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Effects of management and site history on plant succession and seedbank composition in old-fields at the UWM Field Station

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Abstract: Vegetation succession and seedbank composition were studied in eleven oldfields with differing crop histories. All the fields had been abandoned from agriculture in the mid-1960's, and some fields are currently receiving periodic management in the form of burning, mowing, and/or removal of exotic species. Oldfield plant composition was found to be most strongly influenced by management history since abandonment. Recently-managed fields had a greater abundance of certain early-successional non-native species in the herbaceous layer, whereas unmanaged fields contained greater abundances of many later-successional, native perennial herb species. Woody plants showed the most significant response to management. Woody plant densities and species richness were significantly lower in recently-managed fields, whereas unmanaged fields had well-developed sapling and shrub layers. In contrast to the vegetation, the soil seedbanks contained many early-successional, non-native species irrespective of management history. In general, the management techniques are meeting the desired goals of maintaining diverse stages of successional vegetation and reducing establishment of invasive exotic shrubs.

Introduction

Secondary plant succession on abandoned agricultural fields is known to be influenced by many factors. Initial conditions (such as soil type, farming practices, the nature of the last crop, and season of abandonment) can have lasting effects on oldfield species composition, although the magnitude of these effects is thought to diminish with time (Keever 1950, Beckwith 1954, Myster and Pickett 1990). Germination of stored seed from the soil seedbank also contributes to the early vegetation stages of oldfield succession (Marks and Mohler 1985), and disturbances after abandonment can further affect succession by favoring the persistence of colonizing species that would otherwise decline

in abundance over time (Beckwith 1954, Connell and Slatyer 1977, Miller 1982).

The UW-Milwaukee Field Station property includes former agricultural fields which were abandoned from cultivation in the mid-1960's. The fields had varied crop histories prior to abandonment, and they have been under different management regimes since then. Some are now managed to maintain a variety of successional stages of vegetation in order to increase local plant and animal diversity. Others are being manipulated to encourage restoration of native prairie species or to discourage the establishment of invasive non-native (exotic) species such as glossy buckthorn (*Rhamnus frangula*). To accomplish these goals, some fields have been left unmanaged since abandonment, whereas others have been managed to varying degrees by means of burning, mowing, and/or physical removal of woody plants and exotics.

In 1990, we began research to determine the effects of site history and management regime on plant species composition, woody plant succession, and seedbank composition in these oldfields. From a survey conducted in 1990, analysis of herbaceous-layer vegetation indicated that species composition was most influenced by the amount of time since the last management treatment (Krause and De Steven 1991). Fields with very recent management (mowing or burning within the previous 5 years) were distinguished by the presence of a group of non-native weedy species such as quackgrass (*Agropyron repens*), dandelion (*Taraxacum officinale*), and medick (*Medicago* spp.), whereas there was a greater abundance of many native perennial herbs in fields without recent management. Crop history and soil type did not appear to have strong influences on species composition.

Based on 1991 surveys, we report on some additional aspects of plant community composition, including the nature of the soil seedbank and the effectiveness of management in slowing woody plant succession. Seedbank composition is significant not only because it may reflect past management history, but also because seedbanks will contribute to the above-ground vegetation if future site disturbances stimulate seed germination.

Methods

Ten abandoned agricultural fields under different management regimes were studied (Fields 2-11; Fig. 1). All are upland fields which had been abandoned from agriculture in the mid- to late 1960's; a complete history of the

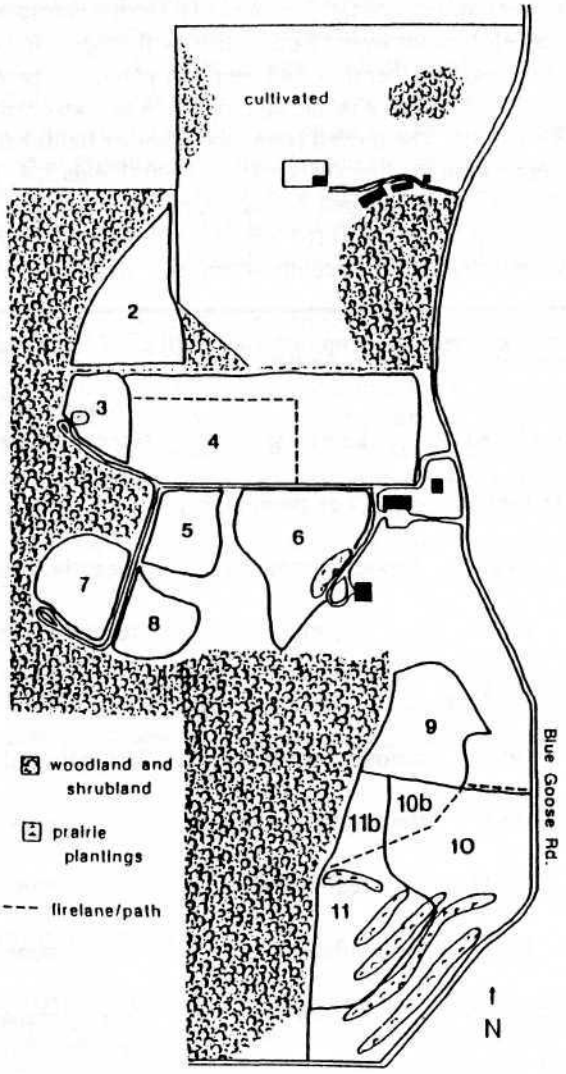

Figure 1. Map of the upland oldfields at the UW-Milwaukee Field Station.

