Journal of Applied Ecology 2005
42, 129–138

Vegetation–site relationships of roadside plant communities in West Virginia, USA

J. S. RENTCH,* R. H. FORTNEY,† S. L. STEPHENSON,‡ H. S. ADAMS,§
W. N. GRAFTON* and J. T. ANDERSON*

**Division of Forestry, West Virginia University, Morgantown, WV 26506, USA; †Department of Civil and Environmental Engineering, West Virginia University, Morgantown, WV 26506, USA; ‡Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701, USA; and §Dabney S. Lancaster Community College, Clifton Forge, VA 24422, USA*

Summary

1. In mountainous regions, road construction is accompanied by large-scale physical disturbance associated with cut and fill operations that drastically alter the landscape. Cut operations remove soil and rock from the hillside above the proposed road, while soil and rock are deposited on the down-slope area in fill operations. The resultant roadsides are highly disturbed habitats characterized by plant communities maintained at an early successional stage. They are often planted with non-native species and frequently provide vectors for the introduction and spread of invasive species. Public transportation managers need to balance the rapid revegetation of roadsides with the goal of maximizing use of native species and minimizing the introduction of non-native species.

2. This study examined vegetation–site relationships along 13 major four-lane highways in West Virginia, USA, using analysis of variance, multiresponse permutation procedures and indicator species analysis.

3. Mean soil nutrient values showed some differences with respect to highway, but fewer when highway positions were compared. Similarly, when highway position was considered, there were no significant differences in mean plant species richness, evenness or diversity.

4. Results of multiresponse permutation procedures suggested that different highways may be characterized by distinct vegetation assemblages. This hypothesis was supported by indicator species analysis: 54 species showed a statistically significant ($P < 0{\cdot}05$) affinity to one highway over all others. More than half of these were classified as non-native and exotic invasive species. When highway position was considered, no significant differences in community composition were found, and indicator species analysis found only 25 species that exhibited a significant affinity to one type of position. Of these, only eight were exotic.

5. Of the 33 most abundant herbaceous species, 11 showed a significant relationship between cover and distance from pavement. For all but one, average cover declined in a linear fashion with increasing distance.

6. *Synthesis and applications*. Despite extensive topographic disturbance associated with highway construction, the resultant vegetative communities do not differ with respect to type of construction or resultant landform. This suggests that highway agencies can manage roadside vegetation using similar, standard techniques. Roadsides are optimal growing sites for exotic invasive species that out-compete native vegetation. Management goals should therefore include techniques for limiting the establishment of these species, and substitution of non-native species planted for erosion control with suitable native species.

Key-words: management, non-native exotic species, roadside vegetation, species indicator analysis

Journal of Applied Ecology (2005) **42**, 129–138
doi: 10.1111/j.1365-2664.2004.00993.x

Correspondence: J. S. Rentch, PO Box 6125, Division of Forestry, West Virginia University, Morgantown, WV 26506, USA (fax +304 203 2441; e-mail jrentch2@mail.wvu.edu).

Introduction

Highways are important components of modern societies in that they provide critical corridors for transporting goods and humans. They also occupy major portions of the landscape and there is growing concern about the effects of roads on local and regional ecosystems (Parendes & Jones 2000). The effect of a road on the environment is complex and includes disturbances during construction, alteration of normal hydrological flows (Forman & Alexander 1998), the introduction of chemicals, including salts (Davison 1971; Rutter & Thompson 1986) and heavy metals (Atkins *et al*. 1982), and fragmentation of natural habitats (Heilman *et al*. 2002). Vehicle exhaust emissions include solid particle emissions, oxides of carbon, sulphur and nitrogen, and gases such as ozone and ethylene (Kammerbauer *et al*. 1986; Ball, Jenks & Aubourg 1998), all of which may affect plant photosynthesis, composition, competition and growth (Angold 1997). Wind gusts, artificial light, noise and dust are additional effects (Spellerberg 1998). Finally, there is growing concern regarding roads as vectors for the introduction and spread of non-native and invasive species (Wilcox 1989; Westbrooks 1991; Brothers & Spingarn 1992; Parendes & Jones 2000; Gelbard & Belnap 2003). Baker (1965) summarized the ecological attributes of roadsides as (i) disturbed habitats; (ii) planted with non-native species; (iii) forming discontinuous vegetation patterns with adjacent sites; (iv) perpetually maintained in an early successional stage; (v) consisting of extensive edge habitats; (vi) having high light intensities; and (vii) used as transportation routes by humans and animals.

Because highway corridors are perpetually disturbed areas, they are commonly considered unnatural. As a consequence, they have largely been excluded from vegetation studies. However, in most regions, highways form a complex matrix on the landscape, and the area in which significant ecological effects occur may be as much as 15–20% of the total land area of the USA (Forman & Alexander 1998). Interstate and other major four-lane highways typically continue for thousands of kilometres and traverse different ecoregions, with a footprint that can exceed 150 m in width. In many areas, they may appear to be the dominant feature on the landscape. However, in areas where much of the native vegetation has been removed for urban, industrial or agricultural land use, roadsides can also function as reservoirs for native plants that may otherwise be under threat (Ross 1986; Forman & Alexander 1998), a phenomenon observed more than half a century ago by Leopold (1949) in the central prairies of the USA.

Some effects of highways in West Virginia and the Appalachian Region, USA, may be the result of large-scale physical disturbances associated with initial construction. Modern highways in this mountainous region are constructed in a series of cuts and fills (Fig. 1). Cut slopes range from near vertical rock cuts with narrow benches to moderately sloping cuts with wide benches. Cut depths may be as much as 100 m deep from the pre-construction grade, at a greater than 1 : 1 slope. Soils applied to cuts, if present, often originate from lower horizons and are typically thinner than native soils, resulting in a reduced volume of soil from which plants may absorb water and nutrients. Fill slopes vary from steep rock fills to moderate to flat compacted fills consisting of unconsolidated material, and may exceed a height of 60 m from pre-construction grade. Fill slopes may also have benches to add slope stability, and the original soil profile may be compacted so that plant root growth is restricted (Miller, Sencindiver & Skousen 2002). These soils may also be mixed with acid, neutral or alkaline parent materials, thus giving rise to diverse soil conditions that require amendments to recreate suitable growing sites (Miller, Sencindiver & Skousen 2002). Where the topography and proposed highway routing require no cuts or fills, highways may be constructed along the existing contour (on-grade).

