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The Role Of Land Use History In Structuring
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THE ROLE OF LAND USE HISTORY IN STRUCTURING AN OLD-FIELD PLANT COMMUNITY

By

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ABSTRACT

THE ROLE OF LAND USE HISTORY IN STRUCTURING AN OLD-FIELD PLANT COMMUNITY

By

Bryan L. Foster

I examined the role of land use history and soil drainage characteristics in influencing the development of a 27 year old-field plant community in southwest Michigan. A divergence in species composition that occurred within the field between 1964 (year of abandonment from agriculture) and 1991 is reflected in the current plant community as a distinct west to east zonation in the abundance of woody vegetation. A similar zonation among the early successional species dominating the field in 1970 indicates that the divergence may be related to the initial colonizing patterns of the dominant perennial grasses (*Agropyron repens*, *Poa compressa*, and *Poa pratensis*), and their differential impact on patterns of woody plant establishment. It appears that an early successional spatial segregation of *Agropyron repens* and *Poa* species was not strongly related to variation in soil texture but rather to the effects of pre-abandonment weed control practices.

ACKNOWLEDGMENTS

I would like to express my sincere appreciation to my major professor, Dr. Katherine Gross, for her guidance and encouragement throughout the course of this project. I thank the additional members of my committee, Dr. Gary Mittelbach and Dr. Stephen Tonsor for their comments on a previous draft of this thesis. I acknowledge and thank Dr. John Cantlon and Dr. Patricia Werner for allowing me to use the Cantlon fields data set. To Paco Moore and Lisa Huberty I extend my appreciation for the many insightful discussions which greatly contributed to the completion of this work. Finally, I would like to thank my wife, Ann O'Neill, for her patience and support.

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INTRODUCTION

Vegetation change has always been a central theme in plant ecology. The study of temporal changes in community composition, structure and function (the process of succession), and the factors controlling these changes are of great importance to the understanding of ecological systems. The most desirable method of studying vegetation change is to make repeated measurements on a given site over time (Watt 1960, vanden Bergh 1979, van der Maarel 1979, Pickett 1982). However, because of time constraints this method has seldom been used for studies other than those of short duration (Drury and Nisbit 1973, Picket 1982). As a result, much of successional theory is based upon comparisons of multiple plant communities in a landscape that differ in their successional ages (Bazzaz 1968, Pickett 1982, Boerner 1985, Pickett 1987), an approach termed space-for-time substitution by Pickett (1987). The primary problem with this approach is that spatial variation is often confounded with the temporal changes that ecologists aim to understand. This is because each community examined is likely to be unique in some aspect of development (Turkington and Mehrhoff 1990).

The rates and patterns of succession at any given location result from complex interactions among multiple levels of organization (organism, population, community, landscape etc.; McDonnell 1988). These interactions affect those factors which determine the probabilities of plant establishment and persistence (dispersal, emergence, competition, herbivory, predation etc.; McDonnell 1988). For example, the roles of dispersal, herbivory, and predation in structuring community development within a given site depend largely on the structural heterogeneity of the surrounding environment which affects the abundance and movements of animals and seeds throughout the landscape. Community level patterns of vegetation change within a site, as well as variation among sites, cannot be fully understood without recognizing the potential impacts of such landscape level processes on local population and community dynamics.

Numerous studies have shown considerable variation in the rates and patterns of succession among sites, even sites within the same geographic area that have similar soils and topography (Keever 1983, Boerner 1985). Many investigators have cited historical factors associated with past agricultural land-use as possible causes of the between-site variability observed in their studies (Boerner 1985, Keever 1983, Turkington and Mehrhoff 1990). Boerner (1985) showed that the initial composition of sites on several Lake Erie islands differed significantly with pre-abandonment land-use (orchards, vineyards, quarries). Keever (1983) recognized that crop history and the seasonal timing of disturbance and abandonment were important determinants of variation in the patterns of early vegetation development among abandoned agricultural fields in the Eastern United states. She showed that plowing and fallowing during different times of the year affected which species dominated the initial colonizing community, and that this in turn tended to influence the subsequent patterns of early species replacement. Keever (1983) also found that the successional age of the vegetation being disturbed and patterns of prior herbicide use can influence the initial species composition of early successional communities.

There is some question as to what the long-term consequences of such differences in initial species composition might be. One well-established view is that sites of differing initial composition will show convergence over time (Drury and Nisbet 1973, Peet and Christensen 1980, Boerner 1985). However, several studies show that species composition can diverge with time in some systems, indicating that no clear generalization can be made (Mathews 1979, Glenn-Lewin 1980).

Though aspects of land-use history have been shown to be an important determinant of successional variability, few studies have specifically examined how land-use factors can affect initial conditions at the time of abandonment and what the consequences of these conditions are for the subsequent patterns of vegetation development.

In this investigation, I use a case study approach to examine the potential determinants of a succession that has occurred over a 27 year period in an old-field at the Kellogg Biological Station in southwest Michigan. The field, which has a well documented land-use history, was abandoned from row crop cultivation in 1964 and one hectare section (known as Cantlon fields), was set aside for a study of early old-field succession by Dr. John E. Cantlon. During this study, patterns of vegetation change over the first six years post-abandonment were recorded annually in replicated permanent plots, providing a record of early species establishment patterns.

Three aspects of land-use history reported to have affected the early species composition in these plots include: 1) the introduction of *Rhus typhina* L., a clonal shrub, approximately 26 years before abandonment from agriculture, 2) weed control applications applied within two years of abandonment and 3) a post-abandonment disturbance regime implemented as part of a succession field experiment (B. Holt, personal communication).

The purpose of the present study was to assess which factors were most important in determining patterns of vegetation development within Cantlon fields and to determine whether variation in the composition and structure within the community that currently occupies Cantlon fields (1991) is more strongly related to historic factors such as prior land-use or to permanent site characteristics such as topography and soil drainage. General patterns of vegetation change and their relationships to historical and site factors were assessed by comparing two sets of species abundance data: 1) current community data from a vegetation survey carried out in Cantlon fields during 1991, and 2) historic data from the permanent plots censused during the first six years following abandonment of the site.

SITE HISTORY

Pre-Abandonment History

The Cantlon experimental fields were established in 1964 in a three hectare old-field located at Kellogg Biological Station in Kalamazoo County Michigan (Figure 1). The soil is a well drained Oshtemo Sandy Loam located upon gently rolling glacial till. The entire three hectare field was taken out of row crop agriculture in the fall of 1964 and a 100 x 100 meter area was set aside for experimental studies of old-field succession which were conducted from 1964 to 1970. The site has been left virtually undisturbed since the termination of the studies in 1970.

Prior to abandonment in 1964, the three hectare field had been under continuous cultivation for approximately a century (Holt 1969, Werner 1972, Werner and Harbeck 1982). In 1938, the field was planted in hybrid walnut trees which were grown there until the early 1950's when the field was returned to row crop cultivation. It was during the walnut cropping period (approximately 1938-1955) that staghorn sumac (*Rhus typhina* L.), a fast-growing clonal shrub, was planted throughout the field, apparently to serve as a nurse crop for the developing walnut trees (B. Holt, personal communication,

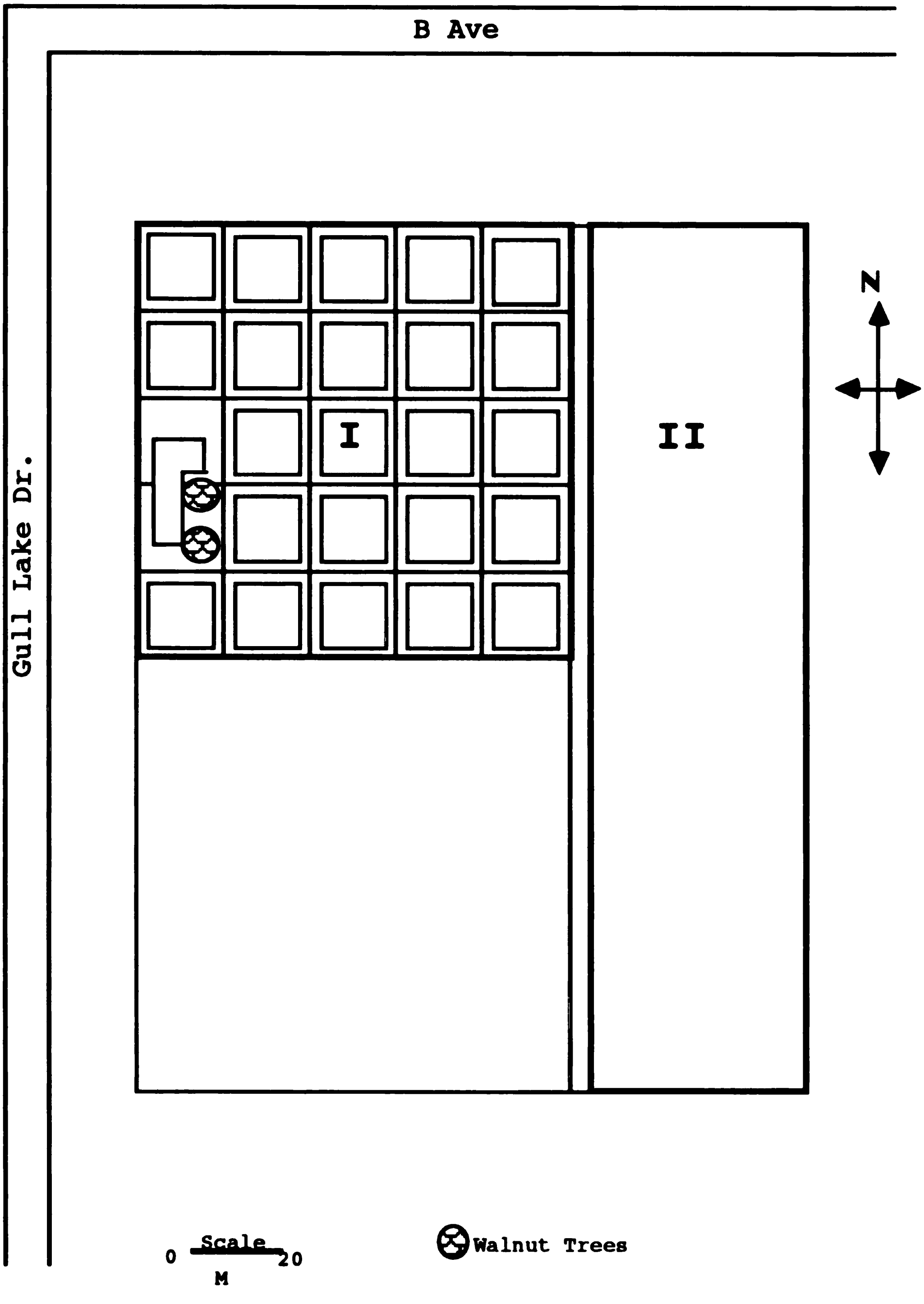

Figure 1. Three hectare old-field at Kellogg Biological Station that was used for several studies of old-field succession between 1964 and 1970. I) Cantlon's experimental fields. II) Field used for patch size study. (Modified from Cantlon, unpublished report).

