CASTANEA 74(4): 327–339. DECEMBER 2009

Vegetation Structure of Field Margins and Adjacent Forests in Agricultural Landscapes of the North Carolina Piedmont

J.D. Fridley,* A.R. Senft, and R.K. Peet
Department of Biology CB #3280, University of North Carolina, Chapel Hill,
North Carolina 27599-3280

ABSTRACT Irregularly disturbed forests surrounding crop fields in agricultural landscapes often serve as ecological buffers that separate undesirable agricultural elements such as agrichemicals and weedy species from adjacent ecosystems. However, the nature of this interface between fields and forests remains little studied, particularly within the context of how species composition changes with field distance and how far exotic species penetrate into forest interiors. In three agricultural landscapes in the North Carolina Piedmont, we surveyed plant communities in multi-scale, nested quadrats arrayed along transects perpendicular to field boundaries and penetrating >200 m into adjacent forests. Rates of species turnover, patterns of species richness, and the distribution of exotic species were assessed for 18 transects. Plant communities exhibited high rates of compositional turnover within 50 m of field boundaries, but species turnover was considerably reduced beyond this threshold. Vegetation composition within borders immediately adjacent to cornfields was dominated by a relatively predictable set of weedy forb and graminoid species, of which a substantial proportion was exotic. Composition of surrounding forest communities more reflected local environmental conditions and contained few exotic species overall. Species richness was not influenced by field proximity. We suggest that agricultural influences on landscape-scale vegetation patterns are most apparent in plant communities located very close (<50 m) to continuous agricultural operations. Although weed communities associated with agricultural management are represented by a large pool of exotic species, relatively few of these species are able to penetrate forest boundaries.

INTRODUCTION The ubiquity of agricultural ecosystems and their significant role as a major source of nutrients (Rew et al. 1992, Weathers et al. 2001), pesticides (Marshall 1987, de Snoo et al. 1999), species (crops, weeds), and even new genes (Marvier 2001), makes the documentation and understanding of ecological communities surrounding intensively cropped agricultural fields of great importance in planning and management of both agricultural landscapes and nearby natural communities (Le Coeur et al. 1997, 2002; Marshall and Moonen 2002). In agricultural landscapes the vegetation surrounding crop fields can serve as an ecological buffer, potentially isolating undesirable agricultural elements such as agrichemicals and weedy species from adjacent non-agricultural ecosystems (Moonen and Marshall 2001). One concern is whether weedy borders of crop fields operate as source populations of invasive exotic species that may spread to surrounding communities (Fraver 1994, Honnay et al. 2002, Merriam 2003). Unfortunately, there are relatively few studies of the structure and composition of plant communities surrounding agricultural fields in relation to their distance from those fields (but see Fraver 1994, Boutin and Jobin 1998, Honnay et al. 2002, Harper et al. 2005, Piessens et al. 2006). Of particular interest is the distribution of exotic species with respect to distance from field edges, whether particular species traits are associated with distance from field, and whether there are structural patterns to the

---

*email address: fridley@syr.edu
Present address: Department of Biology, Syracuse University, 107 College Place, Syracuse, New York 13244.
Received November 24, 2008; Accepted April 24, 2009.

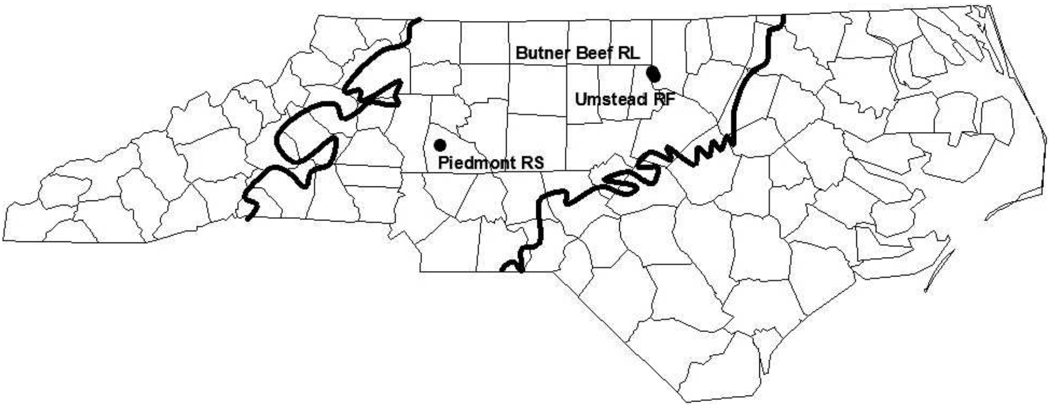

Figure 1. Map of North Carolina with the Piedmont region delineated and sampling locations labeled, including Piedmont Research Station, Umstead Research Farm, and Butner Beef Field Laboratory.

field-forest ecotone that are common to agricultural landscapes over a large geographic region (Kleijn et al. 1998).

We surveyed the vascular plant communities of three agricultural landscapes located within the Piedmont of North Carolina. Our survey design focused on documentation of change in vegetation structure and composition relative to field proximity, as well as broad geographic patterns of species composition for weedy borders and surrounding forests. We specifically sought to determine 1) how overall vegetation composition and its predictability change with distance from field, 2) how vegetation structure and plant species richness change with distance from field edge, 3) how variations in vegetation composition relate to soil texture and nutrient availability, 4) which species and plant growth forms characterize different distances from field edge, and 5) how exotic species frequency and abundance vary with distance from field edge.

METHODS

Study Area

Our study sites included three Agricultural Research Stations of the North Carolina Department of Agriculture and Consumer Services located in the Piedmont region of central North Carolina: Piedmont Research Station (Salisbury, NC; 35.698°N 80.616°W); Umstead Research Farm (Butner, NC; 36.132°N 78.757°W); and Butner Beef Field Laboratory, NC State University (Bahama, NC; 36.175°N 78.810°W) (Figure 1). Annual rainfall in the region averages ca. 100 cm, with no particular rainy season. Normal monthly average temperature ranges from about 4°C in January to 26°C in July (State Climate Office of North Carolina 2006). All sites are typical rural central North Carolina landscapes containing a mosaic of large, tilled crop fields, cattle grazing pastures, and fragmented forest stands of various sizes. Forested areas include relatively large tracts of second- and third-growth yellow pines (*Pinus taeda* and *P. echinata*) and older mixed hardwoods typically dominated by *Quercus* and *Carya* species. Regularly mown, weedy field margins of annual and perennial herbs and grasses surrounding crop fields are typically 5–25 m wide and represent the transition from intensively-managed crop fields to closed-canopy hardwood forests.