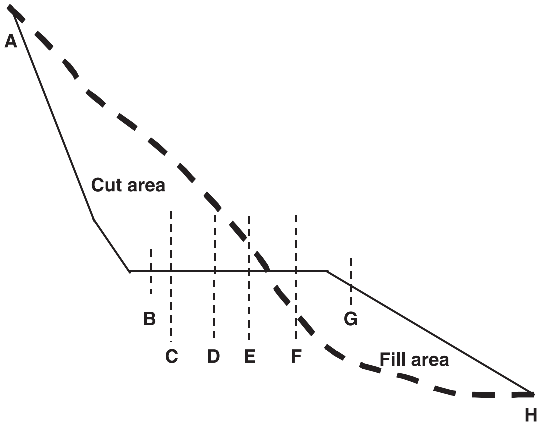

Fig. 1. Sketch of typical roadway components, showing pre- (dotted line) and post-construction (solid line) contours. AB and GH are sampled areas. BC and FG are mowed, unsampled areas. CD and EF are paved travel lanes, and DE is a mowed, vegetated median. Drawing not to scale.

During construction, roadside soils are typically fertilized, mulched and seeded with non-native grasses and legumes that are selected for rapid growth and effectiveness in erosion control. Frequently used combinations on West Virginia highway corridors include tall fescue *Lolium arundinaceum* Schreb. S.J. Darbyshire, red fescue *Festuca rubra* L., love grass *Eragrostis curvulata* (Schrad.) Nees, sericea lespedeza *Lespedeza cuneata* (Dum-Cours.) G. Don, bird's foot trefoil *Lotus corniculatus* L. and crown vetch *Coronilla varia* L.

In 2000, the West Virginia Division of Highways (WVDOH, West Virginia) funded a study to describe the vegetation of the highway corridors that it maintains. This study was, in part, conducted in response to Executive Order 13112 (EO) on Invasive Species. R. H. Fortney, D. W. Grafton, S. L. Stephenson & R. Coxe (unpublished data) reported on invasive species infestations and the distribution of roadside vegetation for major highways and physiographical regions.

The present study examined several vegetation–site relationships. (i) Does the vegetation associated with particular highways, or with particular highway positions, i.e. cut slopes, fill slopes and on-grade highway positions, form distinct, identifiable communities? (2) Are some plant species more likely to occur on one highway or one type of highway position than others? (3) Is there a relationship between the abundance of more abundant herbaceous plant species and distance from roadway pavement?

Methods

We sampled the roadside vegetation of major four-lane highways of the state, including interstate highways, Appalachian corridors and upgraded, limited-access state and federal highways, between 15 June and 30 September 2000. We randomly selected a total of 296 plots from more than 1450 km (900 miles) of roadways. We used two vegetation sampling routines. First, to characterize the overall vegetation at each sample site, we established a 20-m wide plot that extended from the clear line (the limit of mowing) to the end of the slope cut, fill or highway fence, whichever came first (Fig. 1). The shortest and longest transects sampled were 10 m and 45 m, respectively. We then estimated percentage cover in the entire 20-m wide (and variable length) plot for each species in each of three strata (herbaceous, shrub, tree) using the following cover class ratings: < 1% (0·5% mid-point), 1–10% (5·5% mid-point), > 10–50% (30% mid-point), 50–100% (75% mid-point). Additional plot variables recorded at each sampled site included plot position (cut, fill, on-grade), slope aspect and slope inclination.

Secondly, to assess the relationship between species cover and distance from the clear line, we tallied species by cover class in a series of nested 1 × 1-m (herbs) and 5 × 5-m (shrubs) subplots placed 5 m and 10 m apart, respectively, along the centre line of the 20-m wide transect. Plant identifications were made using Radford, Ahles & Bell (1968), Strausbaugh & Core (1977) and Gleason & Cronquist (1991), as well as voucher specimens in the Herbarium at West Virginia University (Morgantown, WV). Nomenclature follows Kartesz (1999).

We sampled roadside soils from a subsample of 80 plots that were randomly selected from the total of 296 plots. We collected samples from four locations (0–10 cm depth) in each plot and thoroughly mixed the soil. Samples were dried and sieved through a 6-mm mesh, and analysed by a commercial soils laboratory for the following soil characteristics: pH, cation exchange capacity (mE/100 mL), percentage organic matter, and soluble sulphur, calcium, magnesium potassium and sodium (in p.p.m). We also estimated micronutrients boron, iron, aluminium, manganese, copper and zinc (all in p.p.m), as well as easily extractable phosphorous and concentrations of N-NO_3 and N-NH_4 (all in p.p.m).

DATA ANALYSIS

We calculated sample plot species richness, evenness and diversity using PC-ORD software (McCune & Mefford 1999). Species evenness (E) is a measure of the degree to which all species share dominance in an area, and the Shannon diversity index (H') is a measure of uncertainty associated with correctly predicting the next species: given plant$_i$ = species$_i$, how likely is it that plant$_{i+1}$ will not be species$_i$? To evaluate differences by highway and highway position for mean plot richness, evenness and diversity for each vegetative stratum, we used analysis of variance (PROC GLM; SAS Institute Inc. 2002). We also used analysis of variance to compare soil means for the smaller subsample of 80 plots. Because two highways (I-81/US-340 and I-70/US-22/WV-2) were represented by only three and two soil samples, respectively, these highways were not included in a comparison of soil means. For this analysis, we transformed percentage organic matter using an arcsine conversion and transformed soil pH values to hydrogen ion concentration. When highway or highway position showed a significant effect, we used Duncan's multiple range test as a method of mean comparison.

