A Comparison of Rate of Succession Over 18 Yr in 10 Contrasting Old Fields

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A COMPARISON OF RATE OF SUCCESSION OVER 18 YR IN 10 CONTRASTING OLD FIELDS[1]

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Abstract. We explored local variation in rate of plant succession by computing three contrasting measures of change for 10 New Jersey old fields through the first 18 yr after abandonment. We found that all three measures, euclidean distance in ordination space, turnover analysis, and regression analysis of species loss from the initial cohort, showed the same trend of decrease in the rate of plant succession with time. However, we did not find a monotonic decrease, and the specific years of transient increase differed with the analytical measure used. Both turnover and regression analysis showed that those old fields that had previously been planted in orchard grass (*Dactylis glomerata*) had a much lower initial change than fields previously in soybeans, or soybeans and sorghum, but this difference dissolved after 10 yr of succession. The study fields compared favorably to other mesic successions and agreed with the general pattern of more rapid rate decrease in mesic compared to xeric successions. Our results echo the general decrease in the rate of plant succession with time reported in the literature and also show important relationships between this decrease and the land-use history of particular fields.

Key words: euclidean distance; land-use history; New Jersey; old fields; species turnover; succession rate.

INTRODUCTION

Historically, experimental and theoretical studies of succession have sought fundamental parameters common to all successions (Jassby and Goldman 1974). Ideally, these should be high-level, integrating parameters (Pickett et al. 1987) that can be used to quantify successional dynamics (Shugart and Hett 1973) and the effects of natural and human disturbances (Jassby and Goldman 1974). In addition, identification of such parameters is important for the development and evaluation of successional models (Shugart and Hett 1973). Succession is synonymous with community change in composition and structure (Pickett and McDonnell 1989), and so indices of change fit logically among these fundamental parameters. Separate measures of change could be calculated for such properties as total species richness, diversity, equitability, and architecture (Major 1974, Veno 1976, Bornkamm 1981); however change in plant composition (Jassby and Goldman 1974, Lewis 1978, Bornkamm 1981) is the most commonly computed measure and can, therefore, be used for comparative studies (Shugart and Hett 1973).

Comparisons between contrasting successions at various scales is critical for understanding succession (Shugart and Hett 1973, Glowacinski and Jarvinen 1975, Lewis 1978). For example, communities differ greatly in the rate of plant species change, which may depend on local conditions such as soil moisture (Shugart and Hett 1973, Glowacinski and Jarvinen 1975, Helle and Monkkonen 1985) or amount of organic matter (Major 1974, Glowacinski and Jarvinen 1975). Successions should show a slowing or decrease in plant species change with time (but see Facelli and D'Angela 1990) with periodic fluctuations (Armesto et al. 1991). Such a decline is expected because pioneer species are replaced by later species which generally live longer (Connell and Slatyer 1977) and are more resistant to further invasions (Lepš 1987). Here we test the following hypotheses, explore local variation in plant successional change, and compare the variation with a geographically extensive study using three contrasting measures of change for 10 New Jersey old fields through the first 18 yr after abandonment.

Hypothesis 1.—Old field plant species change will decrease monotonically with time (Odum 1969, Glowacinski and Jarvinen 1975, Bornkamm 1981). Euclidean distance between consecutive years in ordination space (Austin 1977, Dunn and Sharitz 1987), species turnover (Diamond 1969), and regression of the fraction of the initial species present vs. years of succession (Shugart and Hett 1973) should all show this trend. Because each index highlights a different aspect of successional change and because conclusions concerning plant successional change can be influenced by methodologies (Helle and Monkkonen 1985), a comparison using several different computations is

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warranted (Major 1974, Glowacinski and Jarvinen 1975, Veno 1976, Bornkamm 1981, Helle and Monkkonen 1985).

Hypothesis 2.—Old fields with similar abandonment characteristics and soils will have similar succession patterns (Keever 1983, Myster and Pickett 1990) including the rate of plant species change. Old fields that were abandoned in certain years may have a lower rate due to effects of drought on soil moisture levels (Myster and McCarthy 1989) or the invasion of new exotic species (Pickett 1982, Marks 1983). Old fields abandoned in the same season may be influenced by species dispersal phenology (Busing and Clebsch 1983, Keever 1983), and old fields may change faster if plowed (Monte 1973, Marks and Mohler 1985). In addition, some final crops persist after abandonment (Bazzaz 1968, Myster and Pickett 1990), compete with invading later species, and therefore slow succession. Alternatively, past planting of legumes (Dancer et al. 1977) can quicken plant successional change. Turnover and regression analysis will be used to test this hypothesis.

