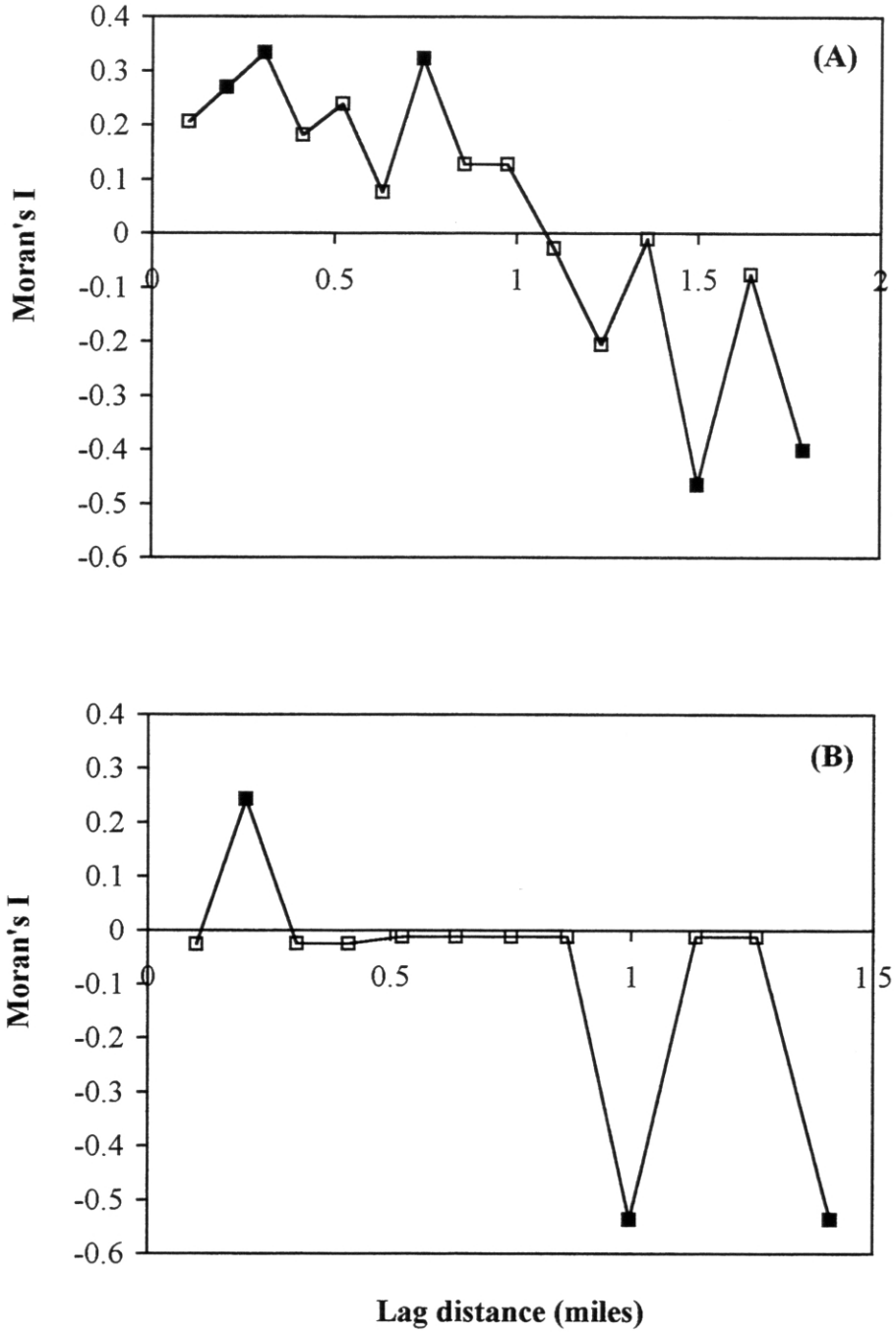

Figure 4.8. Examples of significant correlograms: (A) *Chrysanthemum leucanthemum*, Road 320; and (B) *Cytisus scoparius*, Road 360. Solid symbols represent statistically significant values ($p < 0.05$).

One of the roads at HJA, Road 1507, showed evidence of a patchy spatial structure for all six target species in this analysis (Figure 4.9, Table 4.2). The patch sizes were significant for all species except *Cytisus scoparius* and ranged fairly consistently from 0.1 to 0.3 miles. The interpatch spacing was more variable and, where significant, ranged from about 0.4 to 1.7 miles. The patch–interpatch distance was significant for only two species (*Hypericum perforatum* and *Chrysanthemum leucanthemum*) and varied from about 2 to 2.7 miles (Figure 4.9, Table 4.2).

4.3.2.2 Spatial gradient

The shape of the semivariogram (plot of semivariance versus lag distance) can provide evidence for a gradient in the spatial structure of the target species occurrence along the roads at HJA. Because fitting a curve to a semivariogram is a subjective process (Turner et al. 1990), in this analysis, the shapes of the semivariogram curves were classified in one of only two categories: flat (no gradient structure) or linear (evidence of a spatial gradient) (Legendre and Fortin 1989). Figure 4.10 includes examples of a "flat" semivariogram and two "linear" semivariograms.

Cirsium vulgare had the strongest evidence of a spatial gradient, with linear trends in the semivariograms for six of the seven roads used in this analysis (Table 4.2). *Chrysanthemum leucanthemum* had evidence of a spatial gradient along four of the roads (Table 4.2). As with the correlograms, patterns of target species along Road 1507 showed

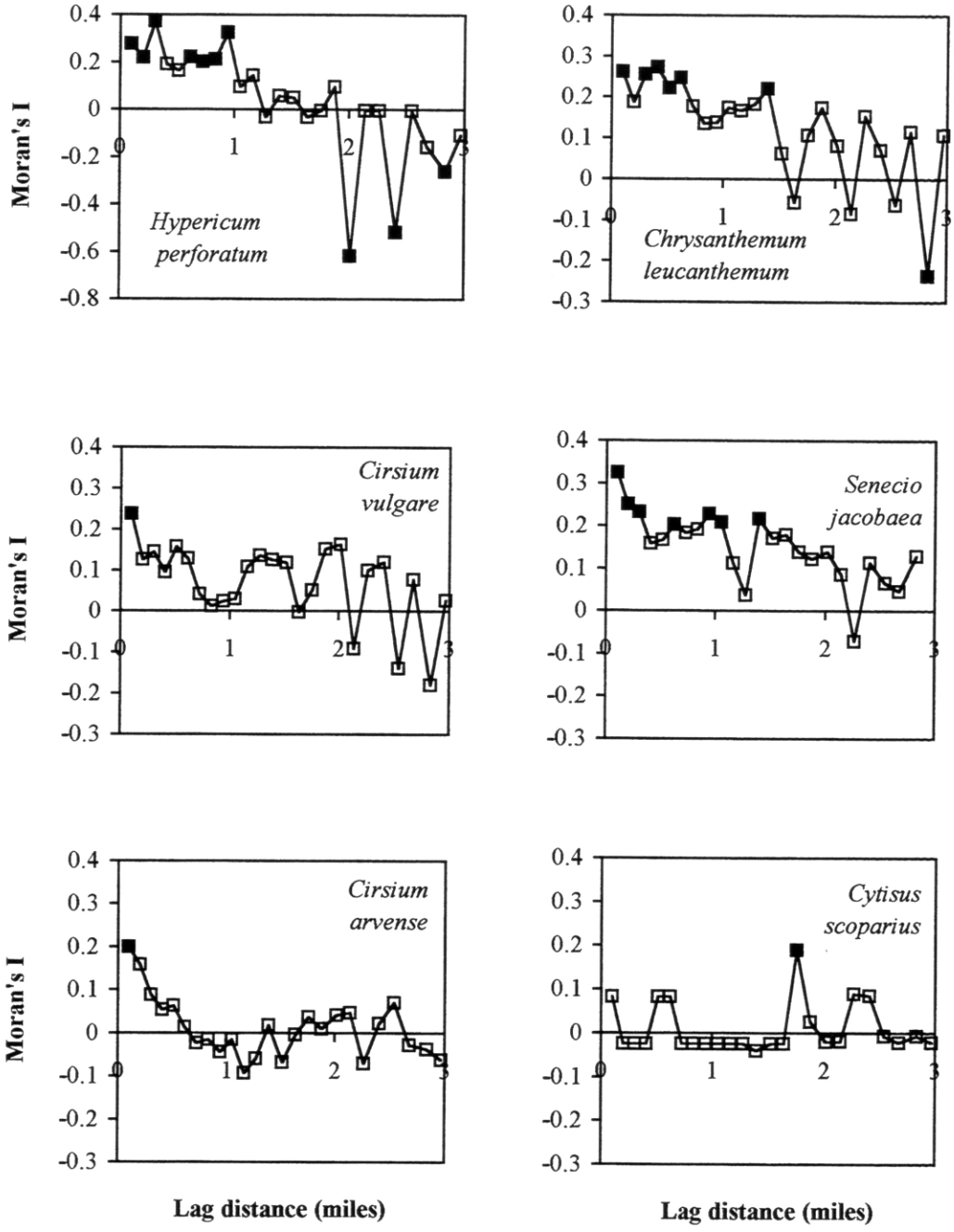

Figure 4.9. Correlograms for six target species along Road 1507. Solid symbols represent statistically significant values ($p < 0.05$).

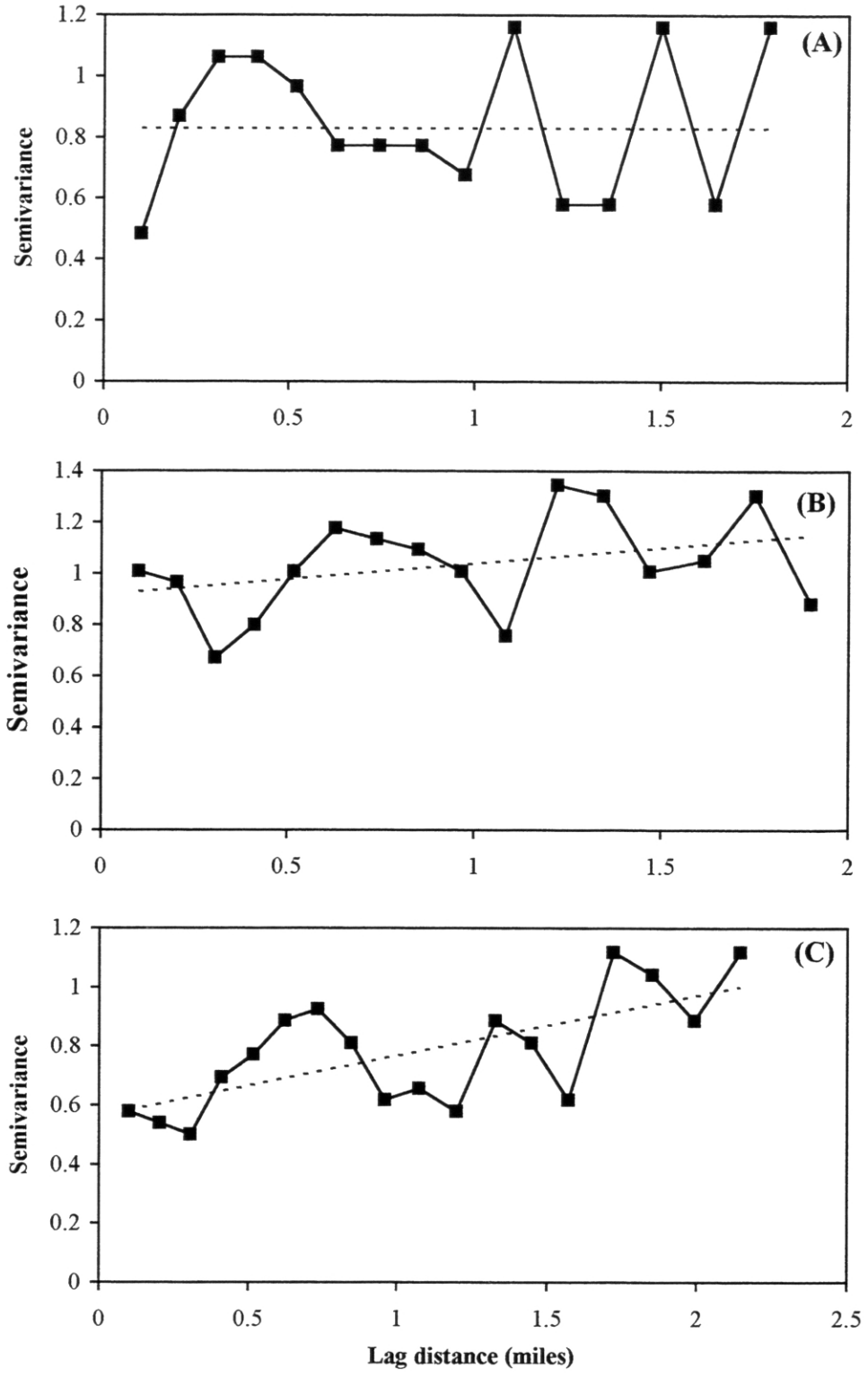

Figure 4.10. Standardized semivariograms for *Cirsium vulgare* : (A) "flat" [Road 320], (B) slight "linear" [Road 130], and (C) "linear" [Road 350]. Dashed lines indicate gradient trendlines.