The selection of the three piedmont research locations for a single pooled analysis of vegetation composition in relation to crop field proximity was made from a larger set of study locations that spanned both piedmont and coastal plain North Carolina Agricultural Research Stations. Our decision to limit the present analysis to the three piedmont locations, but pool data across these three sites was based on 1) preliminary multivariate analysis of species composition that showed extensive overlap of forested piedmont sites (see also Figure 3B in Results), but large separation in coastal plain composition due to differences in coastal plain cropping systems, disturbance histories, and local edaphic conditions; 2) a convergence of field margin and edge community composition across the three piedmont sites (see also Figure 3A in

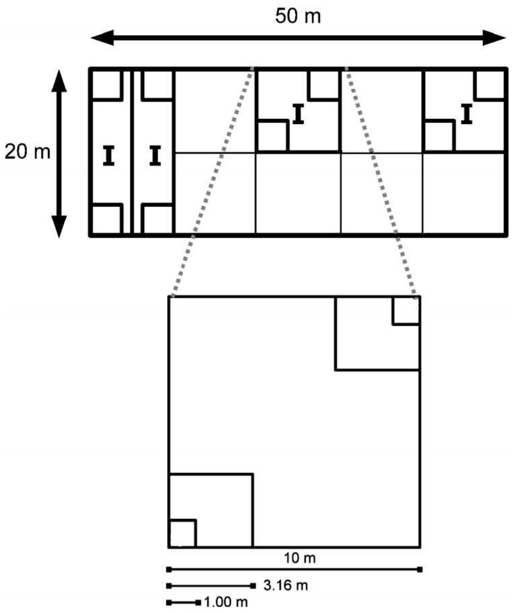

Figure 2. Nested quadrat vegetation plot design. 1000 m^2 plots of 20 × 50 m included 10 modules of 10 × 10 m, four of which were sampled intensively (labeled "I," illustrated below) with nested subplots sized 0.01 to 10 m^2 in two corners (indicated as corner squares).

Results), and 3) obtaining a large enough sample size for piedmont locations of distance-from-field transects to adequately characterize field proximity effects.

Vegetation Surveys

We surveyed the vegetation surrounding selected crop fields (typically a rotation including maize) at each site in May and June 2003. Our survey was intended to measure the composition and structure of vascular plant communities at multiple spatial scales using a nested quadrat design (Figure 2). Typically, we spaced three 1000 m^2 (20 × 50 m) plots along transects running perpendicular to field boundaries. The first plot was placed immediately adjacent to the perceived most recent boundary of tilled soil (or occasionally planted maize; note that field boundaries fluctuate up to a few meters each year) with its longitudinal (50 m) axis parallel to the transect. Second and third 1000 m^2 plots were spaced at uneven distances further along the transect from the field boundary, depending on local topography and distances to nearest streams. Occasionally only two plots were placed along a transect due to stream proximity. In total, we established 18 transects of lengths varying from 52–283 m: four at Piedmont, five at Umstead, and nine at Butner Beef.

Within each 1000 m^2 plot we measured presence and abundance (cover) of all vascular plant species in nested quadrats of six different sizes, following a modified version of the Carolina Vegetation Survey protocol (Peet et al. 1998, Figure 2). Four 100 m^2 quadrats within each plot were sampled intensively: two consecutive 5 × 20 m quadrats were located at the front edge (first 0–10 m of plot with respect to field orientation), one 10 × 10 m quadrat in the middle (20–30 m), and one 10 × 10 m quadrat at the far end (40–50 m). The modification of rectangular intensive quadrats on the leading edge of each 1000 m^2 plot (Figure 2) was intended to capture fine-scale variation in species composition associated with edge distance. We sampled a total of 162 100 m^2 quadrats: 38 at Piedmont, 52 at Umstead, and 72 at Butner Beef.

All sampled 100 m^2 quadrats received smaller-scale surveys in each of two corners, comprising nested areas of 10 and 1 m^2 (Figure 2). Cover estimates of each species were recorded for each surveyed 100 m^2 quadrat and each whole 1000 m^2 plot using the Carolina Vegetation Survey cover class system (Peet et al. 1998). Species nomenclature follows United States Department of Agriculture, Natural Resources Conservation Service (USDA, NRCS) (2006).

We collected soil samples in concert with vegetation surveys to quantify co-variation in edaphic factors. Samples were removed from the A soil horizon (ca. 0–10 cm depth) from the center of each surveyed 100 m^2 quadrat (four per 1000 m^2 plot). Samples were analyzed by Brookside Laboratories, Inc. (New Knoxville, Ohio) for textural and nutrient analysis. Nutrient analyses included *p*H, estimated N release, exchangeable and % base saturation of Ca, Mg, K, and Na, cation exchange capacity, and extractable P, S, Mn, Zn, B, Cu, Fe, and Al (Mehlich 1984). Textural analysis included percent clay, silt, and sand.

