Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach

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Abstract

Chronosequence and permanent plot studies are the two most common methods for evaluating successional dynamics in plant communities. We combined these two approaches by re-sampling an old-field chronosequence at Cedar Creek Natural History Area (Minnesota, USA) to: (1) measure rates of secondary succession; and (2) to test the ability of the chronosequence approach to predict actual successional dynamics over a 14-year survey interval. For each of 19 chronosequence fields we calculated four complimentary indices of succession rate for community changes that actually occurred within each of these fields between 1983 and 1997. We found that measures of compositional dissimilarity, species turnover, and the change rates of perennial and native species cover over this 14-year period were all negatively correlated with field age, indicating that the rate of successional change in these old-fields generally declines over time. We also found that data collected from the initial static chronosequence survey (1983) accurately predicted many of the observed changes in species abundance that occurred between 1983 and 1997, but was a poor predictor of changes in species richness. In general, chronosequence re-sampling confirmed the validity of using the chronosequence approach to infer basic patterns of successional change.

Introduction

The chronosequence approach to studying vegetation dynamics (space-for-time substitution, Pickett 1989), has provided significant insights into the patterns and mechanisms of plant succession (Cowles 1899; Cooper 1926; Olson 1958, van der Maarel & Werger 1978; Inouye et al. 1987; Pickett 1989; Olff et al. 1997). The examination of a chronosequence can reveal broad, regional-scale successional trends by averaging across site-to-site differences in species composition that occur because of differences in environmental conditions and site history (Pickett 1989; Bakker et al. 1996). However, the chronosequence approach has some well-recognized limitations. First, regional averaging limits the level of detail at which successional dynamics can be ascertained (Pickett 1989). Second, correlations of species abundances and community attributes with site age cannot be unam-

biguously attributed to successional processes if other confounding site factors, including site status at the time of abandonment, also covary with age (Bakker et al. 1996). Despite this latter shortcoming, there have been only a few attempts to test the validity of the chronosequence approach by re-sampling each site in the chronosequence after some time period to see if the predicted successional dynamics actually occur (Collins & Adams 1983; Debussche et al. 1996).

Chronosequence re-sampling can potentially give other insights into successional processes that are not accessible by a single chronosequence survey. For example, the rate of successional change following disturbance (e.g. Shugart & Hett 1973; Bornkamm 1981; Olff & Bakker 1991; Myster & Pickett 1994) cannot be easily ascertained from a static survey and require time-series data gathered from particular locations (Nilsson & Nilsson 1985; Debussche et al. 1996). Several studies have shown that the rate of species

replacement declines after disturbance or upon cessation of chronic disturbance as fast-growing, short-lived species are replaced by slow-growing, long-lived species (Shugart & Hett 1973; Leps 1987; Myster & Pickett 1994). Because most permanent plot studies are of relatively short duration, direct measurement of successional rates over long time periods (i.e. greater than 15–20 years) are rare. By revisiting sites in a chronosequence, successional rates can be inferred by measuring change rates over the re-sampling interval for each individual site in the chronosequence and then relating these changes to site age.

Here, we present data from a chronosequence of old-fields in east-central Minnesota that was re-sampled 14 years after the initial survey. Our objectives were: (1) to measure rates of successional change and test the hypothesis that these rates decline over time; and (2) to test how well patterns of successional change in species richness and species abundances (functional/life history groups and individual species) inferred from a static survey of the chronosequence predicts the actual dynamics of succession.

Methods

Study area

Our old-field chronosequence is located at the 2200 ha Cedar Creek Natural History Area (University of Minnesota), 50 km north of Minneapolis Minnesota, USA (45°24′ N, 93°12′ W). Cedar Creek is located on the 222 000 ha Anoka sand plain which was formed by glacial outwash during the last glacial retreat. The upland soils are well-drained sands that are low in nitrogen and water holding capacity (Grigal 1974). The climate is mid-continental, characterized by hot summers and cold winters. Mean annual temperature is 6 °C and mean annual precipitation is 775 mm, most of which falls between May and October.