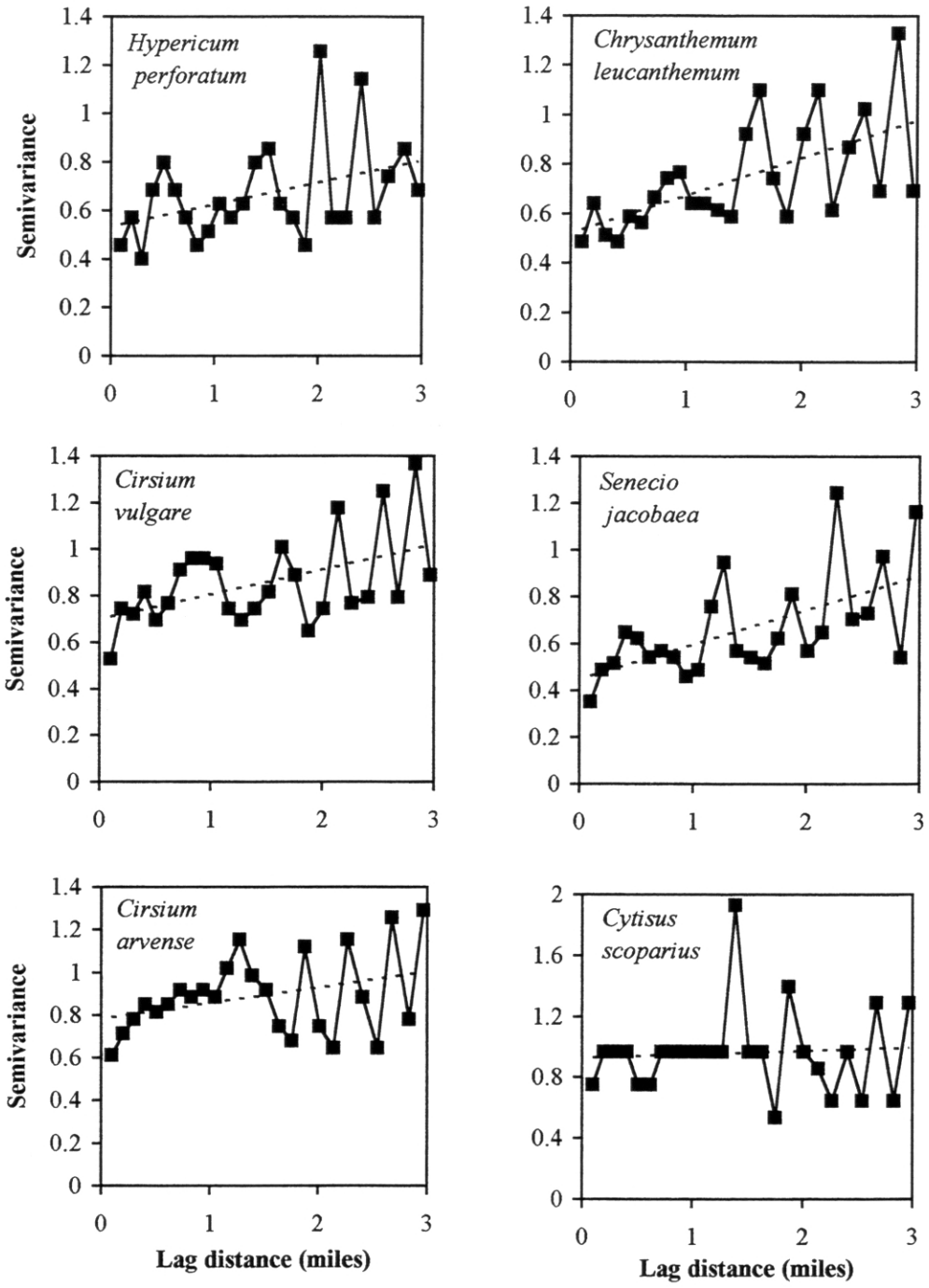

Figure 4.11. Standardized semivariograms for six target species along Road 1507. All species except *Cytisus scoparius* have a "linear" gradient. Dashed lines indicate gradient trendlines.

the strongest spatial structure; five of the six species had evidence of a spatial gradient along this road (Figure 4.11).

4.3.3 Relationship with environmental attributes

Seven environmental attributes of the HJA landscape were examined with respect to the presence of the target species. Four of these represent physical/climatic factors: elevation, precipitation, aspect, and solar radiation . The other three represent human disturbances on the landscape: age of adjacent cut unit, road age, and road-use level. Relative frequencies of six of the eight target species for each class of each environmental attribute are reported below. As in the spatial analysis, *Digitalis purpurea* and *Rubus discolor* were so infrequent that their relative frequencies do not yield any insight about their relationship with environmental attributes of the landscape; for these two species, only presence within a particular environmental attribute class is reported.

4.3.3.1 Elevation

The HJA landscape has a steady elevation gradient from west to east, with the highest elevations along the southern and eastern boundaries (Figure 4.12A). The road network passes through all elevation classes except the highest class (>1500 m), but almost half of the road network is within the 600–900 m elevation class (Figure 4.12B).

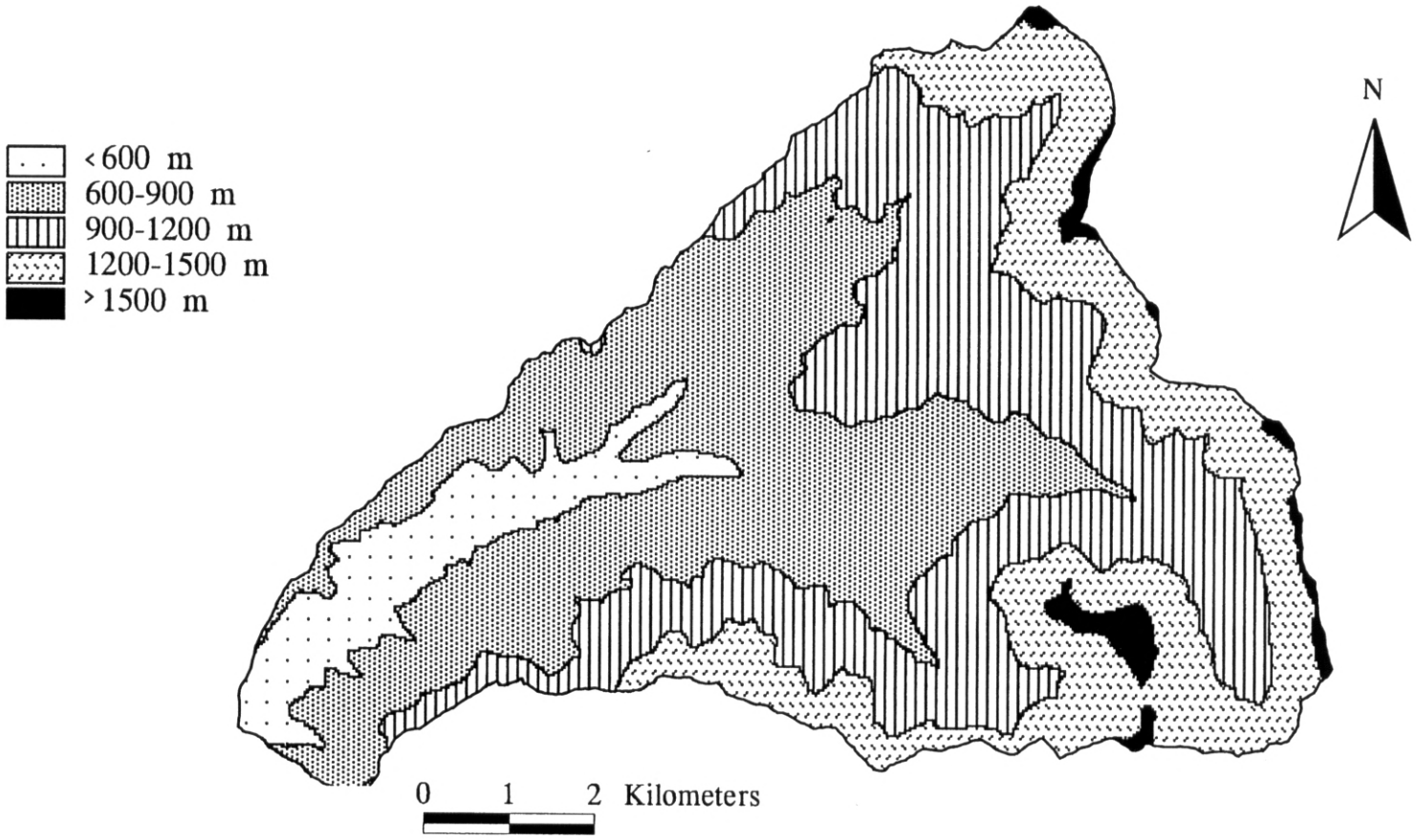

Figure 4.12. Elevation in the H.J. Andrews Experimental Forest: (A) landscape pattern.

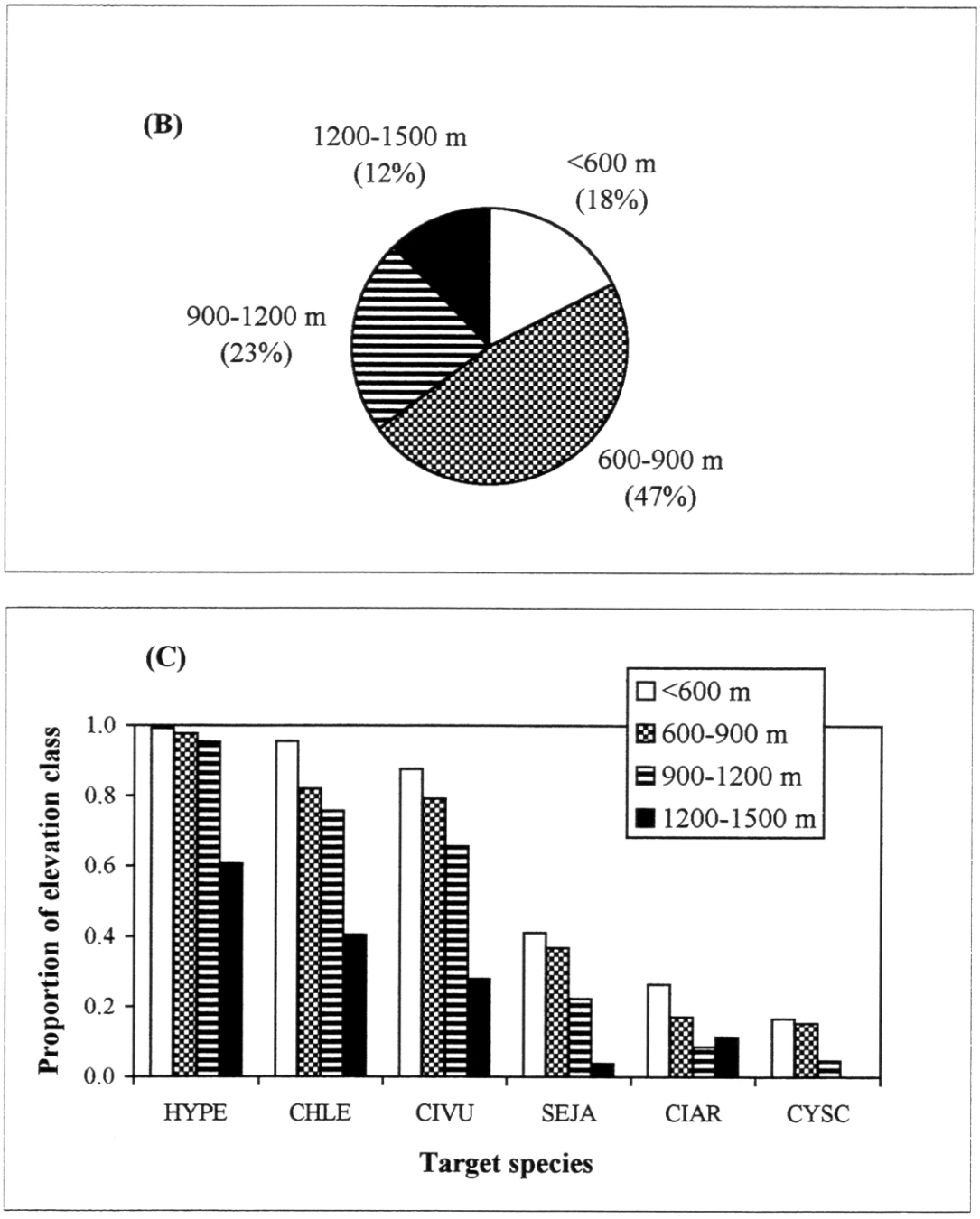

Figure 4.12, Continued. (B) percentage of road network within each elevation class, and (C) frequency distribution of target species in each elevation class. (HYPE = *Hypericum perforatum* ; CHLE = *Chrysanthemum leucanthemum* ; CIVU = *Cirsium vulgare* ; SEJA = *Senecio jacobaea* ; CIAR = Cirsium arvense; *CYSC* = *Cytisus scoparius*)

Most of the target species had a fairly steady decline in relative frequency with elevation, with a markedly lower relative frequency in the highest elevation class (1200–1500 m) (Figure 4.12C). Only *Cytisus scoparius* was absent along roads in this highest class (Figure 4.12C). *Digitalis purpurea* was present in the two lowest elevation classes (<600 m and 600–900 m); *Rubus discolor* was only present in the 600–900 m class.

4.3.3.2 Precipitation

Average annual precipitation varies from <2400 to >3200 mm. As with elevation, the spatial distribution of precipitation at HJA has a general west to east gradient (Figure 4.13A). Only 2% of the roads are in areas with the highest annual precipitation (>3200 mm) (Figure 4.13B). Most of the roads (68%) are in areas with the lowest annual precipitation (<2400 mm) (Figure 4.13B). The relative frequency of most target species was generally lower in higher precipitation classes (Figure 4.13C). *Digitalis purpurea* was only present in the lowest annual precipitation class (<2400 mm); *Rubus discolor* was present in the two lowest classes (<2400 and 2400–2800 mm).

4.3.3.3 Aspect

North-, south-, and west-facing slopes dominate much of the HJA landscape, with a significant amount of western exposure as well (Figure 4.14A). The percentage of the

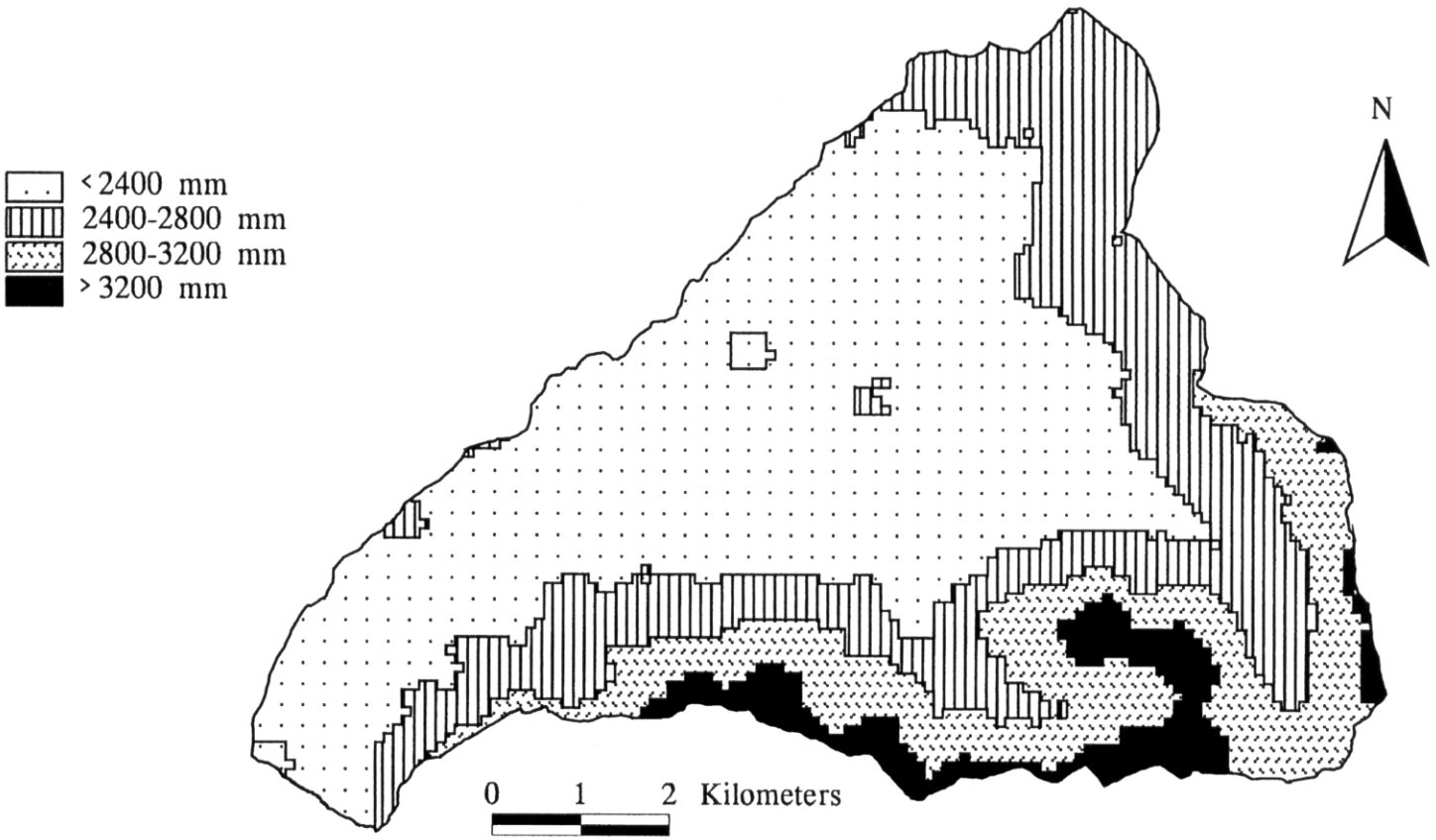

Figure 4.13. Average annual precipitation in the H.J. Andrews Experimental Forest: (A) landscape pattern.