fields is provided in Krause and De Steven (1991). Areas 10b and 11b, which have similar topography and are north of a firelane, were combined and analyzed as an additional eleventh field because of differing management from their adjoining parcels. Fields were characterized with respect to two factors (Table 1). The first was whether they had been last planted in perennial hay crops (Fields 3, 6, 7, 9, 11/11b) or in annual crops such as corn or small grains (Fields 2, 4, 5, 8, 10/10b). The second factor was whether fields had received recent management within the five years prior to 1990 (Fields 3, 4, 10, 11), or whether fields had been unmanaged or last managed more than 15 years previously (Fields 2, 5, 6, 7, 8, 9, 10b/11b). For analysis, these two management-history groups were designated "Recently-managed" and "Unmanaged".

Table 1. Brief management and crop histories of 10 UWM oldfields.

Field	Date abandoned	Last crop	Management since abandonment*
2	late 1960's?	corn(?) or small grains	none
3	1965	timothy/brome hay	recently managed
4	1965	corn	recently managed
5	1964?	corn	none
6	1965	timothy/brome hay	last managed 1970's
7	1965	timothy/brome hay	none
8	1964?	wheat or oats	none
9	1965	alfalfa/brome hay	none
10	1964 or '65	corn	recently managed (except 10b)
11	1965	alfalfa/brome hay	recently managed (except 11b)

* see Methods for details

In mid-summer 1991, the herbaceous-layer species of each field were sampled for presence and coverage using ten 0.5 m^2 randomly-placed quadrats per field (similar to sampling in 1990; see Krause and De Steven 1991). Species cover was visually estimated using a coarse decimal scale (see Londo 1976). In addition, tree and shrub layers (defined as individuals >1 m tall, or for low shrubs, individuals >0.5 m crown diameter) were sampled using strip transects (cf. Barbour *et al.* 1980). Depending upon the size of the field, three or four 100-m transects were oriented along the elevational gradient in each field, and all trees and shrubs present were recorded within a 10-m width along each transect. Individuals of each woody species were classed into one of three size categories: *shrubs*, tree *saplings* (<10 cm dbh), or larger *trees* (>10 cm dbh).

Seedbank analysis was accomplished by collecting 20 soil cores from each field in November 1991. The sample cores of each field were combined and thoroughly mixed, and then cold-stratified at 5°C for about 10 weeks to break seed dormancy. Subsamples of each combined sample were placed in flats and allowed to germinate in the UWM Greenhouse from February to August 1992. In each flat, the soil was spread to a depth of 1.25 cm over about 4 cm of a soilless growing medium. One flat containing only growing medium was maintained as a control to account for any input to the flats from seeds of neighboring greenhouse plants. All seedlings were counted and removed upon being identified.

Vegetation composition was analyzed by the multivariate ordination method of detrended correspondence analysis (see Krause 1995 for details). Statistical differences among group means were tested with non-parametric Mann-Whitney U tests.

Results

Herbaceous-layer vegetation

Similar to the 1990 results, ordination analysis of the 1991 herbaceous-layer data indicated that management history had the strongest influence on differences in herb species composition among the fields (cf. Krause 1995). In general, the oldfield flora is dominated by perennial species regardless of management history; however, there were differences in the distributions of native species and of woody species (Table 2). Of the herb-layer species that showed greater abundance in unmanaged fields, 76% were native, whereas the

Table 2. Life history traits of species found in the herb layer of 11 oldfields. Species are categorized into one of 3 groups: those equally abundant ('Common') in both managed and unmanaged fields, those more abundant in 'Recently managed' fields, and those more abundant in 'Unmanaged' fields.

Life history trait	Species group 'Common'	'Recently managed'	'Unmanaged'
% of species native	43	43	76
% of species perennial	78	86	76
% of species in life form:			
grass/sedge	14	14	8
forb	78	86	56
woody	7	0	36
Number of species in group	14	7	25

species that showed greater prevalence in recently-managed fields or that were common in all fields were more likely to be non-native species (57%). Seedlings of woody species also occurred in greater numbers in unmanaged fields (Table 2). Data for herb-layer species abundances are given in Appendix 1. Species that were more prevalent in unmanaged fields included the natives *Asclepias verticillata* (whorled milkweed), *Solidago canadensis* and *S. gigantea* (goldenrods), *Monarda fistulosa* (wild bergamot), and *Vitis riparia* (wild grape). Species that were more prevalent in recently-managed fields included the non-natives *Agropyron repens* (quackgrass), *Medicago sativa* (alfalfa), and *Taraxacum officinale* (dandelion). Some of the herb species common and equally prevalent in nearly all the fields included the non-natives *Poa* spp. (bluegrass), *Bromus inermis* (bromegrass), *Hypericum perforatum* (St. Johnswort), and *Verbascum thapsus* (mullein), as well as the natives *Asclepias syriaca* (common milkweed), and *Solidago altissima* (tall goldenrod).