Werner & Harbeck 1982). Evidently *Rhus* rhizomes and or seeds remained viable in the soil throughout the row cropping period which followed walnut cultivation. As a consequence, *Rhus* became a dominant species within a few years after the site was abandoned from agriculture (Werner and Harbeck 1982).

In the four years prior to abandonment, the field was planted to wheat in 1960; alfalfa 1961-1962; and corn 1963-1964 (Holt 1969, Werner & Harbeck 1982). The final corn crop in 1964 was fertilized at a rate of 250 lbs. per acre (6-24-24; 100 lbs actual nitrogen; Holt 1969). Various herbicide formulations and a prescribed burn were applied to the field in parallel strips during the fall of 1962 and spring of 1963 as part of a quackgrass (*Agropyron repens* (L.) Beauv.; also known as *Elytrigia repens* (L.) Nevski.) control demonstration (Holt 1969, Davis and Cantlon 1969). The approximate spatial distributions of these treatments relative to the study area are shown in Figure 2b.

The Cantlon Studies

The Cantlon experimental succession plots were established in the fall of 1964 to examine how the year of abandonment affected species establishment and replacement patterns. The 100 x 100 meter area was divided into five experimental blocks each containing five 20 x 20 meter plots (Figure 2a). The experimental blocks were primarily

Figure 2. A) Experimental plot array and block arrangement in the 100 x 100 meter study site. Roman numerals indicate blocks, and arabic numerals indicate year of abandonment. Bold lines indicate block boundaries. B) Approximate distribution of weed control treatments applied to the study area during 1962 and 1963. The back ground grid represents the 20 x 20 plot borders and the shaded regions indicate the distribution of weed control treatments (After Holt 1969).

Br = Burned in May 1963.

L = Lorox [3-(3,4-dichlorophenyl)-1-methoxy-1-methylurealurea] applied at 1.5 lbs./acre in 1963.

AT1 = Atrazine (2-chloro-4-ethylamino-6-isopropylamino-1,3,5-triazine) applied at 4 lbs./acre in May 1963.

AM = Amitrol-T (3-amino-1,2,4-triazole with ammonium thiocynate) applied at 2 lbs./acre in May 1963.

AT2 = Atrazine applied at 2 lbs./acre in the spring 1963.

Dal 2,4D = Dalapon (2,2-dicholopropionic acid) applied at 12 lbs./acre in November 1962. 2,4D (2,4-dichlorophenoxyacetic acid) applied at 1.5 lbs./acre in may 1963.

AT2 2,4D = Atrazine applied at 2 lbs./acre in the spring 1963. 2,4D applied at 1.5 lbs./acre in May 1963.

AT3 2,4D = Atrazine applied at 4 lbs./acre in November 1962. 2,4D applied at 1.5 lbs./acre in May 1963.

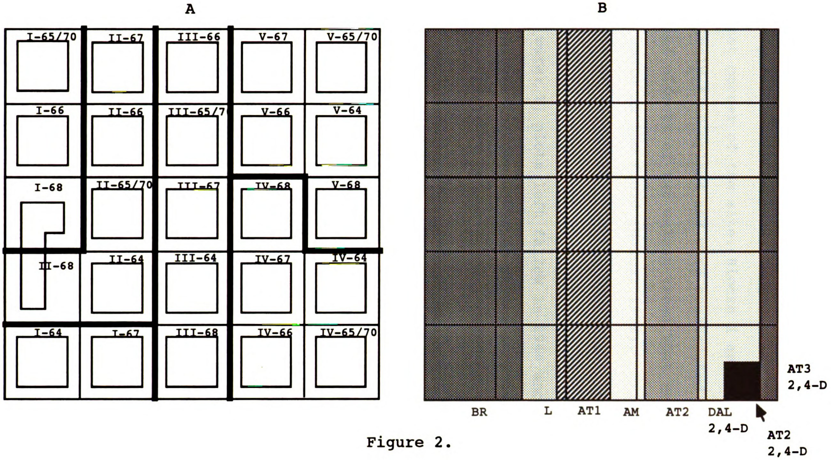
A
I-65/70
II-67
III-66
V-67
V-65/70
I-66
II-66
III-65/7
V-66
V-64
I-68
II-65/70
III-67
IV-68
V-68
II-68
II-64
III-64
IV-67
IV-64
I-64
I-67
III-68
IV-66
IV-65/70
B
AT3
2,4-D
BR
L
AT1
AM
AT2
DAL
2,4-D
AT2
2,4-D

Figure 2.

established with respect to topography (Figure 3). Blocks III, IV, and V are located on a gentle east facing slope of approximately 4-8% which descends toward a low depression in the northeast corner of the site. Blocks I and II are located on a relatively flat upland and were constructed to minimize the potential effects of two walnut trees that were present and still remain in the field (Werner 1972).

A series of sequential plowing treatments were randomly assigned to plots within each block (Figure 2a). The five treatments were: 1) plots left fallow in 1964 and never re-plowed; 2) plowed in June 1965; 3) plowed in June 1966; 4) plowed in June 1967; 5) plowed in June 1968. The 1965 plots were re-plowed and again abandoned in the summer of 1970. This plowing regime created a series of replicated plant communities which differed in year of abandonment. For this reason the treatments will be referred to below as time-since-last-disturbance treatments. Plots common to a particular treatment will be referred to by the year in which they were last disturbed (ie. 1964 plots).

An important aspect of the experimental design is that each set of five plots differed with respect to the successional age of the vegetation which occurred in them before they were plowed and abandoned. Only the first set of five plots (those selected in 1964) followed corn, a situation which is most representative of a typical old-field abandonment. The remaining plots were plowed into natural fallow vegetation that was undergoing succession following

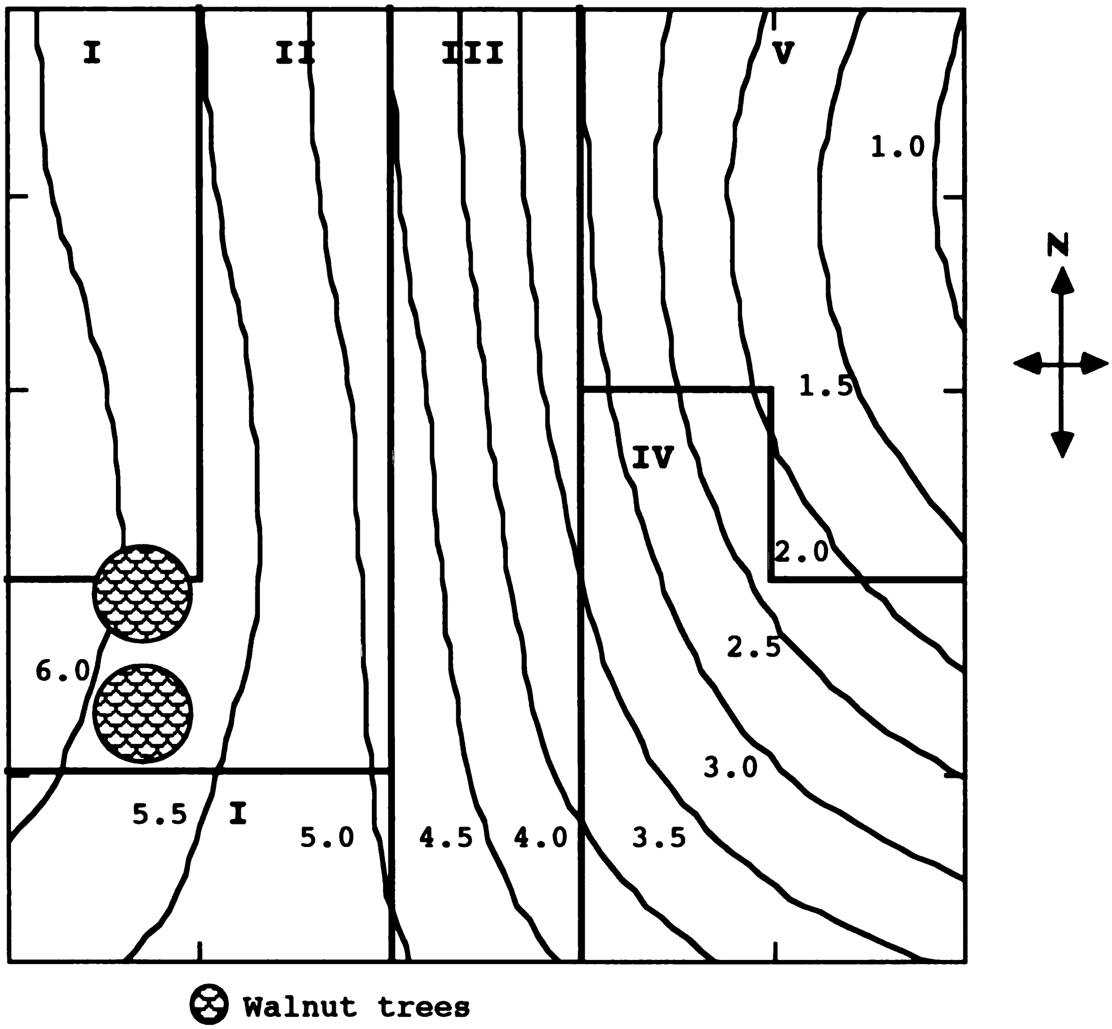

Figure 3. Topographic map of the 100 x 100 meter study area. Values are elevation in meters relative to the lowest point in the field. Experimental blocks are indicated by roman numerals and bold lines.

abandonment. In addition, only the central 16 x 16 meter portion of each plot was plowed leaving a 2 meter buffer zone as an unaltered matrix of vegetation. As a result, all plots were surrounded by a strip of vegetation that was the same age as that within the 1964 plots.