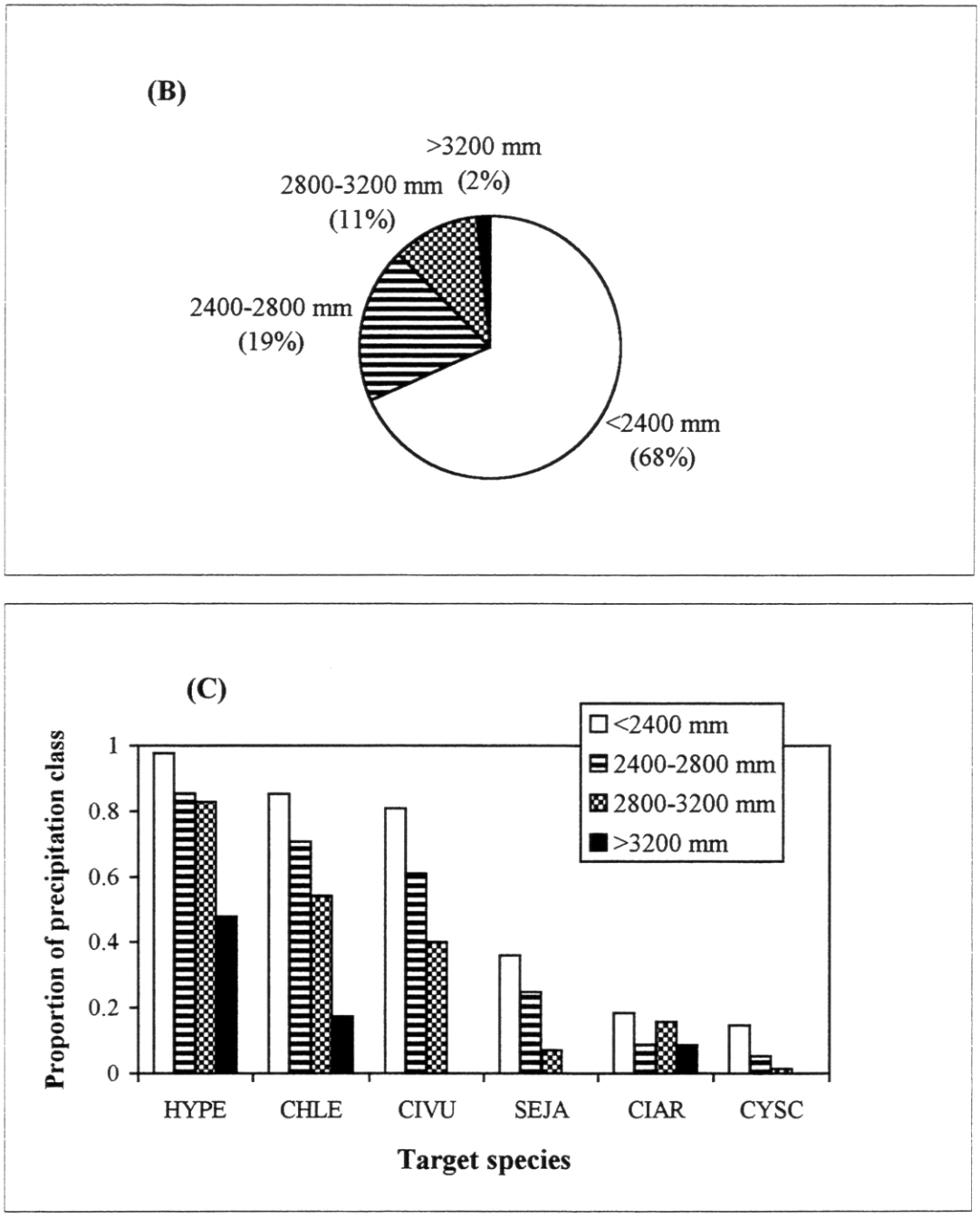

Figure 4.13, Continued. (B) percentage of road network within each precipitation class, and (C) frequency distribution of target species in each precipitation class. (HYPE = *Hypericum perforatum* ; CHLE = *Chrysanthemum leucanthemum* ; CIVU = *Cirsium vulgare* ; SEJA = *Senecio jacobaea* ; CIAR = Cirsium arvense; *CYSC = Cytisus scoparius*)

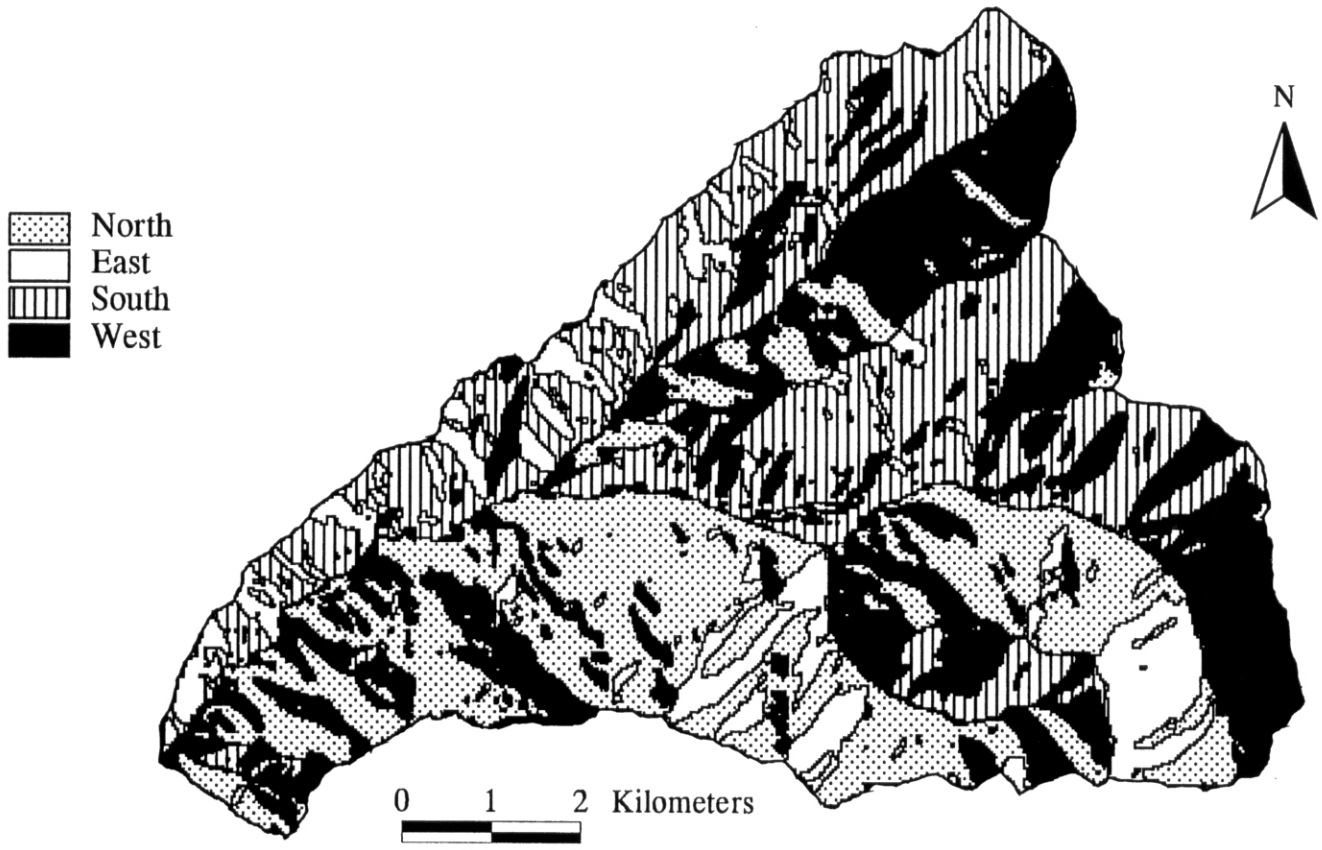

Figure 4.14. Aspect in the H.J. Andrews Experimental Forest: (A) landscape pattern.

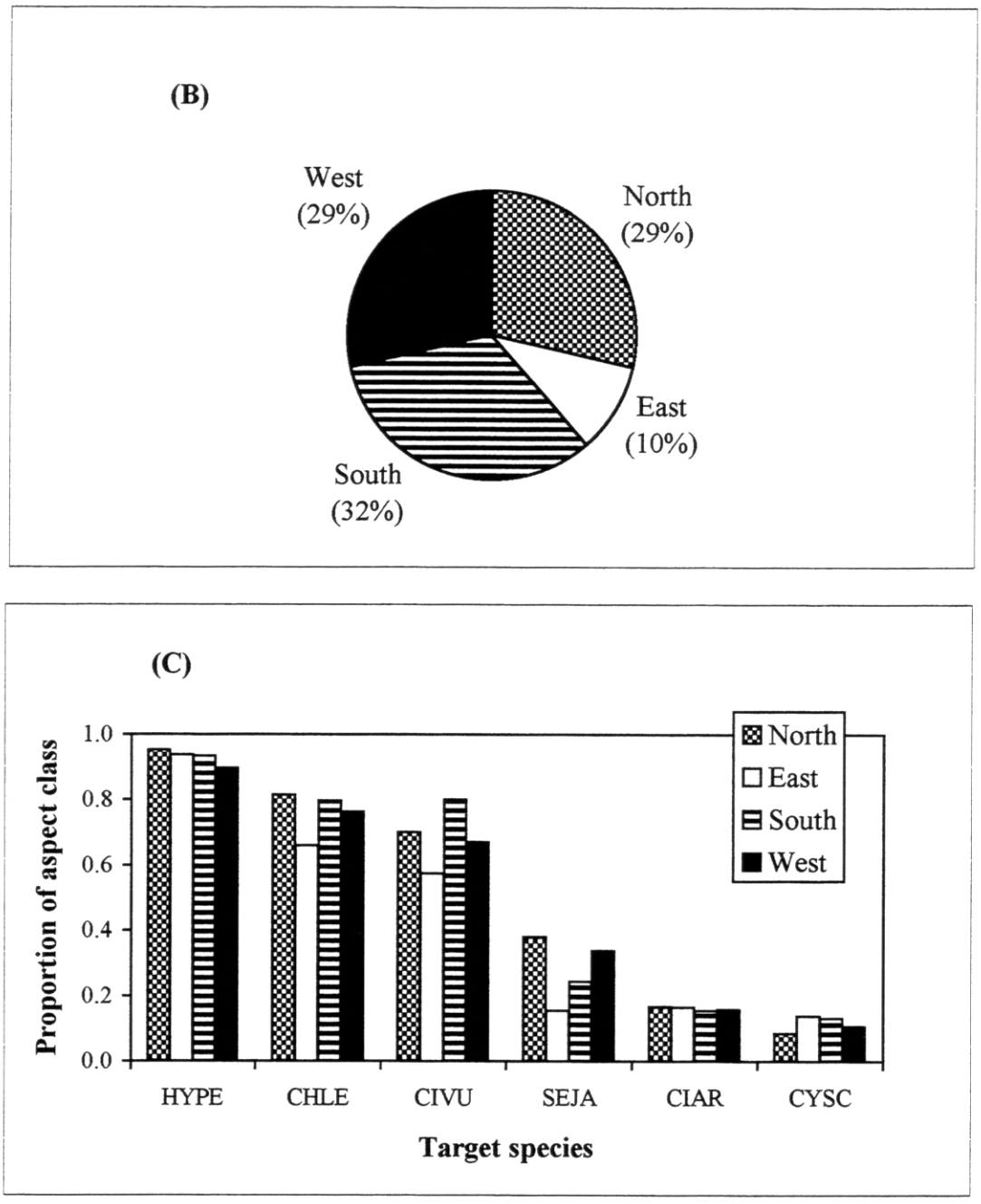

Figure 4.14, Continued. (B) percentage of road network within each aspect class, and (C) frequency distribution of target species in each aspect class. (HYPE = *Hypericum perforatum* ; CHLE = *Chrysanthemum leucanthemum* ; CIVU = *Cirsium vulgare* ; SEJA = *Senecio jacobaea* ; CIAR = *Cirsium arvense* ; CYSC = *Cytisus scoparius*)

road network within each aspect class follows a similar pattern, with the lowest percentage of roads along east-facing slopes (Figure 4.14B). Three of the target species (*Chrysanthemum leucanthemum*, *Cirsium vulgare*, and *Senecio jacobaea*) appeared to have a relationship with aspect; each of these species were proportionately less frequent on road sections with east-facing exposures than on other aspects (Figure 4.14C). The other three species (*Hypericum perforatum*, *Cirsium arvense*, and *Cytisus scoparius*) had fairly similar proportions of occurrence in all four aspect classes (Figure 4.14C). *Digitalis purpurea* was present in north, south, and west aspects; *Rubus discolor* was present in south and west aspects only.