Across all fields, a total of 63 species was found in the herb layer, including many species of infrequent occurrence. The average number of species in unmanaged fields (26.1 species) was somewhat greater than in recently-managed fields (18.7 species), although the difference was not statistically significant (Table 3).

Table 3. Species richness and similarity between the herb-layer vegetation and the seedbanks of 11 oldfields categorized as either 'Recently-managed'(n=4) or 'Unmanaged' (n=7). Data are means ± s.e. Significance of difference between managed and unmanaged fields: * = P<0.05, ns = not significant.

	Recently-managed fields	Unmanaged fields	Signif.
Number of species in:			
herbaceous layer	18.7 ± 4.3	26.1 ± 2.6	ns
seedbank	8.5 ± 0.6	12.3 ± 0.9	*
Number of shared species	4.5 ± 1.2	5.8 ± 1.0	ns
Community coefficient (% similarity)	32 ± 7	30 ± 4	ns

Soil seed bank

A total of 37 species was found in the seedbank samples, which is fewer than in the herb-layer vegetation. The mean number of species in the seedbanks of unmanaged fields was significantly greater than in recently-managed fields (Table 3). However, species composition was not substantially different between recently-managed and unmanaged fields (Table 4). About 46% of seedbank species were non-natives, and all were herbaceous species. Higher species richness in unmanaged fields was largely the result of a greater number (and percentage) of perennial species in the seedbanks (Table 4).

On average, only 4-6 species per field were shared between the soil seedbank and the above-ground vegetation, thus similarity was relatively low (~30%) in each management group (Table 3; see Krause 1995 for a detailed analysis). Species abundances in the seedbank samples are presented in Appendix 2. Common seedbank species included the non-natives *Hypericum perforatum* (St. Johnswort), *Daucus carota* (Queen Anne's lace), and *Poa* spp. (bluegrass), all of which were also common in the herb layer. *Verbascum thapsus* (mullein), a non-native biennial species, was found in the seedbanks of 9 of 11 fields, whereas in the herb layer it was found mainly in a few recently-managed fields. Species that were common in the herb layer but that were notably absent from or rare in the seedbank included the native *Asclepias*

syriaca (common milkweed), and the non-natives *Bromus inermis* (bromegrass), and *Linaria vulgaris* (toadflax). Similarly, many of the herbaceous species that were more abundant in unmanaged fields, such as *Achillea millefolium* (yarrow). *Medicago lupulina* (black medick), *Monarda fistulosa* (wild bergamot), *Vitis riparia* (wild grape), and *Asclepias verticillata* (whorled milkweed), were rare in or absent from the seedbank. Of the species unique to the seedbank samples, more were found in unmanaged fields, and many were annuals such as *Chenopodium album* (lamb's quarters), and *Panicum capillare* (witch-grass).

Table 4. Life history traits of species found in the seedbanks of 11 oldfields. Fields are categorized as either 'Recently-managed'(n=4) or 'Unmanaged' (n=7).Number of species was summed over all fields in each category.

Life history trait	Recently-managed fields	Unmanaged fields
% of species native	46	47
% of species that are:		
annual	33	23
biennial	17	15
perennial	50	62
% of species in life form:		
grass/sedge	17	15
forb	83	85
woody	0	0
Number of species	24	34

Tree- and shrub-layer vegetation

Management history very strongly influenced woody plant succession (Table 5). Densities of shrubs and saplings, total woody plant density, and woody species richness were all significantly higher in the unmanaged fields. There were also no trees found in the recently-managed fields, compared to low densities of trees in unmanaged fields. Species composition also differed between recently-managed and unmanaged fields across size classes (see Appendix 3). In unmanaged fields, five early-successional species were found

Table 5. Woody plant stem density (per 1000 m^2) by size category, and woody species richness in 11 oldfields categorized as either 'Recently managed'(n=4) or 'Unmanaged' (n=7). Data are means $\pm$ s.e. Significance of difference between managed and unmanaged fields: * = $P<0.05$, + = $0.05<P<0.10$, ns = not significant.

Size-class	Recently-managed fields	Unmanaged fields	Signif.
Trees	0.0 ± 0.0	1.2 ± 0.6	ns
Saplings	4.5 ± 3.7	84.2 ± 48.8	*
Shrubs	6.0 ± 4.1	58.7 ± 34.4	+
Total stems	10.5 ± 7.7	144.1 ± 82.4	*
Number of species	4.8 ± 1.2	16.3 ± 2.4	*