Cedar Creek lies within the ecotone between deciduous forests to the east and the Great Plains to the west. The upland vegetation is currently composed of a mosaic of successional old-fields, fire-maintained oak savanna, and mixed forest. Prior to settlement in the mid-19th century, the vegetation consisted primarily of tallgrass prairie, oak savanna, and mixed forest. By 1900, about half of the uplands had been cultivated for row-crop agriculture. Field abandonment in the region has ranged from 1–80 years following the first cultivation, but with most fields being abandoned after 10–20 years (Pierce 1954).

Table 1. The 18 most abundant species in the chronosequence (relative cover greater than or equal to 1%). Relative cover values are averages from all 22 fields surveyed in 1983. Species are listed in descending order of abundance.

Species	Relative cover
Poa pratensis	0.209
Agropyron repens	0.097
Schizachyrium scoparium	0.070
Andropogon gerardi	0.057
Erigeron canadensis	0.043
Crepis tectorum	0.034
Agrostis scabra	0.031
Cyperus sp.	0.028
Ambrosia artemisiifolia	0.025
Setaria lutescens	0.022
Rumex acetosella	0.020
Berteroa incana	0.019
Solidago gigantea	0.016
Carex sp.	0.013
Hedeoma hispida	0.011
Rubus sp.	0.010
Polygonum convolvulus	0.010
Vicia villosa	0.010

Chronosequence sampling

The Cedar Creek chronosequence contains 22 old-fields that ranged in age from 1–56 years post-abandonment in 1983 when the initial survey was conducted (Inouye et al. 1987). Subsequent surveys included all 22 fields in 1989, and 19 of the original fields in 1994 and 1997. For this study we examined species percent cover data collected in the 1983 and 1997 surveys only. In 1983, four parallel transects were established in 20 of the fields. On each of these transects, species percent cover was visually estimated within 25, 0.5 × 1 m quadrats (100 per field) that were spaced 1.5 m apart. In the remaining two fields, six transects were established giving a total of 150 quadrats for these fields (see Inouye 1987 and Tilman 1987 for details). In the 1997 survey, 19 of the original fields were resampled within the same quadrats, utilizing the same methods as the initial survey.

Analyses

To evaluate broad-scale compositional variation among the 22 chronosequence fields in the initial static survey (1983), we used non-metric multidimensional scaling (MDS) to summarize between-field dissimilarities (Euclidean distance – see below) in dominant species abundances (Faith et al. 1987; Clarke 1993). Dissimilarities were based on field differences in the relative cover of the eighteen most abundant species, each of which represented at least 1% of the total plant cover when averaged across all 22 fields (Table 1). This 1% cut-off eliminated many infrequent species from the analysis, but allowed a general assessment of between-field variation in dominant species composition. MDS is a multivariate procedure that projects a set of points (in this case the points represent fields), initially defined in n dimensions (in this case n dimensions are defined by the number of species; $n = 18$), into low dimensional space such that the distances between the points are as close as possible to the calculated dissimilarities. We chose to use MDS because this method assumes no statistical distribution assumptions (Schiffman et al. 1981; Wilkinson et al. 1992). Initial inspection of the data suggested that linear methods such as principal components analysis were inappropriate due to diffuse and non-linear relationships among species. Our application of Detrended Correspondence Analysis (CANOCO version 3.10; ter Braak 1990) to the data produced similar results as MDS. For brevity, only the MDS results are presented.

Succession rate

To test the hypothesis that succession rate declines following field abandonment we computed four complementary indices to assess changes in the community actually observed within each field between the two survey dates (1983 and 1997). Each index emphasizes a different aspect of change in plant community structure over this period. To measure the actual changes in overall floristic composition between the two survey dates, we calculated Euclidean distance dissimilarity (Kent & Coker 1992) for each field based on the relative abundances of the same 18 species used in the MDS analysis described above. These dissimilarities were then related to field age using regression analysis. Euclidean distance was calculated for each field as:

$$\left[\sum_{n}^{K=1} (X_{83,K} - X_{97,K})^2 \right]^{1/2},$$

where n = number of species, $X_{83,K}$ = relative abundance of the kth species in 1983, and $X_{97,K}$ = relative abundance of the kth species in 1997.