Vegetation composition in these treatments was characterized annually in August of each year following abandonment, beginning in 1965, until termination of the study in 1970. In each 16 x 16 meter plot, species cover estimates were recorded in thirty randomly located 1 x 1 meter quadrats.

Additional Experimental Studies of Succession

In addition to the primary study of succession initiated by Dr. Cantlon, several other studies were carried out at the site between 1968 and 1971 to investigate causal factors influencing species recruitment patterns. Within a 10,000 square meter area (50 x 200 meter) adjacent to Cantlon fields (Figure 1), vegetation was removed from replicated plots of varying sizes to examine the influence of disturbance patch size on species recruitment patterns (Davis and Cantlon 1969).

Two experimental species addition studies were also carried out in Cantlon fields during this period. The effects of immigration time on the establishment success of wild carrot (*Daucus carota* L.) was carried out between 1966 and

1968 in all replicates of the 1964 and 1966 plots (Holt 1969). Seeds of *Daucus* were sown into 260 0.24m^2 quadrats in each age of fallow vegetation (two and four years). Seedling emergence, survivorship, and fecundity were quantified over a three year period. The quadrats were located in strips which were placed on the west and east borders of the 1964 and 1966 16m^2 plots (Figure 4).

Between 1969 and 1971 the effects of an introduced biennial on early old-field community composition, structure and diversity was investigated (Werner 1972). Seed of teasel (*Dipsacus sylvestris* Huds.) were sown into 8 strips of 52 0.25m^2 quadrats located on the west and east sides of five of the 16m^2 plots (four strips in 1967 plots, and four strips in 1968 plots; Figure 4). Community parameters within treatment and control (no *Dipsacus*) quadrats were compared over a three year period.

Following the termination of the primary study in 1970 the vegetation in Cantlon fields was left virtually undisturbed. However, in 1979 patterns of tree seedling establishment were investigated at the site (Werner and Harbeck 1982). The results of this study suggest that staghorn sumac (*Rhus typhina*) likely played an important role in the development of the vegetation in Cantlon fields. All trees within five 10 year-old and five 16 year-old fields (replicates of the 1964 and 1970 plots respectively) were identified and aged. Tree seedling densities were then related to the distribution of *Rhus* which dominated the plant

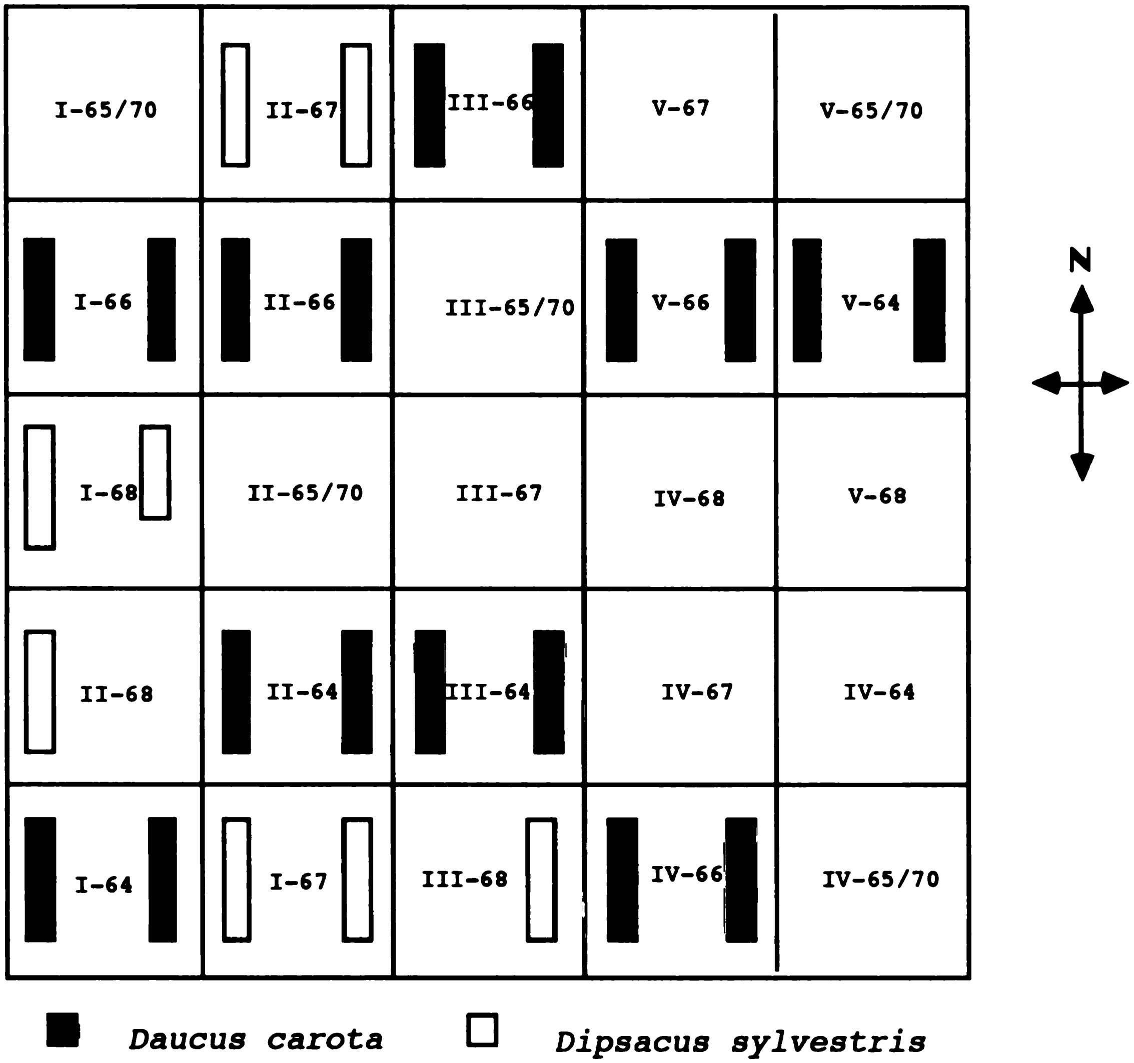

Figure 4. Quadrat locations for the two species introduction studies carried out in Cantlon fields (Holt 1969, Werner 1972). Dimensions of the quadrat strips are not drawn to scale (Modified from Holt 1969, and Werner 1972).

community at the time. This study revealed that tree seedling density was significantly higher beneath the canopy of *Rhus*. Werner and Harbeck (1982) suggested that *Rhus* may have indirectly promoted tree establishment success by reducing herbaceous cover through shading and by facilitating seed dispersal.

Current Community

In 1990 the vegetation occupying the entire 100 x 100 meter area was classified as a mixed copse plant community composed of dense shrubs, trees and vines intermixed with patches of perennial grasses and forbs (Burbank et al. 1992). Much of the site is covered by shrub thicket. However, the eastern third of the area, where the field slopes towards a depression in the northeast corner (Area occupied largely by blocks IV and V), has few woody species and is occupied primarily by perennial grasses and forbs. The boundary between the thicket and the more open area is quite abrupt giving the appearance of a distinct west to east zonation in the vegetation. Possible determinants of this zonation investigated in this study include: 1) the presence of a strong soil moisture gradient along the slope of the field which may have influenced woody plant establishment patterns and 2) the influence of prior land use history and the early establishment patterns of the initial dominant species.

METHODS

Vegetation Sampling

In the summer of 1991, the species composition and structure of the current plant community within the Cantlon fields experimental area was determined. The field was surveyed in a manner to allow comparison of the vegetation patterns to the permanent site characteristics (soil texture and topography), early successional vegetation patterns, and factors associated with prior land-use history. The original boundaries of the 100 x 100 meter study area were relocated and the locations of the 25, 20 x 20 meter plots (16 x 16 meter plots plus buffer zones) were marked with wooden posts at corners. No attempt was made to locate the positions of the 150 quadrats (30 per plot) from which cover data was originally recorded.