in the tree size-class, four of which were wind-dispersed species (*Acer negundo*, boxelder; *Ulmus rubra* (slippery elm); *Fraxinus americana* and *F. pennsylvanica*, white and green ash), and one a bird-dispersed species (*Prunus serotina*, black cherry). The sapling layer of recently-managed fields contained five species of similar composition to the tree layer of unmanaged fields, whereas a more diverse group of fourteen sapling species was found in unmanaged fields. These 14 species included not only early-successional wind-dispersed species, but also animal-dispersed and later-successional species such as *Crataegus* spp. (hawthorns), *Juglans cinerea* (butternut), *Quercus rubra* (red oak), and *Acer saccharum* (sugar maple). The shrubs consisted mainly of animal-dispersed species. Of the species found in recently-managed fields, the three most common were the exotics *Rhamnus frangula, R. cathartica*, (buckthorns) and *Lonicera tatarica* (honeysuckle). In contrast, the shrub layer of unmanaged fields was diverse (17 species) and consisted largely of native species. Common natives included *Cornus stolonifera* and *C. racemosa* (red-osier and gray dogwood), *Juniperus communis* (juniper), *Prunus virginiana* (chokecherry), *Rhus typhina* (staghorn sumac), and *Viburnum lentago* (nannyberry).

Discussion

Previous studies have shown that the early stages of oldfield succession are varied in composition and are greatly influenced by initial factors such as the season of abandonment and the nature of the last crop. However, over time, the vegetation tends to converge towards greater similarity (Myster and Pickett 1990). Later successional stages may be influenced by subsequent disturbance, and extensive disturbances (such as burning or mowing) can favor the persistence of colonizing, early-succession species in the community.

If time since initial abandonment were the only significant factor, the oldfields at the UWM Field Station should show a great deal of convergence in species composition. This is generally the case in that all fields share a number of common oldfield species such as the grasses *Bromus inermis* and *Poa* spp. and the forbs *Solidago altissima*, *Asclepias syriaca*, *Linaria vulgaris*, and *Hypericum perforatum*. However, the management regimes are maintaining some diversity among the fields. As in the 1990 study (Krause and De Steven 1991), overall herbaceous-layer composition best correlated with the amount of time since the last management treatment. Of the species that were more abundant in recently-managed fields, more than 50% were non-native; other non-native herbaceous perennials were also common across all fields. Many of these non-natives have been naturalized for many years and are typical components of oldfield vegetation. In contrast, unmanaged fields had higher species richness overall and a greater proportion of native herbaceous and woody species. Exotic species are often successful early colonizers, characterized by high rates of growth, reproduction, and/or dispersal. Thus the results support the idea that disturbances (*e.g.* management treatments) promote the maintenance of weedy, early-successional species in oldfield vegetation and that reduction of disturbance favors later-successional species such as native perennials and woody plants (Connell and Slatyer 1977, Miller 1982). The fields were also differentiated from each other by the presence of many uncommon species: of the 63 herb-layer species found across all 11 fields, over 25% occurred in only a single field, and in relatively low abundances. Some of these may be remnants of earlier stages of oldfield vegetation.

Some interaction between the seedbank and the aboveground vegetation was indicated by the number of shared species. With increasing time since abandonment, oldfield vegetation should be less influenced by the seedbank and more by dispersal of new species into the site and by vegetative reproduction of already-established species. This trend is supported by the presence of early-successional annual and biennial species in the seedbanks that were absent from

the above-ground vegetation. However, the presence of such species is still significant, because this seedbank may contribute to the composition of the vegetation in the event of new disturbances. A trend for oldfield species richness to increase with successional time is evidenced by greater numbers of species in the vegetation of unmanaged fields, and this more diverse above-ground vegetation in turn has contributed to increased numbers of species in the seedbanks of these unmanaged fields.

Woody species showed the most significant response to the management regimes, which have had the effect of slowing woody plant succession. The fields had been abandoned for less than 30 years, thus larger trees were absent from recently-managed fields and consisted of only a few early-successional species in unmanaged fields. The relatively few tree saplings in recently-managed fields were early-successional species, whereas later-successional species were among the more abundant saplings in the unmanaged fields. Similarly, shrubs were less abundant in recently-managed fields, and about half of the species were aggressive exotics such as buckthorn (*Rhamnus*) and honeysuckle (*Lonicera*). In contrast, the shrub layer of unmanaged fields was well-developed and contained many native species in addition to the non-natives. Having received minimal disturbance since abandonment, the unmanaged fields are on a successional pathway towards forest, and their woody plant cover will continue to develop.

One of the management goals at the UWM Field Station is to maintain oldfield habitats in a broad range of successional stages. The vegetation differences among the fields, which were all abandoned about the same time, indicate that the management regimes are having the desired effects, particularly in preventing succession towards dominance by woody plants. Another management goal is to discourage the establishment of aggressive exotic species, but it appears that the management to set back succession in some fields may also be favoring the persistence of some non-native species. Knowledge of the seedbanks may be a useful contribution to this second management goal. It may be possible to predict what management techniques would be most effective in maintaining oldfield conditions, yet cause the least amount of disturbance and germination from the seedbank, which is a significant source of weedy exotic species.

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Appendix 1. Relative abundance (cover class value) of species found in the herbaceous layer of 11 oldfields with differing management. Values are mean cover class per 10 sample quadrats. Species are listed in four groups (A-D) according to their relative distribution in recently-managed fields versus fields with no recent management ("unmanaged"): A. those equally abundant in both management groups; B. those more abundant in recently-managed fields; C. those more abundant in unmanaged fields; D. incidental species found in only one field.
* = non-native species; LH = life history; P = perennial, B = biennial, A = annual.