Analysis

Our 162 100 m^2 quadrats contained 324 series of nested subplots. We selected scales of 100, 10 and 1 m^2 for analysis, as there were too few 1000 m^2 surveys along each transect

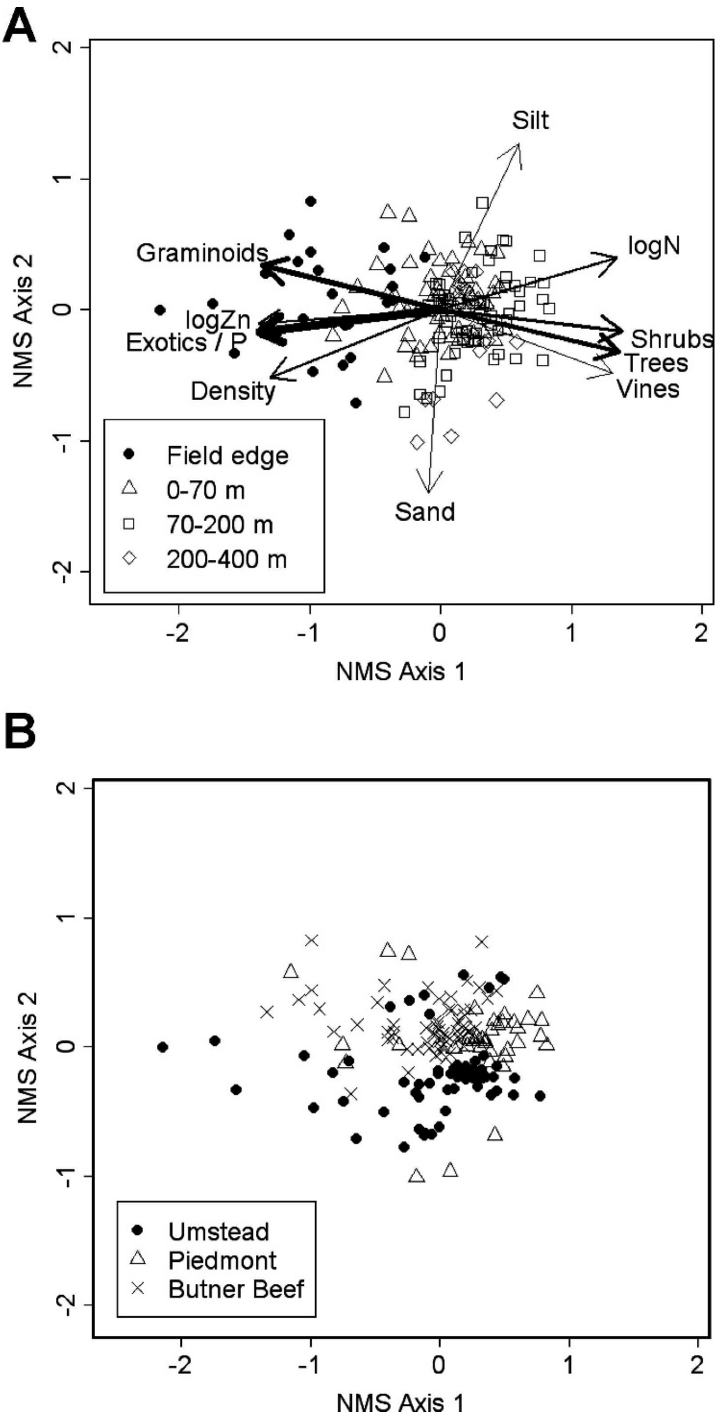

Figure 3. Non-metric multidimensional scaling ordination of 162 100 m^2 vegetation quadrats from the three piedmont sites. A. Vector diagram representing the correlation of selected environmental variables to compositional dissimilarity, as indicated by Mantel tests (all Mantel $r > 0.20$). Symbols represent distance-from-field categories. B. Same ordination as in (A), but with symbols indicating research site.

for rigorous analysis. We quantified trends in compositional variation at the 100 m^2 scale by means of multivariate analysis of species abundance (cover classes) using non-metric multidimensional scaling (NMS; Kruskal 1964), a nonparametric ordination technique that aims to best represent a plot-by-plot similarity matrix in a few spatial dimensions. We calculated plot similarity matrices for species cover values with the Sorensen (Bray-Curtis) index (Legendre and Legendre 1998) and chose the lowest stress configuration of all two-dimensional solutions, following McCune and Grace (2003). The correlation of environmental factors with major axes of compositional variation in multivariate space was assessed with Mantel tests (Mantel 1967) that provided correlations of factors to axes of multivariate ordination. NMS and Mantel tests were performed with the VEGAN statistical package for R 2.2.0 (Oksanen et al. 2007).

For each quadrat (whether 100, 10, or 1 m^2) we established distance-from-field boundary values using the center of the quadrat. For example, a 5 × 20 m (100 m^2) quadrat immediately adjacent to a field would be 2.5 m distant; a 10 m^2 quadrat adjacent to the field would be 1.58 m distant; and an adjacent 1 m^2 quadrat would be 0.5 m distant from the field edge. Distances for quadrats nested within plots not adjacent to fields were taken from field GPS measurements accurate to within 10 m.

Following the approach of Nekola and White (1999), we analyzed the decay in compositional similarity with distance from field boundary using log-transformed Jaccard similarity matrices (Legendre and Legendre 1998) of compositional similarity. Based on the results of this analysis plus obvious structural changes (i.e., transition from herbaceous vegetation to woody cover) we constructed five distance-from-field classes. We then determined the species characteristic of each class using the indicator species analysis approach of Dufrene and Legendre (1997). The Dufrene and Legendre algorithm creates indicator values by scoring species according to both their frequency within a plot group and their absence from other groups. This procedure was performed in PC-ORD for Windows 4.20 (McCune and Mefford 1999).

We analyzed the abundance and distribution of particular groups of species with respect to distance from field boundary by collecting trait and growth-form data. Growth-form (herb, graminoid, shrub, tree, vine) assignment and whether a species was native to North America (pre-European colonization) followed United States Department of Agriculture PLANTS (USDA, NRCS 2006). We consider "exotic" all vascular plant species listed as "Introduced" by the USDA. We used locally-weighted regressions (Cleveland 1979) to compare scatterplot patterns of different datasets.

RESULTS

Compositional Trends in Plant Communities from Field Edge to Forest Interior

The major trend in vegetation composition was associated with the transition from a distinct zone of weedy, field-margin communities to communities dominated by woody canopy. Field margin quadrats (adjacent to field boundary and not including those that overlapped forest canopy) emerged as a relatively well-defined group in NMS ordination of all 100 m^2 quadrats (solid circles, Figure 3A), as did those forested quadrats within 70 m of field boundary (triangles, Figure 3A), while groupings of communities at larger distances generally overlapped one another in two-dimensional ordination space (Figure 3A). Overall, distance of quadrat from field boundary was significantly correlated with compositional dissimilarity (Mantel $r = 0.10$, $P < 0.05$). A secondary axis of compositional variation was related to soil texture (Figure 3A, percent silt $r = 0.26$, percent sand $r = 0.22$, both $P < 0.001$) and partly geography, with a slight separation of Umstead and Butner Beef plots and broadly overlapping composition of Piedmont plots (Figure 3B).

