Forest herb colonization of postagricultural forests in central New York State, USA

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Summary

1 The recovery of forest vegetation following abandonment of agriculture was followed by surveying forest herbs in central New York State at 25 sites where postagricultural forest occurred directly adjacent to old-woods (forest that has never been ploughed).
2 The abundance, richness and diversity of 50 forest herbs were on average lower in postagricultural forests than in old-woods.
3 Thirty of 39 forest herbs that were found in at least four stands were less frequent (number of plots present out of 60) in postagricultural forests than in old-woods. Three species (*Aster divaricatus*, *Dryopteris intermedia* and *Polystichum acrostichoides*) had significantly higher frequency in old-woods, while none was significantly more common in postagricultural forests.
4 Although differences among species in their frequency in the two forest types were not strongly related to dispersal mode, species with rapid clonal expansion were significantly more frequent in postagricultural stands.
5 Several species that were less frequent in postagricultural forests than in old-woods showed decreases in density in postagricultural forests with increasing distance from the adjacent old-woods.

Key-words: colonization, dispersal limitation, forest herb diversity, habitat limitation, human disturbance

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Introduction

Human disturbance has become an increasingly important factor influencing the distribution of individual species, the composition of ecological communities and the biogeochemistry of ecosystems. Despite the general trend towards increased activity, some regions are currently recovering from the discontinuation of human disturbances and thus provide the opportunity to study the long-term consequences of human activities. Many areas within the temperate deciduous forest biome are now recovering from a particularly severe form of human disturbance, the conversion of forest to arable agricultural land. This practice is fundamentally different from many forms of natural disturbance, such as fire and windthrow, because the clearing of trees and repeated ploughing of the soil eliminate both the forest plants and any residual seeds and sprouts of forest species. As a result, the recovery of forest communities on abandoned cropland depends upon colonization from outside seed sources. In this study, we focus on the recovery of native forest herb diversity in postagricultural forests in central New York State. While there have been many studies of the processes of old-field succession and invasion of abandoned farmland by trees (e.g. Oosting 1942; Bard 1952; Bazzaz 1968; Buell *et al*. 1971), patterns of recolonization by forest herbs are much less well-understood.

In many areas of eastern USA, most of the forest was cleared for agriculture during the eighteenth and nineteenth centuries. In some areas of New England and New York, over 80% of the original forest was cleared, primarily for farmland, by the late 1800s (Glitzenstein *et al*. 1990; Foster 1992; Smith *et al*. 1993). Over the past century, much of the farmland has been abandoned, due to a decline in agriculture. While many areas have returned to forest, there is evidence that some native forest plant species, particularly herbs, are rare in temperate postagricultural stands, both in North America and Europe (e.g. Rackham 1980; Peterken & Game 1984; Matlack 1994a; Brunet & von Oheimb 1998).

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Studies comparing forests on former farmland with those that were never cleared for agriculture have consistently revealed differences in plant species composition and diversity (Nyland *et al.* 1986; Whitney & Foster 1988; Glitzenstein *et al.* 1990). For example, in central New England, a number of herb and shrub species were associated with either primary (never cleared for agriculture) or secondary (postagricultural) forests (Whitney & Foster 1988). Similarly, in eastern New York State, Glitzenstein *et al.* (1990) found three distinct forest communities on sites that differed in land-use history: former woodlots, former pastures and former cultivated fields. In addition, there were fewer forest herb species in postagricultural forests than in older forests in Pennsylvania and Delaware, USA (Matlack 1994a), in Lincolnshire, UK (Peterken & Game 1984), in north-western Germany (Wulf 1997) and in southern Poland (Dzwonko & Loster 1988). Bossuyt *et al.* (1999) did not find differences in overall herb abundance or diversity between recent and ancient forests, but they did find that the herb species associated with ancient forests were particularly slow to colonize recent forests.

One difficulty with interpreting results from such studies is that factors other than land-use history could vary between forest types, so species differences between postagricultural and other forests could reflect underlying differences in the environment, such as soils or topography, rather than the effects of agriculture. This is particularly true if the selection of agricultural sites by settlers was biased toward particular environments when the land was originally cleared. Several studies used postagricultural forest directly adjacent to older stands, which should help control for some of the likely environmental differences, and found that forest herbs often decreased with distance from older forest (Matlack 1994a; Brunet & von Oheimb 1998; Bossuyt *et al.* 1999).

In the present study, we present results from an extensive survey of forest herbs in Tompkins County, in the Finger Lakes region of central New York State. Prior to European settlement in the 1790s, this region was dominated by northern mixed hardwood forest (Braun 1950; Marks & Gardescu 1992). By 1900, over 80% of the county had been cleared, and today over 50% of the county is in forest, roughly half of which is postagricultural (Smith *et al.* 1993). We sampled forest herb abundance in 25 sites with paired stands, where relatively mature postagricultural forests were contiguous with old-woods (forest that has never been ploughed for agriculture). Forest herb data from the paired postagricultural and older forest stands were used to address several questions. (i) What are the differences in forest herb abundance and diversity between these two forest types? Because forest species will be present in formerly cultivated sites only when they have colonized from elsewhere, we expect forest herbs to be less abundant and less diverse in postagricultural forest. (ii) Are there certain species that are particularly rare or abundant in postagricultural forests? Knowing which species are successful at establishing in such stands may suggest what processes affect the colonization of these forests. (iii) Does the abundance of herb species decline with an increase in distance from the older, less disturbed forest? The pattern of species abundance along this gradient may suggest factors affecting the distribution of these species (e.g. a decrease in abundance with distance from older forest would be consistent with limited seed movement).

Methods

SITES

Each of the 25 sites in Tompkins County, New York State, had adjacent stands of two forest types. Postagricultural forests were defined as mature forest stands with closed canopies that had developed on land abandoned from agriculture between roughly 1900 and 1930 (based on aerial photos from 1936 to 1938). All the stands showed evidence of being ploughed, based on field features such as an absence of treefall pits and mounds and the presence of stone piles or fences (Marks 1994). The adjacent old-woods were mesophytic forests that had never been cleared for agriculture. Although most old-woods had been selectively logged at some point, none of them showed evidence of logging or other major disturbance within the 10 years prior to the survey in 1994. Stand characteristics at the 25 sites are given in Appendix 1, in the *Journal of Ecology* archive on the World Wide Web (http://www.demon.co.uk/bes/journals), and in Singleton (1998).

In 23 of the 25 old-woods, dominant canopy species included *Acer saccharum* and/or *Fagus grandifolia* (nomenclature follows Gleason & Cronquist 1991). Of the remaining two old-woods, one was dominated by *Tsuga canadensis* and *Quercus rubra*, and the other by *Tilia americana*. Dominant canopy species of the postagricultural forests included *Acer rubrum* and/or *Fraxinus americana*, except for one stand dominated by *Prunus serotina* and *Robinia pseudoacacia*. Soils were Inceptisols and Alfisols, primarily silt loams derived from glacial till (USDA 1965).