Second, we categorized all species by life history (annual, biennial, and perennial) and then calculated observed rates of cover change for species grouped as perennials. We did this to examine the rate at which perennials replaced annuals and biennials in each field between the two survey dates. Third, we categorized all species by historical origin (native versus non-native) and then calculated observed rates of cover change for native species. Change rates for species grouped as perennials and native species were calculated for each field as:

$$[\ln(RC_{97}/RC_{83})]/(t_1 - t_2),$$

where RC_{97} is relative cover in 1997, RC_{83} is relative cover in 1983, and $t_1 - t_2$ is the time interval (14 years). Finally, to examine rates of species turnover between the two surveys we calculated the Sorenson's coefficient of dissimilarity for each field (Kent & Coker 1992; Debussche et al. 1996). This was calculated as:

$$1 - [2C/(S_{83} + S_{97})],$$

where C is the number of species in common within a field between the two observation dates, and S_{83} and S_{97} are the total number of species in 1983 and 1997 respectively. To further evaluate species turnover we also calculated the number of species lost and gained in each field over the survey time interval. Species losses and gains are expressed as a proportion of total species richness in 1983.

Tests of the chronosequence

If successional patterns inferred from the initial static survey of the chronosequence are indicative of true successional dynamics, then the actual dynamics observed in each field between the two survey dates should correspond with these static patterns. To evaluate the predicted successional patterns from the initial chronosequence survey we used simple correlation analyses to examine the dependence of species richness and species abundances in 1983 on field age. For these analyses we focussed on total species richness (total number of species recorded in a field, hereafter referred to as species richness or richness), and the richness and relative abundances of species categorized into several different life history and functional groups. Life history groups categorized species as annuals or perennials. Functional groups categorized species as forbs (herbaceous dicots), grasses,
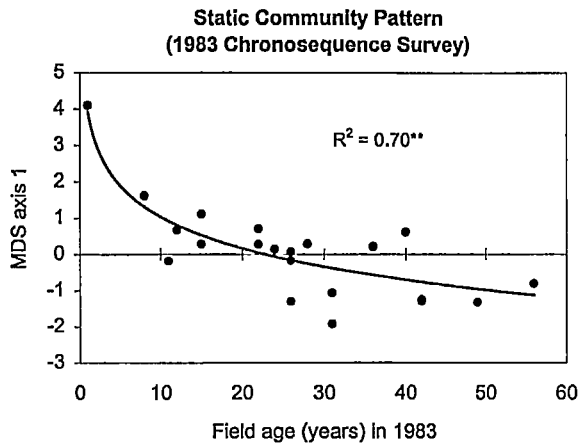
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**Static Community Pattern
(1983 Chronosequence Survey)**

Figure 1. Relationship between the first multi-dimensional scaling (MDS) axis of floristic composition in 1983 (initial chronosequence survey) and field age (*P* < 0.05, **P* < 0.01, ***P* < 0.001).

sedges, and woody plants. We also categorized species as native or non-native. Correlation analyses involving absolute cover of some of these groupings are presented in Inouye et al. (1987).

To test the ability of a static chronosequence survey to predict actual dynamics of change observed between the two survey dates (1983–1997), we evaluated the overall mean change in species richness and abundance (calculated using all fields as replicates) between 1983 and 1997 and tested the significance of these changes using paired *t*-tests. We then used paired *t*-tests to evaluate observed changes in the relative abundances of species groups on a field by field basis using individual plots within fields as replicates. Statistical analyses were performed using SPSS version 8.0. Nomenclature follows Gleason & Cronquist (1963) and Hitchcock (1971).

Results

Successional rates

Static chronosequence patterns
The first MDS axis, derived from measures of plant cover in the initial static survey of the chronosequence, was significantly correlated with field age, suggesting that among-field compositional variation in 1983 was generally indicative of successional change (Figure 1). The negative logarithmic slope of this relationship leads to the prediction that the rate of compositional change will decelerate as fields age, as would be

expected for any dynamic process approaching an asymptote.

Observed dynamics
The four indices of successional change, which measure actual community changes observed between 1983 and 1997, support the above interpretation (Figure 2). As measured by euclidean distance, overall community composition tended to change more rapidly within younger fields than in older fields over the survey interval (Figure 2A). In addition, the rates of change in the cover of perennials (Figure 2B) and of native species (Figure 2C) declined from younger to older fields over the survey interval, indicating that perennials displaced annuals at a faster rate in young fields, as did native species as they displaced non-native species. Sorensen's dissimilarity coefficient also declined from younger to older fields (Figure 2D), indicating that the rates of species turnover between the two observation dates were slower in older fields. This occurred because older fields gained fewer species over the 14-year interval (Figure 3).

