

# Microhabitat factors and the distribution of exotic species across forest edges in temperate deciduous forest of southern Illinois, USA<sup>1</sup>

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HONU, Y. A. K. AND D. J. GIBSON (Southern Illinois University at Carbondale, Department of Plant Biology, Center for Ecology, 1125 Lincoln Drive, Carbondale, Illinois 62901-6509, USA). Microhabitat factors and the distribution of exotic species across forest edges in temperate deciduous forest of southern Illinois, USA. *J. Torrey Bot. Soc.* 133(2): 255–266. 2006.—The study of microhabitat factors has attracted the attention of ecologists for about half a century. We examined crop-forest, access road-forest, and hay field-forest edge types in temperate deciduous forest in Southern Illinois to obtain information that may contribute to the control and management of exotic species. Forest edges have different abiotic factors compared to the interior, a phenomenon known as an edge effect. To investigate microhabitat factors, three 90 m transects were established from the forest boundary into the interior at each of the three edges in July 2002. Twelve 3.14 m<sup>2</sup> circular plots at 5 m intervals from each other for the first 20 m and 10 m apart thereafter were established along each transect. A 550 cm<sup>3</sup> soil core was extracted from the six cm A-horizon in each plot along the three transects in August 2002 and analyzed for soil texture, pH, and major soil nutrients. To quantify the edge effect, the Distance of Edge Influence (DEI) was calculated by contrasting the value of microhabitat factors in plots  $\leq 50$  m from the forest boundary with the value of microhabitat factors in plots  $> 50$  m from the boundary (interior plots) using a permutation approach. The DEI is calculated as the distance where two or more consecutive plots from the forest boundary have values that differ significantly from the expected value of the interior plots. Percent clay and sand generally declined across the crop-forest and access road-forest edges into the interior while the opposite relationship was observed at the hay field-forest edge. Percent silt showed a pattern that was opposite to those exhibited by percent sand and clay at all the three edge types. The DEI of the percent sand, clay, and silt varied between 15 to 50 m at the three edges. Seven exotic species were present in the vegetation and the relationship of the abundance of three of them to 11 microhabitat factors was tested. *Lonicera japonica* and *Allium vineale* were absent when canopy openness was  $< 15\%$  while the presence of *Cardamine hirsuta* was independent of canopy openness. Management strategies for the control of the invasive *L. japonica* and *A. vineale* should consider canopy closure among other factors. By contrast, management prescriptions for the exotic *C. hirsuta* may pose a challenge to forest managers and conservation biologists as a result of its insensitiveness to the 11 microhabitat factors including light (canopy openness) measured in this study. For conservation purposes, a buffer strip of 50 m around a conservation area would eliminate most of these microhabitat edge effects.

Key words: *Allium vineale*, *Cardamine hirsuta*, edge effect, edge habitat, exotic species, invasion ecology, *Lonicera japonica*, microhabitat factors.

Numerous microhabitat factors such as soil nutrients (Franklin et al. 1993, Frelich et al. 2003), light (Gibson and Good 1987), and soil pH (Gough et al. 2000) have been shown to affect the distribution of plant species within forest

habitats. The magnitude of microhabitat factors generally decreases from forest boundaries into the interior. A forest boundary can be defined as the point where two different landscape elements meet (e.g., hay field and forest) (Yahner and Cypher 1987, Harris 1988, Matlack 1994). Forest edges have different values of abiotic factors compared to the interior (Matlack 1993, Hester and Hobbs 2000), a phenomenon known as the edge effect (Leopold 1933). For example, during the day, forest edges have elevated photosynthetically active radiation (PAR) (Geiger 1957, Kapos 1989, Brothers and Spingarn 1992, Matlack 1993), soil temperature (Brothers and Spingarn 1992), air temperature (Kapos 1989, William-Linera 1990), and decreased soil moisture (Kapos 1989) compared with the forest interior. These studies suggest that microhabitat factors at the forest edge and the interior may affect the distribution of plant species (Ashmun

<sup>1</sup> Partial funding was provided by the USDA Forest Service, North Central Research Station, James E. Ozment Achievement Award, and a Southern Illinois University Carbondale Dissertation Research Award.

<sup>2</sup> We thank Dale Vitt, Charles Ruffner, Sedonia Sipes, Andrew Carver, and two reviewers for their useful comments and discussion on a draft of this paper; Karen Harper, Ellen Macdonald, and John Connolly for their direction on the data analysis; Shibi Chandy and Eric Lees for assisting with the field work.

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Received for publication May 14, 2005, and in revised form December 19, 2005.

and Pitelka 1984, Piper 1989, Honnay et al. 1999).

The diverse microhabitats at forest edges serve as an entry point for exotic species (Fraver 1994, Hoffmann et al. 2004); i.e., species that have moved from their local habitat and established in a new habitat (U.S. Congress 1993, Richardson et al. 2000b, Colautti and MacIsaac 2004). Most exotic species were initially introduced by humans for specific purposes (e.g., medicinal benefits, soil conservation, wildlife conservation) but have later become an economic and ecological nuisance (Groves and Burdon 1986, Vitousek et al. 1996, Williamson 1996, Stein and Flack 1996, Sneed 1996, Cox 1999, Novak and Mack 2001, National Invasive Species Council 2001, Wu et al. 2004). For example, *Lonicera maackii* and *Lythrum salicaria* were introduced into North America as ornamental plants but have escaped from parks and gardens into natural habitats (Luken 1988, Blossey et al. 1994, Gould and Gorchov 2000, National Invasive Species Council 2001). There are estimated to be over 2,000 exotic plant species in the United States out of which more than half have become noxious weeds and threaten native biodiversity (U.S. Congress 1993, Vitousek et al. 1996, Williamson 1996, Sneed 1996, Cox 1999). By contrast, some of the exotic species have become integrated into their new environment and become part of the native plant community (Stein and Flack 1996). Those species that become integrated into their new environment are described as naturalized (Mack 1996).

The study of microhabitat factors has attracted the attention of ecologists for over a decade (Kapos 1989, Matlack 1993, Mucia 1995, Frelich et al. 2003). However, there is limited information on how microhabitat factors might affect the distribution of exotic species (Mark 2000, Richardson et al. 2000a, Von Holle 2005) especially along the edge to interior gradient of a forest stand (Fox and Fox 1986, Mucia 1995). In other words, there is inadequate information on the ecological niche of exotic species (Richardson et al. 2000a).

The objective of this study was to examine the variation of 1) microhabitat factors from the forest boundary into the interior of three edge types (crop-forest, access road-forest, and hay field-forest) and 2) investigate microhabitat factors that may be related to the distribution of exotic species at the three edges. We tested the following hypotheses: (H<sub>1</sub>) microhabitat factors

(canopy openness, soil nutrients, and pH) will decrease from the forest boundary into the interior. A decrease in the extent of canopy openness from the edge into the forest interior may be due to the decreasing effect of damage caused by exogenous disturbances such as storms to forest stands that open up the canopy from the forest boundary into the interior (Brothers and Spingarn 1992, Woods 1993). Decreasing levels of soil nutrients from the forest boundary into the forest interior may be due to the decline in accumulation and deposition of litter at the forest edge as a result of decrease of litterfall from the edge to the interior because of the high light at the edge compared to the interior (Matlack 1993). H<sub>2</sub>: Canopy openness associated with exotic species will be higher than in areas where exotic species were absent while soil nutrients and pH will exhibit the opposite pattern. Most exotic species are early successional light demanding species and it is expected that their microhabitat will include high canopy openness. One proposed mechanism of exotic species dominance/invasion is through their enhanced ability to utilize nutrients better than natives (Davis et al. 2000, Hierro et al. 2005). Consequently, it is expected that the microhabitat near exotic species will have low levels of soil nutrients. Knowledge of environmental and soil nutrients that affect the distribution of exotic species across forest edges is critical for the control of exotic species and management of forest stands (Monk 1968, Matlack 1994).