All field sites conformed to a number of additional criteria chosen to minimize variation between the two forest types at each site in factors other than agricultural history. Postagricultural forest and old-woods at a site had to (i) be directly adjacent, (ii) be similar in slope and aspect, (iii) have closed tree canopies at the time of the survey, (iv) be of sufficient size and suitable shape to allow placement of sampling transects (discussed later) at least 50 m from open field edges and, in postagricultural stands, at least 50 m from potential sources of colonization (woods or hedgerows), other than the adjacent old-woods, and (v) whenever possible, be on soil of the same type (USDA 1965). This last criterion was fulfilled at 17 of the 25 sites, while at two others the same soil type ran through parts of both forest types. We thereby minimized differences between forest types that could have resulted from bias when settlers originally selected forested areas for agricultural clearance.

Table 1 The 50 forest herb taxa from Survey I (nomenclature as in Gleason & Cronquist 1991). Categories of clonal expansion are described in Methods: Survey I. Parentheses indicate 11 species excluded from species-level tests; the other 39 each occurred in a minimum of four stands.

Species	Dispersal mode	Clonal expansion
Actaea alba and *A. rubra*	Ingested	0
Allium tricoccum	None?	1
(*Anemonella thalictroides*)	None?	1?
Aralia nudicaulis	Ingested	3
*Arisaema triphyllum**	Ingested	1
Asarum canadense	Ant	2
*Aster acuminatus**	Wind	3
*Aster divaricatus**	Wind	2
(*Aster macrophyllus*)	Wind	2
*Caulophyllum thalictroides**	Ingested	1
Circaea lutetiana and *C. alpina*	Adhesive	3
Dryopteris carthusiana	Spore	2
Dryopteris intermedia	Spore	2
Dryopteris marginalis	Spore	2
Erythronium americanum	Ant	1
(*Galium circaezans* and *G. lanceolatum*)	Ant and none?	0?
Geranium maculatum	Ballistic	0
(*Geranium robertianum*)	Adhesive	0
*Hepatica acutiloba**	Ant	1
(*Hepatica americana*)	Ant	1
(*Hydrophyllum canadense*)	None?	2
(*Hydrophyllum virginianum*)	None?	2
(*Impatiens capensis* and *I. pallida*)	Ballistic	0
(*Lycopodium clavatum*)	Spore	3
*Lycopodium digitatum**	Spore	3
Lycopodium lucidulum	Spore	2
Lycopodium obscurum	Spore	3
*Maianthemum canadense**	Ingested	3
*Medeola virginiana**	Ingested	2
Mitchella repens	Ingested	3
(*Mitella diphylla* and *Tiarella cordifolia*)	None?	2
(*Osmorhiza claytonii* and *O. longistylis*)	Adhesive	0
Oxalis acetosella	Ballistic	3
Podophyllum peltatum	Ingested	2
Polygonatum pubescens	Ingested	2
Polystichum acrostichoides	Spore	2
Prenanthes altissima and *P. alba**	Wind	0
Smilacina racemosa	Ingested	2
*Solidago caesia**	Wind	1
Solidago flexicaulis	Wind	2
Thalictrum dioicum	None?	?
Thelypteris noveboracensis	Spore	2
*Trientalis borealis**	None?	3
Trillium erectum	Ingested/ant	2
Trillium grandiflorum	Ant	1
Uvularia perfoliata	Ant	2
*Uvularia sessilifolia**	Ingested	2
Viola rotundifolia	Ant?	1
Viola spp. (not stemmed)	Ant and ballistic	1
Viola spp. (with stems)	Ant and ballistic	1

*The 12 species also included in Survey II.

It is likely that many of the forest stands in this survey differed in land-use history as a consequence of historical property boundaries and differences in land ownership rather than underlying environmental differences.

SPECIES

We limited the plant surveys to herbaceous species that are common in mesophytic forests in the Finger Lakes Region of New York State (C.L. Mohler and P.L. Marks, unpublished data; Wiegand & Eames 1926; Corbit *et al*. 1999). Fifty of these taxa were found in the 25 sites (Table 1); for simplicity, taxa are referred to as species throughout the paper. Spring ephemerals that senesce particularly early in the growing season were excluded because stands were surveyed in the summer. Sedges and grasses were excluded in order to simplify field identification (they were also relatively rare at the study sites).

SURVEY I

In June–August 1994, forest herbs were sampled in the paired stands at all 25 sites. Within each forest stand (postagricultural or old-woods) at a site, the presence of each forest herb species was recorded for 60 plots along three parallel transects at 25 m, 40 m and 55 m from the edge between the two forest types. Each of the three transects was 49 m long, with 20 plots (each 1.5 m × 2 m) separated by 1 m intervals.

We tested whether herb abundance and diversity differed between the two forest types. Total abundance was calculated for each forest type at a given site by summing the occurrences (presence in sample plot) of all 50 forest herb species in the 60 plots. Two measures of species richness were used: forest level and plot level. Forest level richness was calculated as the total number of species in the sample plots within a stand. Plot level richness was the mean number of species in the 60 plots. The Shannon–Wiener index (Kent & Coker 1996) was used to estimate species diversity.

Species-level tests were done for 39 of the 50 species (Table 1), which were each found in at least four stands of the 50 forests sampled. We excluded eight that were in only one to three stands, the two annuals (*Geranium robertianum* and *Impatiens*), and *Mitella–Tiarella*, as those two genera as non-flowering plants could not be differentiated. We tested whether individual species were associated with a particular forest type (i) at the plot level, by comparing the mean frequency of each of the species (number of occurrences out of 60 plots) in the two forest types averaged over all sites, and (ii) at the stand level, by comparing the presence of each species in both forest types at each of the paired stands at the 25 sites.

For the same 39 species, relative frequency in the two forest types was used to explore whether dispersal mode or the potential for clonal growth affects their ability to colonize postagricultural forests. Dispersal modes (Table 1) were obtained from a number of sources (Wiegand & Eames 1926; Gleason 1952; Harper *et al.* 1970; Culver & Beattie 1978; Beattie & Culver 1981; Handel *et al.* 1981; Bierzychudek 1982; Sorensen 1986; Grime *et al.* 1988; Gleason & Cronquist 1991; Matlack 1994a; Weiblen & Thomson 1995; Cain *et al.* 1998; Corbit *et al.* 1999). For a stand-level test of dispersal mode, we used a Kruskal–Wallis test of relative frequency (percentage of stands in which each species occurred that was postagricultural) with five dispersal categories: wind, spore, ant (including two species listed in Table 1 as 'ant and ballistic'), animal (ingested, 'ingested/ant' and one 'adhesive' species); and short-distance (two ballistic species and three 'none?'). For dispersal modes with enough species to test (ant, spore and ingested), we also compared relative plot-level frequency in the two forest types using Wilcoxon signed-ranks tests with paired stands, alpha-corrected for multiple comparisons as in Rice 1989. Plot-level frequency was also used for a test for association between clonal growth

and forest type, with a Kruskal–Wallis test for row and column independence (exact probabilities, as in Mehta & Patel 1992) for a 4 × 5 contingency table with four categories of clonal expansion and five categories of each species' difference in mean plot frequency between forest types, excluding one species with unknown clonal habit (*Thalictrum*). Categories of clonal expansion (Table 1), based on Matlack (1994a) and personal observations, were: 0 = not clonal, 1 = clonal at the plant base, 2 = annual clonal expansion up to a horizontal distance equivalent to the plant's height, 3 = longer expansion distances. Our categorization differed from that of Matlack (1994a) for only one species (*Allium tricoccum*).