Species richness

Static chronosequence patterns
In the 1983 static survey of the chronosequence, species richness increased significantly with field age (Table 2). The richness of annual and non-native species declined, while the richness of perennials, and species grouped as forbs, grasses, woody species, and as natives all increased significantly with field age.

Observed dynamics
The majority of the predictions for change in species richness, inferred from the single static survey of the chronosequence, were not supported by actual changes in richness observed between the survey dates (Table 2). Mean species richness (total species richness per field averaged across all fields) which was predicted to increase, showed no significant change between the survey dates. In fact, the tendency was for mean richness to decline rather than to increase. On a field by field basis, species richness declined in the majority of fields over the survey interval. Of the various species groupings, only the richness of annuals and forbs showed significant increases or decreases over the survey interval. The mean richness of annuals and species categorized as non-native declined significantly as predicted. However, the mean
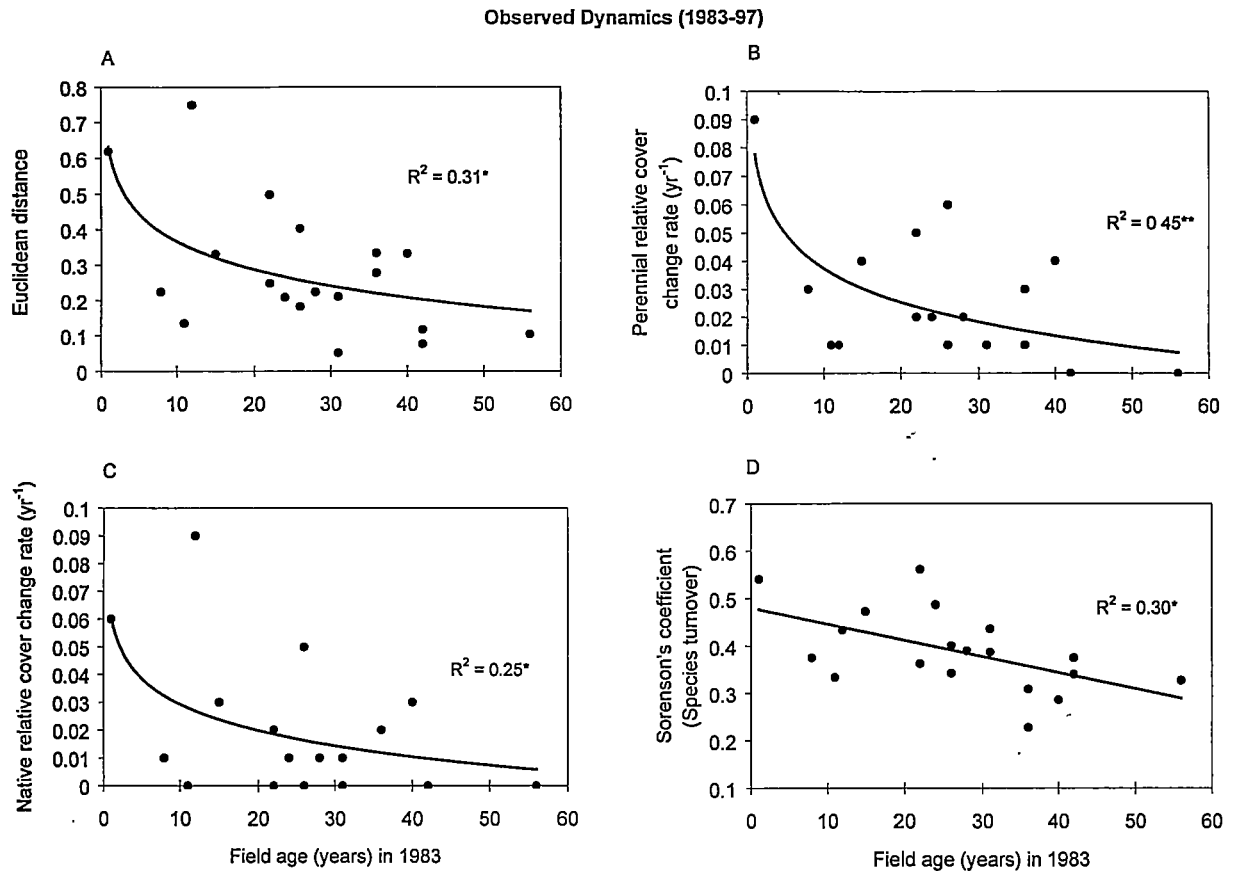
Observed Dynamics (1983-97)