The axis of compositional variation that corresponded to distance-from-field was strongly correlated with variation in several environmental and plant attribute factors as determined by Mantel tests. Soil phosphorus concentration was strongly positively associated with field margin vegetation ($r = 0.37$, $P < 0.001$ for this and all reported nutrient Mantel correlations), while soil nitrogen was negatively associated with margin vegetation ($r = 0.23$). Zinc ($r = 0.34$) patterns were similar to those of phosphorus; other positive correlations with increasing distance from field included soil bulk density ($r = 0.24$) and concentrations of iron and potassium (r

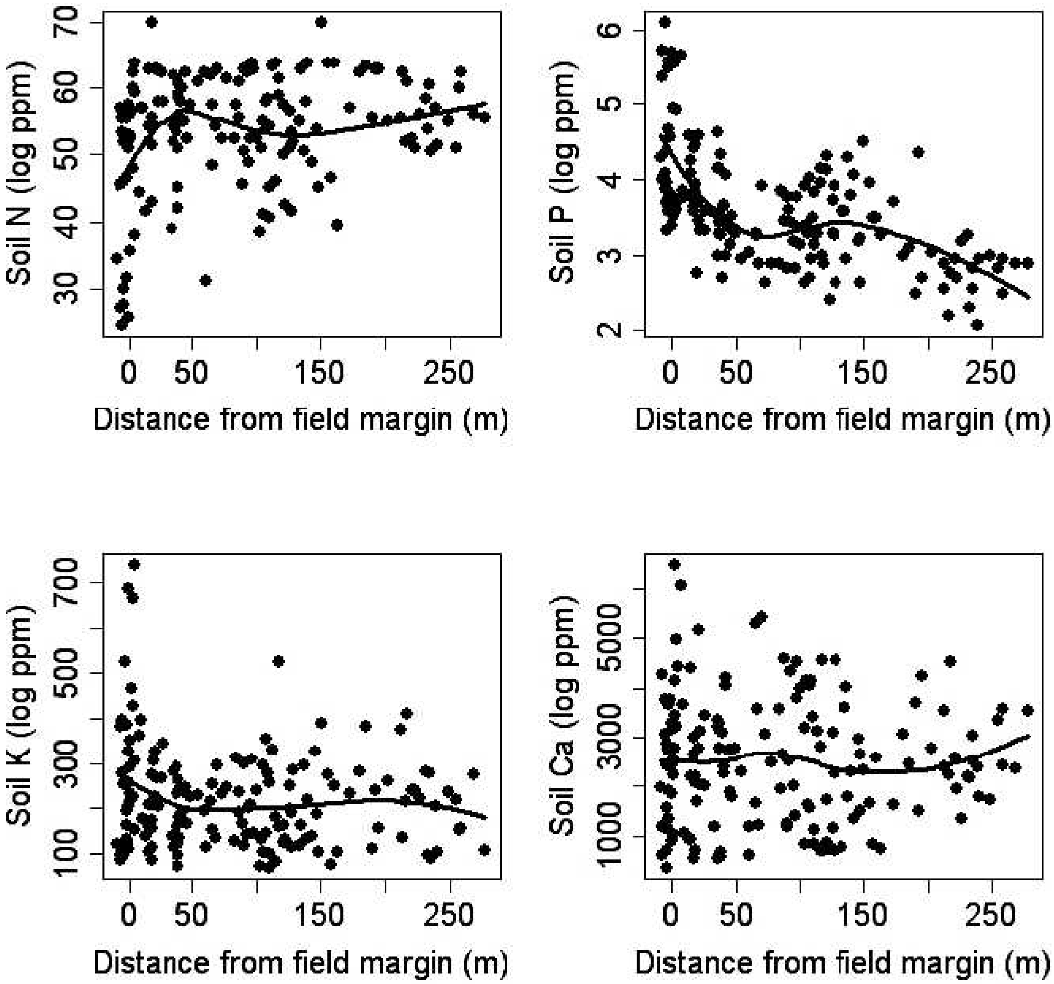

Figure 4. Distribution of selected soil nutrient concentrations (in log parts per million) in relation to distance from field margins. Lines are robust, locally-weighted regressions.

= 0.19 and 0.14, resp.). Availability of important soil nutrients was also directly related to field proximity (Figure 4). Soil phosphorus and potassium were generally more abundant near fields while soil nitrogen was more abundant further from fields. For the major soil nutrients nitrogen, phosphorus, potassium, and calcium, concentrations were much more variable in quadrats adjacent to fields than further away (Figure 4).

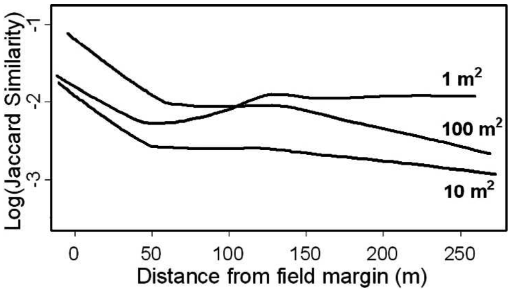

Figure 5. Decay of compositional similarity with reference to first (field-adjacent) quadrat along each transect, for three quadrat sizes. Lines are robust, locally-weighted regressions.