		FIELDS WITH RECENT MANAGEMENT				FIELDS WITH NO RECENT MANAGEMENT						
SPECIES	LH	3	4	10	11	10B&11B	2	5	6	7	8	9
GROUP A.												
**Poa* spp.	P	1.6	6.0	4.0	2.2	5.7	3.2	3.4	3.4	3.8	2.4	2.4
**Bromus inermis*	P	2.6	0.1	2.6	6.2	3.2	2.8	1.1	3.0	2.2	4.6	4.0
Solidago altissima	P	0.4	1.0	0.3	0.3	0.7	1.9	2.0	1.5	0.3	0.9	0.9
Asclepias syriaca	P	0.1	0.7	0.9	0.6	0.2	0.5	0.4	0.7	0.3	0.3	0.5
**Hypericum perforatum*	P	0.7	0.5	0.1	0.1	.	1.1	1.2	0.6	1.3	1.3	0.2
**Linaria vulgaris*	P	0.3	0.4	0.2	0.1	0.3	0.2	.	.	0.2	0.7	0.3
**Daucus carota*	B	2.5	0.7	.	.	.	0.5	1.8	0.4	0.7	0.2	0.7
Aster pilosus	P	0.9	.	.	.	.	0.3	0.4	0.2	0.1	0.2	.
Physalis heterophylla	P	.	0.1	0.1	.	.	0.5	0.1	.	0.1	0.1	.
Solidago ulmifolia	P	0.1	0.1	.	.	.	.	0.3	0.2	.	0.1	.
Oenothera biennis	B	0.5	.	.	.	.	.	0.1	.	0.1	0.2	.
**Tragopogon pratensis*	B	.	.	0.1	.	.	.	.	.	0.1	0.1	.
**Cirsium arvense*	P	0.1	.	.	.	.	.	.	.	0.1	.	.
**Rhamnus frangula*	P	0.1	.	.	.	.	.	.	.	.	.	0.1
GROUP B.												
**Taraxacum officinale*	P	0.9	0.5	0.1	0.3	0.1	.	0.3	0.3	0.1	.	0.1
**Agropyron repens*	P	1.2	2.4	1.4	.	0.7	.	0.5	.	0.4	.	.
**Medicago sativa*	P	0.8	.	.	0.1	0.2	0.2	.	.	.	.	0.4
Aster sagittifolius	P	0.6	0.1	.	.	.	0.2	.	0.1	0.1	.	.
**Verbascum thapsus*	B	0.3	.	0.3	.	.	.	.	.	0.1	.	.
Oxalis stricta	P	.	0.4	.	.	.	0.1	.	.	0.1	.	.
Aster lateriflorus	P	0.1	0.2	.	.	.	.	.	.	.	.	.

Appendix 1, continued.

SPECIES	LH	FIELDS WITH RECENT MANAGEMENT 3	4	10	11	10B&11B	FIELDS WITH NO RECENT MANAGEMENT 2	5	6	7	8	9
GROUP C.												
Asclepias verticillata	P	.	0.1	0.2	.	0.4	0.1	0.5	0.2	0.4	0.4	0.1
Equisetum spp.	P	0.1	0.3	.	.	.	0.4	.	0.2	0.1	0.4	0.2
Monarda fistulosa	P	0.2	0.1	.	.	.	0.9	.	0.1	0.8	0.1	0.1
Vitis riparia	P	.	0.3	.	.	.	0.1	0.5	0.1	0.4	0.3	0.1
**Achillea millefolium*	P	.	0.1	.	.	0.1	0.1	0.2	0.1	0.1	0.1	.
**Medicago lupulina*	A,B	0.1	0.1	.	.	0.2	.	0.6	0.5	.	0.3	.
Solidago gigantea	P	.	.	.	.	0.1	0.5	0.1	.	0.1	0.2	0.1
Solidago canadensis	P	.	.	.	.	.	0.5	.	0.4	0.3	0.3	0.4
**Melilotus officinalis*	A,B	.	.	.	0.1	0.2	.	0.1	0.4	.	0.2	.
Ulmus rubra	P	.	0.3	.	.	.	0.1	.	.	0.3	0.2	0.1
Erigeron annuus	A	0.1	.	.	.	.	.	0.1	.	0.1	0.1	0.1
**Phleum pratense*	P	.	0.1	.	.	.	0.1	.	0.2	.	.	0.2
Fraxinus americana	P	0.1	.	.	.	.	.	.	.	0.3	0.1	0.1
Ambrosia artemisiifolia	A	.	0.1	.	.	.	0.2	.	0.1	0.1	.	.
**Lactuca serriola*	A,B	.	0.1	.	.	.	0.1	0.1	.	0.2	.	.
Acer saccharum	P	.	.	.	.	.	0.1	0.1	.	0.1	0.1	.
Anemone virginiana	P	.	.	.	.	.	0.2	0.4	.	0.2	.	.
Aster simplex	P	.	.	.	.	0.1	.	.	0.1	.	.	0.1
Cornus stolonifera	P	.	.	.	.	.	0.1	0.5	.	.	.	.
Rhus typhina	P	.	.	.	.	.	.	0.1	.	0.4	.	.
**Melilotus alba*	A,B	.	.	.	.	.	.	0.1	0.3	.	.	.
Rubus sp.	P	.	.	.	.	.	.	0.3	.	0.1	.	.
Carex spp.	P	.	.	.	.	.	0.2	.	0.2	.	.	.
Parthenocissus quinquefolia	P	.	.	.	.	.	.	0.2	.	0.2	.	.
Fraxinus pennsylvanica var. *subintegerrima*	P	.	.	.	.	.	0.1	.	0.1	.	.	.