**Methods.** STUDY SITES. Three Research Natural Areas (RNAs) in the Shawnee National Forest (SNF), southern Illinois were selected for the study. To minimize the influence of environmental factors, flat, well-defined and south-facing forest edges were chosen. Three quite different types of forest edges were sampled to allow an assessment of general patterns.

The southern boundary of Baker Bluff RNA (SAF cover type, 40 = Post oak-black jack oak) (24 ha, 37° 29.270 N, 88° 08.894 W) (Hutchison et al. 1987b) was bordered by a crop (*Glycine max*—Soybean) field at the time of the study and represented a crop-forest edge. The farm was established in the early 1930s (Hutchison et al. 1987b). The length of the crop-forest edge was estimated to be 200 m. The northern boundary was bordered by a hay field and the rest of the boundary around the RNA had continuous forest vegetation (Hutchison et al. 1987b). *Allium vi-*

*neale*, *Cardamine hirsuta*, and *Lactuca serriola* were the exotic species observed in the crop field.

The southern boundary of Dennison Hollow RNA (SAF cover types, 40 = Post oak-black jack oak, 52 = White oak-black oak-northern red oak, 53 = White oak, and 110 = Black-oak) (83 ha, 37° 39.268" N, 88° 26.104" W) was bordered by Forest Service access road number 581 (Hutchison et al. 1987c) and was studied to represent an access road-forest edge. The road was constructed in the early 1930s (Hutchison et al. 1987c). The length of the access road-forest edge was estimated to be 300 m. The south-western portion of the external boundary of the RNA was bordered by a *Pinus echinata* plantation and the rest of the boundary was continuous forest vegetation (Hutchison et al. 1987c).

The southern boundary of Panther Hollow RNA (SAF cover type, 40 = Post oak-black jack oak, 52 = White oak-black oak-northern red oak, and 60 = Beech-sugar maple) (73 ha, 37° 32.475" N, 88° 07.284" W) was bordered by a hay field at the time of the study and represented a hay field-forest edge. The hay field was established in the early 1930s (Hutchison et al. 1987a). The length of the hay field-forest edge was estimated to be 100 m. The western boundary was bordered by a *Pinus taeda* plantation and the rest of the boundary was bordered by continuous forest vegetation (Hutchison et al. 1987a). *Festuca arundinacea*, *Lespedeza cuneata*, and *Setaria faberi* were the exotic species observed in the hay field.

All the three sampled forested areas were all natural forest that had a well defined junction, that is, not a transitional zone known as an ecotone with the crop field, access road, and the hay field, respectively (Yahner 1988).

**ASSESSMENT OF MICROHABITAT FACTORS.** To test hypothesis H<sub>1</sub>, three 90 m transects were established approximately at the center of each edge from the forest boundary into the interior of each of the three RNAs along the crop field, hay field, and the access road edges in July 2002. The transects were selected in a random manner and were approximately 30 m apart. Twelve 3.14 m<sup>2</sup> circular plots five m away from each other for the first 20 m and 10 m apart thereafter were established along each transect. In this study, plots at zero meter distance from the forest boundary are those plots that have the edge of the circular plot at the junction of the two landscape elements. A 550 cm<sup>3</sup> soil sample

was collected from the 6 cm A-horizon in each plot along the three transects in August 2002. Five equal distances (10, 20, 30, 40, and 50 cm) were marked along each cardinal axis within each plot and the soil sample taken at one of the five locations by writing the numbers of those five locations and picking one of them. An additional sample was taken from the remaining 16 locations. The five soil cores were mixed thoroughly and 4/5 separated for seed bank germination studies presented elsewhere (Honu 2004). Briefly, the soil samples were transported to the Department of Plant Biology at Southern Illinois University at Carbondale (SIUC) and kept in cold storage at 4° C for four months. The soil samples were analyzed for soil pH, potassium (K μg g<sup>-1</sup>), phosphorus (P μg g<sup>-1</sup>), calcium (Ca μg g<sup>-1</sup>), magnesium (Mg μg g<sup>-1</sup>), cation exchange capacity (CEC), and organic matter (% OM) following Mehlich (1978, 1984). Percent sand, clay and, silt were determined based on dispersion and settlement of particles in water (Ball 1986).

Hemispherical photographs were taken to quantify canopy openness of the forest edges (Frazer et al. 1999). The photographs were taken at a height of 76 cm above the ground level. Measurements were taken in August 2002 during overcast days. Gap Light Analyzer (version 2.0) was used to quantify the canopy openness of the forest edges (Frazer et al. 1999). Although Photosynthetically Active Radiation (PAR) and canopy structure and transmitted gap light (CSTGL) are indicators of canopy openness, CSTGL is a better ecological factor to measure than PAR because CSTGL takes into account the canopy structure. Our study measured canopy openness using CSTGL.

The presence of exotic species in the plots along the three transects were recorded and their frequency distribution determined. The frequency of exotic species at the three edge types ranged from 1 to 27 occurrences in 36 plots (Table 1). The three species (*Allium vineale*, *Cardamine hirsuta*, and *Lonicera japonica*) that occurred in at least 8–16 of the 36 plots at any of the study sites were tested to address H<sub>2</sub> (Table 1). Less or more frequent occurrences were too few or too large for statistical analysis. The microhabitat factors (see above) for all plots along the three transects in which these three species occurred were compared with plots in which the species did not occur (Table 1). Nomenclature follows Gleason and Cronquist (1991).

Table 1. Frequency of seven exotic species present in the vegetation at the crop-forest, access road-forest, and hay field-forest edges in temperate deciduous forest, southern Illinois. + Frequency of exotic species that were examined in subsequent analyses ( $n = 36$ , 3.14 m<sup>2</sup> plots). — = Absent. \* Frequency of five (*Cardamine hirsuta*, *Elaeagnus umbellata*, *Lespedeza cuneata*, *Prunella vulgaris*, & *Rosa multiflora*) of the seven exotic species. *Allium vineale* and *Lonicera japonica* were not added to the combined analysis because they were either very abundant or were affected by microhabitat factors.