The rate of decay in compositional similarity with distance from field margins displayed three distinct regions (Figure 5). For the 100 and 10 m^2 quadrats, compositional similarity declined most steeply over the first 50 m moving away from the field boundary, exhibited little decay from 50 to 150 m, and then gradually declined again to the end of our transects, where many transects ended in close proximity to stream systems. Quadrats of 1 m^2 were less similar overall because they contained fewer species, but showed the same

Table 1. Indicator Species Analysis. Species were analyzed based on five distance from field boundary classes: 1 = within weedy margin; 2 = within 5 m of forest edge; 3 = 10–50 m into forest; 4 = 50–140 into forest; 5 = >140 m into forest. Indicator species are listed in order of group importance value and all listed were significantly associated with group as determined by Monte Carlo test ($P < 0.05$). Asterisks indicate exotic species

Weedy margin	Forest border	Forest, 10–50 m	Forest, 50–140 m	Forest, >140 m
Oxalis stricta	_*Trifolium repens_	_Botrychium virginianum_	_Quercus alba_	_Aristolochia serpentaria_
Conyza canadensis	_Toxicodendron radicans_	_Phryma leptostachya_	_Bignonia capreolata_	_Fraxinus americana_
Plantago virginica	_Rubus argutus_	_Vitis rotundifolia_	_Carpinus caroliniana_	_Euonymus americana_
Poa annua	_*Stellaria media_	_Cornus florida_	_Viburnum dentatum_	_Acer barbatum_
*Polygonum persicaria	_Campsis radicans_	_Liquidambar styraciflua_	_Desmodium rotundifolium_	_Betula nigra_
Pseudognaphalium obtusifolium	_Festuca_ sp.	_Parthenocissus quinquefolia_	_Maianthemum racemosum_	_Passiflora lutea_
*Rumex crispus	_*Lolium perenne_			_Carex typhina_
Solanum carolinianum	_*Medicago lupulina_			_Morus rubra_
Triodanis perfoliata	_*Rosa multiflora_			_Agrostis stolonifera_
*Veronica arvensis	_Actaea racemosa_			
Eupatorium capillifolium	_Geranium maculatum_			
*Sorghum halapense	_*Lonicera japonica_			
*Bromus communtatus				
*Lespedeza cuneata				
Allium canadense				
*Ranunculus parviflorus				
Geranium carolinianum				
Juncus tenuis				
Ambrosia artemisiifolia				
*Trifolium campestre				
*Vicia sativa				
*Triticum aestivum				
*Cynodon dactylon				
Ranunculus recurvatus				
Acalypha virginica				
*Taraxacum officinale				
Rhus copallina				
Hypericum hypericoides				
Solidago sp.				
*Dactylis glomerata				
*Ailanthus altissima				

rates of similarity decay with distance from field. Quadrats of 1 m^2, however, showed few trends overall (Figure 5).

We combined results from distance decay and ordination analyses to create groupings of species characteristic of certain distance classes. We defined five distance groups based on the three regions assigned by distance decay, plus two regions based on obvious structural transitions (herbaceous margin and the zone of transition from herbs to forest cover): 1) within herbaceous margin; 2) within 5 m of forest edge on either side; 3) 10–50 m into forest; 4) 50–140 into forest; 5) > 140 m into forest. Table 1 presents results of indicator species analysis for these groups; group importance was established by significant Monte Carlo tests. Species characteristic of the mown field margin were a relatively large group of annual and perennial forbs and grasses, including many exotic species. Forest edge species, including 5 m on both sides of the weedy border-forest interface, were a smaller set of some weedy, exotic herbaceous species (*Trifolium repens*, *Stellaria media*, *Lolium perenne*, *Medicago lupulina*) and native (*Toxicodendron radicans*, *Campsis radicans*) and exotic (*Lonicera japonica*, *Rosa multiflora*) vines. Indicator species in zones greater than 10 m from the forest edge were mostly common native canopy and understory tree species. These groups contained fewer distance-specific character species due to the greater

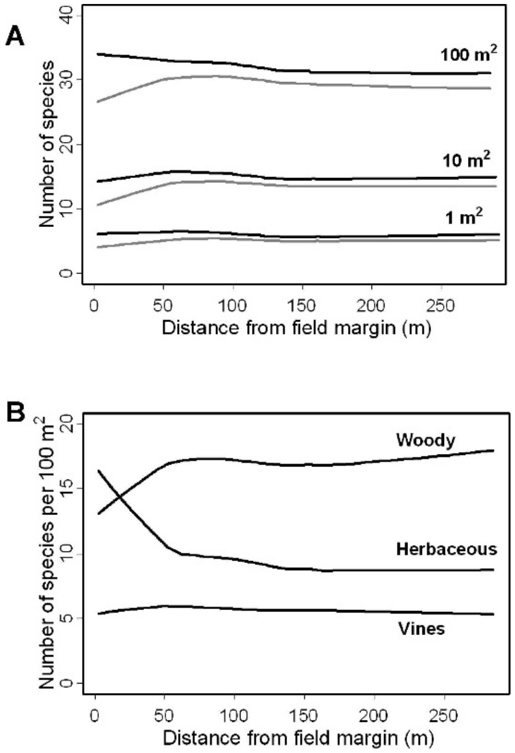

Figure 6. A. Species richness of plant communities of three quadrat sizes in relation to distance from field margin. Black lines are total species richness; grey lines are native species only. B. Richness of selected plant growth forms in $100\ m^2$ quadrats in relation to distance from field margin. Lines are robust locally weighted regressions.

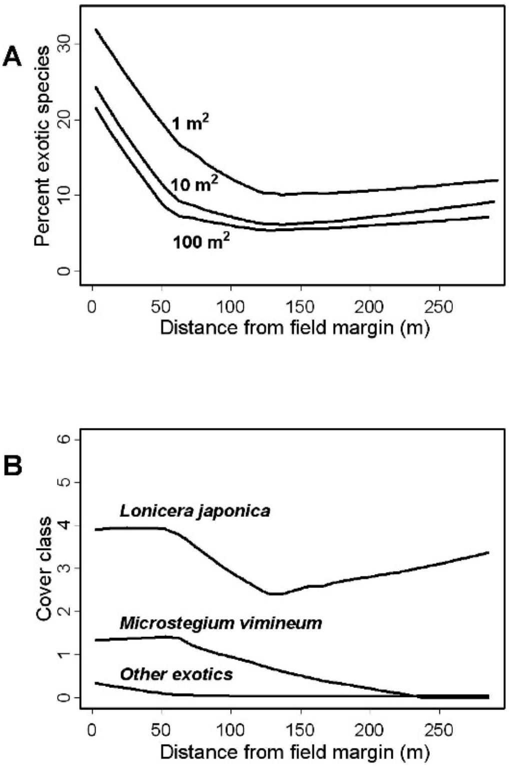

Figure 7. A. Percent exotics (of total richness) in 100, 10, and 1 m^2 quadrats in relation to distance from field margin. B. Exotic abundance in relation to distance from field margin. Cover classes are log-based indices of species horizontal percent cover in a $100\ m^2$ quadrat, and correspond to: (1) trace amount, (2) 0–1%, (3) 1–2%, (4) 2–5%, (5) 5–10%, and (6) 10–25%. Lines are robust locally-weighted regressions.

compositional variability of these communities, and also included several species associated with streams (e.g., *Betula nigra*, *Carpinus carolinana*, *Morus rubra*).