SURVEY II

In a second survey, we sampled forest herbs along transects perpendicular, rather than parallel, to the boundary between the two forest types. We recorded the stem density of each species, thus allowing analyses of differences in densities of individual species between the two forest types at a given site, as well as of patterns of density in postagricultural stands with distance from adjacent old-woods. In June–July 1996, the paired stands were surveyed at nine sites of the 25 that had a relatively high diversity of herb species and were readily accessible. Twelve species (marked with an asterisk in Table 1) were chosen to represent a variety of dispersal modes, and to include species associated with each forest type, as well as those for which Survey I showed no clear association.

In each forest type, we recorded the stem density of each of the 12 species in 1-m^2 plots at 1-m intervals along each of four transects perpendicular to the boundary between the paired stands. Areas within postagricultural forests that were closer to outside sources of colonization (such as old-hedgerows or additional old-woods) than to the adjacent old-woods, were not sampled. As a result, transects extended different distances into the postagricultural forests: 50 m at five sites, 70 m at three, and 100 m at one, and these distances were also used for the half of the transect extending into the adjacent old-woods. For each species, we tested for differences in density between forest types with paired comparisons, using mean densities from the four parallel transects for the plots within 50 m of the common boundary, so all nine sites could be included.

We estimated colonization distance into postagricultural forests for each of the 12 species as the furthest point at which stem density was half its peak value (as in Matlack 1994a). To test for declines with distance from the boundary between forest types, we used a negative logarithmic model to regress mean density at each 1 m interval (from the four plots on the parallel transects) on distance, including data from 50 m, 70 m and 100 m transects. Species present in fewer than 10 plots in a forest type were not tested.

Table 2 Measures of forest herb abundance, richness and diversity in the two forest types (*n* = 25 for each forest type, sampled with 60 plots each 1.5 m × 2 m). Total abundance in each stand was calculated by summing the plot occurrences of each of the 50 forest herb species. Significances are from paired two-tailed *t*-tests, corrected for multiple comparisons

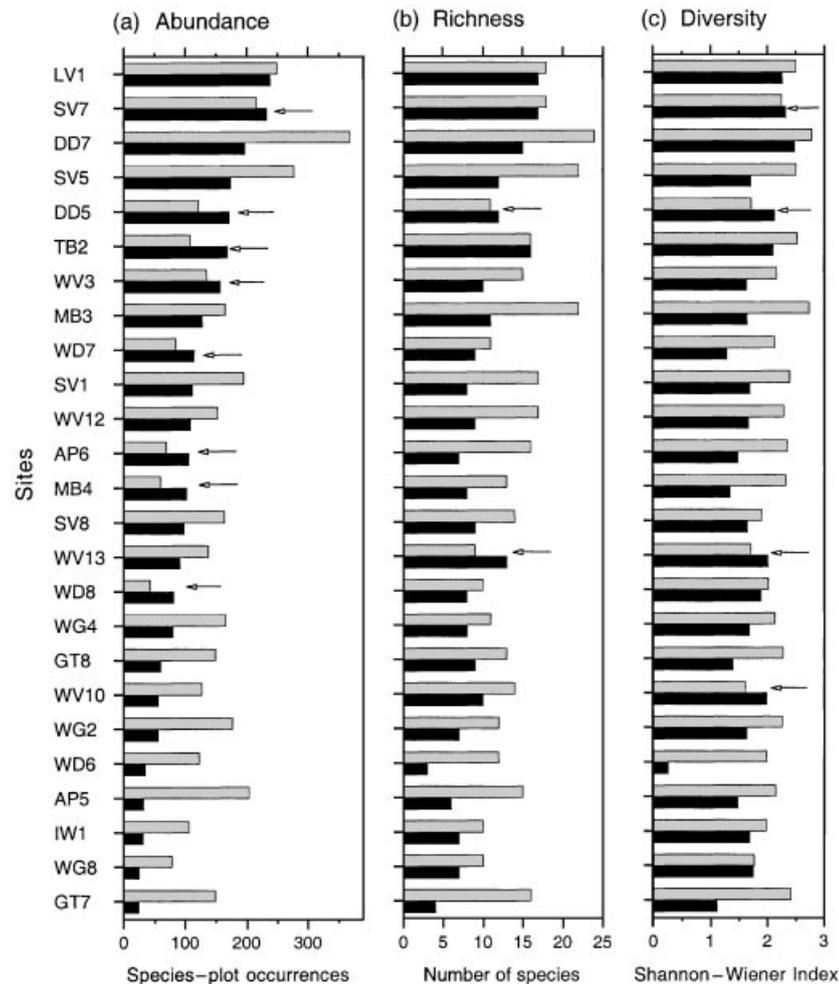|	Old-woods		Postagricultural forest		
	Mean	SE	Mean	SE	*P*-value
Total abundance (no. occurrences per stand)	153	15	107	13	< 0.01
Stand-level richness (no. species per stand)	14.6	0.8	9.7	0.7	< 0.001
Plot-level richness (mean no. species per plot)	2.7	0.3	1.9	0.2	< 0.01
Species diversity (Shannon–Wiener index)	2.2	0.1	1.7	0.1	< 0.001
Contribution of most abundant species to total abundance (%)	24	2	38	3	< 0.001

Fig. 1 Abundance and diversity of 50 forest herb taxa in old-woods (shaded bars) and adjacent postagricultural stands (black bars) at 25 sites, shown ranked by decreasing order of abundance in postagricultural forests. Arrows indicate sites where the value in the postagricultural forest is greater than in the adjacent old-woods. (a) Forest herb abundance, the summed occurrences of each species in the 60 plots (3 m² each) per stand. (b) Species richness, the total number of forest herbs. (c) Forest herb species diversity for the stand; the Shannon–Wiener Index. Stand characteristics at the 25 sites are given in Appendix 1 (WWW).

Results

SURVEY I

Community patterns

Forest herb abundance, richness and diversity were all greater in old-woods than in postagricultural forests (Table 2). The total abundance of forest herbs was roughly 50% greater in old-woods than in postagricultural forests, and the difference in mean abundance between the two forest types was statistically significant (Table 2). Old-woods had greater herb abundance (all species combined) than corresponding postagricultural forests at 17 of 25 individual sites (Fig. 1a), frequently (nine sites) more than twice as high.