Figure 2. Relationships between the four measures of observed succession rate and field age. (A) Euclidean distance between survey dates (1983 and 1997). (B) Perennial cover change rates between survey dates. (C) Native species cover change between survey dates. (D) Sorenson's coefficient of species turnover between survey dates ($^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$).

Table 2. Predicted and observed changes in species richness. Predicted changes are represented by correlations (Pearson correlation coefficients) between richness and field age in the 1983 static survey. Observed changes are presented as overall mean changes and changes in richness on a field by field basis between the two survey dates (1983 and 1997). NC = no change in richness. ($^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$).

| Groups	Corr. w/ field age in 1983	Mean richness 1983	Mean richness 1997	Mean change	t-value	No. of fields exhibiting a given change		
						−	+	NC
Field richness	0.56**	43.10	38.78	−4.32	1.94	12	5	2
Annual	−0.55**	12.31	5.95	−6.36	8.63***	18	1	0
Perennial	0.73***	24.21	24.53	+0.31	0.29	10	8	1
Forb	0.45*	27.79	22.94	−4.85	3.14**	14	3	2
Grass	0.57**	9.96	8.37	−1.59	1.65	12	6	1
Woody	0.75***	1.89	1.74	−0.16	0.47	6	7	3
Native	0.71***	32.05	29.74	−2.31	1.40	12	7	0
Non-native	−0.58**	11.05	9.05	−2.00	2.34*	14	4	1

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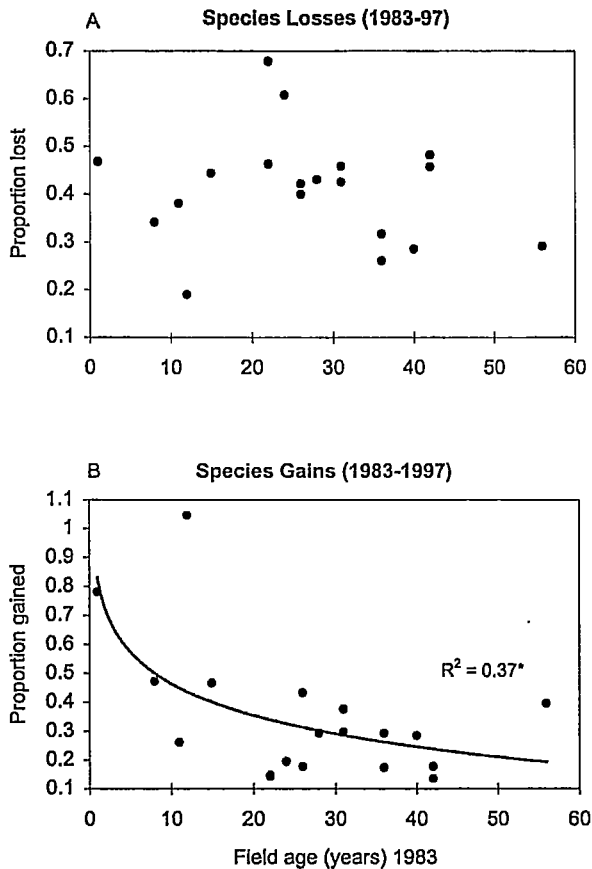
Figure 3. Relationships of species loss (A) and gain (B) between survey dates with field age. Losses and gains are presented as a proportion of the 1983 species richness ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$).

richness of forbs, which was predicted to increase, actually decreased significantly over the survey interval. Although the mean richness of grasses and species grouped as natives did not change significantly over the survey interval, on a field by field basis the richness of these species groups declined in the majority of fields.