Species richness, measured as the number of plant species per quadrat, did not vary systematically with distance from field margin for any spatial scale (Figure 6A). There was an approximate doubling of total species richness with each 10-fold increase in area, which corresponds to a log-area:log-species richness scaling factor of 0.3. Restricting species richness to natives had minor effects on richness patterns except within the first 50 m of field borders (Figure 6A) where the importance of exotics is apparent, even down to 1 m^2 (Figure 7A).

Penetration of Exotic Species into Forest Interior

Exotic species were much more characteristic of field border communities and represent the strongest correlation with the distance from field axis of compositional variation ($r = 0.46$, $P < 0.001$, Figure 3A). We encountered 29 species listed as non-natives by United States Department of Agriculture PLANTS (USDA, NRCS 2006). Table 2 lists exotics by frequency of occurrence in $100\ m^2$ quadrats and distribution in relation to distance from field boundary. Only *Lonicera japonica* (present in 81% of quadrats) and *Microstegium vimineum* (35%) were encountered frequently enough to make generalizations about their patterns of abundance in relation to distance from field (Figure 7B). The $100\ m^2$ abundance of *L. japonica*, the most frequent and locally abundant exotic species in our survey, was on average constant until 70 m distant from fields, where its abundance declined before increasing again beyond 130 m (Figure 7B) with approach to streams. *M. vimineum* was generally less abundant than *L. japonica*, but

Table 2. Exotic species in relation to distribution of occurrence along transects. *%* is percent occupancy in 100 m^2 quadrats (N = 162), followed by minimum, median and maximum distance of occurrence in relation to field boundary in meters. A minimum distance of zero indicates the species was present in the first 5 × 20 m quadrat, immediately adjacent to the field boundary

Species	%	Min	Median	Max
Lonicera japonica	80.8	0	67.5	276
Microstegium vimineum	35.1	0	45	165
Lonicera fragrantissima	20.9	7.5	92.3	285
Stellaria media	12.3	0	0	45
Ligustrum sinense	11.7	0	45	265
Bromus commutatus	8.6	0	7.5	67.5
Trifolium repens	8.6	0	0	7.5
Lolium perenne	8	0	7.5	25
Cynodon dactylon	7.4	0	0	7.5
Polygonum persicaria	6.1	0	7.5	25
Rumex crispus	4.9	0	0	7.5
Lespedeza cuneata	4.9	0	5	7.5
Taraxacum officinale	4.9	0	5	211.5
Rosa multiflora	4.3	7.5	98.5	245
Trifolium campestre	4.3	0	0	7.5
Bromus japonicus	4.3	0	45	155
Veronica arvensis	3.7	0	5	7.5
Bromus catharticus	3.7	0	16.3	45
Medicago lupulina	3.7	0	0	7.5
Ailanthus altissima	3.7	0	7.5	7.5
Vicia sativa	3.7	0	5	7.5
Dactylis glomerata	3.7	0	0	7.5
Sorghum halapense	3	0	0	7.5
Ranunculus parviflorus	3	0	0	7.5
Duchesnea indica	2.4	0	61.3	153
Triticum aestivum	2.4	0	5	7.5
Rumex acetosella	2.4	0	0	7.5
Wisteria sinensis	2.4	7.5	35	265
Verbascum thapsus	2.4	0	13.8	45

displayed a similar decline in abundance with distance into the forest, though it lacked the upturn with stream proximity displayed by *L. japonica*. Most other exotic species were restricted to the mown field margins within ca. 20 m of field edges, with the exceptions of *Rosa multiflora*, *Ligustrum sinense*, *Lonicera fragrantissima*, *Wisteria sinensis*, *Taraxacum officinale*, *Duchesnea indica*, and *Bromus japonica* (Table 2).

As a percentage of all species, exotic species richness in 100, 10, and 1 m^2 declined with field distance up to 130 m (Figure 7A). We detected a slight increase in the representation of exotics after 130 m, due in part to the increasing frequency of *Lonicera japonica* at this distance and possibly the increasing influence of streamside vegetation for some transects. Overall, exotic richness was proportionally higher in smaller quadrats, although differences between 100 and 10 m^2 were small (Figure 7A).

Exotic species richness was strongly correlated with the availability of soil nutrients, even after accounting for their covariance with distance from field. A simple multiple regression approach using Type I sums of squares could explain 39% of the variance in exotic species richness in 100 m^2 quadrats by using the independent variables of field distance, soil phosporus, nitrogen, potassium and calcium (in that order in the stepwise regression model), each of which significantly predicted exotic richness.

DISCUSSION Regularly mown plant communities immediately adjacent to cornfields in North Carolina appear to be a relatively distinct and predictable set of a mixture of annual and perennial forbs and grasses, particularly within the Piedmont region. Such consistency in community composition closest to cornfields was unexpected and contrasts with other studies reporting greater variance in community properties near edge habitats (Ranney et al. 1981, Chen et al. 1992, Fraver 1994). Predictability of edge communities in our study could to be due to a regular mowing regime or moisture and temperature regimes distinct from those found in the forest interior (Williams-Linera 1990, Chen et al. 1993, Matlack 1994).

Although forest edge habitats are often perceived as ''meeting grounds'' for species of different habitat affinities, and thus areas of greater species richness (Gysel 1951, Brothers and Spingarn 1992, Fraver 1994, but see Matlack 1994), we found species richness in quadrats of all sizes to be relatively unaffected by field proximity. Boutin and Jobin (1998) obtained similar results from field-perpendicular transects in woodlot edges of agricultural systems in Quebec. As expected, the composition of natives vs. exotics and woody vs. herbaceous species was somewhat dependent on field distance, especially within the first 100 m. Exotic species were better represented in smaller quadrats, which would occur if exotic individuals were on average more regularly distributed than native individuals. Overall, the scaling of species richness with area was consistent with that found in an array of other habitat types at fine spatial scales (Fridley et al. 2005).