We evaluated the uniqueness of species composition by highway and highway position using multiple response permutation procedures (MRPP; McCune & Mefford 1999). MRPP is a non-parametric multivariate procedure for testing the hypothesis of no difference between species composition of two or more a priori groups of plots (McCune, Grace & Urban 2002). This procedure calculates two statistics. Initially, a weighted mean within-group distance in species space is calculated using Sorenson distance. Then the T statistic is calculated as the ratio of the difference between the observed and expected mean distance and the standard deviation of the expected difference. This statistic describes the separation between groups; the more negative T is, the stronger the separation between groups. A P-value is used to evaluate the likelihood of achieving the observed difference (T) by chance. This procedure then calculates an A statistic that is an estimate of the within-group homogeneity, compared with random expectation. This statistic provides an estimate of the 'effect size' that is independent of the sample size (McCune, Grace & Urban 2002). When all plots are identical within groups, $A = 1$; if heterogeneity within groups equals expectation by chance, then $A = 0$. In community ecology, values for A are commonly $< 0{\cdot}1$ (McCune, Grace & Urban 2002).

We contrasted the affinity of species occurrence by highway and highway position using indicator species analysis (Dufrene & Legendre 1997). This method combines information on the species abundance at a particular highway or highway position and the faithfulness of occurrence of a species at a particular highway or position. First, we calculated an indicator value for each species (the product of the relative abundance and relative frequency); this value ranges from 0 (no indication) to 100 (perfect indication). Secondly, we tested the statistical significance of the highest indicator value (IV_{max}) for each species using a Monte Carlo method that randomly assigns each sample plot to groups 1000 times. The null hypothesis is that IV_{max} is no larger than would be expected by chance (i.e. that the species has no indicator value). To test for significance, we set α at 0·05. We used PC-ORD software (McCune & Mefford 1999) to conduct all procedures.

We also used transect data (1 × 1-m and 5 × 5-m nested subplots) and analysis of variance (PROC GLM, Version 8.2; SAS Institute Inc. 2002) to evaluate the relationship between cover values of more common species and distance from the clear line. In this analysis, we did not control for highway position or highway number. We combined subplot distances into three distance classes: 5 m (5–10 m from the clear line), 15 m (10–20 m) and 35 m (20–45 m). For those species that showed distance as a significant effect ($P \leq 0·05$), we used Duncan's multiple range test to determine which distance classes were associated with significantly different species cover values. For these species, we also evaluated whether the relationship between distance and cover was linear or non-linear, using 1 degree of freedom orthogonal comparisons (SAS Institute Inc. 2002).

Results

We identified a total of 538 vascular plant species from the 296 sample plots. The plot × herbaceous species matrix was quite large (115 736 cells) so to make the matrix more manageable we considered only herbaceous species that occurred on three or more sample plots ($n = 211$). All shrub ($n = 59$) and tree ($n = 68$) species were evaluated. Sample plots were distributed among highway positions as follows: 150 plots were at fill positions, 112 were at cut positions, and 25 occurred at on-grade positions ($N_{tot} = 287$). Nine plots had no information on highway position and were deleted from the analysis.

PLOT MEANS COMPARISON

Appendix 1 contains mean values for species richness, species evenness and species diversity for 287 sample plots, and Appendix 2 includes soil nutrient means for 80 plots. For the herbaceous stratum, US-50 had the highest species richness (19·3), evenness (0·78) and diversity (2·26) values, while I-81 / US-340 had the lowest values (11·7, 0·57 and 1·40, respectively). Although I-81 / US-340 was represented by only 11 plots, the relatively lower values for this highway did not appear to be the result of sample size; the correlation coefficient between overall highway sample size and highway species richness was quite low ($r = 0·25$). For the shrub and tree strata, differences in means were significant but also quite low in magnitude and of doubtful ecological significance. When highway position was considered, means for richness, evenness and diversity were surprisingly uniform. No differences were found for any of these indices.

A comparison of soil nutrient means showed a similar pattern: some differences were apparent by highway, but fewer occurred when values for highway position were compared. No differences were observed by highway for the following soil variables: pH, percentage organic matter, sulphur, phosphorous, manganese, aluminium, nitrate and ammonium. For base cations, US-50, I-79 and I-77 generally scored highest for calcium, magnesium, potassium and sodium, while US-19 and I-64 scored lowest. When we compared soil means by highway position, only phosphorous, sodium, manganese and aluminium showed significant differences. Of these four, all but sodium showed the greatest concentrations at on-grade positions.

COMMUNITY COMPARISON

Results of MRPP suggest that different highways may be characterized by somewhat different vegetation assemblages (Table 1). The T statistics for herb, shrub and tree strata, representing separation between highways, were negative (range –16·2 to –11·8) and highly significant ($P < 0·0001$) for all three strata. The A

Table 1. Summary statistics for multiple response permutation procedures (MRPP) for herbaceous, shrub and tree strata. Input data were species plot cover values. Plots were grouped by (a) highway and (b) highway position (cut, fill, on-grade). The *T* statistic is the weighted mean within-group distance, and the *A* statistic is the chance-corrected within-group agreement. See text for discussion of statistics

Stratum	Observed average Sorenson distance*	Expected average Sorenson distance	*T*	*P*	*A*
Highway					
Herbs	0·798	0·825	–16·236	< 0·0000001	0·033
Shrubs	0·848	0·869	–10·336	< 0·0000001	0·024
Trees	0·867	0·891	–11·845	< 0·0000001	0·027
Highway position					
Herbs	0·822	0·825	–4·012	0·002	0·0043
Shrubs	0·868	0·869	–0·503	0·284	0·0006
Trees	0·889	0·891	–1·687	0·059	0·0021

*Sorensen distance is a proportion coefficient measured in city-block space. Sorensen distance = 1 when within-group homogeneity = 0.

statistics, indicating within-group homogeneity, ranged between 0·024 and 0·033. However, when highway position was considered, results supported the hypothesis that there were few differences in vegetation between plots on cut, fill and on-grade positions. Although the T statistic for the herbaceous stratum was negative (−4·012) and statistically significant ($P = 0{\cdot}002$), within-group observed average distance was also relatively high (Sorenson distance = 0·822). In addition, the A statistic, a measure of within-group homogeneity, was an order of magnitude (0·0043) less than the value for grouping by highway. Statistical significance of the T-value ($P < 0{\cdot}05$) may result even when the 'effect size' (A) is small, if the sample size is large (McCune, Grace & Urban 2002). The high average Sorenson distance and low A statistic together suggest that differences between species composition by highway position were not ecologically meaningful. For the shrub and tree strata, no significant grouping by highway position was suggested.