	Edge type		
	Crop-forest	Access road-forest	Hay field-forest
<i>Allium vineale</i>	5	—	10 <sup>+</sup>
<i>Cardamine hirsuta</i>	8 <sup>+</sup>	—	12 <sup>+</sup>
<i>Elaeagnus umbellata</i>	—	3	1
<i>Lespedeza cuneata</i>	—	—	3
<i>Lonicera japonica</i>	16 <sup>+</sup>	14 <sup>+</sup>	27
<i>Prunella vulgaris</i>	—	1	—
<i>Rosa multiflora</i>	4	5	—
Five exotics*	13 <sup>+</sup>	9 <sup>+</sup>	16 <sup>+</sup>

**DATA ANALYSIS.** The three types of edge surveyed were quite different and so were analyzed separately. The Critical Values Program (CVP) was used for the edge analysis (Harper and Macdonald 2001, 2002). The CVP is presently the only program exclusively developed for edge analysis (Harper and Macdonald 2002). Their CVP consists of 1) determination of Critical Values (see below) by a randomization test of interior forest plots and 2) a comparison of the Critical Values with the observed means at different distances from the forest boundary into the interior (Harper and Macdonald 2001, 2002). Plots located at distances > 50 m from the forest boundary (i.e. plots at 60, 70, 80, 90 m) were considered to represent the forest interior and distances ≤ 50 m were considered as the forest edge. The 50 m distance considered as the forest edge here is consistent with the definition of a forest edge in the review of Mucia (1995) which states that exotic species generally do not penetrate > 50 m from the forest boundary. A total 1320 randomized means (12P<sub>3</sub>) at distances > 50 m were calculated. The means were then sorted and the Critical Values are represented by the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles of the means (i.e. expected values). The CVP compares Critical Values to the observed means of a parameter at different distances from the forest boundary into the interior to see if they are greater or less than expected. Harper & Macdonald (2001; 2002) provide a detailed description of the Critical Val-

ues technique. The Distance of Edge Influence (DEI) (Harper and Macdonald 2001) is calculated as the distance where two or more consecutive plots from the forest boundary have values that differ significantly from the expected value of the interior plots. A microhabitat factor is said to be oriented to the forest edge if the values in these forest boundary plots are higher than the expected value. Conversely, a microhabitat factor is said to be oriented to the forest interior if the values in these plots are lower than the expected values. The start and the end of a DEI were the distances at which the first and the last set of conservative plots with values higher or lower than the expected values occurred. A microhabitat factor that is not oriented to the forest edge or the interior exhibits a neutral pattern.

Logistic regression was used to examine the difference in the probability of occurrence of *A. vineale*, *C. hirsuta*, and *L. japonica* along the edge to interior gradient. Logistic regression was developed to analyze presence and absence data when the predicted probability of a dependent variable is predicted to vary along a certain gradient (e.g., microenvironmental gradient) (SAS 1990). The predicted probability of occurrence of these species from the forest boundary into the forest interior is defined by Eqn. 1 (SAS 1990).

$$p = \frac{e^{a+bx}}{1 + e^{a+bx}} \quad (1)$$

Where  $e$  = the base of a natural log,  $a$  = the intercept,  $b$  = the slope of the curve, and  $x$  = explanatory variable (e.g., canopy opening, see methods). The coefficients were derived from the logistic regression analysis.

A  $t$ -test was used to investigate the difference between microhabitat factors within all plots along the three transects that had *A. vineale*, *C. hirsuta*, and *L. japonica* and those that did not have these three species across the forest edges (SAS 1990). The canopy openness graphs were fitted using a polynomial regression (quadratic) ( $y = y_0 + ax + bx^2$ ) model.

**Results. MICROHABITAT FACTORS.** As predicted ( $H_1$ ), canopy openness declined consistently from the forest boundary into the interior regardless of the edge type (Fig. 1, Table 2). The edge effects (as measured by consecutive distances between plots which were different from the interior values) of the nine abiotic factors we tested extended into the forest interior between 5–50 m (Table 2).

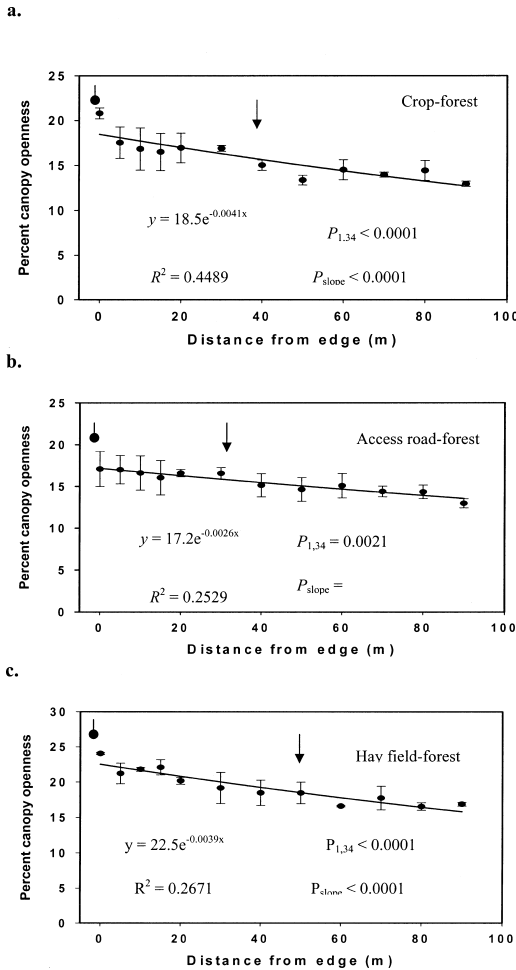


FIG. 1. Variation in percent canopy openness at a) the crop-forest b) access road-forest, and c) the hay field-forest edges into the forest interior in temperate deciduous forest, southern Illinois. Bars show the mean ( $\pm 1$  S.E) based on  $n = 3$ . Dots and arrows are the start and the end of the Distance of Edge Influence (DEI), respectively, based on critical values approach.

Percent sand and clay declined from the forest boundary into the interior at the crop-forest and access road-forest edges while the opposite was observed at the hay field-forest edge (Table 2). The pattern shown by percent silt was opposite to that of percent sand and clay at all the three edge types (Table 2).

There was a pattern of both increasing and decreasing values of the soil nutrients at the three edge types (Table 2). Total calcium was similar across the access road-forest edge (Table 2). Calcium increased from the forest boundary into the interior at the crop-forest edge but de-

creased from the forest boundary into the interior at the hay field-forest edge (Table 2).

Cation Exchange Capacity (CEC) did not follow the same pattern among the three edge types (Table 2). The CEC decreased from the forest boundary into the interior at the crop-forest edge while it increased from the forest boundary into the interior at the access road-forest edge (Table 2). The CEC did not differ across the hay field-forest edge (Table 2).

Soil potassium levels were highest at the forest edge at all the three edge types and the DEI values were  $\leq 30$  m (Table 2). Similarly, soil magnesium decreased from the forest boundary into the interior at the crop-forest and hay field-forest edges however the opposite pattern was shown at the access road-forest edge (Table 2). Soil phosphorus levels increased towards the forest interior at all the three edge types and the DEI values were  $\leq 40$  m (Table 2).

Soil pH increased towards the forest interior at the crop-forest edge while the opposite pattern was observed at the hay field-forest edge (Table 2). The interior and edge distances at the crop-forest edge and hay field-forest edges were the same (Table 2).

Organic matter (OM) content increased towards the forest interior at the three edge types but the start and end of the distances differed among the three forest edges (Table 2). The DEI values were  $\leq 10$  m.