Species relative abundances

Static chronosequence patterns

In the 1983 static survey, the relative cover of annuals and forbs declined significantly with field age (Table 3). The relative cover of grasses showed no significant relationship with field age, while that of perennials, woody species, sedges, and species grouped as natives all increased significantly with field age.

Observed dynamics

The actual changes in cover observed between the two survey dates for five of the seven species groupings were successfully predicted by the initial static survey (Table 3). Mean relative cover of annuals and forbs declined significantly between the two survey dates, while the cover of perennials, sedges and natives all increased over this interval. In contrast to expectation, the mean relative cover of grasses actually increased significantly, while that of woody species showed no significant change over the survey interval. Changes in relative cover for these species groupings on a field by field basis were largely consistent with the above results.

Of the 40 most abundant species recorded in the two surveys, seventeen exhibited statistically significant changes in abundance (measured as relative cover and or relative frequency) between the two survey dates when examining changes across all 19 fields (Table 4). Of these species, five increased in mean relative abundance and twelve decreased. All of the increasing species were perennials. Of the decreasing species, nine were annuals, one was biennial, and two were perennial.

Discussion

In this study, several aspects of successional change that were expected to occur, based on inferences from the initial static survey of the chronosequence, were supported by the observed changes over the 14-year time interval, while other aspects were not. Results from the MDS analysis using data from the initial static survey predicts that the overall rate of compositional change will decelerate during succession. This inference was supported by four separate measures of successional rate that we calculated for each field over the 14-year interval. These measures indicate that during the first 50-60 years of succession at Cedar Creek, the rate of change in the relative abundances of species, and the turnover rate of species declines over time.

The declining succession rate observed here has been documented in other studies (Shugart & Hett 1973; Lewis 1978; Leps 1987; Myster & Pickett 1994) and is consistent with several general mechanisms of successional change (Myster & Pickett 1994), including the declining availability of establishment microsites (Harper 1977; Gross 1980) and the intensification of interspecific interactions (Bazzaz 1979;

Table 3. Predicted and observed changes in the relative abundance of life history and functional groups. Predicted changes are represented by correlations (Pearson correlation coefficients) between relative abundance and field age in the 1983 static survey. Observed changes are presented as overall mean changes in abundance and changes on a field by field basis between the two survey dates (*P < 0.05, **P < 0 01, ***P < 0.001).

Groups	Corr. w/ Field age in 1983	Mean Rel. Cov. 1983	Mean Rel. Cov. 1997	Mean change	t-value	No. of fields exhibiting significant change		
						−	+	NC
Annual	−0.68**	0.183	0.056	−0.127	4.41***	19	0	0
Perennial	0.66**	0 684	0.915	+0 231	5.85***	0	19	0
Forb	−0.58**	0 276	0 159	−0 117	4.51***	15	1	3
Grass	0.16	0.522	0.697	+0.175	4.53***	1	17	1
Woody	0.67**	0.027	0.018	−0.009	1.43	5	2	9
Sedges	0.45*	0.044	0.089	+0 045	4.40***	0	12	7
Native	0.66**	0.665	0.832	+0.167	2.59*	3	11	5

Wilson 1999). The most apparent cause of a declining rate of succession relates to species differences in growth rate, life history, and longevity. As in most examples of old-field succession, newly abandoned fields at Cedar Creek are dominated by fast growing annuals and short-lived perennials that exhibit fairly rapid rates of abundance change. These species are generally displaced over time by the slower-growing, longer-lived perennial grasses that tend to be superior competitors for limiting soil nitrogen (Tilman & Wedin 1991). Once established, competitive, late-successional species may be more resistant to invasion (Leps 1987), contributing further to a slowed rate of succession. The idea that resistance to invasion may increase over time following abandonment is supported in this study by our finding that species gains observed between the two survey dates declined with field age.

Inferences from the initial chronosequence survey indicate that total species richness increases over time in these old-fields (Inouye et al. 1987). However, this prediction was not supported by the observed changes in richness over the 14-year interval. Species richness did not increase significantly in these old-fields from 1983–1997. The richness of annual species did decline significantly as expected. However, the even greater increase in perennial species needed to offset the declines in annuals did not occur. Forb richness, predicted to increase, actually declined significantly over the 14-year interval. Grass richness, also expected to increase, did not change significantly between the

two survey dates. Woody species richness also did not increase as expected.