Appendix 1, continued.

SPECIES	LH	FIELDS WITH RECENT MANAGEMENT 3	4	10	11	FIELDS WITH NO RECENT MANAGEMENT 10B&11B	2	5	6	7	8	9
GROUP D.												
Aster novae-angliae	P	0.1	.	.	.	.	.	.	.	.	.	.
**Barbarea vulgaris*	B,P	.	.	0.1	.	.	.	.	.	.	.	.
**Convolvulus arvensis*	P	.	.	0.3	.	.	.	.	.	.	.	.
Geum aleppicum	P	0.1	.	.	.	.	.	.	.	.	.	.
**Nepeta cataria*	P	0.1	.	.	.	.	.	.	.	.	.	.
Rosa carolina	P	0.1	.	.	.	.	.	.	.	.	.	.
**Trifolium pratense*	P	.	0.4	.	.	.	.	.	.	.	.	.
**Agrostis stolonifera*	P	.	.	.	.	.	.	.	0.5	.	.	.
Antennaria plantaginifolia	P	.	.	.	.	.	.	.	0.3	.	.	.
Apocynum androsaemifolium	P	.	.	.	.	.	.	.	.	0.1	.	.
Erigeron strigosus	A,B	.	.	.	.	.	.	.	0.1	.	.	.
**Ranunculus acris*	P	.	.	.	.	.	.	.	.	.	0.1	.
Ratibida pinnata	P	.	.	.	.	.	.	.	0.1	.	.	.
**Rhamnus cathartica*	P	.	.	.	.	0.1	.	.	.	.	.	.
**Trifolium repens*	P	.	.	.	.	.	.	.	.	0.2	.	.
**Vicia angustifolia*	A	.	.	.	.	.	0.1	.	.	.	.	.
Zanthoxylum americanum	P	.	.	.	.	.	.	.	.	0.3	.	.
Total Species		27	25	14	9	15	29	27	28	37	26	21

Appendix 2. Relative abundance (%) of species found in seedbank samples taken from 11 oldfields with differeing management. Species are listed in four groups (A-D), organized as in Appendix 1. Group E represents species unique to the seedbanks (*i.e.* not found in the herb-layer).
* = non-native species; LH = life history; P = perennial, B = biennial, A = annual.

		FIELDS WITH RECENT MANAGEMENT				FIELDS WITH NO RECENT MANAGEMENT						
SPECIES	LH	3	4	10	11	10B&11B	2	5	6	7	8	9
GROUP A.												
**Poa* spp.	P	3.0	44.3	61.0	47.0	70.2	12.8	13.3	23.2	13.9	4.9	12.9
*Bromus inermis	P	.	.	.	.	.	.	.	1.3	.	.	.
Solidago altissima	P	.	8.2	.	.	.	.	1.6	0.6	.	0.4	1.5
Asclepias syriaca	P	.	.	.	.	.	.	.	.	.	.	.
**Hypericum perforatum*	P	60.6	19.7	5.1	.	.	41.4	55.5	21.3	70.8	67.8	.
**Linaria vulgaris*	P	.	.	13.6	.	.	.	.	.	.	.	.
**Daucus carota*	B	7.5	11.5	.	.	.	8.6	4.7	5.2	0.9	.	1.5
Aster pilosus	P	3.0	.	.	.	2.1	.	0.8	1.3	.	.	.
Physalis heterophylla	P	.	.	.	.	.	.	.	.	.	.	.
Solidago ulmifolia	P	.	.	.	.	.	.	.	.	.	.	.
Oenothera biennis	B	1.5	1.6	.	.	.	1.4	.	.	.	0.4	.
**Tragopogon pratensis*	B	.	.	.	.	.	.	.	.	.	.	.
**Cirsium arvense*	P	.	.	.	.	12.8	.	.	.	.	.	.
**Rhamnus frangula*	P	.	.	.	.	.	.	.	.	.	.	.
GROUP B.												
**Taraxacum officinale*	P	.	.	.	.	.	.	.	.	.	.	.
**Agropyron repens*	P	.	.	10.2	.	.	.	.	.	.	.	.
**Medicago sativa*	P	.	.	.	.	.	.	.	.	.	.	.
Aster sagittifolius	P	.	.	.	.	.	.	.	.	.	.	.
**Verbascum thapsus*	B	12.1	.	5.1	11.8	4.2	2.8	3.9	.	2.7	2.3	3.0
Oxalis stricta	P	6.1	3.3	.	8.8	.	.	.	.	0.9	.	.
Aster lateriflorus	P	.	.	.	.	.	.	.	.	.	.	.