4.3.3.4 Solar radiation

The average daily total solar radiation values for HJA during the growing season (April to September) ranged from <400 to >550 cal/(cm^2·day) (Figure 4.15A). Only 3% of the roads at HJA were within the highest or lowest radiation classes; over 80% were within two classes: 450–500 and 500–550 cal/(cm^2·day) (Figure 4.15B). Figure 4.15C summarizes the proportion of each solar radiation class in which each target species was present. Because the highest and lowest classes represent such a low percentage of the whole road network, the patterns of species occurrence in these classes may not provide much useful information. Patterns in the other three classes suggest a slight negative relationship with solar radiation for a few species; the pattern is strongest for *Senecio jacobaea* (Figure 4.15C). Only *Cytisus scoparius* appears to have a slight positive

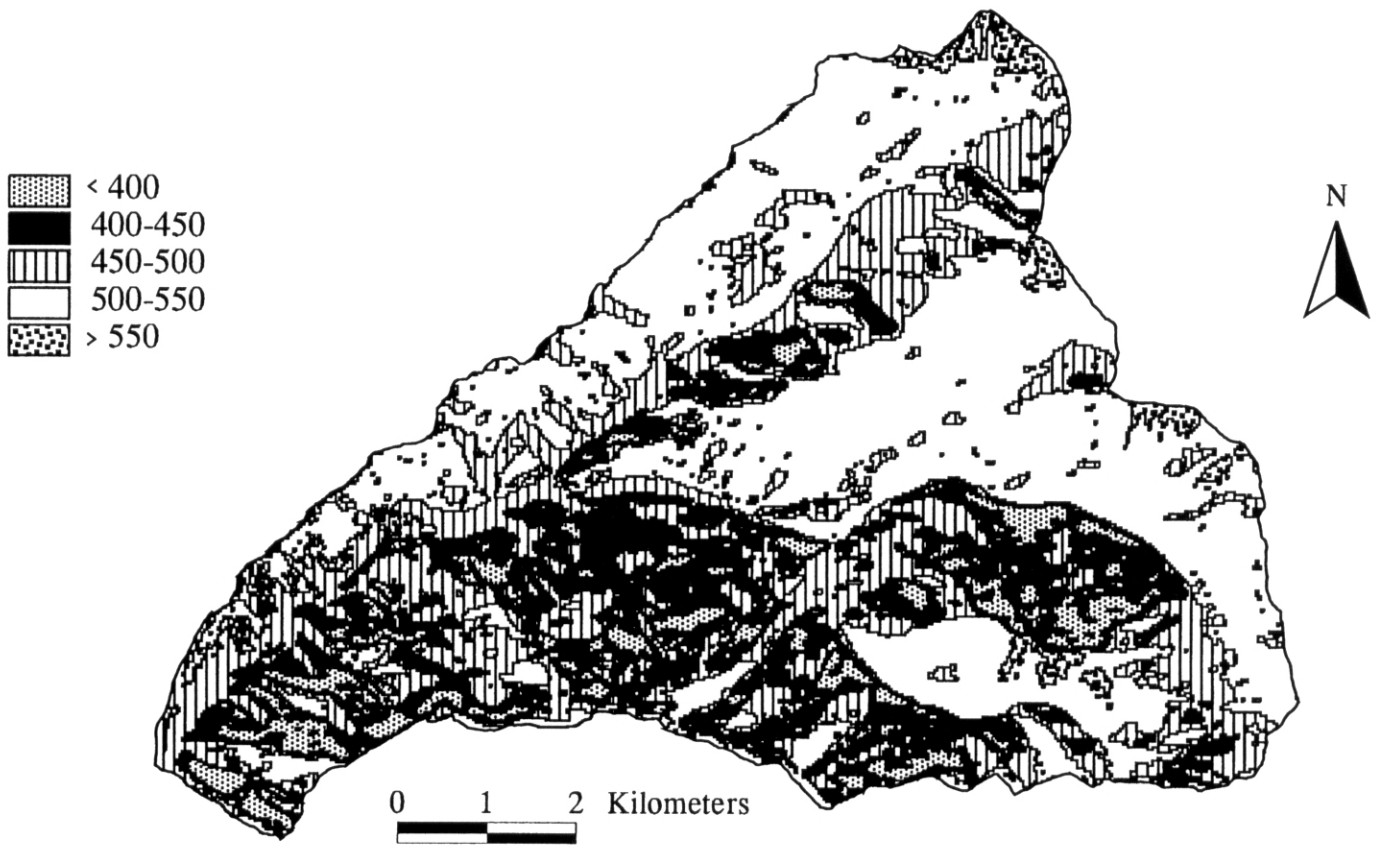

Figure 4.15. Average daily total solar radiation in the H.J. Andrews Experimental Forest: (A) landscape pattern [units are cal/(cm2 day)].

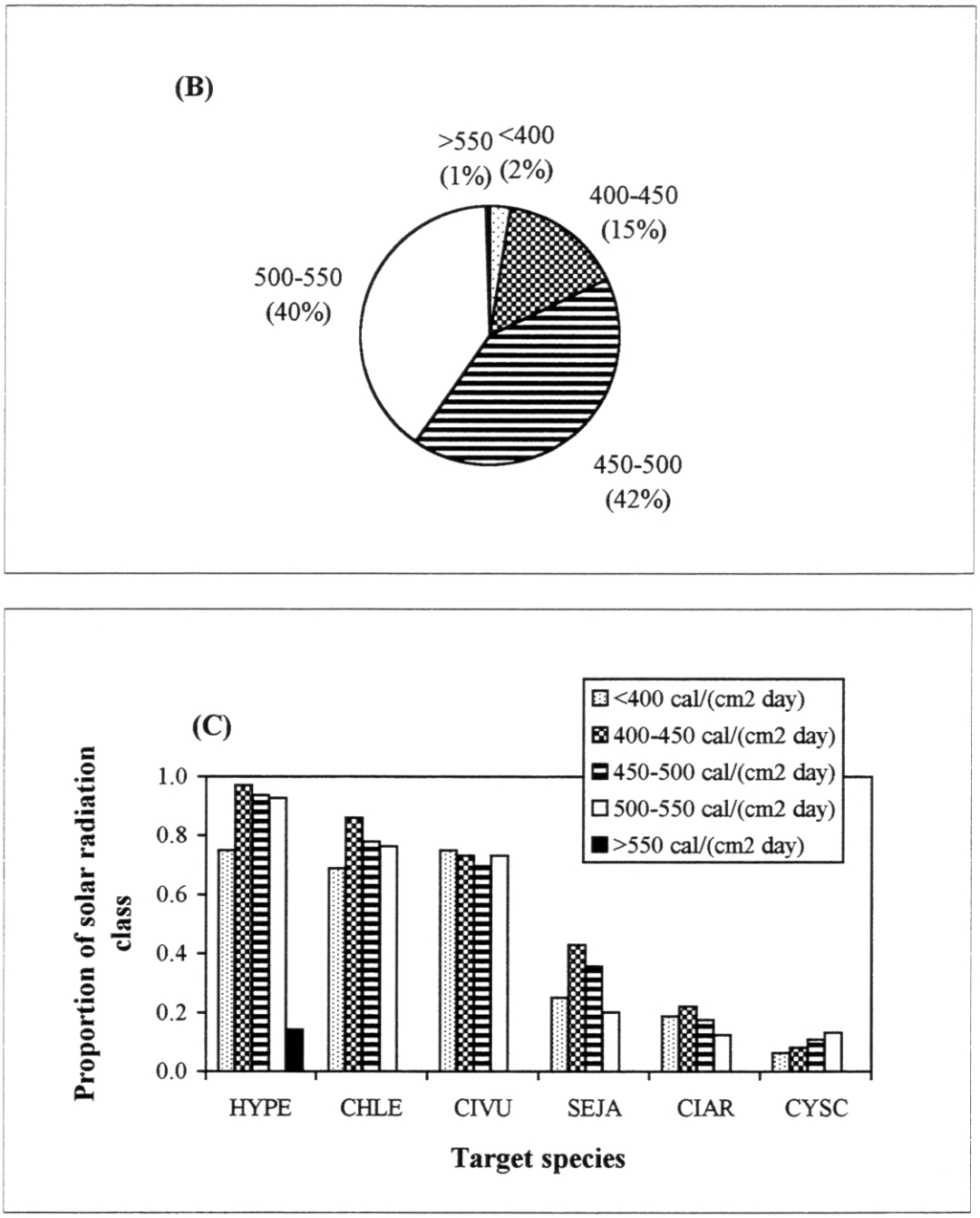

Figure 4.15, Continued. (B) percentage of road network within each solar radiation class (units are cal/(cm^2 day)), and (C) frequency distribution of target species in each solar radiation class. (HYPE = *Hypericum perforatum*; CHLE = *Chrysanthemum leucanthemum*; CIVU = *Cirsium vulgare*; SEJA = *Senecio jacobaea*; CIAR = *Cirsium arvense*; CYSC = *Cytisus scoparius*)

relationship with radiation (Figure 4.15C). *Digitalis purpurea* was present in the three middle classes [400–450, 450–500, and 500–550 cal/(cm^2·day)]; *Rubus discolor* was only present in the 450–500 cal/(cm^2·day) class.

4.3.3.5 Age of adjacent cut unit

Most of the timber harvest units at HJA were cut during the 1950s and 1960s, although some additional harvest took place in the 1970s and 1980s (Figure 4.16A). Over half (61%) of the road network is adjacent to a unit that had been cut, with the highest percentage of the roads adjacent to 1950s- and 1960s-era cut units (Figure 4.16B).

All target species had relative frequencies along roads adjacent to 1950s-era cut units that were comparable to or greater than frequencies along roads adjacent to uncut units (Figure 4.16C). The same was generally true for 1980s-era cut units relative to uncut units (except for *Cirsium arvense* and *Senecio jacobaea*). However, relative frequencies on roads adjacent to 1960s- and 1970s-era cut units were generally lower than those on roads adjacent to uncut units (except for *Hypericum perforatum* and *Cytisus scoparius*) (Figure 4.16C). *Digitalis purpurea* was present on roads adjacent to uncut units and units that were cut in the 1950s and 1960s; *Rubus discolor* was present on roads adjacent to 1960s- and 1970s-era cut units.

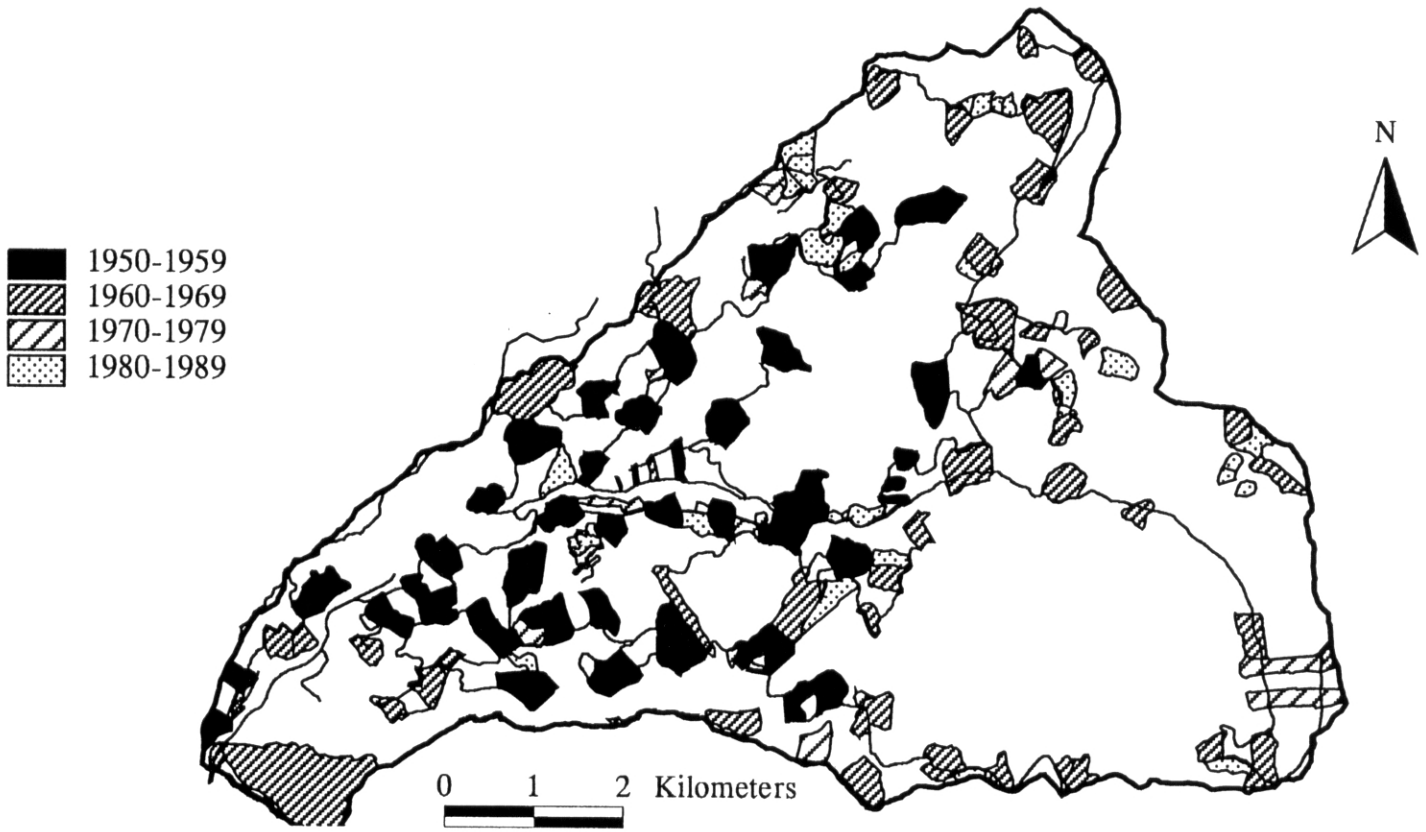

Figure 4.16. Ages (by decade) of cut units in the H.J. Andrews Experimental Forest: (A) landscape pattern.