We observed high rates of spatial turnover in species composition up to around 50 m into forest interiors, followed by relatively stable communities that exhibited further turnover along transects beyond 150 m. The species turnover located toward the extreme ends of transects were probably influenced by proximity of those plots to stream systems. Our observations are strikingly similar to those of Fraver (1994), who documented regular change in forest community composition along edge-to-interior gradients in mixed hardwood stands in North Carolina up to 50 m for south-facing edges and 20 m for north-facing edges. However, in contrast to Fraver (1994) and other edge effects studies (e.g., Wales 1972), we detected no significant influence of forest edge orientation (predominant north or south aspect) on rates of species turnover along field proximity gradients or the extent to which certain edge factors (e.g., exotic abundance) penetrate into surrounding forests (data not shown), although we note our study was not designed to examine transect orientation effects. The 50-m penetration threshold of edge effects on vegetation composition is also remarkably consistent with the review of Harper et al. (2005), who found a mean distance-of-edge influence of 50 m for across forest edge studies from both temperate and topical locations, although the variance was large.

Soil nutrients showed a variety of patterns related to field distance. Of particular interest is the opposing patterns shown for inorganic nitrogen and phosphorus—the two nutrients most heavily input into agricultural systems. We found that phosphorus decreased with increasing distance from field, which is constant with the nutrient's relative immobility in soil. On the other hand, soil nitrogen concentration increased with increasing distance from fields: this nutrient is water soluble and so it may be migrating away from fields into surrounding intact communities. Soil nitrogen may also have displayed higher concentrations at the largest distances in some transects because of stream proximity or the greater organic matter content of forest soils.

Soil nutrients did not appear to be a major factor influencing vegetation composition. We found high variability in all nutrients in plots adjacent to fields, perhaps the consequence of different fertilization regimes among the fields we surveyed. Given such variability in soil nutrient availability near fields, it is surprising that field margin communities are relatively predictable. This suggests that, for most species, nutrient availability is not as important in determining community membership as the regular mowing and compacting disturbance regime of most cornfield borders in the North Carolina piedmont. In contrast, Piessens et al. (2006) found edge effects on vegetation composition in heathlands were most associated with cropland fertilizer runoff. Nonetheless, we were unable to determine the degree to which the gradient in exotic richness was driven by a mass effect of propagule rain from the forest edge versus the somewhat increased soil phosphorus concentration near the field boundary.

Closest to the fields we found abundant small-stature native and exotic herbaceous annuals and perennials followed by a strip of native and exotic vines. Beyond 50 m from the field margin, communities consisted primarily of native woody species. Exotic species were concentrated very close to field boundaries, and most of these species were not pernicious invaders that competitively displace native species. Edge habitats such as those associated with agriculture or riparian areas are well known source areas for the spread of exotic species (Ambrose and Bratton 1990, Brothers and Spingarn 1992, Fraver 1994, Merriam 2003), but our study suggests that in an agricultural landscape exotics are often confined to edge of field habitats, similar to the results of Honnay et al. (2002).

In agricultural edge habitats in the Roanoke River Basin of North Carolina, Fraver (1994) found little penetration of exotic species into the interior of mixed hardwood forests, with the exception of *Lonicera japonica*. Similarly, we found very few exotic invasive species able to substantially penetrate forest communities surrounding agricultural fields. Important exceptions were *L. japonica* and *Microstegium vimimeum*, both species of special concern to natural areas. *L. japonica* is a partially shade-tolerant vine that is capable of persisting under heavy canopies, although it is often associated with disturbance for propagation and establishment and appears to spread quickly through edge habitats in North Carolina (Merriam 2003). Vegetation studies in the Duke Forest region of the North Carolina Piedmont have shown a recent decline in the abundance of *L. japonica* around field borders (R.K. Peet, unpubl.), possibly due to excessive deer browse. This may explain its decreasing abundance in forested areas ca. 100 m from fields in our study. *Microstegium vimineum* is rapidly spreading into southeastern ecosystems via riparian corridors and may pose a threat to other herb-layer species in mesic habitats. Another invasive exotic, *Rosa multiflora*, while found in a variety of sites including those with dense canopies, is typically associated with disturbance and high light levels and is more abundant in the mountains of North Carolina (Merriam 2003).

Our study is one of the first to document vegetation patterns in agricultural landscapes of the southeastern United States, and mirrors other studies demonstrating strong influences of agricultural management practices and land-use histories on surrounding plant communities (Fraver 1994, Burel et al. 1998, de Snoo and van der Poll 1999, Le Coeur et al. 2002, Marshall and Moonen 2002, Schippers and Joenje 2002). Future studies should incorporate estimates of other important environmental and management factors that determine the structure of plant communities specific to agricultural landscapes, such as mowing, increased soil phosphorus, and soil compaction regimes, as well as the landscape histories and configuration of the surrounding communities.

ACKNOWLEDGMENTS We gratefully acknowledge field and laboratory assistance from C. Bernhard, A. Clements, A. Dollander, E. Fridley, J. Gramling, T. Jobe, M. Kudla, J. Long, J. Mayer, and C. Zakas. Logistical support was provided by T. Wentworth of North Carolina State University and the North Carolina Department of Agriculture and Consumer Services, including Agricultural Research Station superintendents D. Askew, Sandy Barnes, Steve Barnes, C. Bogle, R. Coltrain, F. Smith, and T. Marshall. We thank J. Gonzalez-Valero for advice and discussion. This study was supported by a grant from the Collaborative Funding Assistance Program of the North Carolina Biotechnology Center.

LITERATURE CITED

Ambrose, J.P. and S.P. Bratton. 1990. Trends in landscape heterogeneity along the borders of Great Smoky Mountains National Park. Conserv. Biol. 4:135–143.

Boutin, C. and B. Jobin. 1998. Intensity of agricultural practices and effects on adjacent habitats. Ecol. Appl. 8:544–557.

Brothers, T.S. and A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conserv. Biol. 6:91–100.