INDICATOR SPECIES ANALYSIS

Results from indicator species analysis suggest that some species were more likely to occur on particular highways and highway positions than others (Tables 2 and 3). Routes I-81/US-340, in the Ridge and Valley physiographic province in the Eastern Panhandle, had the greatest number of species associates (16), even though it was one of the shortest highway corridors sampled. Japanese honeysuckle *Lonicera japonica* Thumb. and tree of heaven *Ailanthus altissima* (P. Mill.) Swingle, two widely distributed and invasive species, were most strongly associated with I-81/US-340 ($P \leq 0{\cdot}002$). Conversely, although I-64 and I-77/US-460 were among the longest highways sampled (20 and 14 sample plots, respectively), neither had species that were statistically associated with them. *Lespedeza cuneata* and *Lolium arundinaceum*, two commonly seeded grasses, occurred on all eight highway groups but were most strongly associated with US-50.

Plots on cut slopes had only one species with a statistically significant indicator value, *Barbarea vulgaris* Ait. f. (Table 3). While *Dipsacus follonum* L., *Cirsium arvense* (L.) Scop., *Cirsium vulgare (Savi) Ten.* and *Daucus carota* L. occurred at all three highway plot positions, they all showed the strongest affinity to fill slope positions. On-grade plots showed the greatest number of significant species indicator values (20). This group also contained several highly invasive, problematic weeds, such as *Setaria viridis* (L.) Beauv. and *Lonicera japonica*. On-grade plots also supported a number of plant species that are common in wetland habitats: *Juncus effusus* L., *Osmunda cinnamomea* L. and *Carex lurida* Wahl.

RELATIONSHIP BETWEEN DISTANCE FROM PAVEMENT AND ABUNDANCE

Of the 33 most common herbaceous species, 11 showed a significant relationship between distance from pavement and cover (Table 4). For all but *Dichanthelium clandestinum* (L.) Gould, average cover declined with increasing distance, and the relationship was linear for all but *Panicum virgatum* L. Differences between average cover values nearest and furthest from the clear line were generally quite low (i.e. < 5%). However, for *Lolium arundinaceum*, a planted species, average percentage cover was 13·3% closest to the pavement and 6·1% at distances greater than 20 m.

Discussion

The vegetation of West Virginia roadsides is represented by a combination of native and non-native species. Species composition of any highway is likely to be influenced by what combinations of species were planted as part of the construction revegetation. Many seed mixtures included *Lolium arundinaceum*, *Festuca rubra*, *Eragrostis curvulata*, *Lespedeza cuneata*, *Lotus corniculatus* and *Coronilla varia*. Mixed with planted species are adventive species that were probably introduced by various vectors, including animals, wind, gravity and vehicular traffic. Given the extent of initial site disturbance, residual seed banks would probably be virtually non-existent. However, the composition of the adjacent, off-road, undisturbed habitat may also contribute to roadside vegetation composition, depending on phenology, propagule size and abundance, and dispersal method. Site suitability factors (e.g. physical soil characteristics, pH and nutrient availability) are also of importance. Further, aggressive species, including such native taxa as *Solidago* spp. and *Rhus* spp. and non-native taxa such as *Ailanthus altissima*, *Leucanthemum vulgare* Lam., *Daucus carota* and *Rubus phoenicolasius* Maxim., colonize by a combination of seed and underground rootstock development. Finally, roadway age, type and frequency of maintenance, traffic density and source of traffic (i.e. local or interstate travel) may all influence species composition.

The results we obtained indicate that species richness, evenness and diversity were generally uniform in relation to highway position. That is, plant community structure was apparently more strongly influenced by the magnitude of physical disturbance associated with initial construction than the specific type of disturbance (i.e. whether the site was a fill or cut slope or on-grade). Highway roadside habitats are essentially mineral substrates following construction. Except for bare rock cuts, top dressing applied prior to revegetation is reasonably uniform, composed of crushed rock derived from the most suitable and convenient material available to contractors. In other words, sites are created more or less equal, and whether a site is a cut, fill or on-grade does not appear to greatly influence subsequent site–vegetative development.

There were, however, some differences among mean values for species richness and evenness among highways, with US-50 and I-68/I-79/US-33 generally having higher values, and I-81/US-340 and I-70/US-22/

Table 2. Species indicator values (IV) for eight highways. P-values based on the proportion of randomized trials with expected $IV >$ observed IV. Only species whose observed IV exceeds IVexp at P-values < 0·05 are shown; 1000 randomizations were used in a Monte Carlo test. $IV = 100 \times$ (relative abundance × relative frequency)