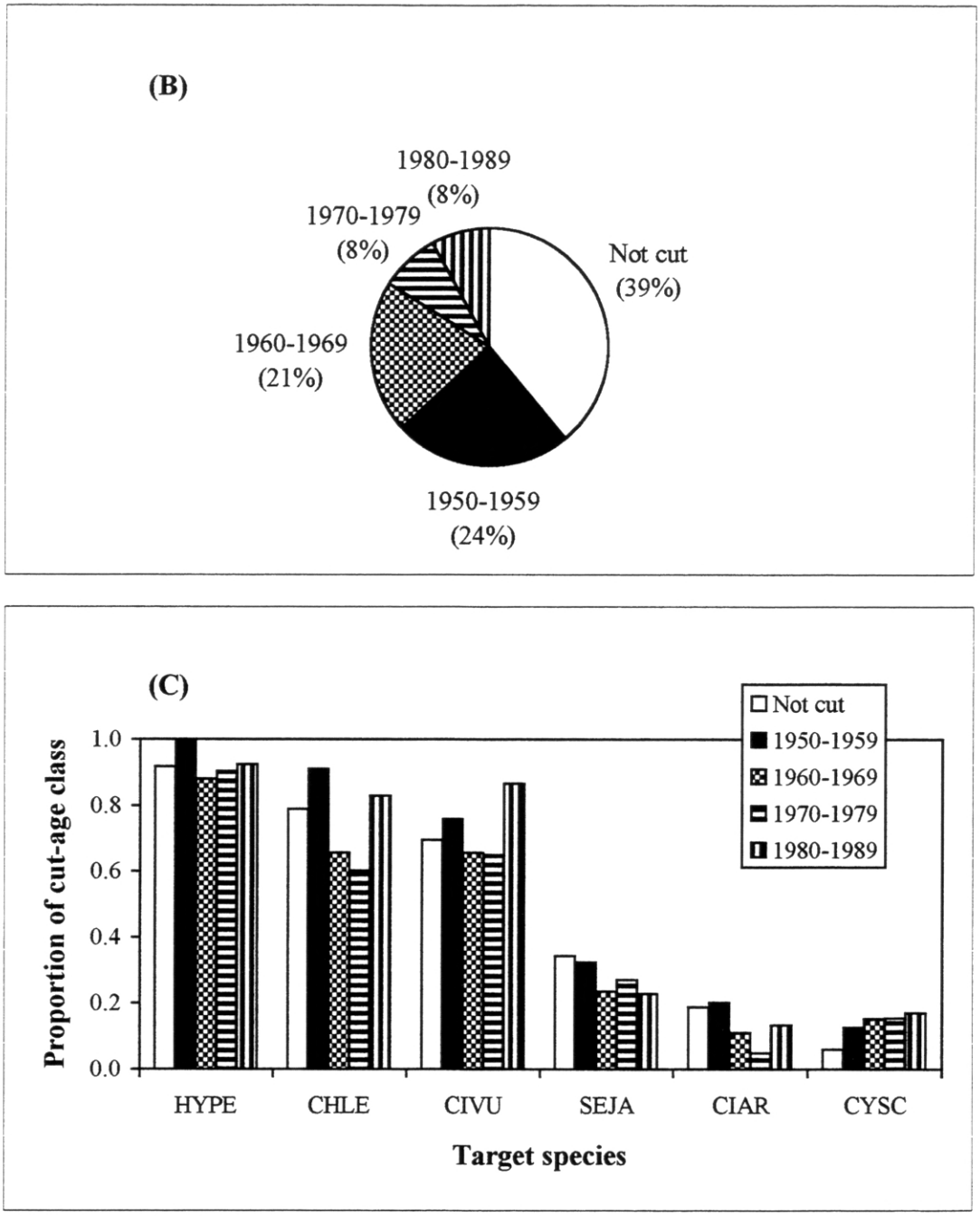

Figure 4.16, Continued. (B) percentage of road network adjacent to each cut unit age, and (C) frequency distribution of target species along roads adjacent to each cut unit age. (HYPE = *Hypericum perforatum*; CHLE = *Chrysanthemum leucanthemum*; CIVU = *Cirsium vulgare*; SEJA = *Senecio jacobaea*; CIAR = *Cirsium arvense*; CYSC = *Cytisus scoparius*)

4.3.3.6 Road age

Road construction at HJA began in the late 1940s, with the bulk of the road network being completed in the 1950s and 1960s; only a few short road segments were built in the 1970s and 1980s (Figures 4.17A and 4.17B). The distribution of target species along roads of different ages is shown in Figure 4.17C. *Hypericum perforatum*, *Chrysanthemum leucanthemum*, and *Cirsium vulgare* had several features of their patterns in common: relative frequencies were similar along 1940s- and 1950s-era roads and were higher along 1970s-era roads than along 1960s- or 1980s-era roads. *Senecio jacobaea* was relatively more frequent along older roads than along newer roads; the opposite was true for *Cytisus scoparius* (Figure 4.17C). For all target species, relative frequencies along 1960s-era roads tended to be lower than along roads of other ages. *Digitalis purpurea* was present along roads built during the 1940s, 1950s and 1960s; *Rubus discolor* was present only along roads built in the 1950s and 1960s.

4.3.3.7 Road use

Most of the "high-use" road segments are part of the main arteries of the HJA road network, whereas most "medium-use" and "low-use" road segments are spur roads or the end sections of main arteries (Figure 4.18A). The highest percentage (42%) of roads were classified as high use, but medium- and low-use roads were also well represented (Figure 4.18B). The relative frequency of target species was higher on high-use roads than on

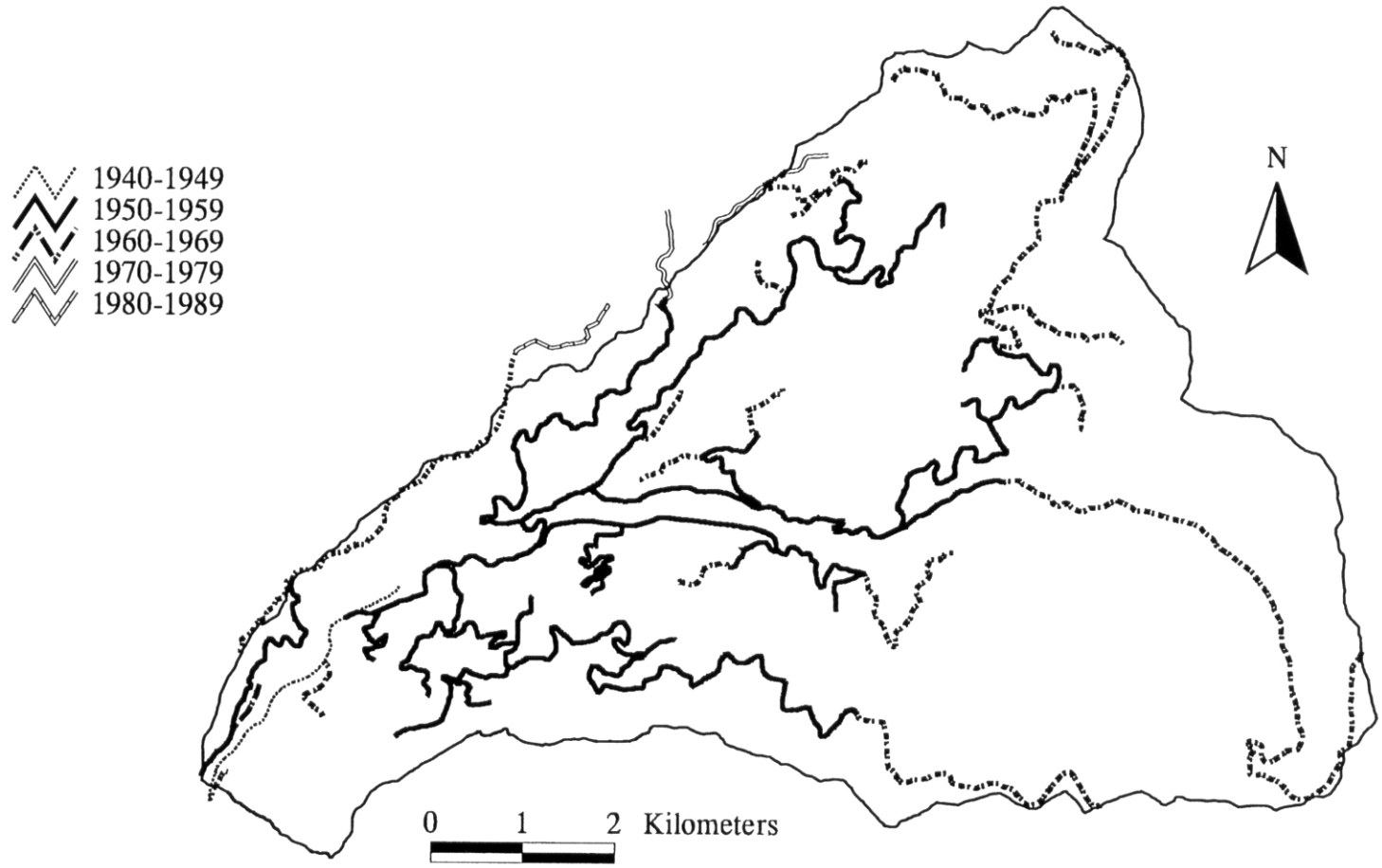

Figure 4.17. Road ages (by decade) in the H.J. Andrews Experimental Forest: (A) landscape pattern.

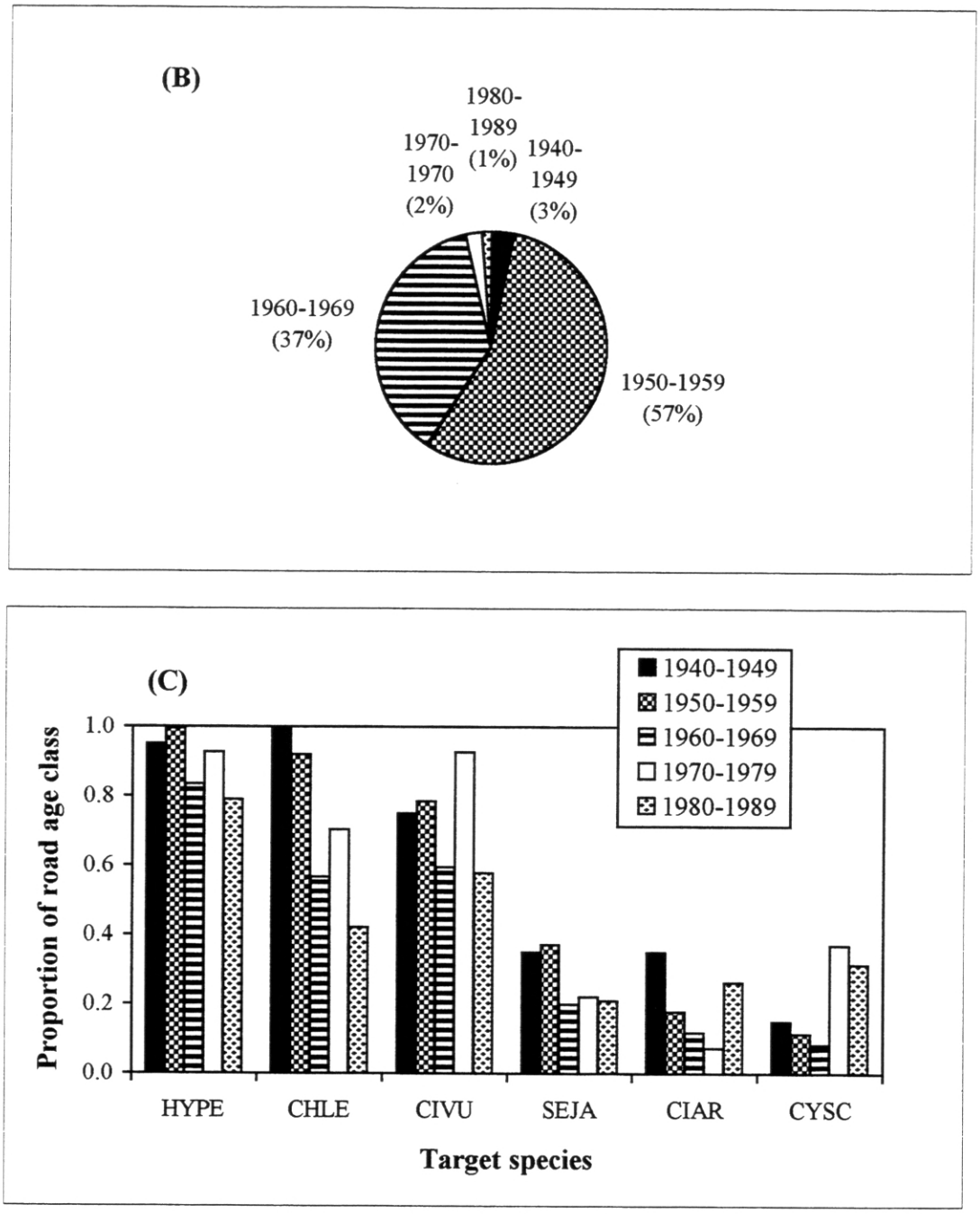

Figure 4.17, Continued. (B) percentage of road network within each road age class, and (C) frequency distribution of target species in each road age class. (HYPE = *Hypericum perforatum* ; CHLE = *Chrysanthemum leucanthemum* ; CIVU = *Cirsium vulgare* ; SEJA = *Senecio jacobaea* ; CIAR = *Cirsium arvense* ; CYSC = *Cytisus scoparius*)

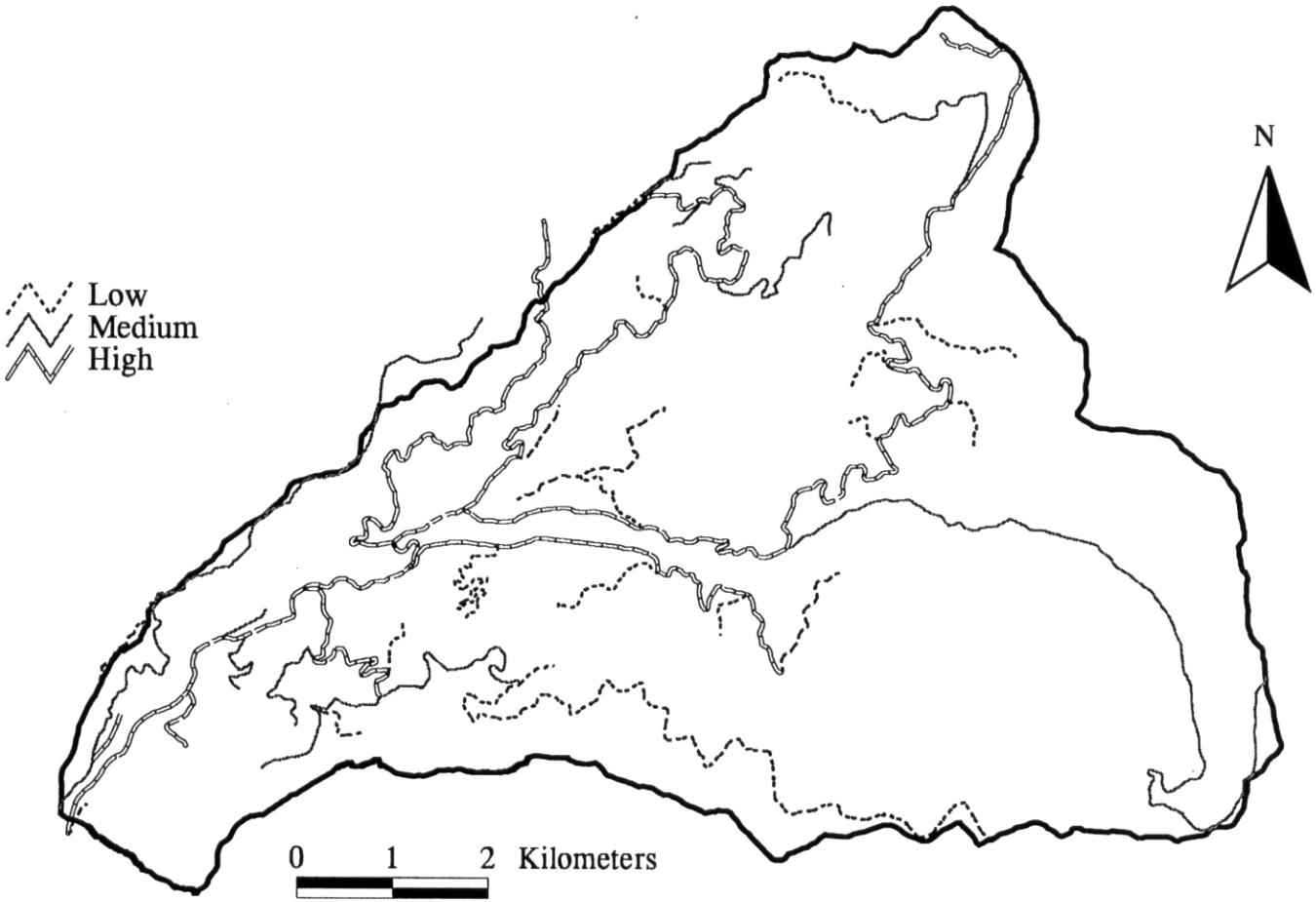

Figure 4.18. Road-use levels in the H.J. Andrews Experimental Forest: (A) landscape pattern.