Similarly, species richness at the level of both forests and plots within forests was significantly greater in
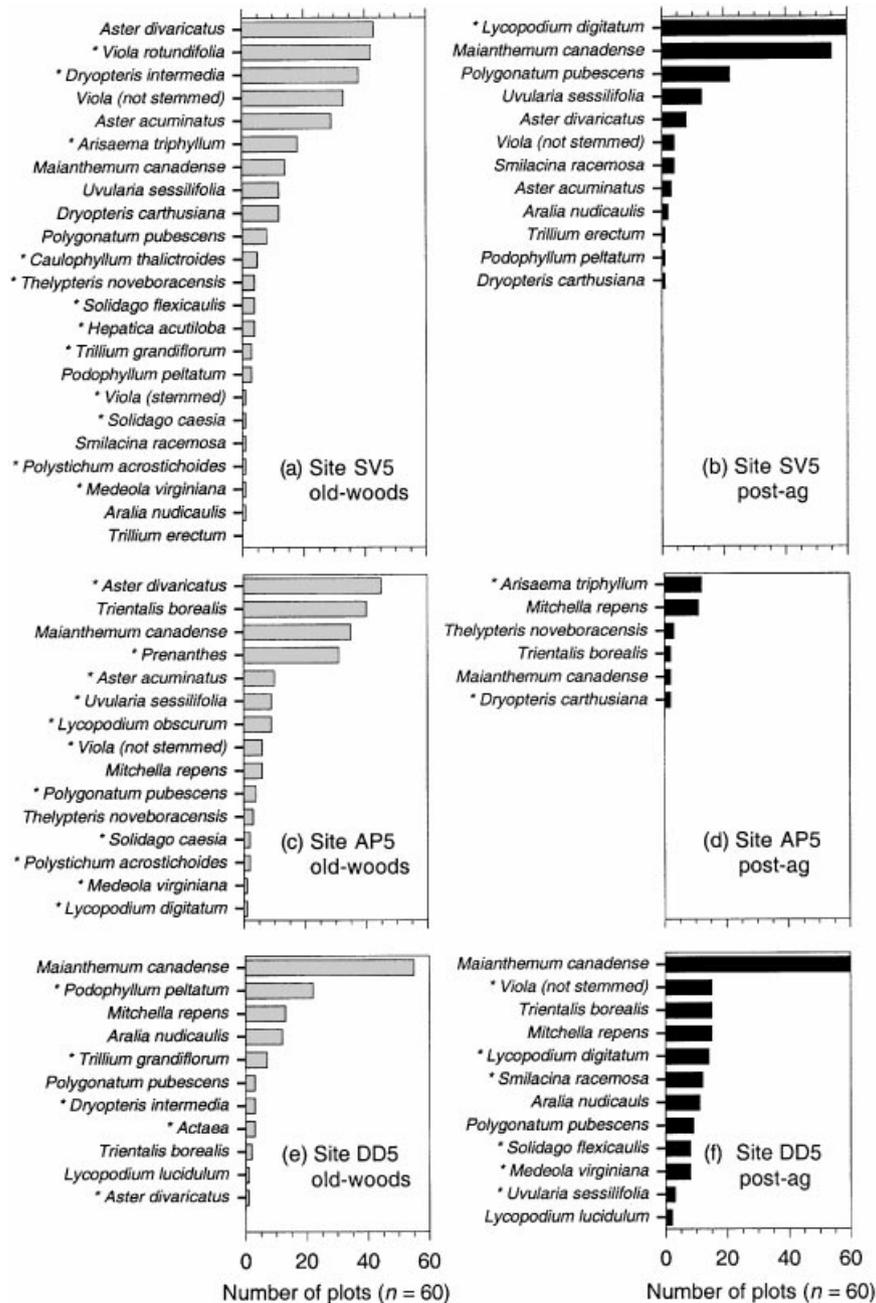
Fig. 2 Patterns of forest herb frequency at sites SV5 (a, b), AP5 (c, d) and DD5 (e, f) in Survey I, in old-woods (shaded bars; a, c, e) and postagricultural stands (black bars; b, d, f), from 60 plots (3 m² each) per stand. Asterisks indicate species not found in the adjacent stand at that site.

old-woods than in postagricultural forests (Table 2). Overall, old-woods contained on average almost five more species of forest herbs than postagricultural forests, and individual sample plots (1.5 m × 2 m) had almost one more species. There were more forest herb species in the old-woods than in the adjacent post-agricultural forests at 22 sites (Fig. 1b), with most (an average of 85%) of the species encountered at a given site present in the old-woods, but only just over half (54%) in the postagricultural forest.

Overall, forest herb diversity (as measured by the Shannon–Wiener index) was significantly greater in old-woods than in postagricultural forests (Table 2),

with the pattern seen in the paired stands at 21 of the 25 sites (Fig. 1c). In addition, old-woods were less dominated by the most abundant species than post-agricultural forests (Table 2).

An example of an individual site that exhibits these overall patterns of herb abundance and diversity is SV5 (Fig. 2a,b; site characteristics listed in Appendix 1 on WWW) where the old-woods contained 23 species compared with 12 species in the postagricultural forest. At this site, the species were distributed more evenly in the old-woods, as shown by a more gradual decline in species frequencies with rank, and indicated by a species diversity value of 2.5 compared with 1.7 in the

postagricultural forest. Even more marked contrasts were apparent in several sites that had especially species-poor postagricultural forests with a low abundance of forest herbs: abundance in the postagricultural forest at site AP5 (Fig. 2c,d) was only 15% of that in the old-woods.

While the overall pattern of higher abundance, richness and diversity in old-woods held for most individual sites, there were exceptions. Total herb frequency, site level richness and diversity were greater in postagricultural forests than in old-woods at eight, two and four sites, respectively (see arrows in Fig. 1 and site DD5 in Fig. 2e,f). Even though *Maianthemum canadense* was almost four times as abundant as the next most abundant species in the postagricultural forest at DD5, diversity was still greater than in the adjacent old-woods (2.1 vs. 1.7). This was due to the gradual decline in abundance with rank of the remaining 11 species (Fig. 2f) whereas in the old-woods, six of the 11 species occurred at low frequency (< 10% of plots, Fig. 2e).

Three of the four sites where species diversity was lower in old-woods than in postagricultural forest (DD5, WV13 and WV10) showed the lowest diversity values of any of the 25 old-woods in the survey (Fig. 1c). At one of these sites (WV10), about half of the old-wood stand was dominated by *Tsuga*, a tree associated with sparse herb cover (Rogers 1982). At the two sites where forest level richness was greater in postagricultural forests than in old-woods (DD5 and WV13, Fig. 1b), the old-woods were dominated by *Fagus*, and had a thick layer of leaf litter and a dense woody understorey, features often associated with low herb abundance (authors' personal observations).

In general, species in each postagricultural forest were a subset of the species in the adjacent old-woods; overall an average of 84% of species in postagricultural forests were also found in the adjacent stand. This pattern can be seen for sites SV5 and AP5 (Fig. 2a–d) where relatively few species were found only in the post-agricultural stand (asterisks in Fig. 2b,d). This pattern did not hold for DD5, one of the two sites where species richness was greater in the postagricultural forest (Fig. 2e,f).

Species patterns

The following analyses included only 39 species that were each present in at least four stands. Frequency (number of plots present out of 60 plots) was higher in old-woods for 30 species, while nine were more frequent in postagricultural stands (Fig. 3a). The differences were only significant, after correction for multiple comparisons, for three species (*Aster divaricatus*, *Dryopteris intermedia* and *Polystichum acrostichoides*), all of which had significantly higher plot-level frequency in old-woods (Wilcoxon signed-ranks tests with paired stands). When significance was not adjusted for multiple comparisons, 12 species had higher frequencies in old-woods and three species had higher frequencies in post-agricultural forests (asterisks in parentheses, Fig. 3a).

A similar pattern was seen for presence at the site level (Fig. 3b). Although it is difficult to determine statistical significance for any individual species when a large number of comparisons are made (39 were made), the overall pattern clearly suggests that more of the forest herb taxa in the survey were associated with old-woods than with postagricultural forests.