Appendix 2, continued.

SPECIES	LH	FIELDS WITH RECENT MANAGEMENT 3	4	10	11	10B&11B	FIELDS WITH NO RECENT MANAGEMENT 2	5	6	7	8	9
GROUP C.												
Asclepias verticillata	P	.	.	.	.	.	1.4	.	.	.	.	.
Equisetum spp.	P	.	3.3	.	.	.	.	.	0.6	.	.	.
Monarda fistulosa	P	.	.	.	.	.	.	.	.	.	.	.
Vitis riparia	P	.	.	.	.	.	.	.	.	.	.	.
**Achillea millefolium*	P	.	.	.	.	.	.	.	.	.	.	.
**Medicago lupulina*	A,B	.	.	.	.	.	.	.	.	.	.	.
Solidago gigantea	P	1.5	.	.	.	4.2	.	3.1	.	.	.	2.3
Solidago canadensis	P	.	.	.	.	.	.	6.2	.	.	.	.
**Melilotus officinalis+*	A,B	.	.	.	.	.	.	.	.	.	.	.
Ulmus rubra	P	.	.	.	.	.	.	.	.	.	.	.
Erigeron annuus	A	.	.	.	.	.	.	.	.	.	.	.
**Phleum pratense*	P	.	.	.	.	.	.	.	0.6	.	.	0.8
Fraxinus americana	P	.	.	.	.	.	.	.	.	.	.	.
Ambrosia artemisiifolia	A	.	.	.	2.9	2.1	.	.	1.3	.	.	0.8
**Lactuca serriola*	A,B	.	.	.	.	.	.	.	.	.	.	.
Acer saccharum	P	.	.	.	.	.	.	.	.	.	.	.
Anemone virginiana	P	.	.	.	.	.	.	.	.	.	.	.
Aster simplex	P	.	.	.	.	.	.	.	.	.	.	.
Cornus stolonifera	P	.	.	.	.	.	.	.	.	.	.	.
Rhus typhina	P	.	.	.	.	.	.	.	.	.	.	.
**Melilotus alba+*	A,B	.	.	.	.	.	.	.	.	.	.	.
Rubus sp.	P	.	.	.	.	.	.	.	.	.	.	.
Carex spp.	P	3.0	.	.	.	.	11.4	.	16.8	.	0.2	.
Parthenocissus quinquefolia	P	.	.	.	.	.	.	.	.	.	.	.
Fraxinus pennsylvanica var. *subintegerrima*	P	.	.	.	.	.	.	.	.	.	.	.

+ Both *Melilotus* spp. are reported together in Group E, because their seedlings could not be distinguished.

Appendix 2, continued.

SPECIES	LH	FIELDS WITH RECENT MANAGEMENT 3	4	10	11	FIELDS WITH NO RECENT MANAGEMENT 10B&11B	2	5	6	7	8	9
GROUP D.												
Aster novae-angliae	P	.	.	.	.	.	.	.	.	.	.	.
**Barbarea vulgaris*	B,P	.	.	.	17.6	.	.	.	.	4.9	1.3	73.5
**Convolvulus arvensis*	P	.	.	.	.	.	.	.	.	.	.	.
Geum aleppicum	P	.	.	.	.	.	.	.	.	.	.	.
**Nepeta cataria*	P	.	.	.	.	.	.	.	.	.	.	.
Rosa carolina	P	.	.	.	.	.	.	.	.	.	.	.
**Trifolium pratense*	P	.	.	.	.	.	.	.	.	.	0.2	.
**Agrostis stolonifera*	P	.	.	.	.	.	.	.	.	.	.	.
Antennaria plantaginifolia	P	.	.	.	.	.	.	.	.	.	.	.
Apocynum androsaemifolium	P	.	.	.	.	.	.	.	.	.	.	.
Erigeron strigosus	A,B	.	.	.	.	.	.	.	.	.	.	.
**Ranunculus acris*	P	.	.	.	.	.	.	.	.	.	.	.
Ratibida pinnata	P	.	.	.	.	.	.	.	.	.	.	.
**Rhamnus cathartica*	P	.	.	.	.	.	.	.	.	.	.	.
**Trifolium repens*	P	.	3.3	.	.	.	.	.	1.3	0.9	.	0.8
**Vicia angustifolia*	A	.	.	.	.	.	.	.	.	.	.	.
Zanthoxylum americanum	P	.	.	.	.	.	.	.	.	.	.	.
GROUP E.												
**Brassica rapa*	A	1.5	.	.	.	.	.	.	.	0.4	.	1.5
Veronica peregrina	A	.	4.9	.	.	.	.	.	.	.	1.3	.
**Chenopodium album*	A	.	.	1.7	.	2.1	.	1.6	1.9	0.4	0.6	.
**Melilotus* spp.+	A,B	.	.	3.4	.	.	7.1	7.0	22.6	2.2	13.4	.
**Silene latifolia*	A,P	.	.	.	5.9	.	.	.	.	1.3	0.6	.
Panicum capillare	A	.	.	.	2.9	.	1.4	.	1.3	0.4	0.2	.
Verbena hastata	P	.	.	.	.	.	.	.	.	.	.	0.8
Verbena urticifolia	A,P	.	.	.	2.9	.	.	.	.	.	.	.
**Cerastium vulgatum*	P	.	.	.	.	2.1	1.4	.	.	.	.	.
**Silene vulgaris*	P	.	.	.	.	.	8.6	.	.	.	6.0	.
Potentilla norvegica	A,P	.	.	.	.	.	1.4	1.6	.	.	0.2	.
Typha spp.	P	.	.	.	.	.	.	0.8	.	.	.	.
Eupatorium perfoliatum	P	.	.	.	.	.	.	.	0.6	.	.	.
**Cirsium vulgare*	B	.	.	.	.	.	.	.	.	.	.	0.8
Total Species		10	9	7	8	8	12	12	15	12	15	12