To examine the observed vegetation patterns in relation to both the original experimental plot array and to the apparent west to east zonation in the woody vegetation, five west to east oriented parallel transects were established across the site. Transects were set 20 meters apart and placed such that each ran through the center of five adjacent plots (Figure 5). Along each transect 31 points were selected

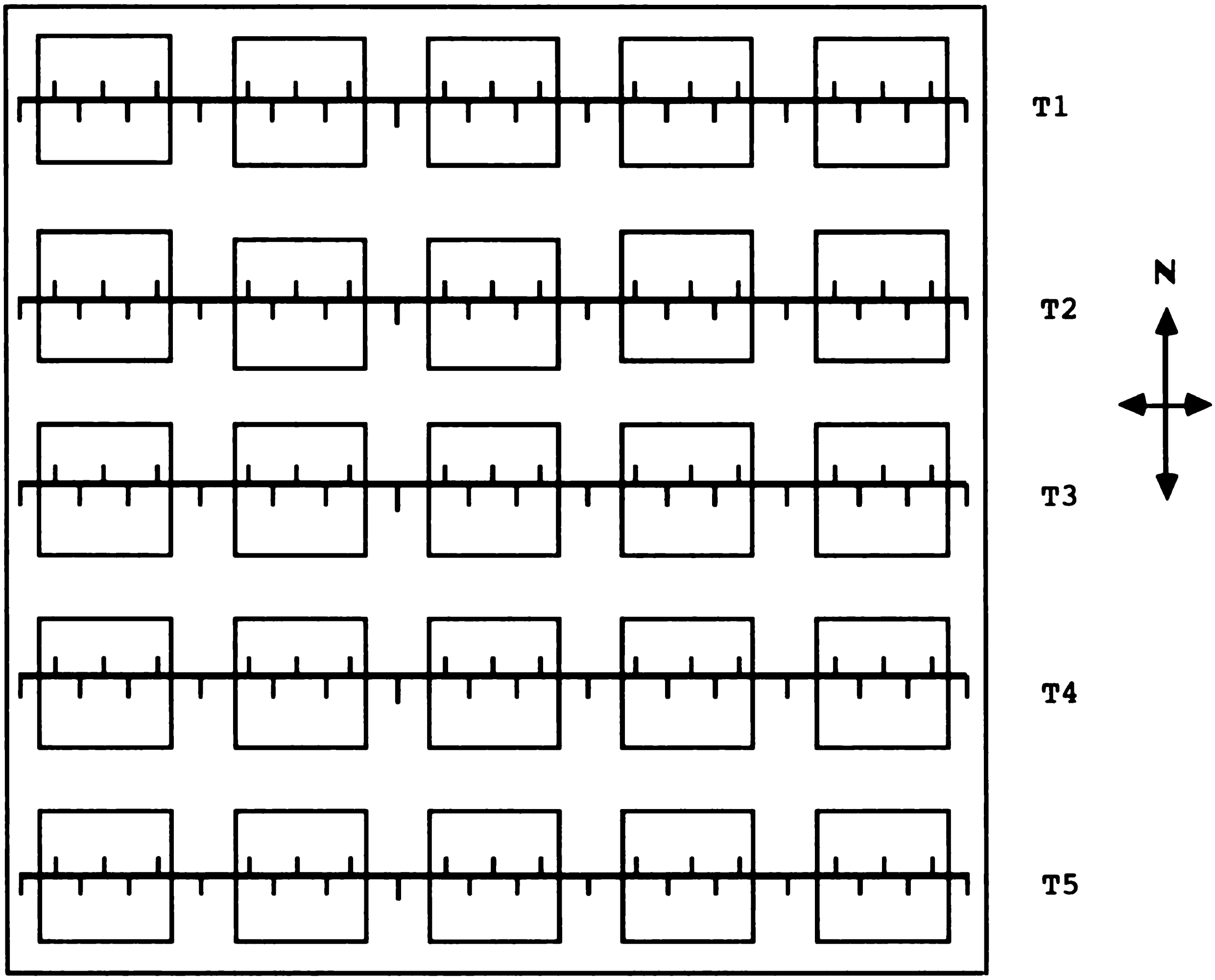

Figure 5. Positions of the five transects used to sample the vegetation in 1991. The short line segments along each transect represent the locations of the 155 $1m^2$ quadrats.

at regular intervals and vegetation composition at each point determined in $1m^2$ quadrats. Quadrats were placed such that five equally spaced (3 meters apart) quadrats lay within each of the five 16 x 16 meter plots crossed by that transect. The remaining six quadrats on each transect were distributed so that one lay in the center of each buffer zone crossed by the transect.

Percentage cover of plant species rooted within each of the 155 quadrats and species projecting downward upon quadrats were visually estimated. At each quadrat position, cover of both rooted and non-rooted species was estimated in relation to the same $1m^2$ quadrat so that the abundance of herbaceous plants as well as shrubs and trees could be estimated on the same scale of measurement. Because it was desired to assess species composition in the immediate area occupied by each quadrat, non-rooted species which projected onto a quadrat, but were rooted more than three meters from the transect point, were not recorded. Because the dominant species in this field were shrubs of fairly low stature and crown diameters that rarely exceeded three meters, only a few of the non-rooted individuals that projected onto a quadrat (large trees) were not recorded. Visual estimates of cover, especially cover projections of shrubs and trees, are very subjective and subject to a high degree of error. However, because only coarse-grained patterns in the vegetation were sought, this method was adequate for the purposes of the study.

Soil Analysis

In addition to species cover, several soil factors and relative elevation were measured within Cantlon fields. Soil samples were taken from within each of the 155 quadrats with a 2.5cm diameter soil tube corer to a depth of approximately 30 centimeters. Each core was separated into the A and B horizons. Samples from 75 of the 155 quadrats (three per 16 x 16 meter plot) were air dried and then processed to determine particle size. Coarse fractions (particles > 2mm) were separated into three size classes by sieving (2-4mm, 4-8mm, >8mm) and then weighed. The fine fraction (particles < 2mm in diameter) was assessed for proportions of sand, silt and clay using the hydrometer method (Brower and Zar 1984). Relative elevation values were estimated for all quadrats by constructing a topographic map of the area and then superimposing quadrat positions upon it. The map was produced by sighting 45 points of known location (relative to plot boundaries) with a transit and then calculating relative elevation (Figure 3).

Data Analysis

Multivariate analyses were used to examine patterns in species composition within both the historic data (collected from 1965-1970) and the current community data (collected in 1991). Two ordinations of the 25 16 x 16 meter experimental plots (based on species cover) were developed using Principal Components Analysis (PCA). The ordination of the plots as they appeared in 1991 (current community patterns) is based on mean percentage cover values of species calculated by averaging over the 5 quadrats located in each plot. The ordination of the plots as they appeared in 1970 (historic community pattern) is based on the mean percentage cover values of species calculated by averaging over the 30 quadrats within each plot. To reduce noise in the data and to allow examination of broad-scale patterns, only species with relative cover values greater than or equal to 2% were included in the analyses (Pielou 1984). Based on this 2% criteria, nine species from the 1991 data set and five species from the 1970 data were retained for use in the multivariate analyses. These species are hereafter referred to as "dominant species".

Correlation analysis was used to examine the possible influence of site factors on the current structure of the community. Spearman rank correlation analysis was used to examine patterns of association between soil texture variables and PC scores of plant community composition (both historic and current data). Canonical correlation analysis (CCA) was used to examine the association between the permanent site factors (soil texture and relative elevation) and the vegetation (species cover) variables simultaneously (current community data only). CCA is a multivariate method that is an extension of simple correlation to situations where information regarding relationships between two sets of interdependent variables are sought. The method constructs a linear function (canonical variate) of one set of variables (in this case the species abundances of the same nine species used in PCA) and a linear function of the second set (site variables) such that the correlation between the two variates is maximized. A second pair of canonical variates can be constructed in the same manner with the correlation being less than between members of the first pair. Additional pairs of canonical variates can be produced, each with smaller correlations between members than the previous pairs (Webster 1977, James and McCulloch 1990). Because this method is designed to maximize correlations between variates, canonical correlation coefficients must be interpreted with caution. Ecological significance must be evaluated by examining the outcome of both a likelihood ratio test, which evaluates the significance of linear association between each pair of canonical variates, and a redundancy analysis (Van den Wollenberg 1977) which evaluates the proportion of the variance within a set of variables (species abundances) predictable from a linear combination of a second set of variables (site factors). CCA was performed on raw cover values obtained from the individual 0.5 x 2 meter quadrats measured in 1991 (n=75).

Portions of the historical data set were analyzed using analysis of variance to test for time-since-last-disturbance and block effects on individual species abundances. Some of the species cover data were square root transformed to meet the normality assumption of ANOVA. For these data, normality and homogeneity of variance were confirmed by normal probability plotting and Bartlett's test respectively. The significance of all statistical tests were assessed at the 5% probability level. All analyses were performed using SYSTAT (version 5.1) and SAS (version 5.4).

Vascular plant nomenclature for species recorded in both the early successional and current communities follows Fernald (1950). For brevity species are often referred to below by genus name only.

RESULTS

Current Community Composition and Structure

A total of 75 plant species were recorded in the 1991 vegetation survey of Cantlon fields (Table 1). Of these species, only nine had relative cover values greater than 2%. These nine dominant species were: *Lonicera tatarica* L., *Celastrus orbiculatus* L., *Solidago canadensis* L., *Poa pratensis* L., *Rhus typhina* L., *Juglans nigra* L. *Agropyron repens* (L.) Beauv., *Achillea millefolium L., and Ulmus rubra* Muhl. Together these species comprised 77% of the total vegetative cover in the community.

The current vegetation within Cantlon fields exhibits a fairly distinct west to east zonation in species abundance and life form composition (Figure 6). The western portion of the site is dominated by dense shrub thickets comprised primarily of *Lonicera tatarica, Celastrus orbiculatus* and *Rhus typhina* with other less frequent species of shrubs, trees and vines intermixed. *Rhus typhina* increases in abundance towards the center of the site where tree species such as *Juglans nigra, Ulmus rubra* and *Morus alba*, which are more numerous at the western extreme of the site, decline in abundance. On the eastern side of the site there is a

Table 1. Relative abundance of the common species (≥1%) observed in the 1991 vegetation survey of Cantlon field. The dominant species (≥2% relative cover) used in PCA are in bold type.

Species	Relative Cover	Frequency**
Lonicera tatarica	0.200	96
Celastrus orbiculatus	0.176	94
Solidago canadensis	0.111	75
Poa pratensis	0.093	102
Rhus typhina	0.075	79
Juglans nigra	0.045	45
Agropyron repens*	0.025	70
Achillea millefolium	0.022	57
Ulmus rubra	0.022	16
Morus alba	0.017	14
Bromus inermis	0.015	11
Rhamnus cathartica	0.015	34
Lonicera mackii	0.014	10
Rubus spp.	0.014	27
Daucus carota	0.014	43
Poa compressa	0.013	44
Fraxinus americana	0.013	18
Vitis spp.	0.012	15
Rhamnus frangula	0.011	15
Remaining 56 Species	0.093	

Total Number Of Species = 75
Nomenclature follows Fernald (1950).
* Species also known as *Elytrigia repens* (L.) Nevski.
** Number of quadrats out of a total of 155.