Species varied considerably in the degree to which they were associated with the two forest types. *Lycopodium digitatum* was the most abundant forest herb in the postagricultural stands (Fig. 3). Although *L. digitatum* is a forest plant (vs. open habitat), it was absent from the old-woods at 10 of 13 sites where it was recorded (Fig. 4a). Where present, it was often found in more than two-thirds of the plots in postagricultural forests (eight sites), but in more than 10% of the plots in the old-woods at only one site. *Trientalis borealis* and *M. canadense* were also relatively common throughout the county (at least 10 sites; dashed line in Fig. 3b) and at individual sites (mean number of plots more than five; dashed line in Fig. 3a). The pattern for *T. borealis* suggests a consistent association with postagricultural forests (Fig. 4b), but although it was in more plots in postagricultural forests at 10 of the 12 sites where it occurred, overall the frequency difference was not significant. The pattern for *M. canadense* was more variable; it was more frequent in postagricultural forests at 10 sites, in old-woods at eight sites, and similar in the two forest types at one site (Fig. 4c).

In contrast, *A. divaricatus* and *Trillium grandiflorum*, two other species common both throughout the county (Fig. 3b) and within stands (Fig. 3a), were relatively rare in postagricultural forests (Fig. 4d,e). Overall, *A. divaricatus* was the most abundant species in the survey. Although *A. divaricatus* was present at 23 of the 25 sites, it was only in 10 postagricultural stands. Interestingly, *T. grandiflorum* occurred in three post-agricultural forests where it was absent (at least from the sample plots) in the adjacent old-woods.

Aster acuminatus (Fig. 4f) was representative of a small number of species that was primarily associated with old-woods but not particularly common. Although *A. acuminatus* occurred only at six sites, it was quite frequent in the old-woods at these sites (found in an average of 25% of plots). At four of the sites it was absent from the postagricultural forest, and in the remaining two postagricultural forests it was present at low frequencies (average 5%). Similar patterns were seen for *Hepatica acutiloba*, *Viola rotundifolia*, *Caulophyllum thalictroides* and *Prenanthes*.

Given that old-woods were the likely source area for herbs colonizing adjacent postagricultural stands, we tested whether the frequency of each species in post-agricultural forest was associated with its frequency in the adjacent old-woods, that is, were species more abundant in postagricultural forests where they were also abundant in the adjacent stand? We used a 3×3 contingency table for each species, with three frequency categories (0, 1–4, > 4 plots) for each of the two forest
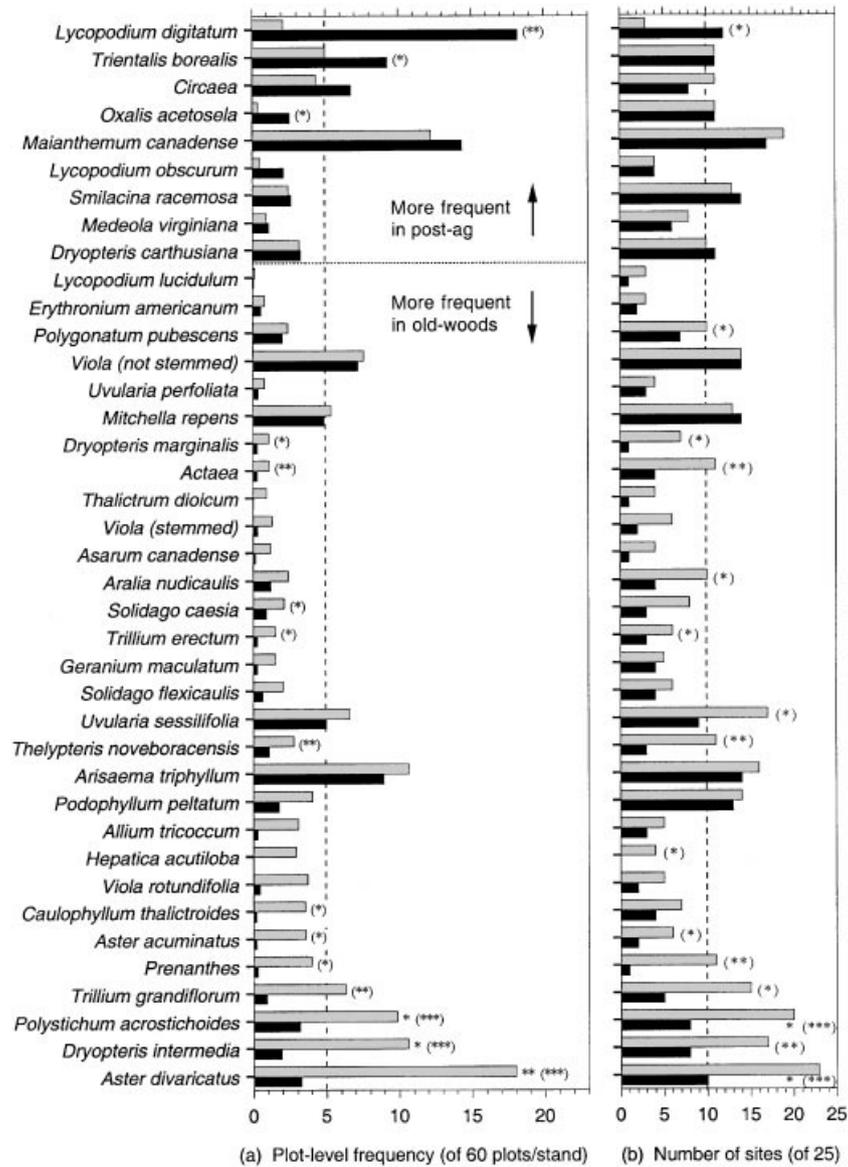
Fig. 3 Forest herb frequency at 25 sites, in old-woods (shaded bars) and adjacent postagricultural stands (black bars), ranked by mean difference in plot-level frequency between the forest types, for 39 species found in at least four stands. Asterisks indicate significance of Wilcoxon signed-rank tests between forest types, using stand pairs: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; asterisks not in parentheses are levels corrected for multiple comparisons (k = 39). (a) Plot-level frequency (of 60 plots) averaged over all 25 stands of a forest type. (b) Stand-level frequency (of 25 sites).

types in the stand pairs, in linear-by-linear association tests with exact probabilities (Mehta & Patel 1992; alpha-corrected for multiple comparisons, as in Rice 1989). There was a significant association for only two species: *T. borealis* and *M. canadense*.

Dispersal mode was not a major factor determining the distribution of forest herbs; species with all modes of dispersal were found in both forest types. Overall stand-level occurrence in postagricultural forests relative to old-woods did not differ significantly ($P = 0.18$, Kruskal–Wallis test) among five dispersal categories (wind, spore, ant, ingested/adhesive, ballistic/none), although the means of the ant and wind groups were slightly lower. However, based on plot-level frequencies within stand pairs, ant-dispersed species (see Table 1) had significantly lower mean frequencies in

postagricultural forests than in old-woods ($P < 0.05$, Wilcoxon signed-ranks test) whereas species with ingested seeds and those with spores (the other dispersal modes with enough species to test) had mean plot-level frequencies that did not differ significantly between the two forest types.