**MICROHABITAT RELATIONSHIP WITH EXOTIC SPECIES.** Out of the 11 microhabitat factors analyzed (Table 2), only one (canopy openness) was related to the distribution of *Lonicera japonica* from the forest boundary into the interior. Canopy openness above plots that *L. japonica* occurred in was higher (15–22%) than in plots that it did not occur in (12–15%) at the crop-forest edge and the access road-forest edge ( $df = 34$ ,  $t = -6.65$  and  $-9.37$ , respectively,  $P > |t| < 0.0001$ , Fig. 2) (at both edges there was a single plot at the very edge of the forest boundary without *L. japonica* that had 20% and 16% openness, respectively). Logistic regression showed that the predicted probability of occurrence of *L. japonica* along the edge to interior gradient varied among the three sites but in all cases declined from the forest boundary into the interior (Fig. 3a). The decreasing predicted probability of occurrence of *L. japonica* at the hay field-forest edge differed from that of the crop-forest and the access road-forest edge (Table 3, Fig. 3a). However, the decreasing predicted

Table 2. Start and end of distance of Edge Influence (DEI, m) of abiotic factors across three edge types in southern Illinois. All DEI values were significant at  $P < 0.05$  (two tailed  $t$ -test). — = microhabitat factors that neither increased nor decreased from the edge into the forest interior. Start = 0 means the microhabitat factor decreased from the forest edge into interior while start  $> 0$  means increased from the edge into the forest interior.

Microhabitat factors	Crop-forest		Access road-forest		Hay field-forest	
	Start	End	Start	End	Start	End
<b>Environmental factors</b>						
% canopy openness	0	40	0	30	0	50
<b>Soil texture</b>						
Percent sand	0	30	0	50	50	0
Percent clay	0	30	0	40	50	0
Percent silt	30	0	40	0	0	50
<b>Soil resources</b>						
Calcium ( $\mu\text{g g}^{-1}$ )	30	0	—	—	0	20
CEC (meq/100 g)	0	50	15	0	—	—
Magnesium ( $\mu\text{g g}^{-1}$ )	0	50	20	0	0	5
Phosphorus ( $\mu\text{g g}^{-1}$ )	20	0	20	0	40	0
Potassium ( $\mu\text{g g}^{-1}$ )	0	5	0	30	0	5
pH	30	0	—	—	0	30
% organic matter	20	0	20	0	40	30

probability of occurrence of *L. japonica* at the crop-forest edge was not different from that of the access road-forest edge (Table 3, Fig. 3a). As with *L. japonica*, canopy openness was the only microhabitat factor that that was related to the distribution of *Allium vineale* at the hay field-forest edge ( $df = 34$ ,  $t = -2.30$ ,  $P > |t| < 0.0273$ , Fig. 2c). The canopy openness above plots that *A. vineale* occurred in at the hay field-forest edge ranged from 15 to 24 %. Plots that *A. vineale* did not occur in had canopy openness from 18 to 24 %. The predicted probability of occurrence of *A. vineale* decreased with increasing distance from the forest boundary into the interior at the hay field-forest edge (Table 3, Fig. 3b). None of the 11 microhabitat factors (see Table 2) were related to the distribution of *Cardamine hirsuta* at the crop-forest edges and the hay field-forest edges (in all cases  $P > |t| > 0.05$ ). *Cardamine hirsuta* was absent at the access road-forest edge (Table 1). The probability of occurrence of *C. hirsuta* declined from the forest boundary into the interior at the two edge types, and the slope of the regression between the two edges did not differ (Table 3, Fig. 3c).

Microhabitat factors in plots in which five infrequent exotic species combined (*Cardamine hirsuta*, *Elaeagnus umbellata*, *Lespedeza cuneata*, *Prunella vulgaris*, and *Rosa multiflora*) occurred in (see Table 1) did not differ from those without those five exotic species (in all cases  $P > |t| > 0.05$ ).

**Discussion. MICROHABITAT FACTORS.** Previous investigations of microhabitat factors at forest edges emphasized environmental factors such as Photosynthetically Active Radiation (PAR), humidity, Vapor Pressure Deficit (VPD), soil moisture, soil and air temperature (Geiger 1957, Kapos 1989, William-Linera 1990, Brothers and Spingarn 1992, Matlack 1993) but did not consider soil nutrients (but see Hester & Hobbs (2000)). The decreasing level of canopy openness that we found from the forest boundary into the interior is consistent with previous studies (Kapos 1989, Brothers and Spingarn 1992, Matlack 1993). The decreasing level of canopy openness across the edge may be due to the decline in the effect of storm damages on canopy openness from the forest boundary into the interior (Brothers and Spingarn 1992, Woods 1993). The Distance of Edge Influence (DEI) values of canopy openness at the three edge types ranged from 30 to 50 m (Table 2). The distances of edge influence, measured as PAR, found by Kapos (1989), Brothers & Spingarn (1992), and Matlack (1993) were between 30 and 50 m. The findings suggest that the abundance of interior species increases significantly only after 30 m from the forest edge while the opposite may hold for edge species. Interior species are those species whose habitat starts some distance from the edge of the forest and edge species are those species whose habitat is located at the forest edge. *Lonicera japonica* and

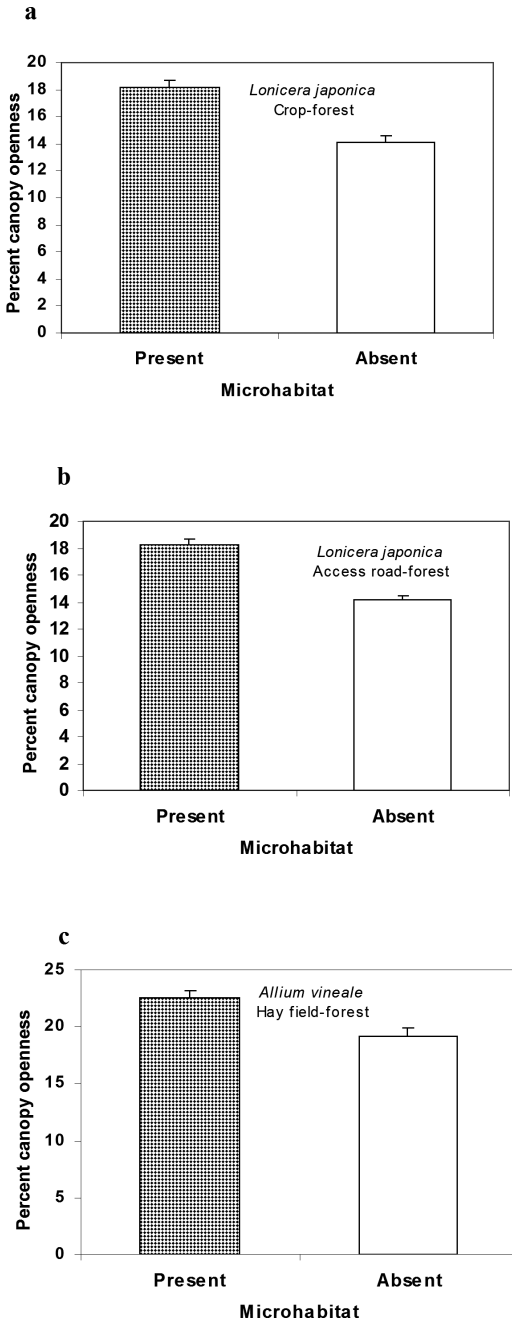


FIG. 2. Percent canopy openness above plots with and without *Lonicera japonica* across a) the crop-forest and b) access road-forest edges and c) *Allium vineale* across the hay field-forest edge in temperate deciduous forest, southern Illinois. Bars show the mean + one S.E.

*Symphoricarpos orbiculatus* are examples of edge and interior species, respectively (Honu 2004).