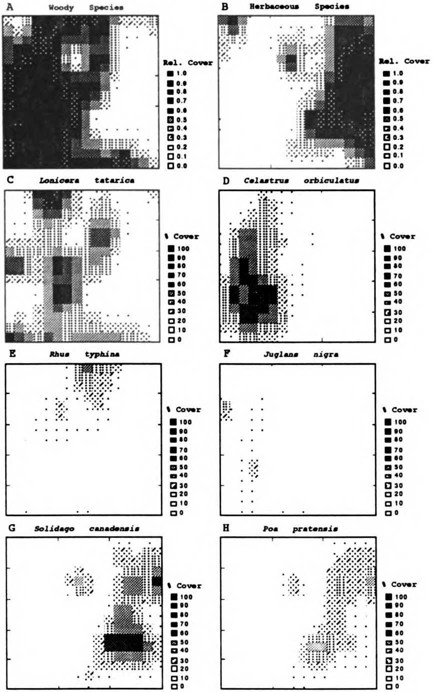

Figure 6. Cover distribution maps of woody (A), and herbaceous (B) relative cover, and the percentage cover of the 6 most common species (C-H) observed in the 1991 vegetation survey of the Cantlon fields experimental area. Each map represents a 100 x 100 meter area.

distinct reduction in woody vegetation and the area is dominated by perennial herbs and grasses such as *Solidago canadensis, Achillea millefolium, Poa pratensis* and *Agropyron repens*.

Current Community Vegetation-Site Relationships

The first three PCA axes of the current plant community composition accounts for 69% of the total variation (50, 10, and 9 percent respectively). The first principal component (PC1) reflects a gradient in woody species cover (Figure 7). This is consistent with the west to east pattern of zonation in woody species apparent in the cover distribution maps (Figure 6). Plots in blocks I and II (except one plot from block I) have negative PC1 scores and tend to occupy the left (woody) side of the ordination space, while all plots from blocks IV and V have positive PC1 scores and tend to occupy the right (herbaceous) side of the ordination space (Figure 7). Plots with PC1 scores near zero are intermediate in woody and herbaceous cover. PC2 appears to primarily represent variation in the cover of *Ulmus rubra*; this axis separates three plots that have conspicuously high amounts of *Ulmus* cover from the rest of the plots.

There is a strong association between the current abundances of the dominant species and relative elevation within Cantlon fields. However there is no such relationship between the current vegetation pattern and soil texture. The

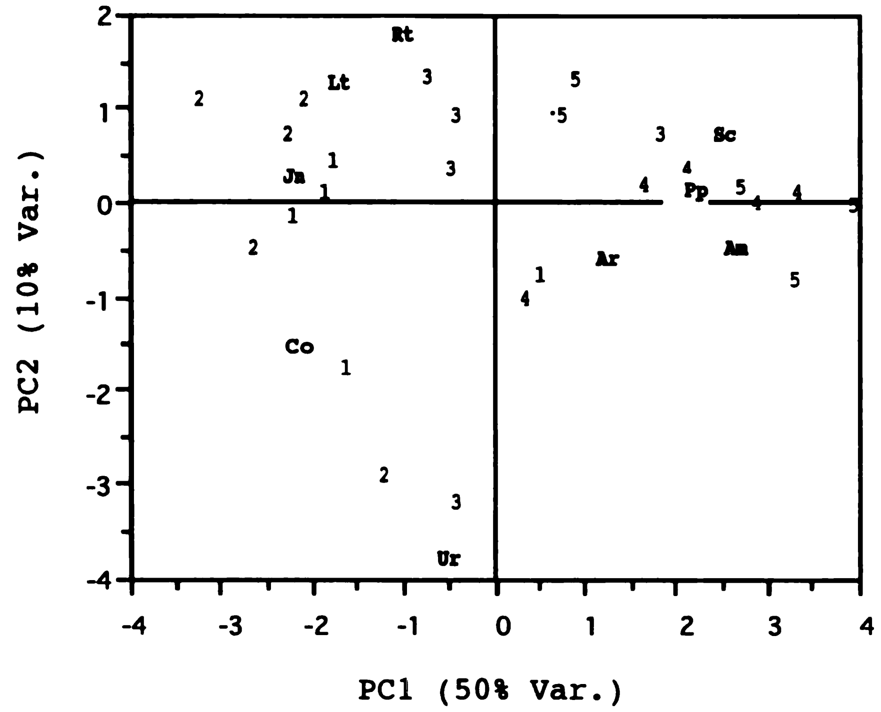

Figure 7. Principal component ordination of all plots censused in 1991. Numbers represent the block in which plots are located. Bold two letter codes indicate species positions in the ordination space. Am = *Achillea millefolium*. Ar = *Agropyron repens*. Co = *Celastrus orbiculatus*. Pp = *Poa pratensis*. Jn = *Juglans nigra*. Lt = *Lonicera tatarica*. Rt = *Rhus typhina*. Sc = *Solidago canadensis*. Ur = *Ulmus rubra*.

first principal component is strongly correlated with relative elevation ($r=-0.81$, $p<0.005$) but is only weakly correlated with the soil texture variables (Table 2). A weak gradient in soil texture along the slope of the field is suggested by the significant negative correlations between four of the coarse fragment variables and relative elevation. These correlations reflect a tendency towards greater amounts of coarse fragments in plots located in the lower areas of the field. However, the range of variation in these variables is fairly narrow as indicated by their standard deviations (Table 2) and thus are not likely to produce strong variation in soil moisture.

The first pair of canonical variates generated by CCA were significantly positively correlated (Table 3a). Examination of the site variable loadings (Table 3b) suggest that this is due primarily to variation in relative elevation across the site and the apparent effects on vegetation patterns. However, it is not possible to distinguish between a possible slope effect and the influence of other factors that might be coincident with the slope of the field (ie. potential herbicide effects etc.). To examine the relationship between the vegetation and soil texture exclusively, a second CCA was performed with relative elevation excluded. In this analysis the correlation between the first pair of canonical variates was reduced (0.69 vs 0.85) but was still significant ($p< 0.05$). The significant correlation between the first pair of canonical variates does

Table 2. Comparison of site variables (plot mean values and standard deviations, N=25) with plot principal component scores and mean relative elevation using Spearman Rank Correlation Analysis. Significance symbols: *, $p < 0.05$; **, $p < 0.005$.

			Rank Corrlation Coefficients			
Site Factors	Mean	SD	PC1	PC2	PC3	Rel.Elev.
Soil Particle size*						
Sand in A	.699	.054	-.14	-.22	.18	.10
Clay in B	.031	.031	.23	.14	-.12	-.26
2-4mm in A	.040	.010	.31	.30	.07	-.47*
4-8mm in A	.033	.011	.01	.24	.27	-.17
> 8mm in A	.036	.017	.07	.14	-.19	-.14
Sand in B	.672	.093	.36	-.20	.29	-.37
Clay in B	.095	.046	-.33	.37	-.19	.34
2-4mm in B	.067	.023	.54*	.30	.02	-.54*
4-8mm in B	.047	.020	.49*	.26	.10	-.52*
> 8mm in B	.039	.031	.31	.19	.18	-.47*
Rel. Elevation.	3.753	1.575	-.81**	-.18	.26	1.00

* Proportion of soil sample comprised of a given particle size.

Table 3. A) Comparison of vegetation and site variables using canonical correlation analysis with and without relative elevation included. B) Site variable loadings (correlations between site variables and their canonical variates). Significance symbols: *, $p < 0.05$; **, $p < 0.005$.

A

Canonical Variates	Canonical Correlation Coefficients With Rel. Elev.	Without Rel.Elev.
First	.85**	.69*
Second	.58	.57
Third	.51	.44

B

Site variables	Correlation Coefficients 1st Variate	2nd variate	3rd Variate
Sand in A	-.07	.24	.23
Sand in B	.38	.44	-.06
2-4mm in A	.20	-.23	.22
4-8mm in A	.23	-.13	.50*
> 8mm in A	.38	-.21	.52*
Sand in B	.36	.52	.14
Clay in B	.20	-.65	.10
2-4mm in B	.61*	.18	.32
4-8mm in B	.56*	-.09	.10
> 8mm in B	.52*	.16	.23
Rel. Elevation	.95**	-.12	.13

not mean that soil texture necessarily explains a significant degree of the variation in the vegetation. Redundancy analysis indicates that the soil texture canonical variate explains only 10% of the variation in species cover. This is an indication that soil drainage was not an important determinate of within site differences in species abundances and that other factors such as prior land use and initial species composition may have been more important in determining the west to east zonation of the vegetation in the current community.

Early Successional Patterns

The species cover data from 1970 reveals the presence of similar patterns of variation in species distributions within the early successional community as that observed in the current community (west to east zonation), possibly reflecting the early stages of development of the current pattern. This early pattern was largely due to variation in the abundance of three perennial grasses: *Agropyron repens*, *Poa compressa* and *Poa pratensis*. *Rhus typhina* did not appear to contribute significantly to this pattern.

Principal component analysis of the 1970 species abundance data reveal both spatial and temporal patterns of variation in the abundance and distribution of the dominant species. PC1, which explains 40% of the total variation, reflects the major spatial gradient in the community. This axis is significantly correlated with the first principal component generated from the 1991 ordination and in both data sets is significantly correlated with relative elevation (Table 4). The component loadings for PC1 indicate complementarity in the abundance of *Agropyron repens* and the other dominant perennial species (*Poa* species and *Rhus typhina;* Table 5). PC2, which explains 30% of the total variation, reflects the influence of time-since-last-disturbance on the distribution of species cover and separates plots plowed three months prior to the 1970 census from those plots plowed and abandoned in earlier years (Figure 8). The species loadings on PC2 indicate that this axis represents a contrast between the abundance of *Agropyron repens*, a rhizomatous perennial, and several annual dicots (e.g. *Amaranthus* species) which were most abundant in the plots last plowed in 1970 (Figure 9a).