Route/species	Observed IV								Maximum expected IV	SD	P
	119	64	68/79/33	70/22/2	77/460	81/340	19	50			
US 19											
Bidens vulgata	0	1	0	0	0	0	21	0	4·8	2·91	0·002
Scirpus cyperus	0	0	0	0	0	0	19	0	4·3	3·06	0·004
Solidago rugosa	0	3	4	0	0	0	23	0	6·6	3·39	0·004
Acer rubrum	1	4	5	0	1	0	23	1	8	3·29	0·005
Cyperus strigosus	0	0	0	0	0	0	14	0	3·7	2·67	0·012
Lolium perenne	0	0	0	0	0	1	12	0	3·9	2·85	0·021
Dichanthelium clandestinum	0	0	5	0	0	0	16	4	7·4	3·87	0·034
US50											
Leucanthemum vulgare	0	2	13	0	11	0	3	46	12·4	3·46	0·001
Lespedeza cuneata	3	4	11	2	11	3	6	25	13	2·89	0·004
Achillea millefolium	0	4	5	1	7	0	5	21	9·6	3·23	0·008
Clinopodium vulgare	0	0	4	0	2	0	1	18	7·2	3·51	0·015
Equisetum arvense	0	0	0	2	0	0	0	13	3·8	2·64	0·021
Tussilago farfara	5	0	1	9	0	0	1	17	6·7	3·31	0·024
Agrostis gigantea	0	0	0	0	0	0	2	10	4·1	2·97	0·026
Erigeron strigosus	0	4	6	0	3	0	1	19	9	3·84	0·030
Lolium arundinaceum	4	8	8	3	10	17	5	18	13·6	2·28	0·040
Onoclea sensibilis	0	0	1	0	0	0	0	9	3·6	2·39	0·044
Gallium mollugo	0	0	8	1	2	0	0	15	7·3	4	0·046
I70, US22, WV2											
Ionactus linariifolius	0	0	0	30	0	0	0	0	3·4	2·44	0·001
Rubus phoenicolasius	1	0	0	32	0	2	0	0	4·6	3·84	0·002
Centaurea cyanus	0	0	0	15	0	0	0	1	3·3	2·3	0·007
Oenothera biennis	2	6	0	16	1	0	1	0	6·2	3·21	0·019
Amaranthus hybridus	0	0	0	9	0	0	0	0	3·1	2·32	0·030
Aralia spinosa	0	0	0	14	0	0	0	0	3·1	2·94	0·031
Spiraea japonica	0	0	0	14	0	0	0	0	3·1	2·95	0·031
Acer platinoides	0	0	0	11	0	0	0	0	2·9	2·3	0·035
I79, I68, US33											
Agrimonia parviflora	0	0	14	0	0	0	0	0	5·4	3·51	0·038
Phalaris arundinacea	0	0	12	0	0	0	0	0	4·9	3·41	0·049
I81, US340											
Allium vineale	0	2	1	0	4	45	1	0	8·2	3·88	0·001
Bromus sterilis	0	0	0	0	0	36	0	0	3·6	2·61	0·001
Carduus acanthoides	0	0	0	0	0	73	0	0	4·1	2·82	0·001
Centaurea biebersteinii	0	0	1	0	0	54	0	0	5·2	3	0·001
Festuca rubra	0	0	0	0	0	27	0	0	3·3	2·38	0·001
Oxalis dillenii	0	0	0	0	0	27	0	0	3·4	2·53	0·001
Celastrus scandens	0	0	0	0	0	48	0	0	4·5	3·36	0·001
Ailanthus altissima	4	0	1	0	0	40	0	0	5·7	3·33	0·001
Ulmus americana	0	0	0	0	0	40	0	0	3·9	2·86	0·001
Lonicera japonica	6	9	1	0	3	36	2	0	9·7	4·22	0·002
Bromus inermis	0	0	0	0	2	26	0	0	5·1	3·37	0·003
Elymus repens	0	1	1	0	0	23	0	0	4·5	3·02	0·004
Carya alba	0	1	0	0	0	11	0	0	3·7	2·45	0·011
Dactylis glomerata	0	1	5	0	0	23	1	2	8·5	4·02	0·013
Carya cordiformis	0	0	0	0	0	16	0	0	3·8	2·85	0·015
Geum laciniatum	0	0	1	0	0	9	0	0	3·7	2·55	0·043
US 119											
Lactuca serriola	20	2	1	0	0	1	0	0	6·1	3·12	0·001
Platanus occidentalis	31	2	0	1	1	0	0	2	7·4	3·4	0·001
Bidens frondosa	31	0	0	0	0	0	0	0	4·5	3·27	0·002
Polygonum cuspidatum	19	0	0	0	0	0	0	0	4·4	3	0·007
Setaria viridis	14	0	0	10	0	0	0	0	4·3	2·66	0·008
Solidago odoura	15	0	0	0	0	0	0	0	3·9	2·71	0·008
Betula nigra	13	0	0	0	0	0	0	0	3·8	2·86	0·014
Acer negundo	19	2	1	3	3	0	0	6	8·1	3·61	0·019
Albizia julibrissin	11	0	0	0	0	1	0	0	3·9	2·73	0·020
Cercis canadensis	21	4	1	0	6	0	0	3	10·6	5·23	0·040

Table 3. Species indicator values (IV) for three highway positions (cut, fill, on-grade). P-values based on the proportion of randomized trials with expected $IV >$ observed IV. Only species whose observed IV exceeds IVexp at P-values < 0·05 are shown; 1000 randomizations were used in a Monte Carlo test. $IV = 100 \times$ (relative abundance × relative frequency)

	Observed IV					
Position/species	Cut	Fill	On-grade	Maximum expected IV	SD	P
Cut position						
Barbarea vulgaris	6	0	0	3·1	1·6	0·043
Fill position						
Dipsacus fullonum	3	28	8	15·1	3·4	0·007
Cirsium arvense	2	24	3	12·4	3·4	0·012
Cercis canadensis	2	23	1	12·9	3·6	0·015
Cirsium vulgare	2	18	3	10·1	3·1	0·030
Daucus carota	17	34	12	25·6	3·6	0·038
On-grade position						
Setaria viridis	0	0	16	3·3	1·7	0·002
Juncus effusus	1	0	17	6·6	2·6	0·005
Asplenium platyneurone	0	0	7	1·7	1·1	0·008
Ulmus americana	0	0	7	2·3	1·3	0·011
Lonicera japonica	6	6	25	13·6	3·5	0·014
Polystichum acrostichoides	1	0	9	3·0	1·6	0·015
Acer saccharum	1	2	16	7·6	2·8	0·022
Oxalis dillenii	0	0	4	1·8	1·2	0·023
Hypericum perforatum	3	0	11	5·3	2·2	0·024
Geum laciniatum	0	0	6	2·4	1·4	0·027
Celastris scandens	0	1	6	2·8	1·6	0·037
Panicum virgatum	3	3	16	9·4	3·0	0·039
Aster divaricatus	0	0	4	1·7	1·2	0·044
Osmunda cinnamomea	0	0	4	1·7	1·3	0·044
Smilax rotundifolia	1	0	8	3·5	2·0	0·045
Festuca rubra	0	0	4	1·8	1·2	0·046
Catalpa speciosa	0	0	3	1·8	1·1	0·046
Carex lurida	0	0	6	2·7	1·6	0·048
Corylus cornuta	0	0	4	1·5	1·1	0·049
Solidago canadensis	8	16	27	20·2	3·6	0·050