There was some evidence that clonal growth influenced which species were most successful at colonizing postagricultural forests, as there was a significant association of categories of clonal expansion (see Table 1) with species' plot-level relative frequencies in postagricultural forest vs. old-woods ($P < 0.05$, Kruskal–Wallis test). This was largely due to a number of species in category 3 (annual expansion greater than plant height) that were more frequent in postagricultural stands. Although the six species with the greatest mean positive
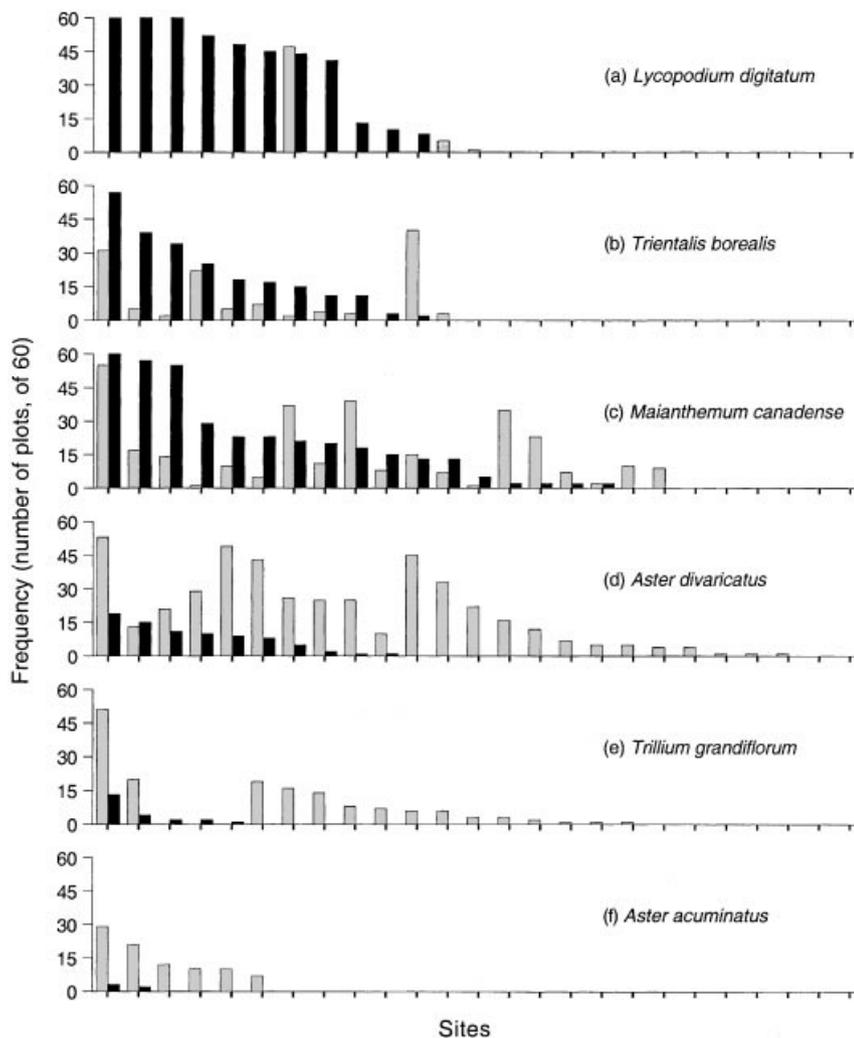
Fig. 4 Examples of forest herbs in old-woods (shaded bars) and adjacent postagricultural stands (black bars). For each species, the sites are shown ranked by decreasing order of its frequency in the postagricultural stands. (a) *Lycopodium digitatum*, (b) *Trientalis borealis*, (c) *Maianthemum canadense*, (d) *Aster divaricatus*, (e) *Trillium grandiflorum* and (f) *Aster acuminatus*.

difference in plot-level frequency between forest types (Fig. 3a: *L. digitatum*, *Trientalis*, *Circaea*, *Oxalis*, *Maianthemum* and *L. obscurum*) all have rapid potential clonal growth, other species in that category showed different patterns (e.g. *A. acuminatus* was strongly associated with old-woods; Fig. 3a).

SURVEY II

Colonization distance in the postagricultural forests for the 12 species sampled ranged from 0 m for *C. thalictroides* and *H. acutiloba* to 53 m for *T. borealis* (Table 3). These estimates of colonization distance were generally consistent with occurrence in postagricultural forests in Survey I; species with low colonization distances such as *H. acutiloba* and *A. divaricatus* were relatively rare, while species with greater colonization distances such as *L. digitatum* and *T. borealis* were more common.

In postagricultural forests, there were seven significant negative logarithmic regressions of species stem density on distance from the adjacent old-woods (each stand analysed separately; Table 3). Other species, including

Prenanthes, clearly declined in abundance with distance from old-woods, but were sufficiently rare that regressions were not significant due to a small sample size. There were also three significant negative logarithmic regressions (decreases in density with distance from the common edge) in old-woods (Table 3).

Stem density of *A. divaricatus* declined with distance from old-woods at all nine sites (significantly so at five; means for all sites shown in Fig. 5a). In all cases its abundance had dropped to zero at least 10 m (five plots) before the end of the transect. *Arisaema triphyllum* and *Aster acuminatus* showed similar, but weaker, patterns, with one significant negative logarithmic regression for *A. triphyllum* (Table 3), but none for *A. acuminatus*, probably due to low stem density.

In contrast, several species (*L. digitatum*, *M. canadense* and *T. borealis*) showed no decline in postagricultural stands with increasing distance from old-woods. For example, although *M. canadense* showed a significant regression in one site, it was generally abundant throughout postagricultural forests and reached its highest recorded density at 85 m from old-woods (Fig. 5b).

Table 3 Results from Survey II of stem densities of 12 forest herbs, in plots on transects perpendicular to the edge between forest types. Species are in order of increasing colonization distance into postagricultural forests, based on the furthest occurrence of half the peak per-plot stem density. A negative logarithmic model was used for regressions of density on distance from the common edge, within each of the nine stands of a forest type