Burel, F., J. Baudry, A. Butet, P. Clergeau, Y. Delettre, D. Le Coeur, F. Dubs, N. Morvan, G. Paillet, S. Petit, C. Thenail, E. Brunel, and J.-C. Lefeuvre. 1998. Comparative biodiversity along a gradient of agricultural landscapes. Acta Oecol. 19:47–60.

Chen, J., J.F. Franklin, and T.A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. Ecol. Appl. 2:387–396.

Chen, J., J.F. Franklin, and T.A. Spies. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. Agric. For. Meteorol. 63:219–237.

Cleveland, W.S. 1979. Robust locally weighted regression and smoothing scatterplots. J. Amer. Stat. Assoc. 74:829–836.

de Snoo, G.R. and R.J. van der Poll. 1999. Effect of herbicide drift on adjacent boundary vegetation. Agric. Ecosyst. Environ. 73:1–6.

Dufrene, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67:345–366.

Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River Basin, North Carolina. Conserv. Biol. 8: 822–832.

Fridley, J.D., R.K. Peet, P.S. White, and T.R. Wentworth. 2005. Connecting fine- and broad-scale patterns of species diversity: species-area relationships of Southeastern U.S. flora. Ecology 86:1172–1177.

Gysel, W.L. 1951. Borders and openings of beech-maple woodlands in southern Michigan. J. For. 49:13–19.

Harper, K.A., S.E. MacDonald, P.J. Burton, J. Chen, K.D. Brosofske, S.C. Saunders, E.S. Euskirchen, D. Roberts, M.S. Jaiteh, and P.-A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conserv. Biol. 19:768–782.

Honnay, O., K. Verheyen, and M. Hermy. 2002. Permeability of ancient forest edges for weedy plant species invasion. For. Ecol. Manage. 161:109–122.

Kleijn, D., W. Joenje, D. Le Coeur, and E.J.P. Marshall. 1998. Similarities in vegetation development of newly established herbaceous strips along contrasting European field boundaries. Agric. Ecosyst. Environ. 68:13–26.

Kruskal, J.B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29:115–129.

Le Coeur, D., J. Baudry, and F. Burel. 1997. Field margins plant assemblages: variation partitioning between local and landscape factors. Landscape Urban Planning 37:57–71.

Le Coeur, D., J. Baudry, F. Burel, and C. Thenail. 2002. Why and how we should study field boundary biodiversity in an agrarian landscape context. Agric. Ecosyst. Environ. 89:23–40.

Legendre, P. and L. Legendre. 1998. Numerical Ecology, 2nd English ed. Elsevier, New York, New York.

Ma, M., S. Tarmi, and J. Helenius. 2002. Revisiting the species–area relationship in a semi-natural habitat: floral richness in agricultural buffer zones in Finland. Agric. Ecosyst. Environ. 89:137–148.

Mantel, N. 1967. The detection of disease clustering and generalized regression approach. Cancer Res. 27:209–220.

Marshall, E.J.P. 1987. Herbicide effects on the flora of arable field boundaries. p. 291–298. *In:* Proceedings of the 1987 British Crop Protection Conference—Weeds. British Crop Protection Council, Thornton Heath, Surrey, United Kingdom.

Marshall, E.J.P. and A.C. Moonen. 2002. Field margins in northern Europe: their functions and interactions with agriculture. Agric. Ecosyst. Environ. 89:5–21.

Marvier, M. 2001. Ecology of transgenic crops. Amer. Scientist 89:160–164.

Matlack, G.R. 1994. Vegetation dynamics of the forest edge—trends in space and successional time. J. Ecol. 82:113–123.

McCune, B. and J.B. Grace. 2003. Analysis of ecological communities. MjM Software, Gleneden Beach, Oregon.

McCune, B. and M.J. Mefford. 1999. PC-ORD: Multivariate analysis of ecological data, version 4.20. MjM Software, Gleneden Beach, Oregon.

Mehlich, A. 1984. Mehlich 3 soil test extraction modification of Mehlich 2 extractant. Comm. Soil Sci. Plant Anal. 15:1409–1416.

Merriam, R.W. 2003. The abundance, distribution and edge associations of six non-indigenous, harmful plants across North Carolina. J. Torrey Bot. Soc. 130:283–291.

Moonen, A.C. and E.J.P. Marshall. 2001. The influence of sown margin strips, management and boundary structure on herbaceous field margin vegetation in two neighbouring farms in southern England. Agric. Ecosyst. Environ. 86:187–202.

Nekola, J.C. and P.S. White. 1999. The distance decay of similarity in biogeography and ecology. J Biogeogr. 26:867–878.

Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, and M.H.H. Stevens. 2007. VEGAN: Community ecology package (R package version 1.8-7). http://vegan.r-forge.r-project.org/

Peet, R.K., T.R. Wentworth, and P.S. White. 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63:262–274.

Piessens, K., O. Honnay, R. Devlaeminck, and M. Hermy. 2006. Biotic and abiotic edge effects in highly fragmented heathlands adjacent to cropland and forest. Agric. Ecosyst. Environ. 114:335–342.

Ranney, J.W., M.C. Bruner, and J.B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. p. 67–95. *In:* Burgess, R.L. and D.M. Sharp (eds.). Forest island dynamics in a man-dominated landscape. Springer-Verlag, New York, New York.

Rew, L.J., A.J. Theaker, and R.J. Froud-Williams. 1992. Nitrogen fertilizer misplacement and field boundaries. Aspects Appl. Biol. 30: Nitrate and farming systems.

Schippers, P. and W. Joenje. 2002. Modelling the effect of fertilizer, mowing, disturbance and width on the biodiversity of plant communities of field boundaries. Agric. Ecosyst. Environ. 93:351–365.

State Climate Office of North Carolina. 2006. Raleigh State University climate normals. North Carolina State University, Raleigh, North Carolina.

United States Department of Agriculture, Natural Resources Conservation Service. 2006. The PLANTS Database, 6 March 2006 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, Louisiana.

Wales, B. 1972. Vegetation analysis of north and south edges in a mature oak-hickory forest. Ecol. Monogr. 42:451–471.

Weathers, K.C., M.L. Cadenasso, and S.T.A. Pickett. 2001. Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. Conserv. Biol. 15:1506–1514.

Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. J. Ecol. 78:356–37.