Soil texture can affect the within-habitat distribution of individual species (Franklin et al. 1993). However, previous studies of forest edges have not examined the variation of soil texture (Mucia 1995). Percent clay and sand generally declined from the crop-forest and access road-forest edges while the opposite was observed at the hay field-forest edge. Dust particles as a result of wind-erosion near the crop-forest and access road-forest edges were observed in the field and may be the cause of the general increase of percent clay and sand near those two forest edges. At the time of the study, the crop-forest edge was more than 50% bare of vegetation after the crop was harvested. The access road-forest edge was heavily used by four wheel motorbikes (ATVs) and horses. The soil along the road was loosened by the tires of the ATVs and the hooves of the horses aiding erosion. Pollution from road materials have been shown to affect soil nutrients (e.g. Mg) and diversity of weedy species generally decrease with increasing distance from roads (Angold 1977, Rummer et al. 1997, Godefroid and Koedam 2004). Unlike the crop field and access road edges the hay field was protected from wind-erosion because of the presence of vegetation on the site. Percent silt generally increased from the crop-forest and access road-forest edges while the opposite was observed at the hay field-forest edge. The pattern shown by silt is expected because the percentage silt depends on the amount of sand and clay present ( $\% \text{ silt} = 100 - (\% \text{ sand} + \text{clay})$ ).

Soil nutrients affect the invasion (Shea and Chesson 2002) and the distribution (Gates et al. 1956) of exotic species. Hester & Hobbs (2000) appear to have been the first to examine variation of soil nutrients across a forest edge but they did not quantify the change in the level of the individual soil nutrients from the forest boundary into the interior as we have here through calculation of the DEI (Harper and Macdonald 2001). Some of the patterns we found agreed with those of Hester & Hobbs (2000) who studied a forest bordered by a pasture land. For instance, our finding that phosphorus was lower at the forest edge than the forest interior at all the three edges we studied was opposite to that of Hester & Hobbs (2000) while our finding that potassium decreased from the forest boundary into the interior at the crop-forest and access road-forest edges we studied

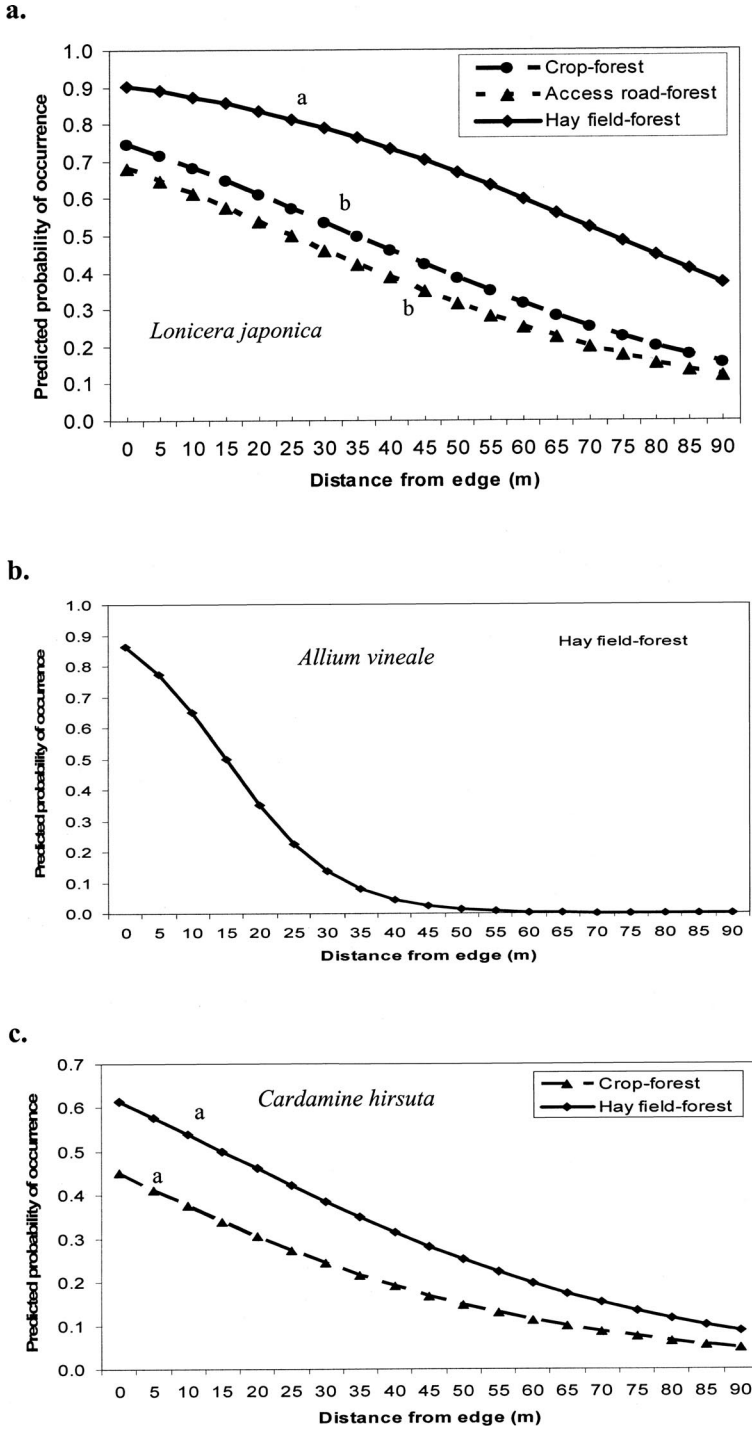


FIG. 3. Predicted probability of occurrence of a) *Lonicera japonica* across crop-forest, access road-forest and hay field-forest edge types, b) *Allium vineale* across the hay field-forest edge, and c) *Cardamine hirsuta* across crop-forest and hay field-forest edges, in temperate deciduous forest, southern Illinois. Different letters indicate that the slopes differ from one another based on logistic regression.

Table 3. Logistic regression of probability of occurrence of *Lonicera japonica*, *Allium vineale*, and *Cardamine hirsuta* from an edge to interior habitat at crop–forest, access road–forest edge and hay field–forest edge types in temperate deciduous forest of southern Illinois.

Parameter	DF	Estimate	Standard Error	Wald	95% Confidence Limits	Chi-Square	Pr > ChiSq
<b><i>Lonicera japonica</i></b>							
Hay field–forest edge (HFE)	1	2.2379	0.6057	1.0507	3.4251	13.65	0.0002
Crop–forest edge (CF)	1	-1.1769	0.6014	-2.3557	0.0019	3.83	0.0504
Access road–forest edge (ARF)	1	-1.4762	0.6044	-2.6607	-0.2917	5.97	0.0146
Distance (slope)	1	-0.0307	0.0106	-0.0515	-0.0099	8.38	0.0038
HFE v CF; HFE v ARF; CF v ARF	1	0.2993	0.5482	-0.7752	1.3738	0.30	0.5851
<b><i>Allium vineale</i></b>							
Hay field–forest edge (HFE)	1	1.8433	0.9142	0.0515	3.6352	4.07	0.0438
Distance (slope)	1	-0.1231	0.0496	-0.2203	-0.0259	6.16	0.0131
<b><i>Cardamine hirsuta</i></b>							
Hay field–forest edge (HFE)	1	0.4681	0.5377	-0.5858	1.5219	0.76	0.384
Crop–forest edge (CV)	1	-0.6657	0.5845	-1.8112	0.4798	1.3	0.2547
Distance (slope)	1	-0.0311	0.0141	-0.5905	0.0035	4.87	0.0274
HFE vs CF	1	-0.6657	0.5845	-1.8112	0.4798	1.3	0.2547

agrees with their findings. The increasing level of phosphorus from the forest boundary into the interior was unexpected and is difficult to explain. We expected decreasing levels of soil nutrients from the forest boundary into the interior as a result of the decreasing accumulation and deposition of litter from the forest boundary into the interior (Matlack 1993, Hester and Hobbs 2000). The decreasing accumulation and deposition of litter at the forest edge may be due to the decreasing effect of species richness from the forest boundary into the interior (Brothers and Spingarn 1992, Fraver 1994). We observed this decrease to occur for soil potassium and cation exchange capacity. The crop and hay field may have been fertilized which may influence the trends we observed. The diverse patterns exhibited by microhabitat factors across forest edges may render forest edge management decisions difficult.