+ Both *Melilotus* spp. are reported together in Group E, because their seedlings could not be distinguished.

Appendix 3. Stem densities (per 1000 m) by size category (tree, sapling, shrub) for woody species in 11 oldfields with differing management.
* = non-native species

SPECIES	FIELDS WITH RECENT MANAGEMENT 3	4	10	11	FIELDS WITH NO RECENT MANAGEMENT 10B&11B	2	5	6	7	8	9
TREES											
Acer negundo	.	.	.	.	.	0.2	.	.	0.3	.	.
Fraxinus americana	.	.	.	.	.	.	1.0	.	0.7	0.3	.
F. pennsylvanica	.	.	.	.	.	.	0.7	.	0.3	.	.
Prunus serotina	.	.	.	.	.	.	.	.	1.0	.	.
Ulmus rubra	.	.	.	.	.	.	0.7	.	1.3	2.0	.
SAPLINGS											
Acer negundo	0.8	0.3	.	.	.	0.8	2.7	0.2	1.7	0.3	.
A. saccharum	.	.	.	.	.	.	16.0	.	8.7	1.0	.
Carya ovata	.	.	.	0.2	.	.	.	.	.	.	.
Crataegus spp.	.	.	.	.	.	.	0.3	0.2	2.3	.	0.2
Fraxinus americana	9.6	1.7	.	0.2	2.0	13.8	103.0	4.2	30.7	11.7	13.2
F. pennsylvanica	.	.	.	.	.	.	46.3	.	.	.	4.8
F. pennsylvanica var. *subintegerrima*	.	.	.	.	.	0.5	4.3	.	0.7	.	3.2
Juglans cinerea	.	.	.	.	.	.	.	.	.	2.0	.
Populus deltoides	.	.	.	.	.	0.2	.	.	.	.	.
P. tremuloides	.	.	.	.	.	0.2	.	.	.	.	.
Prunus serotina	0.8	.	.	.	.	2.5	2.7	.	1.0	.	.
Quercus rubra	.	.	.	.	.	.	.	.	0.3	1.0	.
Salix spp.	.	.	.	.	.	2.2	.	0.2	.	.	.
Ulmus americana	.	.	.	.	.	.	1.0	.	.	.	.
U. rubra	4.4	.	.	.	1.0	1.8	176.3	1.2	108.0	14.3	0.8

Appendix 3, continued.

SPECIES	FIELDS WITH RECENT MANAGEMENT 3	4	10	11	FIELDS WITH NO RECENT MANAGEMENT 10B&11B	2	5	6	7	8	9
SHRUBS											
Cornus racemosa	.	.	.	.	.	.	45.0	.	.	.	.
C. stolonifera	.	0.3	.	.	2.0	21.8	22.7	3.0	0.3	0.3	3.2
**Elaeagnus umbellata*	.	.	.	.	.	3.0	1.7	0.5	0.3	.	.
Hypericum spathulatum	.	.	.	.	.	.	.	.	.	0.3	.
Juniperus communis	.	.	.	.	6.0	4.0	1.0	0.5	0.3	0.7	1.8
**Lonicera tatarica*	0.4	.	0.5	0.2	.	0.2	4.0	.	0.7	1.3	1.0
Prunus virginiana	.	.	.	.	.	2.2	18.3	0.5	2.3	.	0.8
**Rhamnus cathartica*	0.4	.	0.2	.	.	0.8	0.3	.	0.3	.	0.5
**R. frangula*	5.2	0.3	.	0.8	.	0.5	4.3	1.0	0.7	0.3	2.8
Rhus typhina	.	.	.	3.8	.	.	150.3	.	40.7	.	.
Ribes sp.	.	.	.	.	.	.	.	.	.	.	0.5
**Rosa multiflora*	.	.	.	.	1.0	.	0.7	0.2	.	0.3	.
Rubus sp.	.	.	.	.	.	.	1.7	.	.	.	.
Salix discolor	.	.	.	.	.	2.2	.	1.5	.	.	.
Spiraea alba	.	.	.	.	.	26.5	.	.	.	.	.
Viburnum lentago	.	.	.	.	5.0	1.8	8.0	0.5	4.0	0.3	0.8
Zanthoxylum americanum	12.0	.	.	.	.	0.2	.	.	3.7	.	.
Total Species	8	4	2	5	6	20	24	13	23	15	13