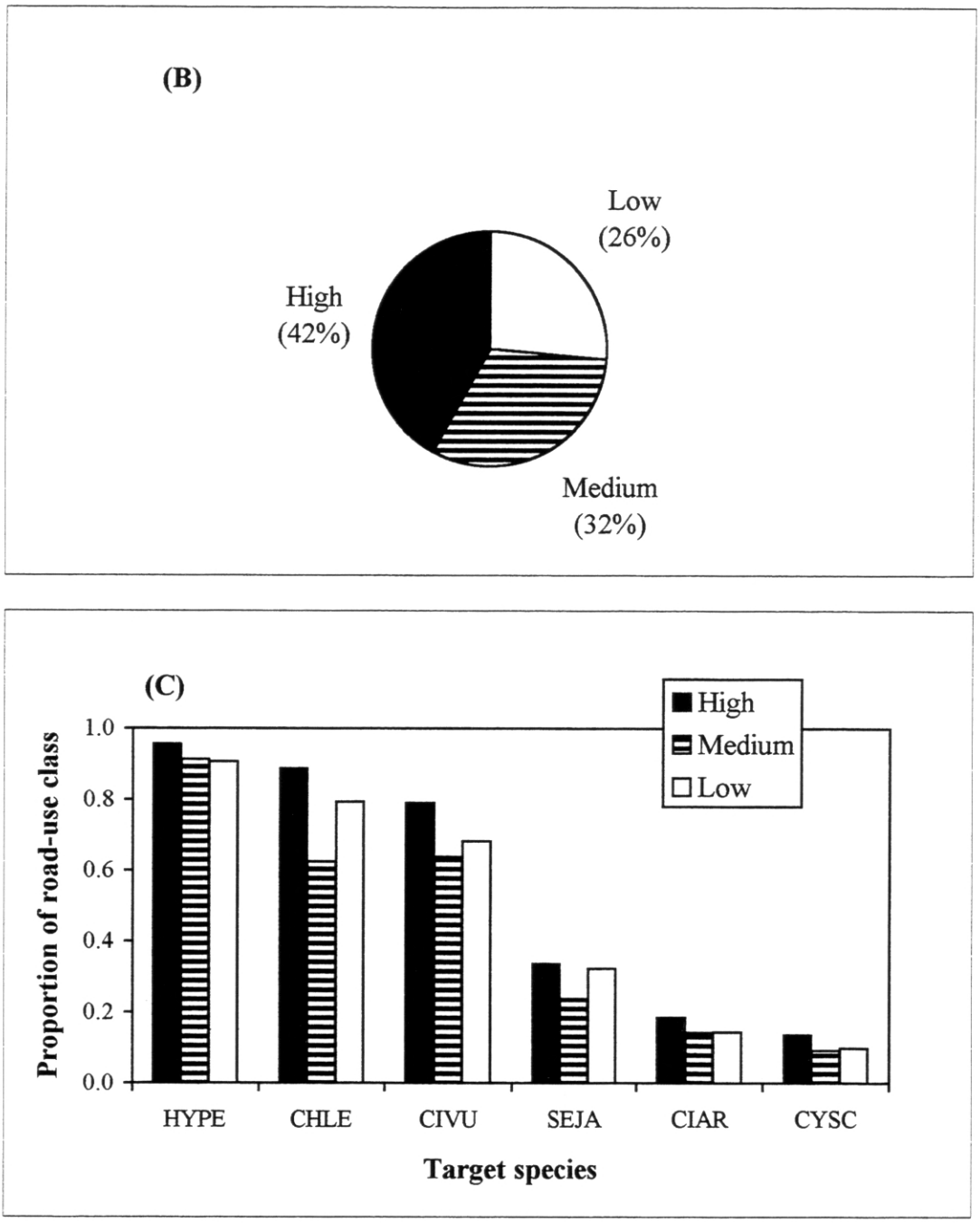

Figure 4.18, Continued. (B) percentage of road network within each road-use class, and (C) frequency distribution of target species in each road-use class. (HYPE = *Hypericum perforatum* ; CHLE = *Chrysanthemum leucanthemum* ; CIVU = *Cirsium vulgare* ; SEJA = *Senecio jacobaea* ; CIAR = *Cirsium arvense* ; CYSC = *Cytisus scoparius*)

roads in the other two classes, although only slightly so for some species (Figure 4.18C). Relative frequencies were similar on medium- and low-use roads for *Hypericum perforatum*, *Cirsium arvense*, and *Cytisus scoparius*, but they were higher on low-use roads for the other three target species (Figure 4.18C). *Digitalis purpurea* was present along high- and low-use roads; *Rubus discolor* was present along roads in all three use levels.

4.4 Discussion

Studies in landscape ecology have shown that spatial patterns affect a variety of ecological processes (Franklin and Forman 1987; Turner 1989; Levin 1992). The current study addressed the process of exotic plant invasion along roads in a forested landscape in western Oregon. Spatial patterns of exotic plants showed significant internal spatial structure and had relationships with environmental attributes of HJA, indicating that patterns of physical and biological phenomena influence the process of invasion in this landscape.

4.4.1 Evidence of spatial structure

All six of the target species used in the spatial analysis in the current study had evidence of patchiness (i.e., significant Moran's I values plotted in correlograms) and a

spatial gradient (i.e., linear semivariograms) along at least one of the roads in the HJA network. The evidence of both patchiness and spatial gradients was strongest for the species that were most frequent (*Hypericum perforatum*, *Chrysanthemum leucanthemum*, and *Cirsium vulgare*), which suggests that these species may be approaching the dynamic equilibrium phase of invasion in the HJA landscape (Figure 4.1A) and the spatial pattern may reflect biological or physical barriers. The lack of spatial autocorrelation for some species along some roads suggests that the invasion patterns are more random along these portions of the road network. These species may be at an earlier phase of invasion in this landscape (Figure 4.1A), and any biological or physical barriers may not be fully reflected in the spatial pattern.

Where they were significant, the linear patch sizes were generally between 0.1 and 0.3 miles for all species. The presence of discrete patches suggests that the process of invasion is not occurring in a wavelike front, but rather species are becoming established in multiple, distinct foci (Moody and Mack 1988) that may expand over time and from which subsequent dispersal to new invasion sites can occur (Figure 4.2B). The significant interpatch spacing was more variable and ranged from 0.4 to 1.7 miles. Likewise, the patch–interpatch distance was also quite variable and ranged from 1 to 3.6 miles. Thus, although patch sizes were fairly similar for the target species, their arrangement in space appears to vary among the species and among the roads.

The semivariograms that were "linear" provided additional evidence for spatial structure among the target species. A spatial gradient indicates that the pattern of species occurrence varied with distance along the road. Of particular interest from an ecological viewpoint is what underlying environmental factor may be related to the gradient pattern.

Elevation may be one of the underlying factors. Several of the species had evidence of a gradient along roads that covered a range of elevations, and the patch structure appeared different at the beginning (lower elevation) than at the end (higher elevation) of the road. However, the lowest elevation also coincides with the oldest roads and with the entrance to HJA, which may be the inital point of introduction for some or all of the target species. Thus, elevation is confounded with other environmental attributes at HJA.

The spatial structure of one of the roads at HJA, Road 1507, is noteworthy: all six target species had evidence of patchiness; five species had evidence of a gradient. Data on the environmental attributes for this road suggest that elevation, precipitation, and road-use level also followed a gradient along this road and that aspect and solar radiation were quite variable. Apparently this environmental variability is related to the spatial structure associated with the invasion patterns along this road. Another road at HJA, Road 1506, also had a gradient of elevation and precipitation as well as variable aspect and solar radiation patterns, but the road-use level gradient was not as strong and fewer target species had evidence of significant spatial structure compared with Road 1507.

Interannual patterns of the target species along the roads at HJA are inconclusive with regard to changes in invasion patterns over time. Observations over two consecutive years (1993 to 1994) are insufficient to determine whether observed changes reflect actual increase in exotic plant occurrence, measurement errors, or population fluctuations due to climate or other factors (such as road maintenance activities). Temperature and precipitation records from HJA climate stations, for example, indicate that 1994 was generally drier and warmer than 1993 (Appendix E). The 1994 conditions may have been more favorable for the target species, resulting in modest increases in their frequencies.

The 1993–1994 data are more appropriate as a baseline from which to compare invasion patterns in the future than as an indication of temporal changes during the study period.

Relative frequencies of target species in this study generally corresponded to frequencies observed at a finer spatial scale. The three most frequent species in the current study were also among the most frequent in a finer scale study, in which 50-m sampling units were surveyed along 1-km transects (Parendes 1997, unpublished). The relative frequencies of *Hypericum perforatum* and *Chrysanthemum leucanthemum* were about 7% and 8% higher, respectively, in the finer scale study than in the current (coarser scale) study. For *Senecio jacobaea*, the relative frequency was about 10% higher in the current study. The differences in relative frequencies for the other target species were ≤3% (Parendes 1997, unpublished).

4.4.2 Relationship between invasion and physical/climatic factors

The physical/climatic factors included in this study represent environmental attributes that vary on regional and landscape scales. Hierarchy theory as applied to landscape ecology suggests that larger scale factors exert control over phenomena at finer scales (O'Neill et al. 1986; Urban et al. 1987), and thus it was expected that these physical/climatic factors would be related to the patterns of distribution of target exotic species in the HJA landscape.

As expected, most target species had a negative relationship with elevation. Frenkel (1974) found similar results along a road on Mount Shasta in California. In the

current study, five species were present along roads in the highest elevation class (1200–1500 m), and their relative frequencies were quite a bit lower than in the other classes. These species may be approaching the limit of their environmental tolerances at these higher elevations. *Cytisus scoparius* was not found above 1200 m, and neither *Digitalis purpurea* nor *Rubus discolor* was found above 900 m. Perhaps these species have narrower tolerances with environmental conditions that are associated with elevation.

The spatial pattern of average annual precipitation at HJA appears to be strongly related to elevation, with the highest precipitation occurring at the highest elevations. As with elevation, most target species had a negative relationship with precipitation. However, more study of the individual target species would be needed to determine if this is a causal relationship, or if the relationship is confounded by other factors that are also associated with elevation (such as road age, likely point of introduction, or temperature). Forcella and Harvey (1983a), for example, found that temperature and moisture conditions in the mid-montane zone of western Montana were adequate for introduced weeds, but that the conditions in the subalpine zone were too cool and moist for most Eurasian species. At HJA, roads at the lowest elevation were also the oldest and the closest to the most likely point of introduction, and thus relationships among several environmental attributes are confounded.

Three target species (*Chrysanthemum leucanthemum*, *Cirsium vulgare*, and *Senecio jacobaea*) were less frequent along roads on east-facing slopes than on other aspects. The other target species appeared to have no relationship with aspect. DeFerrari and Naiman (1994) also found that aspect was not an important indicator of landscape invasibility. However, Brothers and Spingarn (1992) reported higher frequencies of exotic

plants along "warm" (south and west aspects) forest edges than along "cool" (north and east aspects). Perhaps the scale of observation in the current study was too coarse to detect such a relationship with the target species at HJA.

The spatial pattern of solar radiation in the HJA landscape appears to have a strong relationship with aspect, with the highest radiation values corresponding generally with south- and west-facing slopes. The model used to develop the solar radiation data includes aspect as one of the inputs; other inputs were elevation, slope, and cloud cover (Harmon and Marks 1995). Although five classes of radiation could be distinguished at HJA for the growing season (April to September), over 80% of the road network fell within two medium-range classes [450–500 and 500–550 cal/(cm^2·day)]. Surprisingly, several target species appeared to have a slight negative relationship with solar radiation, although the relative frequencies in the highest and lowest radiation classes should be interpreted with caution since they represent such a small percentage of the road network. Other studies have cited a positive relationship between light levels and exotic species presence (Forcella and Harvey 1983a; Brothers and Spingarn 1992; Wilson et al. 1992).

As with aspect, perhaps the scale at which this study was conducted is too coarse to detect relationships between solar radiation and the target species. Quite a few of the 0.1-mile increments along the road network actually fell within two or more radiation classes, but they had to be assigned to just one class for this analysis. This was also a problem for data on aspect and age of the adjacent cut unit, but it was more problematic for solar radiation and the data processing likely oversimplified the pattern of radiation along the roads. Also, the model used to develop the radiation data did not take into

account the effect of topographic shading (M. Harmon, personal communication). Given the varied topographic relief at the HJA, this may be a significant limitation for this type of analysis.

4.4.3 Relationship between invasion and human disturbance on the landscape

Three environmental attributes included in this study represent disturbances on the landscape: age of adjacent cut unit, road age, and road-use level. All of these attributes are a direct consequence of human activity and may influence the patterns of distribution of target species in the HJA landscape.

Age of adjacent cut unit and road age represent relative time since disturbance. *Cytisus scoparius* tended to be more frequent on or adjacent to more recent disturbances, which supports hypotheses that this species requires habitat disturbance for its establishment (Bossard 1991). *Cytisus scoparius* had higher relative frequencies on roads adjacent to more recent cuts and on newer roads, and it had the lowest relative frequency on roads adjacent to uncut units. *Senecio jacobaea* had a trend of occurring on older disturbances, particularly along older roads. Perhaps this pattern indicates that this species takes time to become established after its initial introduction.

For target species other than *Cytisus scoparius* (or *Digitalis purpurea* and *Rubus discolor*, which were too rare for a valid comparison), the relative frequencies along roads adjacent to uncut units were generally similar to or higher than those along roads adjacent to units that had been cut. Also, the relative frequencies on roads adjacent to the most

recent (1980s-era) cut units were not consistently higher than those adjacent to older cut units. In fact, they were lower for some species (e.g., *Cirsium arvense* and *Senecio jacobaea*). These results suggest that the spatial patterns of invasion are confounded by other factors. For example, the environmental conditions created by the road itself, rather than additional light or other factors created by the adjacent cut unit, may also be important.

Several target species had highest relative frequencies on roads constructed in the 1940s, 1950s, and 1970s. However, the relationship between target species and road age is complicated by at least two factors. First, the roads constructed in the 1960s tend to be at higher elevations. Therefore, the lower relative frequencies of target species on these roads may reflect environmental conditions associated more with elevation than with road age. Second, most of the roads in the HJA were constructed before 1970; only 3% of the road network was built in the 1970s or 1980s. Therefore, the distribution patterns should be interpreted with caution.