Time-since-last-disturbance and block location both had significant effects on cover of *Agropyron repens* and the two *Poa* species in 1970. There were no significant treatment or block effects on the cover of *Rhus typhina*. The significant treatment effect on *Agropyron* cover (F=6.2 p<.001) reflects the negative impact of plowing the 1970 plots three months prior to censusing (Figure 9a). The block effect on *Agropyron* cover (F=4.3 p<.05) reflects a tendency toward higher cover within blocks I and II compared to the remaining three blocks (Figure 9b).

The *Poa* species (*Poa compressa* and *Poa pratensis*)

Table 4. Comparison of 1991 principal component scores and site variables (plot mean values) with 1970 principal component scores using Spearman Rank Correlation Analysis (N=25). Significance symbols: *, $p < 0.05$; **, $p < 0.005$

	Rank Correlation Coefficients		
	PC1 (1970)	PC2 (1970)	PC3 (1970)
Principal Components			
PC1 (1991)	.56**	-.40*	-.18
PC2 (1991)	.08	.20	.41
PC3 (1991)	-.22	.19	-.03
Relative Elevation	-.53*	.26	.11
Time-Since-Disturbance	-.33	-.35	.16
Soil Particle Size*			
Sand in A	-.13	-.14	-.11
Clay in A	.08	.15	.18
2-4mm in A	.14	.03	-.01
4-8mm in A	-.13	.09	-.11
>8mm in A	.12	.09	.02
Sand in B	.46*	-.43*	-.08
Clay in B	-.32	.43*	.14
2-4mm in B	.29	-.19	.09
4-8mm in B	.21	-.12	-.05
>8mm in B	.09	.05	-.09

* Proportion of soil sample comprised of a given particle size

Table 5. Species abundance loadings for the first three principal components of the 1970 data.

	Component Loadings		
	PC1	PC2	PC3
Agropyron repens	-0.721	0.711	0.131
Amaranthus spp.	-0.068	-0.694	-0.152
Poa compressa	0.811	0.244	0.299
Poa pratensis	0.654	0.113	-0.157
Rhus typhina	0.658	0.026	0.815

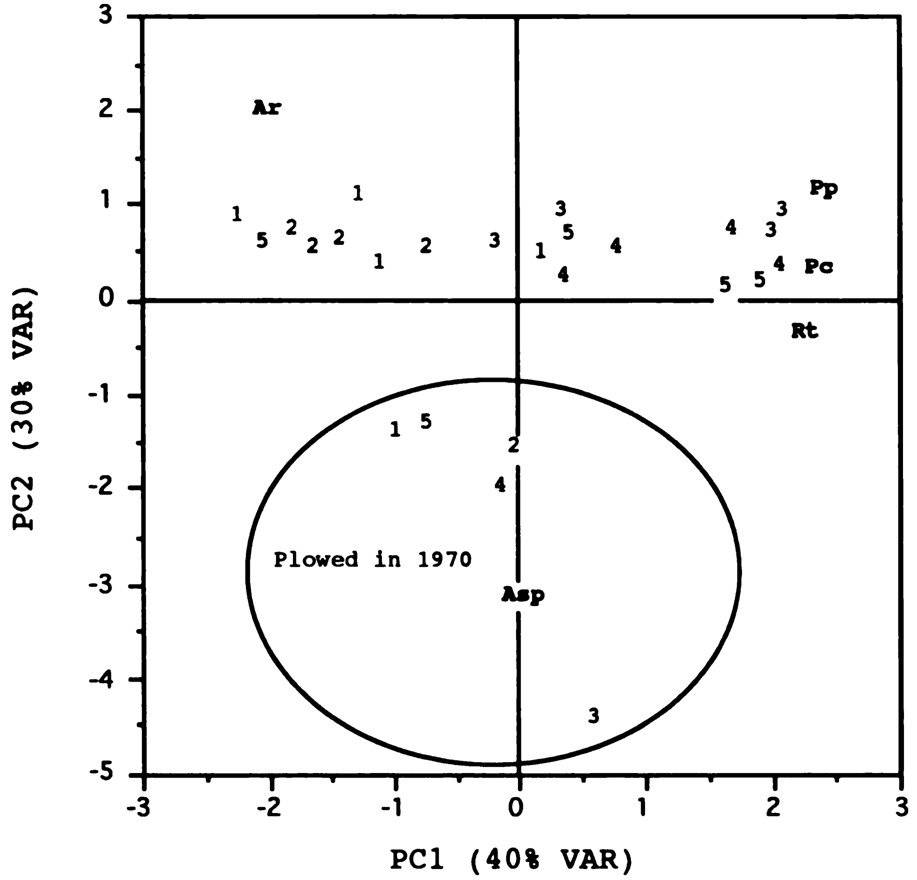

Figure 8. Principal component ordination of all plots censused in 1970. Numbers represent the block in which plots are located. Bold two letter codes indicate species positions in the ordination space. Asp = *Amaranthus* species (*A. albus, A. hybridus, A. retroflexus, A. veridis*). Ar = *Agropyron repens*. Pc = *Poa compressa*. Pp = *Poa pratensis*. Rt = *Rhus typhina*.

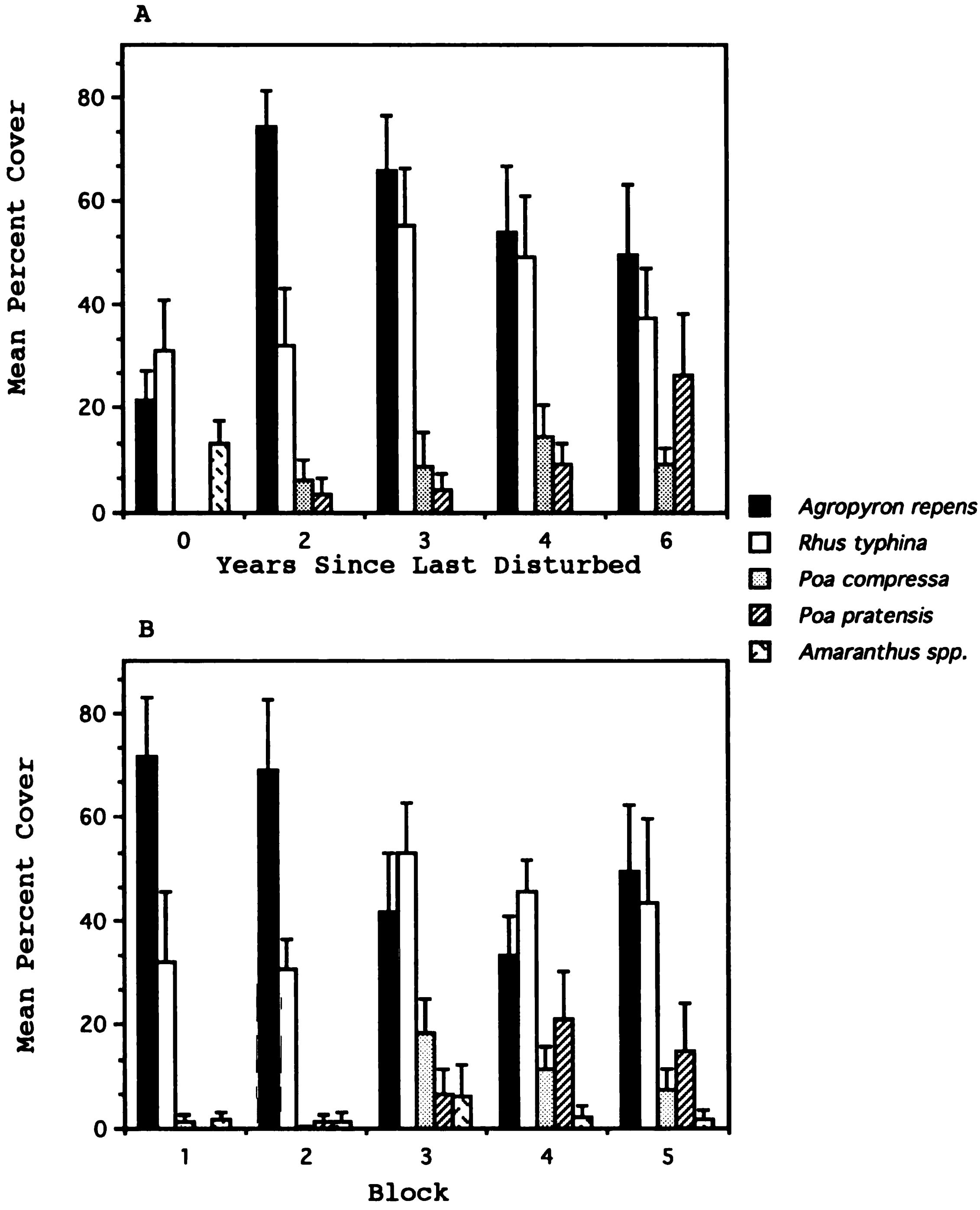

Figure 9. Percentage cover (mean + S.E.) of the species present in Cantlon fields in 1970. A) Species among plots having undergone a different number of years of succession. B) Species among plots in experimental blocks. (*Amaranthus* species = *A. albus, A hybridus, A. retroflexus*, and *A, veridis*).

together had complementary patterns of abundance to that of *Agropyron*. Percent cover of *Poa* species was significantly higher (F=4.8 p<.01) in blocks III-V where *Agropyron* was less abundant (Figure 9b). If the 1964 plots (those not re-plowed after abandonment from agriculture) are excluded from the analysis there is a strong negative correlation between the cover of *Agropyron* and *Poa* species (r=-0.95 p<0.0001) in the field in 1970.

Cover maps of the dominant species illustrate graphically the spatial structure of the early successional plant community as it developed from 1968 to 1970 (Figure 10). The most striking pattern is the high degree of segregation between *Agropyron repens* and *Poa* species cover. This west to east zonation exhibited by the perennial grasses and the high concentration of *Agropyron* cover in the portion of the field that had been previously burned (Figure 2b) suggests that the pre-abandonment weed control treatments may have influenced the distribution of *Agropyron* cover. As was indicated by a non-significant block effect, cover of *Rhus* in 1970 did not exhibit any pattern of variation from west to east across the field as was apparent in the coverage of the dominant perennial grasses (Figure 10).