Table 4. Herbaceous species that showed a statistically significant linear relationship between average cover (%) and distance from pavement edge. Mean values with different letter suffixes are significantly different ($P < 0.05$)

			Mean percentage cover		
Species	F-value	P	0–10 m	10–20 m	> 20 m
Ambrosia artisimiifolia	3·9	0·025	1·8a	0·9ab	0·4b
Apocynum androsaemifolium	3·6	0·031	1·6a	1·3b	0·3b
Daucus carota	6·9	0·001	2·6a	1·4ab	1·1b
Dichanthelium clandestinum	4·9	0·011	0·6b	2·3ab	4·6a
Dipsacus fullonum	4·2	0·018	3·2a	1·5ab	0·8b
Eupatorium fistulosum	3·8	0·042	2·8a	0·0b	0·0b
Leucanthemum vulgare	11·2	< 0·001	2·2a	1·3b	0·5c
Lolium arundinaceum	5·1	0·007	13·3a	8·2ab	6·1b
Melilotus officinalis	3·2	0·049	3·0a	1·8ab	0·2b
Panicum virgatum	3·2	0·05	1·6a	0·0c	0·4b
Plantago lanceolata	2·9	0·049	1·8	1·2ab	0·3c

WV-2 having lower values. Although the geology and soil of roadside habitats are reasonably uniform, these differences may reflect different parent material, varying construction techniques and success of post-construction seeding efforts, management practices (i.e. extent of mowing and herbicide use) and time since initial construction. For herbaceous species, the difference between the most species-rich highway (US-50) and least species-rich highway (I-81/US-340) was approximately eight species. However, for other between-highway comparisons, differences in species richness, evenness and diversity were smaller and of doubtful ecological significance.

Comparison of soil mean values by highway and highway position showed a similar trend. There were some differences by highway (principally involving concentrations of base cations) but fewer when highway positions were compared. Some differences for soil nutrients were probably related to parent material. In addition, the application of abrasives and de-icing salts during winter months on road sections with more severe climate may also increase roadside concentrations of manganese and sodium, respectively. Miller, Sencindiver & Skousen (2002) analysed individual plot samples to identify areas and highways that had nutrient deficiencies. These authors found that, although phosphorous and organic matter occasionally occurred at below optimum levels, in most cases soil fertilities of roadsides were not limiting to plant growth. In this study, means by highway and by highway position of the most commonly recognized metrics of soil fertility (e.g. pH, percentage organic matter, calcium, magnesium, potassium and nitrate) were generally in the optimum range (Chapman & Baker 2002; Heckman 2002). We did not address the physical characteristics of roadside soils in this study. However, in view of the generally acceptable levels of soil nutrients, physical characteristics such as texture, bulk density and soil water-holding capacity may exert more influence on species occurrence and plant growth.

Although MRPP did not reveal recognizable groupings by highway position, T statistics indicated that highways had somewhat different species assemblages (Table 1). This was further supported by the indicator species analysis that suggested that some species were more likely to occur on particular highways and highway positions (Tables 2 and 3). Notably, 23 of 54 species that showed a significant affinity to a particular highway were exotics; for those showing an affinity to a particular highway position, eight of 25 were exotics (Harmon & Ford-Werntz 2002). In addition to being more likely to occur on certain highways, exotic species tended to occur with greater frequency and abundance than native species. Mean indicator values for exotics were 27·3 by highway and 20·4 by highway position. Both were significantly greater ($P < 0{\cdot}006$) than comparable values for native species (means = 18·0 and 8·4, for highways and highway positions, respectively). The dominance of exotic species at I-81/US-340 may be responsible for low values of species richness and diversity values. For example, two exotic species, *Carduus acanthoides* L. and *Centaurea biebersteinii* DC., had relative frequencies of 100% and 85%, respectively, and relative abundance values of 73% and 64%.

Of particular interest is *Ailanthus altissima*, which is becoming increasingly common on roadsides. This shrub is fast growing, a prolific seed producer, a persistent stump and root sprouter and an aggressive colonizer (Hoshovsky 1988). Because the species is shade intolerant, advanced regeneration does not occur under an existing stand; however, after death or injury of the main stem the wide-spreading shallow root system can give rise to an abundance of new plants. It is widespread but not evenly distributed on West Virginia roadsides, occurring on a total of 24 sample plots; however, its average cover was highest (10·2) of the more common tree species. It was most consistently present on I-81/US-340 in the Eastern Panhandle (Table 2), where it was present in eight of 10 sample plots. It was also common along sections of I-79 and US-119, particularly in the north-central and northern sections of the highway. Because this species is drought tolerant (Burns & Honkala 1990), relatively resistant to insect predation (Goor & Barney 1968), alleopathic (Mergen 1959; Heisey 1990), tolerant of low pH, low phosphorous and high salinity in soils (Plass 1975) as well as airborne ozone (Davis, Miller & Coppolino 1978) and sulphur (cited in Hoshovsky 1988), it is likely to become increasingly common along highways in the near future. In addition, there is evidence that the species can establish a ramet bank in interior forests, and capture overstorey space after canopy gaps occur (Kowarik 1995; Knapp & Canham 2000).

We found significant relationships between species abundance and distance from the clear line for only 11 out of the 33 most common species, and differences between average cover values nearest and furthest from the clear line were generally low. The absence of stronger relationships may in part be due to the relatively short length of the transects sampled (maximum = 45 m). Other studies have examined transects 100 m long or greater (Angold 1997; Parendes & Jones 2000; Watkins *et al.* 2003); however, the sample length varies with the question being considered. In this study, we were contractually confined to the road right-of-way, and direct assessment of the similarities between roadside and interior vegetation was not a primary research question.