Road-use levels were included to represent relative frequency and intensity of disturbance (vehicle traffic and road maintenance). All target species occurred on roads of all three use levels (high, medium, and low), except that *Digitalis purpurea* was not found on medium-use roads. In general, all target species (except *Digitalis purpurea* and *Rubus discolor*, which were too rare for a valid comparison) were more frequent along high-use roads than along medium- or low-use roads, although the difference was quite modest in some cases. A few species had higher relative frequencies on low-use roads than on medium-use roads, although again the difference was sometimes modest. These results complement those conducted at a finer scale, in which the distribution of individual exotic

plants along high-use and low-use roads at the HJA had some modest differences, but the overall invasion patterns were similar along roads in these two use levels (Parendes 1997, unpublished).

4.4.4 Relationship between invasion and dispersal potential

Spatial patterns in this study correspond, in general, to potential for dispersal. The patterns of dispersal can have a significant effect on the speed with which an invading species occupies new sites (Kot et al. 1996). The three most frequent target species in this study either have lightweight seeds (*Hypericum perforatum* and *Chrysanthemum leucanthemum*) or have plumed fruits/seeds (*Cirsium vulgare*). Both of these morphological characteristics may promote wind dispersal, which may help explain the species' widespread distribution. *Cytisus scoparius* and *Rubus discolor* have the heaviest seeds of the target species and would therefore be less likely to be wind dispersed for very long distances. *Cytisus scoparius* was the more frequent of these two species, occurring on about 11% of the road network in patchy locations throughout the HJA. It may be that dispersal by vehicles (including those used during road maintenance) is an important mechanism for this species (Smith and Harlen 1991), which would help explain its pattern of distribution along the roads. *Rubus discolor*, in contrast, has fleshy fruit that is likely dispersed by birds (Ridley 1930), which may help explain why it was only found in a few isolated locations along the roads.

However, potential for dispersal is not adequate to explain all of the spatial patterns. *Digitalis purpurea* has the lightest seeds of the target species, yet it was only found along 1% of the road network. *Senecio jacobaea* and *Cirsium arvense* have plumed fruits/seeds, but were not as widely distributed as *Cirsium vulgare* was. Perhaps these species have stricter environmental requirements for invading new sites than do the more frequent target species. It also may be that these species have not yet reached their full potential for establishment in this landscape. A newly introduced species is typically maintained in small populations of low frequency for some time (often many years) before it expands its range, often quite rapidly. Although all of the target species have been at HJA since at least the early 1970s (Franklin and Dyrness 1971), perhaps these less frequent target species are still in the initial lag phase of invasion (Figure 4.1A), and their current distribution represents small nascent foci (Moody and Mack 1988) from which they may expand their range with time.

4.5 Conclusions

Result of this study support a general conceptual model of the spatial and temporal process of invasion in a landscape. Exotic plants do not appear to be invading this landscape as an advancing wavefront. Rather, the process of invasion is generating multiple, discrete "foci" (Moody and Mack 1988) from which further invasion can occur. This conceptual model is supported by the spatial analysis results, which indicated that target species occurred in detectable patches or along detectable spatial gradients on some

of the roads at HJA. The patch sizes were significant and were within a similar size range for several species and along several roads, but the interpatch spacing and patch–interpatch distance were more variable. The heterogeneous arrangement of patches across the landscape suggests that each target species may be at a different phase in its respective invasion curve (as conceptualized for hypothetical species in Figure 4.1B).

The distribution of the target species at the HJA appears to be related to some of the environmental attributes examined in this study, although there is a fair amount of variation. For example, most target species were more frequent at lower versus higher elevations, and several target species were less frequent on east aspects (which tend to be cooler than west or south aspects). Also, target species were more frequent on high-use roads than on either medium- or low-use roads, although the difference was quite modest in most cases. However, confounding factors are likely to be influencing the spatial patterns of invasion on this landscape. For example, 1960s-era roads tended to be at higher elevations, and thus the lower frequencies of some species along these roads may reflect environmental conditions associated more with elevation than with road age.

Dispersal mechanism also helps explain some of the spatial patterns of invasion. The most frequent target species have the highest potential for dispersal, but other species with high dispersal potential were not as widely distributed. Confounding factors (e.g., relationships among environmental attributes; time since introduction; length of the lag phase; or biological/physical barriers to invasion) are likely influencing the patterns of invasion on this landscape.

A future study of the exotic plant invasion at the landscape scale could include a measure of relative abundance of the target species and field-based assessments of canopy

cover. Such data might provide stronger view of the spatial structure of the target species across the landscape and might yield more insight on the relationship between exotic plant distribution and important environmental attributes than was obtained in the current analysis. The spatial analysis tools used in the current study are also appropriate for abundance data. The biggest potential problem would be gathering data in a rigorous, consistent manner. Assessments of both abundance and canopy cover are somewhat subjective; care would be needed in designing an appropriate sampling scheme.

The overall results of the current study could be used as a basis for modeling the susceptibility of this landscape to invasion. Recent literature in invasion ecology has continued to consider what makes plant species successful invaders (Scott and Panetta 1993; Mack 1996; Rejmanek and Richardson 1996; Williamson and Fitter 1996a; Reichard and Hamilton 1997) and how best to model the process of invasion over space (Walker and Dowling 1991; Hastings 1996a, 1996b). Any modeling approach should include life history characteristics, a spatial component, and a mechanism for modeling rare, long-distance dispersal events. Life history characteristics may help elucidate specific biological barriers that influence invasion patterns. A spatial component can help account for the significant spatial structure associated with invasion patterns on the landscape. Long-distance dispersal events may play a large role in the invasion process (Hastings 1996b). Some of the environmental attributes considered in the current study (such as aspect and solar radiation) could be re-examined at a finer scale to determine if a significant relationship is present.

A predictive model may help identify landscapes or portions of landscapes that are particularly susceptible to invasion and may also be useful for establishing a monitoring

program. Kareiva et al. (1996) suggested that invasion theory can make a significant contribution in this regard, by developing ways to detect an invasion "problem" (assumed to include either ecological or economic concerns) before it is too late or too costly to prevent further invasion.

Chapter 5

Conclusion

5.1 Overview of results

The central question of this research examined how exotic species characteristics (i.e., biological factors such as dispersal mechanism) and invasibility of landscape features (i.e., physical factors such as disturbance or light availability) interact to produce the observed pattern of invasion by exotic plants in a forested landscape. The results support a general conceptual model, which suggests that invasion can occur when all barriers (Johnstone 1986) are removed. The elements of this model include a propagule source, a corridor (actual or conceptual), and an invasion site (Figure 1.1). Biological or physical/environmental barriers that operate on any or all of these elements may prevent invasion.

5.1.1 Role of roads

The primary focus of this research was on the road system within the forested landscape at the H.J. Andrews Experimental Forest (hereafter, HJA). The results support the hypothesis that roads serve as both corridors and invasion sites for exotic plants. In the seed bank study (Chapter 2), results showed that seed bank densities were much higher

along the road than in the mature forest and that the proportion of exotics in the seed bank was generally higher in samples taken from the roadsides than in those taken 5 m or 50 m from the road. Logistic regression analysis indicated that distance from the road was a significant predictor of whether a seed bank sample had an exotic species. In the study of roads and streams at the 1-km scale (Chapter 3), the number and frequency of exotic species was much higher along roads (both high-use and low-use) than along abandoned roads (which were not accessible to vehicles) or along streams.

5.1.2 Environmental barriers

The results of this study support the hypothesis that environmental barriers at the potential invasion site influence the observed patterns of invasion. Although exotic species were present in the seed bank within the mature forest at HJA, they were not present in the existing vegetation (Chapter 2), suggesting that environmental barriers were preventing their establishment.

In the study at the 1-km scale (Chapter 3), logistic regression analysis indicated that light levels and habitat type (a proxy for disturbance level) were significant predictors of the presence of several target species. As noted above, exotic species were much more frequent along both high-use and low-use roads than along either abandoned roads or streams, which may reflect the more favorable light conditions along the currently used roads. Most target species were more frequent under high light conditions, and the lower light levels along abandoned roads and streams may be barriers to invasion for many

exotics. An exception was *Lactuca muralis*, which was especially frequent along streams and appears to be more tolerant of a broader range of environmental conditions.

The distribution of some target species was related to some of the physical attributes examined at the 100-km scale (Chapter 4), which provides additional evidence that environmental barriers influence the pattern of invasion. For example, the frequency of most target species was lower at higher elevations, and several target species were less frequent on east aspects (which tend to be cooler than west or south aspects). However, confounding factors are likely to be influencing the spatial patterns of invasion on this landscape. For example, although some species had lower frequencies along 1960s-era roads, this pattern may reflect environmental conditions associated more with elevation than with road age since roads built during this decade tended to be at higher elevations.

5.1.3 Dispersal barriers

The results of this study also support the hypothesis that dispersal barriers may influence the patterns of invasion by exotic plants. Several exotic species were only found in the seed bank samples taken along the road at HJA (Chapter 2), suggesting that dispersal barriers prevented their movement into the mature forest. The exotics that were found in the seed bank in the mature forest had a high potential for dispersal, especially by wind. Seeds/fruits of these species either have special morphological features (e.g., plumes) or are lightweight. At both the 1-km scale (Chapter 3) and the 100-km scale (Chapter 4), the most frequent species also had a high potential for dispersal. However,

potential for dispersal did not explain all of the spatial patterns observed in this study. Other species with lightweight seeds (e.g., *Digitalis purpurea*) or plumed achenes (e.g., *Taraxacum officinale* and *Cirsium arvense*) were not as frequent. Confounding factors such as time since introduction, length of the "lag phase" after introduction (Figure 4.1A), germination requirements, seed longevity, competition, herbivory, or physical barriers to invasion may have a strong influence on the spatial patterns of invasion at any given observation date.

5.1.4 Landscape implications

Finally, the results of this study support a general conceptual model of invasion over time and space in a landscape. At the 100-km scale (Chapter 4), spatial analysis results indicated that target species had significant spatial structure along at least some of the roads. Data were collected over two growing seasons (1993 and 1994), but the time lag was not sufficient to determine if the increased target species frequencies were due to actual changes in invasion patterns or to population fluctuations in response to climate or other factors. The relative frequencies varied among target species, which suggests that they were at different phases along their respective invasion curves (Figure 4.1A), but additional observations over a longer time period are necessary to determine what shape each invasion curve has in this landscape (e.g., Figure 4.1B).

The evidence of patchiness and spatial gradients for some target species along some roads (Chapter 4) provides additional evidence for the presence of barriers to invasion. The heterogeneous arrangement of patches on the landscape suggests that the process of invasion is generating multiple, discrete "foci" from which further invasion can occur.

5.2 Management implications

One of the consequences of constructing roads in a forested landscape is that the road network provides a corridor for invasion by exotic plants. Invasion patterns were not strongly related to road-use level at the 1-km scale (Chapter 3) or the 100-km scale (Chapter 4). Perhaps the initial disturbance during road construction is more important at these scales than are subsequent differences in vehicle use and maintenance frequency. Some differences were observed at a very fine (2-m) scale (Chapter 3), with more target species detected at higher frequencies along high-use roads than along low-use roads. These results suggest that differences in vehicle use and maintenance frequency along high-use versus low-use roads have more influence on the patterns of invasion at the finer (2-m) scale than at the coarser (1-km and 100-km) scales.

Although many species appear to be restricted to roadsides, some do disperse away from the road. Several exotic species were found in the seed bank in the mature forest (Chapter 2) and, although no exotics were found in the existing vegetation in the mature forest, seeds that retain their viability would be immediately available to colonize a

site after a management-related or natural disturbance creates suitable environmental conditions (i.e., removes any existing environmental barriers).

Fewer exotic species and lower frequencies were found along abandoned roads relative to the other road types (Chapter 3). Although it is impossible to determine what the invasion patterns were along currently abandoned roads when they were accessible to vehicles, the results suggest that management strategies that include road closure may be an indirect way of controlling invasion by exotic plants. Natural resource management goals are changing in public lands from an emphasis on resource (i.e., timber) extraction to an emphasis on watershed restoration. These changing goals, in combination with reduced budgets for maintenance activities, may lead to more road closures in the future. Given the strong relationship between high light levels and the occurrence of most target exotic species in the current study, any management activity that promotes canopy closure (such as over an old road bed) is also likely to reduce the numbers of exotics in the existing vegetation.

The landscape patterns observed for the target species (Chapter 4) suggest that exotics are establishing in discrete patches that coalesce over time, rather than as an advancing wavefront. Efforts to control or eradicate exotic species should focus on "nascent foci" (Moody and Mack 1988), the discrete patches that could be easily monitored. Results from the current study could be used to identify species and populations that may warrant specific management activities. Some species such as *Hypericum perforatum* and *Chrysanthemum leucanthemum* are too widespread for complete eradication to be a reasonable goal at this point. However, other species such as *Cytisus scoparius* and *Rubus discolor* are currently distributed in fairly discrete locations

at HJA. Given that these two species have become serious pests in other similar habitats, it may be appropriate to consider proactive control measures before their populations expand too much farther.

The results of this study could also be used as a baseline to monitor invasion patterns in the future. The methods used for the survey at the 100-km scale could be repeated in a few years to assess the status of the target species and to determine if additional management activities are warranted. A repeat survey of the whole road network would take one person several days to complete. The process could be accelerated with two people: one to drive the vehicle and the other to record observations. Also, a repeat survey could gather data on both frequency (as was noted in the current study) as well as an appropriate measure of abundance. Although abundance is somewhat subjective and may be confounded with frequency, density, and cover (Cain and Castro 1959), some measure of relative abundance may provide additional information on the spatial pattern of invasion that was not available in the current analysis.

5.3 Summary

Among the many consequences of human activity, especially the development of complex transportation systems, has been the introduction of exotic species. There are few landscapes that are immune to some level of invasion, and the presence of exotics may be important in both ecological and management contexts. The forested landscape examined in the current study appears to have some barriers to invasion (i.e., few exotics present in

mature forest), but the extensive road network provides a corridor and habitat for a suite of exotic species to enter and become established.

Landscape ecology concepts of pattern and process are well suited to research on biological invasions. This study examined exotic species distribution patterns in various ways: in the soil seed bank, in various habitats along roads and streams, along the entire road network, and in relation to environmental attributes. The results contribute to an ecological understanding of the process of invasion in this landscape, especially along roads. The results also lend themselves to future work on developing a susceptibility model and monitoring regime, which would link the ecological issues with management concerns.