The lack of an observed increase in total species richness between the two survey dates could be due to several reasons:

— a 14 year interval may be too short to detect the expected increase in richness;
— species richness might increase with field age in the chronosequence in a non-linear fashion, making it difficult to detect dynamic changes with the methods used in this study;
— a static chronosequence survey may not be reliable for predicting changes in richness during succession; or
— some type of perturbation occurred between 1983 and 1997, temporarily preventing richness from increasing over this interval.

The first possibility is unlikely because richness was predicted to increase by seven species in these fields over the 14-year interval based on the slope of the regression of total species richness on field age in 1983 (Figure 4). If such a change had actually occurred in these fields our methods should have detected it. The best-fit relationship between species richness and field age is clearly linear (Figure 4), ruling out the possibility that non-linearity explains our inability to detect the predicted changes. We cannot clearly distinguish between the third and fourth alternatives, but the fourth seems likely. A severe drought occurred at Cedar Creek in 1988, reducing species richness in the old-fields by as much 30% (Tilman & El Haddi 1992). Species richness in these fields did

Table 4. The 40 most abundant species in the chronosequence fields listed as either increasing or decreasing in mean relative cover between the two survey dates. Species in bold differed significantly in mean relative cover and or mean frequency (average proportion of quadrats occupied in a field) using paired t-tests (*P < 0.05, **P < 0.01, ***P < 0.001). Within each list, species are listed from the most to least abundant in terms of relative cover. A = Annual; B = Biennial; P = Perennial; G = Grass; C = Cyperaceae; F = Forb; W = Woody.

Species	Life hist.	Funct. group	Relative cover (%)		Frequency (%)	
			1983	1997	1983	1997
Increasing species						
Poapratensis	P	G	22.50	34.95**	70.05	91.37
Schizachyrium scoparium	P	G	4.03	13.47	14.84	32.00*
Rumex acetosella	P	G	2.11	2.40	24.53	24.84
Carex sp.	P	C	1.50	8.75*	11.58	38.53**
Vicia villosa	P	F	1.24	1.64	12.37	20.21
Achillea millefolium	P	F	0.57	1.63	13.42	20.42
Fragaria virginiana	P	F	0.56	0.67	4.26	3.84
Tragopogon dubius	B	F	0.36	0.58	14.58	11.74
Lathyrus venosus	P	F	0.35	0.69	4.37	4.84
Panicum praecocious	P	G	0.20	0.24	4.58	5.32
Arabis divaricarpa	B	F	0.13	0.15	4.32	4.58
Sorghastrum nutans	P	G	0.01	1.64	0.05	9.89**
Decreasing species						
Agropyron repens	P	G	9.77	8.67	59.84	59.26
Andropogon gerardi	P	G	6.63	6.28	18.32	18.63
Erigeron canadensis	A	F	4.18	0.49**	49.37	9.58**
Crepis tectorum	A	F	4.05	0.75	26.68	8.47*
Agrostis scabra	P	G	3.08	0.86**	36.95	5.74**
Cyperus sp.	P	C	2.94	0.19	26.16	3.26*
Setaria lutescens	A	G	2.64	0.04**	34.32	0.84*
Ambrosia artemisiifolia	A	F	2.43	0.79**	40.37	19.74
Berteroa incana	B	F	1.90	1.08	22.47	12.11
Solidago gigantea	P	F	1.90	1.47	7.26	8.74
Polygonum convolvulus	A	F	1.14	0.59*	45.21	17.42**
Rubus sp.	P	W	1.05	0.39	6.32	3.89
Panicum oligosanthes	p	G	1.03	0.78	20.68	13.68
Hedeoma hispida	A	F	0.87	0.63	31.26	14.00*
Lychnis alba	p	F	0.86	0.42	13.32	7.74
Lespedeza capitata	p	F	0.76	0.58	13.53	12.53
Ambrosia cornopifolia	p	F	0.75	0.18	7.47	4.37
Solidago nemoralis	p	F	0.71	0.23	5.53	5.05
Aristida basiramea	A	G	0.70	0.54	16.42	3.58*
Rosa arkansana	p	W	0.67	0.47	8.05	6.58
Eragrostis spectabilis	p	G	0.53	0.18	6.11	2.16
Artemisia caudata	B	F	0.40	0.05	7.16	1.32
Polygonum tenue	A	F	0.33	0.01*	9.37	0.01**
Asclepias syriaca	p	F	0.31	0.14	5.89	2.00
Physalis virginiana	p	F	0.27	0.24	5.95	6.47
Lepidium denisiflorum	A	F	0.26	0.02*	12.53	1.37**
Anemone cylindrica	p	F	0.25	0.22	8.00	8.95
Silene antirrhina	A	F	0.06	0.04	6.11	1.74