**MICROHABITAT RELATIONSHIP WITH EXOTIC SPECIES.** Varying levels of microhabitat factors cross forest edges may affect the distribution of plant species differently (Ashmun and Pitelka 1984, Piper 1989). In this study, canopy openness was the important microhabitat factor that affected the distribution of exotic species across the forest edges. Invasion of exotic species are promoted by disturbance events (Macdonald and Richardson 1986, Williamson 1996, Shigesada and Kawasaki 1997) that increase the availability of PAR (Fox and Fox 1986, Hobbs 1989, 2000). The results of our study suggest that canopy openness of < 15% may minimize the oc-

currence of at least two invasive exotics (*L. japonica* and *A. vineale*) in forest stands (Fig. 2). At the crop-forest and the access road-forest edges, *L. japonica* was generally absent in areas that had < 15% canopy openness (Fig. 2a–b). The abundance of *L. japonica* at the hay field-forest edge may be due to > 15% canopy openness (Fig. 1c). Similarly, *A. vineale* was generally absent in areas that had < 15% canopy openness at the hay field-forest edge (Fig. 2c). Exotic species can be classified based on their eco-physiological characters as 1) light demanding or gap adaptors, 2) shade tolerators, 3) generalists, 4) competitors, 5) risk-takers, and 6) those that easily adapt to habitat changes (Newsome and Noble 1986, Geldenhuys et al. 1986, Shigesada and Kawasaki 1997, Myers and Bazely 2000, Shea and Chesson 2002). Based upon our results, *L. japonica* and *A. vineale* can be regarded as gap adaptors. The resistance of forest stands to invasion by exotic species may be due to environmental factors (e.g., canopy opening, soil nutrients), biotic resistance of the invaded community (e.g., competition), and demographic factors (e.g., number of propagules introduced) (Swincer 1986, Brothers and Spingarn 1992, Von Holle et al. 2003, Howard et al. 2004). Consequently, closed canopy forests resulting from a low level of disturbance (Swincer 1986, Brothers and Spingarn 1992) are less susceptible to invasion than open canopy forests (Fox and Fox 1986). Important microhabitat factors such as light, and soil resources in addition to habitat type and dispersal distance affect the

invasion of plant communities by exotic species (Swincer 1986, Kruger et al. 1986, Honnay et al. 1999, Hester and Hobbs 2000, Burns 2004, Kühn et al. 2004, Underwood et al. 2004). Macdonald (1984) found only 3% of exotic species in closed canopy forests compared to 21% in open canopy forests.

The lack of any relationship in our study between the microhabitat factors and the distribution of the invasive *C. hirsuta* may make the control of this species more problematic than *L. japonica* and *A. vineale*. The occurrence of *C. hirsuta* in a wide range of canopy conditions suggests that it is a generalist.

The predicted occurrence of *Lonicera japonica* and *Cardamine hirsuta* at distances up to 90 m in from the forest edge suggests that some exotic species can occur in forest stands at large distances and longer spatial edge effects than usually observed may be present (Laurance 2000, Honu 2004).

### Conclusion and Management Implications.

The overriding pattern exhibited by the microhabitat factors was that a buffer strip of 50 m around conservation areas would eliminate most of the microhabitat edge effects we examined. Control and management of exotic species is a difficult and a complex task (Matlack 1993, Stein and Flack 1996, Sneed 1996, Myers and Bazely 2000, National Invasive Species Council 2001). Currently, biological, chemical, mechanical, and prescribed burning methods are the main strategies used to control populations of invasive species (Christensen and Burrows 1986, U.S. Congress 1993, Williamson 1996, Stein and Flack 1996, Sneed 1996, Samways 1997, Federal Interagency Committee for Management of Noxious and Exotic Weeds 1998, Guiberson 1999). All these control measures are referred together as Integrated Pest management (IPM) (National Invasive Species Council 2001) but little attention have been given to the silvicultural practices such as canopy closure in the control of exotic species (U.S. Congress 1993; National Invasive Species Council 2001). Management strategies for the control of the invasive *Lonicera japonica* and *Allium vineale* should encourage a canopy closure of > 85% of forest stands in addition to other control measures. Our results suggest that canopy closure of forest stands in which exotic species occur may form a significant component of an IPM strategy. Conversely, management prescriptions for *Cardamine hirsuta* and all exotic species as a group

across forest edges may pose a greater challenge to forest managers and conservationist biologists as a result of their apparent insensitiveness to the 11 important microhabitat factors including light that we measured. Additional study is warranted on the optimum canopy opening that will reduce exotic species but not reduce the population of native species significantly (Linert and Fischer 2003).

### Literature Cited

- ANGOLD, P. G. 1977. The impact of road upon adjacent heathland vegetation: affects on plant species composition. *J. Appl. Ecol.* 34: 409–417.
- ASHMUN, J. W. AND L. F. PITELKA. 1984. Light induced variation in the growth and dynamics of transplanted ramets of the understory herb *Aster accuminatus*. *Oecologia* 64: 255–262.
- BALL, D. F. 1986. Site and soils, p. 215–284. *In* P.D. Moore & S.B. Chapman [eds.], *Methods in Plant Ecology*. Blackwell Scientific Publications, London, UK.
- BLOSSEY, B., D. SCHROEDER, S. D. HIGHT, AND R. A. MALECKI. 1994. Host specific and environmental impact of two leaf beetles (*Galerulla californiensis* and *G. pussilla*) for biological control of Purple Loosestrife (*Lythrum salicaria*). *Weed Sci.* 42: 134–140.
- BROTHERS, T. S. AND A. SPINGARN. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Cons. Biol.* 6: 91–100.
- BURNS, J. H. 2004. A comparison of invasive and non-invasive dayflowers (Commelinaceae) across experimental nutrient and water gradients. *Div. Distr.* 10: 387–397.
- CHRISTENSEN, P. E. AND N. D. BURROWS. 1986. Fire: an old tool with a new use, p. 97–105. *In* R. H. Groves and J. J. Burdon [eds.], *Ecology of Biological Invasions*. Cambridge University Press, Cambridge, UK.
- COLAUTTI, R. I. AND H. J. MACISAAC. 2004. A neutral terminology to define 'invasive' species. *Div. Distr.* 10: 135–141.
- COX, G. W. 1999. *Alien Species in North America and Hawaii*. Island Press, Washington, DC.
- DAVIS, M. A., J. P. GRIME AND K. THOMPSON. 2000. Fluctuating resources in the plant communities: a general theory of invasibility. *J. Ecol.* 88: 528–534.
- FEDERAL INTERAGENCY COMMITTEE FOR MANAGEMENT OF NOXIOUS AND EXOTIC WEEDS. 1998. *Pulling together: National Strategy for Management of Invasive Plants*, 2nd ed. U.S. Government Printing Office, Washington, DC. 22 p.
- FOX, M. D. AND B. J. FOX. 1986. The susceptibility of natural communities to invasions, p. 57–66. *In* R. H. Groves and J. J. Burdon [eds.], *Ecology of Biological Invasions*. Cambridge University Press, Cambridge, UK.
- FRANKLIN, S. B., P. A. ROBERTSON, J. S. FRALISH, AND S. M. KETTLER. 1993. Overstorey vegetation and successional trends of Land Between The Lakes, USA. *J. Veg. Sci.* 4: 509–520.
- FRAVER, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forest of