| Species	No. of sites (of 9)	Mean colonization distance (m)	Sites (of 9) with mean density > in		Significant negative of regressions (of 9)	
			Old woods	Post-agricultural	Old woods	Post-agricultural
Caulophyllum thalictroides	1	0.0	1	0	–	–
Hepatica acutiloba	1	0.0	1	0	–	–
Prenanthes spp.	4	1.0	3	0	–	–
Uvularia sessilifolia	4	11.0	2	0	–	–
Aster divaricatus	9	12.3	7	0	–	5
Medeola virginiana	4	15.0	1	0	–	–
Solidago caesia	2	20.0	1	1	–	–
Aster acuminatus	5	21.7	4	0	–	1
Arisaema triphyllum	5	40.2	1	1	–	1
Lycopodium digitatum	6	44.3	0	6	–	–
Maianthemum canadense	9	48.7	3	2	2	1
Trientalis borealis	5	52.6	0	2	1	–
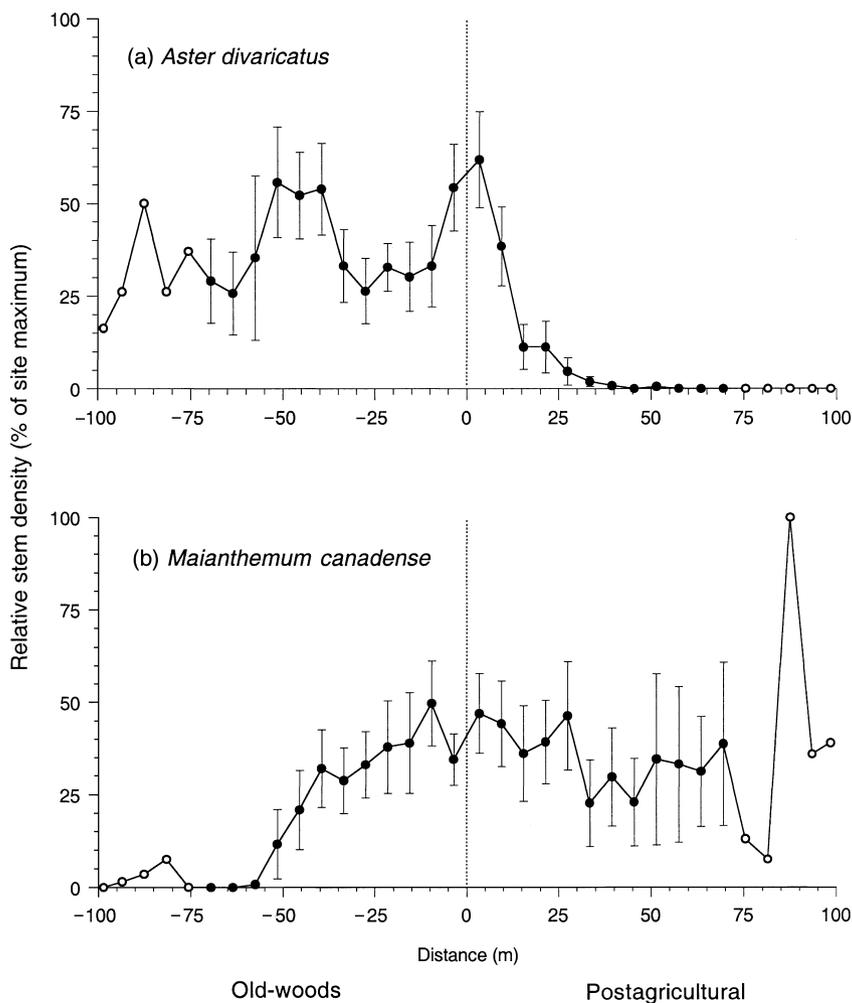
Fig. 5 Relative stem density vs. distance from the edge between old-woods and adjacent postagricultural stands, for the two species, (a) *Aster divaricatus* and (b) *Maianthemum canadense*, found at all nine sites in Survey II. Values are means across sites (± 1 SE; *n* = 9 sites for the first 50 m in both directions, four sites for 50–70 m, and one site, shown as white circles, for > 70 m). Within-site values were mean densities from 12 plots per 6 m of distance (three plots each on four parallel transects), as a percentage of the maximum 12-plot mean at that site.

Discussion

This study indicates that forest herb communities in postagricultural forests in central New York State are still recovering from the effects of agriculture. Even in the oldest postagricultural forests in the region (*c.* 70 years old), and in stands directly adjacent to source populations of these herb species, forest herb abundance, richness and diversity were generally lower than in old-woods. Only one of the characteristic species (*Hepatica acutiloba*, present in four old-woods) was absent from all 25 postagricultural forests. The presence of each of the remaining 38 common forest herbs in at least one postagricultural stand suggests that the habitat in forests recovering from agriculture may be suitable for these species, and that communities might reach former levels of abundance and diversity, given time.

Some general characteristics of forest herbs make them unlikely to be rapid colonizers of postagricultural forests. Sexual reproduction is often infrequent and produces few seeds (Bierzychudek 1982), and seedlings have high rates of mortality (Cook 1980; Bierzychudek 1982) and are associated with specific microhabitats within forests, such as treefall mounds, fallen logs, canopy gaps and particular tree species (Thompson 1980; Ashmun & Pitelka 1984; Beatty 1984; Crozier & Boerner 1984). Such features take centuries to develop in abandoned ploughed fields. In addition, forest herbs often have short dispersal distances, usually less than a few metres (e.g. Beattie & Lyons 1975; Hughes *et al.* 1988; Cain *et al.* 1998; Singleton 1998). Our results are consistent with the expectation that forest herbs are slow to colonize abandoned farmlands. The differences observed between forest types are likely to under-represent those of the region as a whole, because the sampled postagricultural stands were on land abandoned early in the 1900s and were adjacent to old-woods, a likely colonization source, whereas many stands in the region are both younger and more isolated (Smith *et al.* 1993). Other studies have shown that postagricultural stands not connected to older forest have fewer forest understorey species (Dzwonko & Loster 1988; Matlack 1994a; Grashof-Bokdam & Geertsema 1998).

Although the observed differences between forest types in herb abundance and diversity may be due to factors other than agricultural history (e.g. subtle differences in topography or soil properties), it is likely that agricultural history was of paramount importance. The criteria used for site selection were designed to match the two forest types as closely as possible in soils, slope, aspect and recent disturbance history. Furthermore, although early settlers may have selected particularly fertile land for agricultural use, most of our sites were on hillsides in regions of higher elevation in the county, typically the last to be cleared and the first to be abandoned, and therefore less likely to have been chosen because they were particularly fertile for growing crops.

Nevertheless, there were a few sites where postagricultural forests had greater values for abundance, richness or diversity. At two such sites, the old-woods had forest canopies dominated by *Fagus grandifolia*, a dense understorey of *F. grandifolia* saplings, and a deep leaf litter layer. Dense leaf litter has been correlated with the absence of forest herbs in other temperate forests (Sydes & Grime 1981; Whitney & Foster 1988). In addition, individual postagricultural forests where herb abundance was greater than in the corresponding old-woods were typically characterized by one or two very abundant species (usually *Lycopodium digitatum* or *Maianthemum canadense*), rather than a greater abundance of many species.

Overall, *L. digitatum* (= *L. complanatum* var. *flabelliforme*) was the most abundant forest herb in postagricultural stands. Others have found a similar association of *Lycopodium* spp. with forests recovering from agriculture (Eames 1942; Whitney & Foster 1988). Eames (1942) even suggested that the conditions in some postagricultural forests are particularly well suited to the growth of the gametophyte of some *Lycopodium* species, which might explain the distribution of this species, particularly as the dust-like spores make it unlikely to be dispersal-limited (Eames 1942; Whitney & Foster 1988). The high rate of clonal growth of *L. digitatum* also undoubtedly contributed to its high abundance in postagricultural forests. Interestingly, it was often absent from the adjacent old-woods, and as it is unlikely that *L. digitatum* was regularly present in the old-woods but outside the sampled plots, the colonization sources for this species were probably farther away, in drier, more open woodlands (Wiegand & Eames 1926; Gleason & Cronquist 1991), rather than the adjacent closed-canopy maple/beech forests. Long-distance dispersal is also suggested by the frequent presence of *L. digitatum* at > 50 m into postagricultural forests in Survey II. Isolated patches of the species are occasionally found in old fields before the development of a woody canopy (P.L. Marks, personal observation), so *L. digitatum* may have had more time to invade the stands than species that require a more closed forest habitat.