Static Pattern
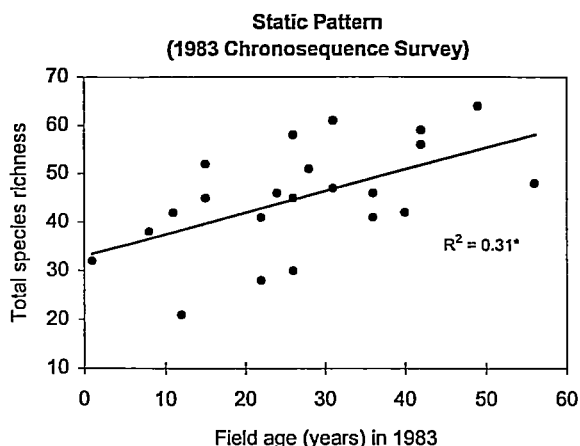### (1983 Chronosequence Survey)

Figure 4. Relationship between total species richness and field age in the 1983 survey of the chronosequence.

not return to pre-drought levels until 1994 (Tilman 1996). Thus an increase in richness may not have been observed between 1983 and 1997 because these old-fields had not recovered from the 1988 drought until 1994, and changes in the following three years would be too small to detect.

Unlike species richness, changes in species abundances between the two surveys were fairly consistent with the qualitative predictions of the initial chronosequence survey. Of the seven species groups examined in this study (species grouped as annuals, perennials, forbs, grasses, woody, sedges, and natives), only the abundance of grasses and woody plants failed to change as expected over the survey interval. Grass abundance, which was not expected to change, increased significantly between observation dates. Our inability to detect the expected increase in woody plant abundance over the survey interval is not surprising given that woody plant invasion is extremely slow in these old-fields, likely due to a combination of dispersal limitation, slow growth rates, and poor competitive ability on low nitrogen soils (Inouye et al. 1987, 1994). Also consistent with the chronosequence, all of the individual species exhibiting significant increases in abundance over the 14-year interval were species with a perennial life history, while the majority of the species showing significant declines over this period were annuals. With the exception of *Cyperus* sp., the remaining species showing significant declines in abundance were either biennials or short-lived perennials.

The different capacity of the initial chronosequence survey to predict changes in species abundances versus species richness over the survey interval may reflect differential sensitivity of these community attributes to climatic variability. Species richness in grassland can vary substantially from year to year in relation to rainfall and can be strongly reduced by drought (Tilman & El Haddi 1992). As a result, species richness within a given field at Cedar Creek will likely fluctuate over time, perhaps exhibiting directional trends only over very long time periods. Because of this, the long-term successional trajectories of species richness may be best assessed by the chronosequence approach rather than through repeated measures on permanent plots, because the chronosequence approach averages across this interannual variability. The successional trajectories in the abundance of life history and functional groups appear to be much more resistant to these types of fluctuations, being detectable from both the examination of fields that differ in age and by observing changes within the same fields over a modest time period.

Chronosequence and permanent plot studies are the most common methods used for evaluating vegetation change. Because these approaches examine succession at different levels of spatial resolution and ecological organization they are potentially complimentary (Bakker et al. 1996). Our results indicate that chronosequence re-sampling, which integrates these two different approaches, provides a valuable tool for gaining additional insights into successional processes. In this study, chronosequence re-sampling confirmed the expectation that succession rate declines over time, and also confirmed the validity of using the chronosequence approach to infer many aspects of successional change.

Acknowledgements

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