There is some evidence that the strong spatial segregation of perennial grasses in this community in 1970 was influenced by the early patterns of colonization by *Agropyron repens*. Analysis of mean cover in plots in each successive census year reveals that *Agropyron* was the

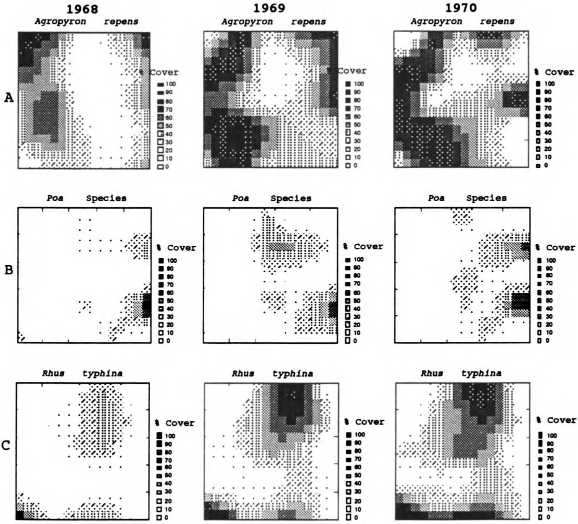

Figure 10. Cover distribution maps of (A) *Agropyron repens*, (B) *Poa* species (*Poa compressa* and *Poa pratensis*) and (C) *Rhus typhina* in 1968, 1969, and 1970 in the Cantlon fields experimental area. Each map represents a 100 x 100 meter area.

dominant species in the field during the first five years of succession (Figure 11). In contrast, the two *Poa* species were present only in trace amounts in the plots during the initial year of succession. Both *Poa* species were first observed in the second year following abandonment and cover increased continuously in successive years (Figure 11).

The dominance of *Agropyron repens* and *Rhus typhina* in the early successional community of Cantlon fields may have been partially due to the effects of time-since-last-disturbance on the initial abundance of these species. Analysis of the 25 plots in their first year after the initiation of each treatment, revealed significant differences between plots left fallow (and never re-plowed) after the final crop harvest (treatment 1) and those plots that were plowed in subsequent years (treatments 2-5) (Figure 12a). The relative cover of *Agropyron*, *Rhus*, and *Poa* species and species diversity, as measured by the Shannon diversity index (H'), significantly differed among the treatments (*Agropyron*, $F=7.6$ $p<.001$; *Rhus*, $F=4.6$ $p<.01$; *Poa* spp., $F=5.99$ $p<.01$; H', $F=14.5$ $p<.001$). The average relative cover of *Agropyron* was lower in treatment 1 (abandoned in 1964) than in any of the other four treatments. In treatment 1 *Agropyron* was less abundant than two other species (*Amaranthus* species and *Erigeron annuus*) and contributed an average of only 10 percent to the total cover among plots in treatment 1 (Figure 12a). In contrast, in Treatments 2-5, *Agropyron* was the species with the greatest average relative

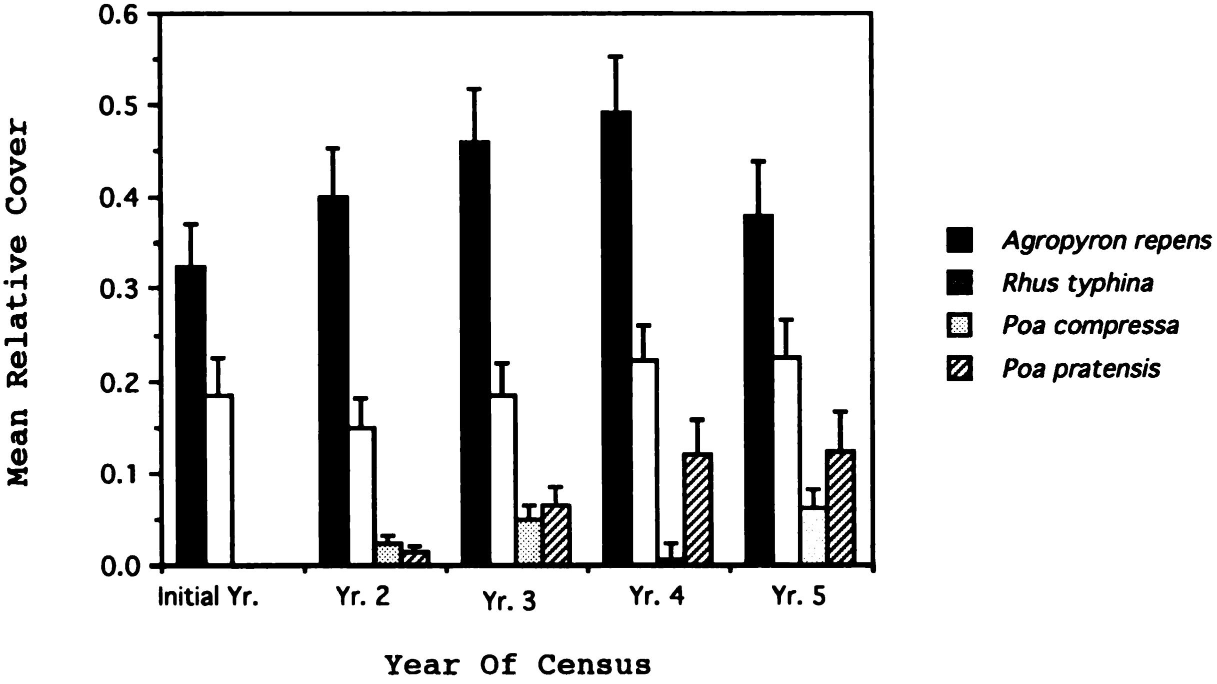

Figure 11. Temporal pattern in relative cover (mean + S.E.) of *Agropyron repens*, *Rhus typhina* and the *Poa* species during the first 5 years of succession within experimental plots (n=25 for the first 3 years; n=20 for year 4, and n=15 for year 5).

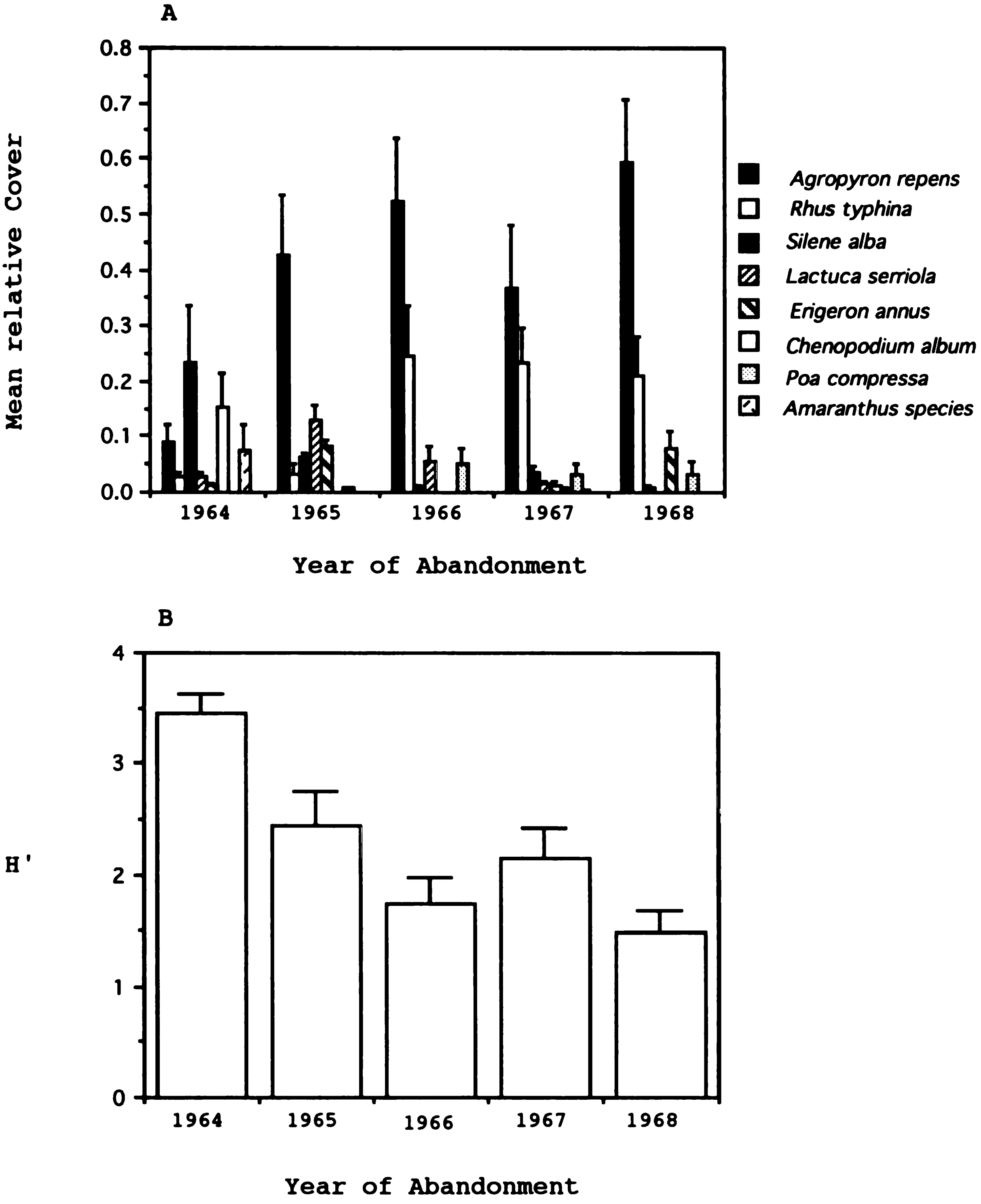

Figure 12. A) Relative cover (Mean + S. E.) of common plant species and B) species diversity (H'; Mean + S. E.) in plots one year after being plowed and abandoned.

cover. Plant species diversity (H') was significantly higher in treatment 1 than in any of the other treatments (Figure 12b) suggesting the presence of a negative relationship between the abundance of *Agropyron* and species diversity in the early successional community. *Rhus* exhibited a similar pattern to that of *Agropyron* with elevated relative cover in treatments 3-5 (Figure 12a).