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APPENDICES

Appendix A. Location of complete data sets

The following complete data sets for this study have been deposited in the Forest Science Data Bank (address below):

Seed bank data by species, site, and sampling location at H.J. Andrews Experimental Forest (Chapter 2)

Survey data for target species along high-use roads, low-use roads, abandoned roads, and streams at H.J. Andrews Experimental Forest (Chapter 3)

Presence/absence data for each target species along the entire road network at H.J. Andrews Experimental Forest (Chapter 4)

Environmental attributes for the entire road network at H.J. Andrews Experimental Forest (Chapter 4) -- Note: existing data sets in the Forest Science Data Bank (address below) were used to develop GIS layers for the following: elevation, precipitation, aspect, age of the adjacent cut unit, and road age

The Forest Science Data Bank is a partnership between the Department of Forest Science, Oregon State University, and the USDA Forest Service Pacific Northwest Research Station, Corvallis, Oregon. For more information, contact

Data Manager
Forest Science Data Bank
Forestry Sciences Lab
3200 Jefferson Way
Corvallis, OR 97331

Appendix B. Life history characteristics of target species

Family	**Species**	**Common name**	**Life form**	**Height** [a]
Asteraceae	*Chrysanthemum leucanthemum*	ox-eye daisy	perennial	2-8 dm
Asteraceae	*Cirsium arvense*	Canada thistle	subdioecious perennial	3-15 (20) dm
Asteraceae	*Cirsium vulgare*	bull thistle	biennial	3-15 (20) dm
Fabaceae	*Cytisus scoparius*	Scotch broom	perennial	to 3 m (1-2 m, per Abrams)
Poaceae	*Dactylis glomerata*	orchard-grass	perennial	to 12 dm
Apiaceae	*Daucus carota*	Queen Anne's lace	biennial	2-12 dm
Scrophulariaceae	*Digitalis purpurea*	foxglove	biennial	5-18 dm
Poaceae	*Holcus lanatus*	velvet-grass	perennial	(2) 5-10 dm
Hypericaceae	*Hypericum perforatum*	klamath weed, St. John's wort	perennial herb from woody base	3-8 dm
Asteraceae	*Hypoachaeris radicata*	cat's ear	perennial	1.5-6 (8) dm
Asteraceae	*Lactuca muralis*	wall lettuce	annual or biennial (or perennial, per Abrams)	3-9 dm

Family	Species	Common name	Life form	Height [a]
Fabaceae	*Lotus corniculatus*	bird's foot trefoil	perennial	numerous prostrate to ascending stems
Plantaginaceae	*Plantago lanceolata*	English plantain	perennial (or biennial, per Abrams)	(1) 1.5-6 dm (scapes)
Plantaginaceae	*Plantago major*	common plantain	perennial	5-25 (40) cm (scapes)
Rosaceae	*Rubus discolor*	Himalaya blackberry	perennial	to 10 m, ascending to nearly erect, eventually sprawling
Polygonaceae	*Rumex acetosella*	red sorrel	dioecious perennial	(1.5) 2-3 (4) dm
Asteraceae	*Senecio jacobaea*	tansy ragwort	biennial or short-live perennial	2-10 dm
Asteraceae	*Taraxacum officinale*	common dandelion	perennial	5-50 cm (scape)
Fabaceae	*Trifolium hybridum*	alsike clover	perennial	
Fabaceae	*Trifolium pratense*	red clover	short-lived perennial	3-10 dm
Fabaceae	*Trifolium repens*	white clover	perennial	1-6 dm

[a] Source: Abrams 1940, 1944, 1951; Abrams and Ferris 1960; Hitchcock et al. 1955, 1959, 1961, 1964, 1969.

Appendix C. Seed sizes and probable dispersal agents of target species

Species	**Fruit type, size** [a]	**Seed size** [a]	**Seed weight** [b]	**Fruit/seed modifications** [a]	**Dispersal** [c]
Chrysanthemum leucanthemum	achene, terete, irregularly ellipsoid ~10 ribs	2 mm	0.22 mg	no pappus	wind, birds, adhesion, animal (dung)
Cirsium arvense	achenes	4 mm, about 1 mm wide	1.575 mg	pappus of staminate fls about 8 mm; of pistillate fls becoming 2 cm in fruit; (for genus) pappus of plumose bristles	wind, water
Cirsium vulgare	achene	<4 mm	2.85 mg [d]	pappus 2-3 cm	wind
Cytisus scoparius	legume, flattened; 25-40 mm	5-12 per fruit	7.6 mg	fruit dehiscent	ballistic, ants
Dactylis glomerata	spikelets compressed, 5-9 mm, 3 (-5)-fld		0.9 mg	disarticulates above the glumes	wind, adhesion, birds, humans
Daucus carota	(family) dry schizocarp consisting of 2 halves (mericarps) that separate at maturity; (genus) fruit slightly compressed	(fr) 3-4 mm long, 2 mm broad; ovoid	1.5 mg [d]	(genus) fruit with stout, spreading, glochidate (barbed at tip) or barbed bristles along alternate ribs, merely bristly or hairy along others	adhesion, animal (dung), birds

Species	Fruit type, size [a]	Seed size [a]	Seed weight [b]	Fruit/seed modifications [a]	Dispersal [c]
Digitalis purpurea	capsule, 12 mm, ovoid	0.5 mm, many, unwinged, reticulate	0.09 mg	capsule loculicidal; mean output: 78,000 to 93,000 seeds per plant	wind
Holcus lanatus	spikelets 4 mm, 2-fld, lower fl M/F, upper M		0.22 mg [d]	disarticulate below glumes; awn of second fl hook-like	wind, animal (dung), adhesion
Hypericum perforatum	capsule, (4) 5-8 mm, ovoid	~ 1.25 mm;	0.126 mg	genus: fr septicidal	wind, rain wash
Hypoachaeris radicata	achene, with slender beak as long as body (or from a little longer to much shorter)	body of achene 4-7 mm	0.81 mg [d] mean output: 970 achenes per plant	pappus plumose; outer shorter pappus bristles commonly merely barbellate	wind, birds, adhesion
Lactuca muralis	achene, flattened	~4 mm, including short beak (~1 mm)	0.43 mg [d] (avg of *L. saligna* and *L. serriola*)	pappus; (for genus) copious, of soft capillary bristles)	wind, adhesion (various animals)
Lotus corniculatus	legume, pod 20-40 mm long, 2-3 mm broad	~1.5 mm, 10-15 per fruit	1.2 mg	pod 2-valved, dehiscent	dehiscent, wind, rain wash, animal (dung), birds

Species	Fruit type, size [a]	Seed size [a]	Seed weight [b]	Fruit/seed modifications [a]	Dispersal [c]
Plantago lanceolata	capsule, 3-4 mm, oblong, very obtuse at apex	2 mm, (1) 2 per fruit; deeply excavated on the face	1.55 mg	(family) fruit a circumscissile capsule, dehiscing by encircling a transverse line, so top comes off as lid or cap	wind, animal (dung), birds, adhesion
Plantago major	capsule, 2.5-4 mm, ovoid	1 mm, 6-30 per fruit; strongly reticulate	0.2 mg	capsule circumscissile near or below middle	wind, animal (dung), birds, adhesion, humans
Rubus discolor	coherent druplets, ~1.5 cm thick, globose; infl 5-20 fld		5.24 mg [d]	berry fleshy, palatable; pit reticulate-pitted	birds
Rumex acetosella	achene, <1 mm	see fruit description	0.412 mg		wind, animal (dung), birds
Senecio jacobaea	achene; of disk fls minutely pubescent; of ray fls glabrous		0.28 mg	pappus; (for genus) of numerous entire or barbellate, capillary bristles	wind, birds, adhesion

Species	Fruit type, size [a]	Seed size [a]	Seed weight [b]	Fruit/seed modifications [a]	Dispersal [c]
Taraxacum officinale	achene, narrowed into a filiform beak (2) 2.5-4 times as long as body of achene	body of achene 3-4 mm	0.858 mg	pappus 6-8 mm; mature achene and pappus form conspicuous ball easily disintegrated by wind; (for genus) of many unequal, filiorm persistent bristles	wind, water
Trifolium hybridum	legume (for genus: usu shorter than and included in calyx); fls 5-9 mm, calyx ½ to 1/3 as long as corolla	1-3 per fruit	0.55-0.88 mg	(genus) indehiscent	
Trifolium pratense	legume; fls 13-20 mm, calyx ½ to 1/3 as long as corolla	2 per fruit	1.9 mg	(genus) indehiscent	animals (dung), birds
Trifolium repens	legume; fls 5-9 mm, calyx ~1/2 length of corolla	1-3 per fruit	0.642 mg	(genus) indehiscent	wind, animal (dung), birds

[a] Source: Abrams 1940, 1944, 1951; Abrams and Ferris 1960; Hitchcock et al. 1955, 1959, 1961, 1964, 1969.
[b] Source: Salisbury 1942 except as noted.
[c] Source: Ridley 1930.
[d] Source: Herbert and Irene 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).

Appendix D. Native and current range of target species

Species	Native range[a]	Current distribution[a]	Habitat[a]
Chrysanthemum leucanthemum	Eurasia	naturalized throughout much of temperate North America; common in Pacific States	fields, roadsides
Cirsium arvense	Eurasia	widely introduced in northern U.S. and southern Canada; found throughout Pacific States	cultivated ground, pastures, fields, waste places
Cirsium vulgare	Eurasia	widespread in North America; common in Pacific Northwest	pastures, fields, roadsides, waste places, disturbed ground
Cytisus scoparius	southern Europe, northern Africa	spreading rapidly in many areas from California to B.C., on west side of Cascades; also currently known from a few locations in eastern Oregon	along roadsides, disturbed places
Dactylis glomerata	Eurasia	introduced in much of North America and common throughout Pacific Northwest	lower elevations; roadsides, waste places, meadows
Daucus carota	Eurasia	established throughout most of North America; well established in western Washington and Oregon	
Digitalis purpurea	Europe	southern B.C. to California, especially west of Cascades and occasionally farther east	roadsides, other disturbed sites

Species	Native range [a]	Current distribution [a]	Habitat [a]
Holcus lanatus	Eurasia	widely introduced in North America from Alaska to California (more common west of Cascades), east to Newfoundland, and south to Georgia, Tennessee, Missouri, and Arizona; not common in Rocky Mountain states, but collected in both Idaho and Montana; spreads rapidly	roadsides, railroad embankments, waste ground to open woods in lower mountains
Hypericum perforatum	Europe	serious pest throughout much of U.S.; B.C. to central California and eastward to Atlantic Coast	fields, pastures, waste ground; very noxious, difficult to exterminate, poisonous to horses
Hypoachaeris radicata	Europe	widely established in U.S. and southern Canada; in Pacific Northwest, rarer east of Cascade Range	lawns, pastures, roadsides, other disturbed sites
Lactuca muralis	northern Europe	(as of late 1950s) sparingly established in northeast U.S. and adjacent Canada; known in Pacific Northwest from selected locations from B.C. to Marion Co., Oregon. Note: has become more widespread in recent decades; listed as "occasional, western Cascades" in Hitchcock and Cronquist 1973	moist places
Lotus corniculatus	Europe	Idaho and western Washington and Oregon; slowly spreading; more common in eastern U.S.	bottomlands or wet places (including lawns); waste places

Species	Native range [a]	Current distribution [a]	Habitat [a]
Plantago lanceolata	Eurasia	cosmopolitan weed, particularly in moister parts of temperate zone; frequent throughout Pacific States and across continent; common west of Cascades and less frequent elsewhere in Pacific Northwest	fields, roadsides, waste places
Plantago major	Europe	variable species of cosmopolitan distribution; in Pacific States, occurs in wide altitudinal range	varied habitats
Rubus discolor	Eurasia	from southern B.C. to California, mostly on west side of Cascade Range; also abundant along Snake River in southeast Washington	common along roads and railroads
Rumex acetosella	Europe	ubiquitous weed throughout most of world; common in much of North America, north of Mexico	along railroads, highways, and waste areas, but also well established in undisturbed, open to lightly wooded areas, from lowlands to lower mountains
Senecio jacobaea	Europe	established in parts of U.S. and Canada; important as weed west of Cascade Range in Oregon and Washington	pasture, other disturbed situations; poisonous to livestock, effect cumulative
Taraxacum officinale	Europe and adjacent Asia	cosmopolitan weed; well established in Pacific States	lawns, fields, roadsides, disturbed sites

Species	Native range [a]	Current distribution [a]	Habitat [a]
Trifolium hybridum	Europe	general in western U.S.; well established in Washington, Oregon, northern California	meadows
Trifolium pratense	Europe and northern Asia	widely introduced throughout much of western U.S.	fields and meadows
Trifolium repens	Europe	established throughout western North America, from Aleutian Islands southward	fields, waysides, waste places, and apparently native habitats such as mountain meadows

[a] Source: Abrams 1940, 1944, 1951; Abrams and Ferris 1960; Hitchcock et al. 1955, 1959, 1961, 1964, 1969.

Appendix E. Temperature and precipitation data from two climate stations at H.J. Andrews Experimental Forest, 1993 and 1994.

Table E1. Mean daily air temperature (°C) for two climate stations at the H.J. Andrews Experimental Forest, 1993 and 1994.

Climate station	Month	1993		1994	
		Max	Min	Max	Min
CS2MET[a]	Jan	0.4	-3.3	5.7	1.0
	Feb	2.8	-3.0	3.8	-1.1
	Mar	8.5	1.9	8.8	0.6
	Apr	10.5	4.0	13.8	3.8
	May	18.8	7.5	18.8	7.3
	Jun	19.7	8.2	20.3	7.7
	Jul	21.4	8.8	29.5	10.6
	Aug	25.1	10.4	26.7	9.7
	Sep	21.9	6.5	19.6	9.0
	Oct	13.5	5.4	11.0	3.4
	Nov	4.1	-1.9	2.0	-0.8
	Dec	3.9	-0.3	1.4	-1.5
RS15[b]	Jan	-0.4	-2.8	6.5	2.7
	Feb	2.3	-0.9	3.7	0.1
	Mar	6.5	2.5	8.3	2.4
	Apr	6.5	2.7	9.4	3.8
	May	14.6	8.1	14.4	7.5
	Jun	15.5	8.9	16.3	8.9
	Jul	16.0	9.8	23.3	12.9
	Aug	19.4	12.0	20.5	11.5
	Sep	20.7	11.8	18.8	11.7
	Oct	13.5	8.2	13.4	7.0
	Nov	5.0	0.2	*[c]	*
	Dec	4.4	1.3	*	*

[a] Watershed 2 Climatic Station, elevation 485 m.

[b] Reference Stand 15, elevation 922 m.

[c] Symbol * indicates data unavailable.

Table E2. Monthly precipitation (mm) for two climate stations at the H.J. Andrews Experimental Forest, water years 1993 and 1994.

Climate station	Month	Water year 1993	Water year 1994
CS2MET[a]	Oct	172	44
	Nov	385	110
	Dec	432	281
	Jan	256	294
	Feb	96	285
	Mar	371	171
	Apr	413	135
	May	235	91
	Jun	94	100
	Jul	53	5
	Aug	7	2
	Sep	0	47
	TOTAL	**2514**	**1565**
RS15[b]	Oct	191	45
	Nov	348	101
	Dec	427	241
	Jan	246	232
	Feb	101	217
	Mar	388	179
	Apr	401	134
	May	243	124
	Jun	155	106
	Jul	70	9
	Aug	25	3
	Sep	0	76
	TOTAL	**2595**	**1467**

[a] Watershed 2 Climatic Station, elevation 485 m.

[b] Reference Stand 15, elevation 922 m.