- the Roanoke River basin, North Carolina. *Cons. Biol.* 8: 822–832.
- FRAZER, G. W., C. D. CANHAM, AND K. P. LERTZMAN. 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Institute of Ecosystem Studies, Millbrook, NY.
- FRELICH, L. E., J. L. MACHADO, AND P. B. REICH. 2003. Fine-scale environmental variation and structure of understorey plant communities in two old-growth pine forests. *J. Ecol.* 91: 283–293.
- GATES, D. H., L. A. STODDART, AND C. W. COOK. 1956. Soil as a factor influencing plant distribution on salt-deserts of Utah. *Ecol. Monog.* 26: 155–175.
- GEIGER, R. 1957. The climate near the ground. Harvard University Press, Cambridge, MA.
- GELDENHUYS, C. J., P. J. ROUX, AND K. H. COOPER. 1986. Alien invasion in indigenous evergreen forest, p. 119–131. *In* I. A. W. Macdonald, J. F. Kruger & A. A. Ferrar [eds.], *The Ecology and Management of Biological Invasions in South Africa*. Oxford University Press, Cape Town, South Africa.
- GIBSON, D. J. AND R. E. GOOD. 1987. The seedling habitat of *Pinus echinata* and *Melampyrum lineare* in oak-pine forest of the New Jersey Pinelands. *Oikos* 49: 91–100.
- GLEASON, H. A. AND A. CRONQUIST. 1991. *Manual of vascular plants of Northeastern United States and adjacent Canada*. New York Botanical Garden, Bronx, NY.
- GODEFROID, S. AND N. KOEDAM. 2004. The impact of forest paths upon adjacent vegetation: effects of the path surfacing material on the species composition and soil compaction. *Biol. Cons.* 119: 405–419.
- GOUGH, L., G. R. SHAVER, D. A. CARROLL, D. L. ROYER, AND J. A. LAUNDRE. 2000. Vascular plant species richness in Alaska arctic tundra: the importance of soil pH. *J. Ecol.* 88: 54–66.
- GOULD, A. M. A. AND D. L. GORCHOV. 2000. Effects of the exotic invasive shrub *Lonicera maackii* on the survival and fecundity of three species of native annuals. *Am. Midl. Nat.* 144: 36–50.
- GROVES, R. H. AND J. J. BURDON, eds. 1986. *Ecology of Biological Invasions*. Cambridge University Press, Cambridge, UK. 166 p.
- GUIBERSON, B. Z. 1999. *Exotic Species: Invaders in Paradise*. Twenty-first Century Books, Brookfield, CT.
- HARPER, K. A. AND S. E. MACDONALD. 2001. Structure and composition of riparian boreal forest: new method for analyzing edge effect. *Ecology* 82: 649–659.
- HARPER, K. A. AND S. E. MACDONALD. 2002. The critical values program for assessing edge influence. *Bull. Ecol. Soc. Amer.* 83: 61–62.
- HARRIS, L. D. 1988. Edge effects and conservation of biotic diversity. *Cons. Biol.* 2: 331–332.
- HESTER, A. J. AND R. J. HOBBS. 2000. Influence of fire and soil nutrients on native and non-native annuals at remnant vegetation edges in the Western Australian wheatbelt. *J. Veg. Sci.* 3: 101–108.
- HIERRO, J. L., J. MARON, AND R. CALLAWAY. 2005. A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *J. Ecol.* 93: 5–15.
- HOBBS, R. J. 1989. The nature and effects of disturbance relative to invasions, p. 389–405. *In* J. A. Drake [ed.], *Biological Invasions: A Global Perspective*. Wiley, New York, NY.
- HOBBS, R. J. 2000. Land-use changes and invasions, p. 55–64. *In* H. A. Mooney & R. J. Hobbs [eds.], *Invasive Species in a Changing World*. Island Press, Washington, DC.
- HOFFMANN, W. A., V. M. P. C. LUCATELLI, F. J. SILVA, I. N. C. AZEVEDO, M. S. MARINHO, A. M. S. ALBUQUERQUE, A. O. LOPES, AND S. P. MOREIRA. 2004. Impact of the invasive alien grass *Melinis minutiflora* at the savanna-forest ecotone in the Brazilian Cerrado. *Div. Distr.* 10: 99–103.
- HONNAY, O., P. ENDELS, H. VEREecken, AND M. HERMY. 1999. The role of patch area and habitat diversity in explaining native plant species richness in disturbed suburban forest patches in northern Belgium. *Div. Distr.* 5: 129–141.
- HONU, Y. A. K. 2004. Diversity of exotic species across forest edges in the Shawnee National Forest, Illinois, USA. Dissertation, Southern Illinois University at Carbondale, Carbondale, IL.
- HOWARD, T. G., J. GUREVITCH, L. HYATT, AND M. CARREIRO. 2004. Forest invasibility in communities in southeastern New York. *Biol. Inv.* 6: 393–410.
- HUTCHISON, M. D., S. OLSON, AND S. J. HARRIS. 1987a. Research Natural Area establishment record for Panther Hollow Research Natural Area within the Shawnee National Forest. USDA, Forest Service, Hardin County, IL.
- HUTCHISON, M. D., S. OLSON, AND S. J. HARRIS. 1987b. Research Natural Area establishment record for the Baker Bluff Research Natural Area within the Shawnee National Forest. USDA, Forest Service, Hardin County, IL.
- HUTCHISON, M. D., S. OLSON, AND S. J. HARRIS. 1987c. Research Natural Area establishment record for the Dennison Hollow Research Natural Area within the Shawnee National Forest. USDA, Forest Service, Saline County, IL.
- KAPOS, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* 5: 173–185.
- KRUGER, J. F., D. M. RICHARDSON, AND B. W. WILGEN. 1986. Processes of invasion by alien plants, p. 145–155. *In* I. A. W. Macdonald, J. F. Kruger & A. A. Ferrar [eds.], *The Ecology and Management of Biological Invasions in South Africa*. Oxford University Press, Cape Town, South Africa.
- KÜHN, I., M. BRANDENBURG, AND S. KLOTZ. 2004. Why do alien plant species that reproduce in natural habitats occur more frequently? *Div. Distr.* 10: 417–425.
- LAURANCE, W. F. 2000. Do edge effects occur over large spatial scales? *TREE* 15: 134–135.
- LEOPOLD, A. 1933. *Game management*. University of Wisconsin Press, Madison, WI.
- LINERT, J. AND M. FISCHER. 2003. Habitat fragmentation affects the common wetland specialist *Primula farisana* in north-east Switzerland. *J. Ecol.* 91: 587–599.
- LUKEN, J. O. 1988. Population structure and biomass allocation of the naturalized *Lonicera maackii* (Rupr.) Maxim. in forest and open habitats. *Am. Midl. Nat.* 119: 258–267.
- MACDONALD, I. A. W. 1984. Invasive alien organisms