DISCUSSION

A number of studies have shown that initial patterns of species composition and abundance can strongly differ among newly abandoned fields because of historical differences in past agricultural use (crop history, herbicide and fertilizer use, timing of abandonment etc.; Keever 1983, Boerner 1985, Squires 1989), even among fields in the same geographic region that are similar with respect to soils, topography, and the species available for colonization. Whether early differences in species composition persist or if sites converge on a similar species assemblage over time depends to some degree upon the biology of the early dominant species and their influence on the subsequent recruitment of later arriving species (Keever 1983, Boerner 1985).

The west to east zonation of the vegetation in the plant community currently occupying Cantlon fields reflects divergent patterns of succession that have occurred over a 27 year period. The western two thirds of the site has developed into a woody thicket, while the eastern third of the site appears to have resisted invasion by woody plants. The results of this study suggest that this divergence is not due to variation in soil drainage or texture across the site, but more likely to the influence of historical factors on the initial abundance and distribution of the early dominant species (*Agropyron repens, Rhus typhina,* and *Poa* species) and the differential affects of these species on patterns of woody plant establishment in Cantlon fields.

The Impact of Prior Land Use on Initial Dominant Species

All of the land use factors considered in this study appear to have influenced the abundance and distribution of *Agropyron repens* and *Rhus typhina* which initially dominated the early successional plant community within Cantlon fields.

The introduction of *Rhus typhina* to the site approximately 26 years prior to field abandonment and a historically high abundance of *Agropyron repens* likely contributed to early dominance by these species once agricultural activities ceased.

The weed control treatments applied to the field prior to abandonment strongly affected the early spatial distribution of *Agropyron*. *Agropyron* cover was highest in 1970 within blocks I and II where a prescribed burn and a broad-leaf herbicide (LOROX) were applied in 1963. LOROX is not considered effective for control of *Agropyron* (Kells and Renner 1990) and a prescribed burn likely enhanced the growth of *Agropyron* by breaking the dormancy of secondary buds and stimulating aggressive clonal spread (Werner and Rioux 1979). The significantly lower early successional cover of *Agropyron* in blocks III-V may have been due to the application of herbicides formulations containing either Atrazine or Amitrol. These two chemicals are generally considered to be effective in controlling *Agropyron* (Kells and Renner 1990).

The plowing treatments applied to the Cantlon field plots between 1965 and 1970, which were originally applied in order to examine the effects of year of abandonment on the early successional community, appeared to have enhanced the early growth of both *Agropyron* and *Rhus* thus contributing to their dominance of the early successional community. Both *Agropyron* and *Rhus* are rhizomatous species capable of rapid clonal spread, a condition generally favored by disturbance. *Agropyron* is known to be encouraged by modern cultural practices and a single tillage operation such as those applied in Cantlon fields, likely enhanced its growth by activating dormant buds and promoting clonal spread (Werner and Rioux 1979). Similarly, disturbances such as frost, fire, and mechanical damage, are known to break apical dominance and stimulate the formation of new stems in several species of *Rhus* (Gilbert 1966, Barnes and Wagner 1989, Luken 1990). Most of the experimental plots in Cantlon fields were plowed one or more years after abandonment from agriculture. As a result, communities supporting developing vegetation were being disturbed. Plowing plots containing established populations of *Agropyron* and *Rhus* likely enhanced the clonal spread of these species.

Impact of Early Dominant Species on Community Development

Interactions between *Agropyron* and *Poa*:

By 1970 a distinct west to east zonation in perennial grasses had developed across Cantlon fields. *Agropyron* colonized much of the site after abandonment in 1964 and quickly dominated much of blocks I and II. Poa species (*Poa compressa* and Poa *pratensis*) colonized more gradually and by 1970 dominated much of the area within blocks III, IV, and V where *Agropyron* was less abundant.

Similar temporal patterns of colonization by *Agropyron* and *Poa* species have been documented in old-field successions elsewhere in the Midwest. Tilman and Wedin (1991) report that among old-fields at Cedar Creek Natural History Area in Minnesota *Agropyron repens* typically colonizes newly abandoned sites, reaches peak relative abundance within 2-3 years after abandonment, and then declines fairly rapidly. In contrast, *Poa pratensis* usually arrives in these fields around year five, rises to dominance within ten years and then can remain dominant for many years. After approximately 40 years the prairie grasses *Schizachyrium scoparium* and *Andropogon gerardi* become the dominant species in these fields. Tilman and Wedin (1991) suggest that the temporal distribution of these grass species at Cedar Creek may be a reflection of differences in patterns of plant allocation which in turn affect the relative colonization and competitive abilities of these species. Early successional species which allocate a high proportion of biomass to reproduction (seed and or rhizome) are typically good colonizers but are poor competitors for soil resources because of low allocation to root. In contrast, later successional species with high allocation to root biomass are typically good competitors, but poor colonizers because of low allocation to reproduction (Tilman 1991).

The trade-off between colonization ability and competitive ability may partially explain the temporal distribution of *Agropyron* and *Poa* species observed in the early succession of Cantlon fields. Tilman and Wedin (1991) showed that allocation to rhizome and root tended to differ between populations of *Agropyron repens* and *Poa pratensis* that were grown in monocultures. *Agropyron* tended to have a higher proportion of biomass in rhizome than *Poa pratensis*. This should allow *Agropyron* to colonize disturbed areas by clonal spread more rapidly than *Poa pratensis*. In contrast, *Poa pratensis* tended to showed greater allocation to root than did *Agropyron* suggesting that this species may be a superior competitor for soil resources enabling it to persist longer than *Agropyron* in the presence of competition. These patterns of allocation are consistent with the patterns of colonization and persistence exhibited by these species in Cantlon fields.

Effects on woody species establishment:

Similarities in the spatial distribution of the dominant species (west to east zonation) between the current and early successional plant communities in Cantlon fields suggest that the early segregation of perennial grasses (a possible reflection of pre-abandonment weed control) may have had persistent effects on the community and resulted in a successional divergence. Much of the area in blocks I and II where *Agropyron* was an early dominant is currently occupied by woody thickets. In contrast, much of the area within blocks III, IV and V, where *Poa* species were present, is currently dominated by herbaceous plants (primarily *Solidago canadensis* and *Poa pratensis*). This pattern suggests that areas dominated by *Agropyron* and *Poa* species may have differed with respect to invasability by woody species, with areas occupied by *Poa* being more resistant to woody plant establishment.

It is likely that *Agropyron* repens and *Poa* species (both rhizomatous grasses) are both capable of inhibiting the establishment of woody plants when forming dense sods. Why areas in Cantlon fields that were dominated by *Poa* species may have been less invasable by woody plants is unclear, but it is possible that its longer persistence in the community may have played a role. *Agropyron,* which initially dominated most plots, was reported to have declined drastically in abundance after 1970, while *Poa* species continued to increase in abundance (Werner and Harbeck 1982). *Poa pratensis* is currently the dominate grass species within Cantlon fields. Werner and Harbeck (1982) suggest that the rapid decline of *Agropyron* in Cantlon fields was due to its shade in-tolerance and report that it died out in areas where staghorn sumac (*Rhus typhina*) canopy developed, thus opening up suitable microsites for woody plant establishment. In contrast, *Poa* species likely persisted longer under the *Rhus* canopy because it is relatively tolerant to shade (Whitford and Whitford 1978, Werner and Harbeck 1982).

Indirect effects of *Rhus typhina*:

Rhus typhina may have indirectly promoted the establishment of other species of woody plants into Cantlon fields after 1970 when it was reported to have developed a significant canopy (Werner and Harbeck 1982). This may explain why much of the current community is currently occupied by a dense thicket of bird-dispersed shrubs and vines. The initial presence of a widely distributed fast growing clonal shrub undoubtedly increased the structural complexity of the community early in its development. Such complexity is known to influence subsequent patterns of vegetation development by affecting light levels and influencing the pattern of seed rain of animal dispersed seeds (Werner and Harbeck 1982, McDonnell and Stiles 1983, McDonnell 1988).

There is evidence that *Rhus typhina* is capable of promoting woody plant establishment beneath its canopy. In

Cantlon fields in 1979, Werner and Harbeck (1982) found significantly greater numbers of tree seedlings in areas dominated by *Rhus* as compared to more open areas. They suggested that the presence of *Rhus* indirectly promoted tree establishment success by 1) creating suitable establishment microsites and 2) by serving as recruitment foci for animal dispersed seeds (especially bird dispersed seed). Once *Rhus* became dominate in these fields the cover of rhizomatous herbaceous perennials such as *Agropyron repens* decreased rapidly, presumably due to shading, and created suitable microsites for tree establishment.

A study examining the role of another *Rhus* species (*Rhus copallina*) in facilitating the establishment of tree seedlings in a Oklahoma prairie (Petranka and McPherson 1979) is consistent with the conclusions of Werner and Harbeck (1982) concerning tree establishment in Cantlon fields. Petranka and McPherson (1979) showed that the density of prairie vegetation typically decreased and numbers of forest tree seedlings increased beneath the canopy as *Rhus* invaded open prairie. They suggested that allelopathy and the reduction of light levels beneath the canopy were the primary determinants of this pattern.

Importance of Dominant Species

The results of this study underscore the importance of dominant species in regulating community dynamics in early successional fields. Though many species may be present in a community, it is likely that interactions among the few species which dominate space and resources will have the greatest impact on community structure and development. Knowledge of how historical factors can influence the species composition of early successional plant communities and how key dominant species might directly or indirectly affect the recruitment of later arriving species is of practical value to land managers and community restorationists who wish to manipulate community change in order to direct successional pathways towards a desired result.

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