Relationships between species abundance and distance from the clear line were generally indirect. Of the 11 species that showed a significant relationship, average abundance for 10 species decreased as distance from the clear line increased. Several dynamics may account for this trend. First, mowing roadside areas may increase the vigour of plant populations that are less sensitive to clipping (Forman & Alexander 1998), providing a seed source for adjacent, unmown areas. Secondly, plants near the clear line tend to grow rapidly because of deep soils (Gelbard & Belnap 2003), ample light and moisture from road drainage (Forman & Alexander 1998), as well as nitrogen and phosphorous from vehicle exhaust (Angold 1997). For example, Spencer *et al.* (1988) found higher nitrogen concentrations in plants that were closest to roadways. Angold (1997) attributed increased abundance, size and vigour of *Molinia caerulea* (L.) Moench. along roadways in the UK to deposition of oxides of nitrogen from vehicle exhausts. Conversely, chemical pollution near roadways also may favour plant species that are tolerant of high levels of soil salt, lead and other heavy metals, all of which commonly decrease in soil and plant tissue concentration with distance from the highway (Chow 1970; Davison 1971; Ross 1986). In this study, the salt tolerance of *Meliotis officinalis* L. Lam. (Eckardt 1987), *Lolium arundinaceum* and *Plantago lanceolata* L. (Ross 1986) may help to account for their greater abundance near roadway pavements.

Population dynamics may also partially account for the rate of establishment and spread as well as the distance effect of these species. Propagule size and dispersal vector may limit the rate of spread. For example, seeds of *Meliotis officinalis* are generally spread by rainwater and stream water (Turkington, Cavers & Empel 1978); this may result in the concentration of the species along paved portions of roadways, and less on up- or down-slope areas that are well-drained and where overland flow is typically collected and diverted to drainage structures (Trombulak & Frissell 2000). Competition also affects species composition and rate of spread. For example, in an experiment to identify limiting processes in restoration of species-rich grassland, Pywell *et al*. (2002) found that sowing of a nurse crop caused a significant reduction in both total species richness and the richness of unsown grass species. They attributed these trends to increased interspecific competition for resources during the establishment phase, caused by the rapidly growing nurse crop. Although increased fecundity may be linked to high population density, the resultant intraspecific competition may also cause reduced seedling growth (Paynter *et al*. 1998; Paynter, Downey & Sheppard 2003), reduced vigour and seed set and delayed flowering (Dale 1974). All of these factors may dampen the rate of spread and the distance effect identified in this study.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our findings suggest that different highways may be characterized by somewhat different species assemblages and that some species show a greater affinity for one (or more) highway over others. These distribution patterns may be related to highway age, variations in revegetation efforts during highway construction, differences in sequences of species colonization and the timing of species introductions. They do not appear to be related to the type of initial construction. There also appears to be minimal variation in edaphic conditions on roadsides in terms of soil fertility, which suggests that soil conditions are not limiting for vegetation development. Non-native species, including those planted during construction for sediment/erosion control, as well as those that become established after construction, often occurred at greater frequency and abundance than native species. However, for all highways surveyed, native species were often well represented.

Three management implications are supported by these findings. First, highway agencies can manage roadside vegetation using similar techniques, as vegetation and site conditions are similar along most highways. Secondly, as roadsides appear to be optimal growing sites for non-native and in many cases invasive species, management goals established by highway agencies should include developing techniques for limiting the establishment and spread of non-native species and, conversely, encouraging the establishment and spread of native species. Thirdly, certain invasive species (e.g. *Ailanthus altissima*), which use highway corridors as migration routes, out-compete native vegetation and pose a threat to adjacent forest communities, should be targeted for control.

Acknowledgements

This study was supported by a grant from the West Virginia Division of Highways (Contract RP-160). This is Scientific Article No. 2883 of the West Virginia University Agricultural and Forestry Experiment Station, Morgantown, West Virginia, USA.

Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE993/JPE993sm.htm.

Appendix 1. Mean species richness, evenness, diversity and total cover by highway route number and highway position.

Appendix 2. Mean soil nutrient values for subsample of vegetation plots.

References

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

Atkins, D.P., Trueman, I.G., Clarke, C.B. & Bradshaw, A.D. (1982) The evolution of lead tolerance by *Festuca rubra* on a motorway verge. *Environmental Pollution (Series A)*, **27**, 233–241.

Baker, H.G. (1965) Characteristics and modes of origins of weeds. *The Genetics of Colonizing Species* (eds H.G. Baker & G. L. Stebbins), pp. 141–172. Academic Press, London, UK.

Ball, J.E., Jenks, R. & Aubourg, D. (1998) An assessment of the availability of pollutant constituents on road surfaces. *Science in the Total Environment*, **209**, 243–254.

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

Burns, R.M. & Honkala, B.H. (1990) *Silvics of North America. Volume 2. Hardwoods*. USDA Forest Service Agricultural. Handbook 654. USDA, Washington DC.

Chapman, S.L. & Baker, W.H. (2002) *Understanding the Numbers on Your Soil Test Report*. Publication FSA-2118. University of Arkansas, Division of Agriculture Co-operative Extension Service, Arkansas. http://www.uaex.edu/Other_Areas/publications/HTML/FSA-2118.asp.

Chow, T.J. (1970) Lead accumulation in roadside grass and soil. *Nature*, **225**, 295–296.

Dale, H.M. (1974) The biology of Canadian weeds. 5. *Daucus carota*. *Canadian Journal of Plant Science*, **54**, 673–685.

Davis, D.D., Miller, C.A. & Coppolino, J.B. (1978) Foliar response of eleven woody species to ozone with emphasis on black cherry. *Proceedings of the American Phytopathology Society*, **4** (Abstract NE-22), 185.

Davison, A.W. (1971) The effects of de-icing salt on roadside verges. I. Soil and plant analysis. *Journal of Applied Ecology*, **8**, 555–561.

Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.

Eckardt, N. (1987) *Element Stewardship Abstract for* Melilotis officinalis*, Sweetclover*. The Nature Conservancy Arlington, VA. http://tncweeds.ucdavis.edu/esadocs/documnts/ailaalt.html.