Plot-level frequency in postagricultural forests was significantly associated with frequency in the adjacent old-woods for only two species (*Trientalis borealis* and *M. canadense*). Because the old-woods were the closest colonization source (although longer-distance dispersal is also a possibility), a positive association was expected for most species. It may be that current abundance in the old-woods is not what it was when it acted as a colonization source, e.g. herbs can temporarily increase in response to canopy openings (Ashmun & Pitelka 1984), and a number of the old-woods showed signs of past tree cutting. Also, potential source populations along the boundary between the stands would not have been recorded in Survey I (transects were 25–50 m from the edge), which might explain why an average of 16% of species at a given site were present only in the postagricultural stand. Matlack (1994b) found that a number of forest herb species in eastern USA showed positive associations with open edge, while Corbit *et al.*

(1999) found a number of forest herbs in both remnant and naturally regenerated hedgerows in Tompkins County, New York State, and suggested that hedgerows might be used as corridors by seed-dispersing animals. Movement along the boundary between postagricultural forests and old-woods could explain why certain species (e.g. *Trillinm grandiflorum*) that were generally associated with old-woods were sometimes present only in the postagricultural forest at a given site (Fig. 4e). Additionally, because of the generally patchy distribution of forest herbs, our sampling may not have been intensive enough to detect associations for some species.

When species first colonize postagricultural sites, migration can be by seed or spore dispersal and, for stands adjacent to sources, by clonal spread, and both modes may be important for subsequent population persistence and spread within the stand. Independent estimates suggest, however, that regardless of means, colonization of new stands is slow. Of the species studied by Matlack (1994a), *Arisaema triphyllum*, which has animal-dispersed seeds, had a relatively high migration rate (1.2 m year^{-1}), comparable with an estimate based on our survey (1.0 m year^{-1}) if colonization distance (Table 3) is divided by an approximate time since canopy closure (40 years). Migration rate estimates for the wind-dispersed *A. divaricatus* were much lower, both in his study (0.25 m year^{-1}; Matlack 1994a) and ours (0.31 m year^{-1}). Estimates of migration rates of forest herbs in postagricultural forests in Europe ranged from 0 to 1.25 m year^{-1} in southern Sweden (Brunet & von Oheimb 1998) and from 0.05 to 1.15 m year^{-1} in Belgium (Bossuyt *et al*. 1999). If these rates are typical, then most postagricultural forests in central New York State are not old enough or close enough to source populations for forest herb communities to have recovered.

The density of individual species of forest herbs in postagricultural stands may be correlated with clonal growth rate, and the two species most strongly associated with postagricultural forests in our study, *L. digitatum* and *T. borealis*, can spread rapidly through vegetative growth. *Trientalis borealis* and *L. clavatum*, a species similar to *L. digitatum*, have been recorded as having maximum annual rates of horizontal rhizome growth of almost 1 m (Sobey & Barkhouse 1977). However, these rates are within the range of typical herb seed dispersal distances and therefore are not necessarily responsible for their high colonization rates, although they may be important for increasing the density and frequency of the species within postagricultural stands. In postagricultural forests in Pennsylvania and Delaware, Matlack (1994a) found no clear pattern: migration of herbs and shrubs was related to clonal expansion when rates were based on half-peak densities, but not on the farthest stem or peak density, and species with little clonal spread had higher rates in some sites. Brunet & von Oheimb (1998) found no relationship between clonal growth rates and migration rates into postagricultural forests in southern Sweden.

Some of our results are consistent with dispersal limitation. In Survey II, there was a decrease in abundance with increasing distance from the edge for several of the species, as Matlack (1994a), Brunet & von Oheimb (1998) and Bossuyt *et al*. (1999) also found for certain of their forest species. There was no evidence from field observations of any environmental gradients across those distances; and dispersal is the likely explanation for the pattern of these species in postagricultural stands. If dispersal is an important factor limiting colonization, colonizing ability might correlate with dispersal mode. Studies in the USA and Europe have generally found that ant-dispersed species have particularly low migration rates (Matlack 1994a; Brunet & von Oheimb 1998; Bossuyt *et al*. 1999). Our plot-level analysis of ant-dispersed species showed they were less frequent in postagricultural forests than in old-woods. However, in an overall comparison of dispersal modes in a stand-level test, ant-dispersed species were not significantly lower, nor species with ingested seeds particularly higher, in their frequencies in postagricultural forest vs. old-woods. Nevertheless, our plot-level results were consistent with Matlack (1994a), who found that the frequencies of species with ingested seeds in isolated postagricultural stands were not significantly lower than in old forests, in contrast with ant-dispersed species. In our survey, all modes were represented in postagricultural forest, and each dispersal mode included some species that were rare in postagricultural forests and others that were not. For example, we found some of the spore-dispersed species (unlikely to be dispersal-limited), such as the ferns *Polystichum acrostichoides* and *Dryopteris intermedia*, were associated with old-woods, while other spore-dispersed species (e.g. *L. digitatum*) were associated with postagricultural forest (Fig. 3). Species of a given dispersal mode may vary in dispersal patterns, such as seeds ingested by mammals vs. birds, and patterns of colonization may vary even within a species. Glitzenstein *et al*. (1990) found *A. divaricatus* to be associated with postagricultural forests in eastern New York State whereas this species was strongly associated with old-woods in our survey.

These observations suggest that the habitat within some postagricultural forests could limit the establishment, growth or reproduction of certain species of forest herbs. In other cases, it may simply be a matter of time; slow growth and limited seedling establishment, rather than persistent environmental alteration, that apparently explain the low abundance of the forest species *Gaultheria procumbens* in postagricultural stands on a sand plain in central Massachusetts (Donohue *et al*. 2000). Despite the fact that a number of studies has shown that forest herbs are slow to colonize postagricultural stands in regions of temperate deciduous forest (e.g. Peterken & Game 1984; Nyland *et al*. 1986; Dzwonko & Loster 1988; Whitney & Foster 1988; Matlack 1994a), there is currently no clear explanation for the overall pattern. Successful colonists vary in characteristics such as degree of clonal growth and dispersal mode, species with

similar dispersal modes sometimes differ in colonizing ability, and the same species may show different associations in different regions. As a result, the question of why some herb species are slower than others to colonize postagricultural forests remains unanswered.

CONSERVATION IMPLICATIONS

Clearing forest and ploughing the soil for the cultivation of crops are particularly intense forms of disturbance because they eliminate all forest plant species and the propagules needed for regrowth. In central New York State, as in other regions, forest herb abundance and diversity are greater in sites that have never been cleared for agriculture, and such forests are therefore generally more valuable reservoirs of biodiversity for forest herbs. However, many of the herb species surveyed are beginning to colonize postagricultural forests, with only one species (*H. acutiloba*) found exclusively in old-woods. Postagricultural forests near old-woods are therefore likely to contain at least some forest herb species as they grow older, suggesting that it may be possible to facilitate restoration by planting forest herbs. However, only experimental plantings will confirm that there is suitable habitat for these herbs in postagricultural stands, and that restoration of forest herb communities is therefore a viable option.

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