- in the terrestrial ecosystems of the fynbos biome, South Africa. *S. Afr. J. Sci.* 80: 396–377.
- MACDONALD, I. A. W. AND D. M. RICHARDSON. 1986. Alien species in terrestrial ecosystems of the fynbos biome, p. 77–91. *In* I. A. W. Macdonald, J. F. Kruger & A. A. Ferrar [eds.], *The Ecology and Management of Biological Invasions in South Africa*. Oxford University Press, Cape Town, South Africa.
- MACK, R. N. 1996. Plant invasions: Early and continuing expressions of global change, p. 205–216. *In* B. Huntley, W. Cramer, A. V. Morgan, H. C. Prentice & J. R. M. Allen [eds.], *Past and Future Rapid Environmental Changes: the Spatial and Evolutionary Responses of Terrestrial Biota*. Springer-Verlag, Berlin, Germany.
- MACK, R. N. 2000. Assessing the extent, status, and dynamism of plant invasions: current and emerging approaches, p. 141–168. *In* H. A. Mooney & R. J. Hobbs [eds.], *Invasive Species in a Changing World*. Island Press, Washington, DC.
- MATLACK, G. R. 1993. Microenvironment variation within and among deciduous forest edge sites in the eastern United States. *Biol. Cons.* 66: 185–194.
- MATLACK, G. R. 1994. Vegetation dynamics of the forest edge—trends in space and successional time. *J. Ecol.* 82: 113–123.
- MEHLICH, A. 1978. New extractant for soil test and acidity of phosphorus, potassium, magnesium, calcium, sodium, manganese and zinc. *Comm. Soil Sci. Pl. Anal.* 9: 477–492.
- MEHLICH, A. 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. *Comm. Soil Sci. Plant Anal.* 15: 1409–1416.
- MONK, C. D. 1968. An ecological significance of evergreenness. *Ecology* 47: 504–505.
- MUCIA, C. 1995. Edge effects in fragmented forests: implications for conservation. *TREE* 10: 58–62.
- MYERS, J. H. AND D. R. BAZELY. 2000. *Ecology and Control of Introduced Plants*. Cambridge University Press, Cambridge, UK.
- NATIONAL INVASIVE SPECIES COUNCIL. 2001. *Meeting the Invasive Species Challenge: National Invasive Species Management Plan*. U.S. Government Printing Office, Washington, DC.
- NEWSOME, A. E. AND I. R. NOBLE. 1986. Ecological and physiological characters of invading species, p. 1–20. *In* R. H. Groves & J. J. Burdon [eds.], *Ecology of Biological Invasions*. Cambridge University Press, Cambridge, UK.
- NOVAK, S. J. AND R. N. MACK. 2001. Tracing plant introduction and spread: genetic evidence from *Bromus tectorum* (Cheat grass). *BioScience* 51: 114–122.
- PIPER, J. K. 1989. Light and flowering within patches of *Smilacina racemosa* and *Smilacina stellata*. *Bull. Torrey Bot. Club* 116: 247–257.
- RICHARDSON, D. M., W. J. BOND, W. R. J. DEAN, S. I. HIGGINS, G. F. MIDGLEY, S. J. MILTON, L. W. POWRIE, M. C. RUTHERFORD, M. J. SAMWAYS, AND R. E. SCHULZE. 2000a. Invasive alien species and global change: a south African Perspective, p. 303–349. *In* H. A. Mooney & R. J. Hobbs [eds.], *Invasive Species in a Changing World*. Island Press, Washington, DC.
- RICHARDSON, D. M., P. PYSEK, M. REJMANEK, M. G. BARBOUR, F. D. PANETTA, AND C. J. WEST. 2000b. Naturalization and invasion of alien plants: concepts and definitions. *Div. Distr.* 6: 93–107.
- RUMMER, B., B. STOKES AND G. LOCKABY. 1997. Sedimentation associated with forest surfacing in a bottomland hardwood ecosystem. *For. Ecol. Manage.* 90: 195–200.
- SAMWAYS, M. J. 1997. Classical biological control and biodiversity conservation. *Biol. Cons.* 6: 1309–1316.
- SAS 1990. *SAS/STAT User's guide version 6*, 4<sup>th</sup> ed. SAS Institute, Cary, NC.
- SHEA, K. AND P. CHESSON. 2002. Community ecology theory as a framework for biological invasions. *TREE* 17: 170–176.
- SHIGESADA, N. AND K. KAWASAKI. 1997. *Biological Invasions: Theory and Practice*. Oxford University Press, Oxford, UK.
- SNEED, B. C. 1996. *Alien Invaders: the continuing threat of exotic species*. Franklin Watts, New York, NY.
- STEIN, B. A. AND S. R. FLACK, EDs. 1996. *America's Least Wanted: Alien Species Invasion of U.S. Ecosystems*. The Nature Conservancy, Arlington, Virginia. 31 p.
- SWINCER, D. E. 1986. Physical characteristics of sites in relation to invasion, p. 67–76. *In* R. H. Groves & J. J. Burdon [eds.], *Ecology of Biological Invasions*. Cambridge University Press, Cambridge, UK.
- UNDERWOOD, E. C., R. KLINGER, AND P. E. MOORE. 2004. Predicting patterns of non-native plant invasions in Yosemite National Park, California, USA. *Div. Distr.* 10: 447–459.
- U.S. CONGRESS. 1993. *Harmful Non-indigenous Species in the United States*, OTA-F565. U.S. Government Printing Office, Washington, DC. 391 p.
- VITOUSEK, P. M., C. M. D'ANTONIO, L. L. LOOP, AND R. WESTBOROKS. 1996. Biological invasions as global environmental change. *Am. Sci.* 84: 468–478.
- VON HOLLE, B. 2005. Biotic resistance to invader establishment of a Southern Appalachian plant community is determined by environmental conditions. *J. Ecol.* 93: 16–26.
- VON HOLLE, B., H. R. DELCOURT, AND D. SIMBERLOFF. 2003. The importance of biological inertia in plant community resistance to invasion. *J. Veg. Sci.* 14: 425–432.
- WILLIAM-LINERA, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *J. Ecol.* 78: 356–373.
- WILLIAMSON, M. 1996. *Biological Invasions*. Chapman & Hall, London, UK.
- WOODS, K. D. 1993. Effects of invasion by *Lonicera tatarica* L. on herb and tree seedlings in four New England forests. *Am. Midl. Nat.* 130: 62–74.
- WU, S. H., C. F. HSIEH, S. M. CHAW, AND M. REJMANEK. 2004. Plant invasions in Taiwan: Insights from the flora of casual and naturalized alien species. *Div. Distr.* 10: 349–362.
- YAHNER, R. H. 1988. Changes in wildlife communities near edges. *Cons. Biol.* 2: 333–339.
- YAHNER, R. H. AND B. L. CYPHER. 1987. Effects of nest location on depredation of artificial arboreal nests. *J. Wildlife Manage.* 52: 158–161.