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

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

Gleason, H.H. & Cronquist, A. (1991) *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*. New York Botanical Garden, Bronx, NY.

Goor, A.Y. & Barney, C.W. (1968) *Forest Tree Planting in Arid Zones*. Ronald Press, New York, NY.

Harmon, P.J. & Ford-Werntz, D. (2002) *Checklist and Atlas of the Vascular Flora of West Virginia*. Draft 21 March, 2002, Wildlife Resources Technical Document 02–6. WV Division of Natural Resources, Natural Heritage Group, Elkins, WV.

Heckman, J.R. (2002) *Soil Fertility Test Interpretation, Phosphorus, Potassium, Magnesium, and Calcium*. Publication FS7. Rutgers Co-operative Extension Service, New Jersey Agricultural Experiment Station, New Brunswick, NJ. http://www.rce.rutgers.edu/pubs/pdfs/fs719.pdf.

Heilman, G.E. Jr, Stritthold, J.R., Slosser, N.C. & Dellasala, D.A. (2002) Forest fragmentation of the conterminous United States: assessing forest intactness through road density and spatial characteristics. *Bioscience*, **52**, 411–422.

Heisey, R.M. (1990) Allelopathic and herbicidal effects of extracts from tree of heaven (*Ailanthus altissima*). *American Journal of Botany*, **77**, 662–670.

Hoshovsky, M.C. (1988) *Element Stewardship Abstract for* Ailanthus altissima*, Tree of Heaven*. The Nature Conservancy Arlington, VA. http://tncweeds.ucdavis.edu/esadocs/documnts/ailaalt.html.

Kammerbauer, H., Selinger, H., Rommelt, R., Zeigler Jons, A., Knoppik, D. & Hock, B. (1986) Toxic effects of exhaust emissions on spruce *Picea abies* and their reduction by the catalytic converter. *Environmental Pollution*, **42**, 113–142.

Kartesz, J.T. (1999) A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland. *Synthesis of the North American Flora* (eds J.T. Kartesz & C.A. Meacham), Version 1.0. North Carolina Botanical Garden, Chapel Hill, NC.

Knapp, L.B. & Canham, C.D. (2000) Invasion of an old-growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. *Journal of the Torrey Botanical Society*, **127**, 307–315.

Kowarik, I. (1995) Clonal growth in *Ailanthus altissima* on a natural site in West Virginia. *Journal of Vegetation Science*, **6**, 853–856.

Leopold, A. (1949) *A Sand County Almanac*. Oxford University Press, Oxford, UK.

McCune, B. & and Mefford, M.J. (1999) *PCORD for Windows: Multivariate Analysis of Ecological Data*, Version 4.0. MjM Software, Glenedon Beach, OR.

McCune, B., Grace, J.B. & Urban, D.L. (2002) *Analysis of Ecological Communities*. MjM Software Design, Glenedon Beach, OR.

Mergen, F. (1959) A toxic principle in the leaves of *Ailanthus*. *Botanical Gazette*, **121**, 32–36.

Miller, R.L., Sencindiver, J.C. & Skousen, J. (2002) *Evaluation of Highways and other Transportation Rights-of-Way in West Virginia as Habitats for Invasive Species: Soil Report*. West Virginia Department of Transportation, Division of Highways, Charleston, WV, in press.

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

Paynter, Q., Downey, P.O. & Sheppard, A.W. (2003) Age structure and growth of the woody legume weed *Cyttisus scoparius* in native and exotic habitats: implications for control. *Journal of Applied Ecology*, **40**, 470–480.

Paynter, Q., Fowler, S.V., Memmott, J. & Sheppard, A.W. (1998) Factors affecting the establishment of *Cytisus scoparius* in southern France: implications for managing both native and exotic populations. *Journal of Applied Ecology*, **35**, 582–595.

Plass, W.T. (1975) *An Evaluation of Trees and Shrubs for Planting Surface Mine Spoils*. Research Paper NE 317. US Forest Service, Northeast Experiment Station, Newtown Square, PA.

Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W. & Peel, S. (2002) Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology*, **39**, 294–309.

Radford, A.E., Ahles, H.E. & Bell, C.R. (1968) *Manual of the Vascular Flora of the Carolinas*. University of North Carolina Press, Chapel Hill, NC.

Ross, S.M. (1986) Vegetation changes on highway verges in south-east Scotland. *Journal of Biogeography*, **13**, 109–117.

Rutter, A.J. & Thompson, N.E. (1986) The salinity of motorway soils. III. Simulation of the effects of salt usage and rainfall on sodium and chloride concentrations in the soil of central reserves. *Journal of Applied Ecology*, **23**, 271–289.

SAS Institute Inc. (2002) *SAS, Release 8.2*. SAS Institute, Inc., Cary, NC.

Spellerberg, I.F. (1998) Ecological effects of roads and traffic: a literature review. *Global Ecology and Biogeography*, **7**, 317–333.

Spencer, H.J., Scott, N.E., Port, G.R. & Davison, A.W. (1988) Effects of roadside conditions on plants and insects. I. Atmospheric conditions. *Journal of Applied Ecology*, **25**, 699–707.

Strausbaugh, P.D. & Core, E.L. (1977) *Flora of West Virginia*. Seneca Books.

Trombulak, S.C. & Frissell, C.A. (2000) Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, **14**, 18–30.

Turkington, R.A., Cavers, P.B. & Empel, E. (1978) The biology of Canadian weeds. 29. *Meliotus alba* Desr. and *M. officinalis* (L.) Lam. *Canadian Journal of Plant Science*, **58**, 523–537.

Watkins, R.Z., Chen, J., Pickens, J. & Brosofske, K.D. (2003) Effects of forest roads on understorey plants in a managed hardwood landscape. *Conservation Biology*, **17**, 411–419.

Westbrooks, R. (1991) Plant protection issues. I. A commentary on new weeds in the US. *Weed Technology*, **5**, 232–237.

Wilcox, D.A. (1989) Migration and control of purple loosestrife (*Lythrum salicaria* L.) along highway corridors. *Environmental Management*, **13**, 365–370.

Received 2 October 2003; final copy received 28 October 2004