STUDY AREA

Hutcheson Memorial Forest Center (HMF) is located in Somerset County, New Jersey, USA (40°30′ N, 74°34′ W). The old-growth forest at HMF has a *Quercus–Carya* canopy and a *Cornus florida* understory (Bard 1952, Myster 1993). We analyzed the 10 old fields adjacent to the old-growth forest or established hedgerow that comprise the Buell–Small Successional Study (BSS; Buell et al. 1971, Pickett 1982, Myster and Pickett 1989). The BSS old fields were abandoned from continuous production agriculture in pairs every other year starting in 1958 and ending in 1966. In addition to year of abandonment, the 10 BSS old fields differ in season of abandonment (3 in spring vs. 7 in fall), mode of abandonment (4 plowed vs. 6 unplowed) and final crop before abandonment (2 in soybeans vs. 4 in soybeans and sorghum vs. 4 in orchard grass [*Dactylis glomerata*]; Myster and Pickett 1990). Forty-eight permanent plots, measuring 2.0 × 0.5 m, were arranged in a grid in each old field at the time of its abandonment. The dimensions of the grid were determined by the size and shape of each field. Every year since abandonment, these plots have been sampled using wooden frames in late July for the percentage of the surface plot that each species covers.

METHODS

We used three different methods to compute plant successional change. We first computed the euclidean distance (ED), or closeness between consecutive years, of the average position of the BSS old fields in PCA ordination space (Austin 1977, Dunn and Sharitz 1987). The PCA used the correlation matrix based on variance in plant abundance and composition.

Second, we computed the species turnover (TO) for each year t after abandonment ($t = 0$ when fields were abandoned) expressed as a percentage:

$$\mathrm{TO}(t) = [100 \cdot (n_1 np_t + n_t np_1)/n_1] + n_t - ni_{1t},$$

where $n_1 np_t$ is the number of species in year 1 after abandonment but not present in year t, $n_t np_1$ is the number of species in year t but not present in year 1, n_1 is the number of species present in year 1, n_t is the number of species present in year t, and ni_{1t} is the number of species invading between year 1 and year t (Diamond 1969). Turnover is a simple modification of Sorensen's formula (Glowacinski and Jarvinen 1975) and may increase after a period of decline because of newly introduced species.

Finally, we calculated lambda (λ) for each year t after abandonment where $\lambda(t) = \ln[(n_t - n_t np_1)/n_1]/t$ and performed a linear regression analysis on $\ln[\lambda(t)]$ vs. $\ln(t)$ (Shugart and Hett 1973). The 1-yr time interval of the BSS data used in the regression is suitable for forest successions (Jassby and Goldman 1974). The regression parameters P value, slope (b), y intercept (a), and R^2 were used to evaluate the hypotheses. The regression residuals were graphed and patterns inspected to ensure that low P values indicated linear relationships between the data (Sokal and Rohlf 1981). λ is an index of plant species change over the time interval t, a is the initial species loss in richness and retention of species, and the slope b is the rate of that change. To avoid overflow errors during computation, $\ln[\lambda(t)]$ could not be negative, therefore we always took the absolute value (R. Vichnevetsky, Computer Science Department, Rutgers University, *personal communication*) which must have been an unspoken assumption of Shugart and Hett (1973).

We also divided the old fields into groups based on abandonment conditions (Myster and Pickett 1990) to investigate the effect of such differences on subsequent succession. We repeated the percent turnover analysis and the regression analysis using the data from these groups in order to test the role of abandonment conditions in affecting plant successional change and to illustrate the variation in these fields. All methods and figures start with year 2 and continue to year 18 where the initial species composition is that at year 1. The three indices focus on different aspects of successional change. ED combines both plant composition and abundance and computes change between consecutive years. Turnover (TO) uses only number of species and computes change in comparison to year 1. λ also uses species richness and compares to year 1 but divides through by the time interval t.

RESULTS AND DISCUSSION

Hypothesis 1.—The mean euclidean distance (ED) between consecutive years of BSS old field succession in PCA ordination space (Myster and Pickett 1990) decreased steadily over the first 18 yr of succession (Fig. 1A). In general, the old fields became more similar

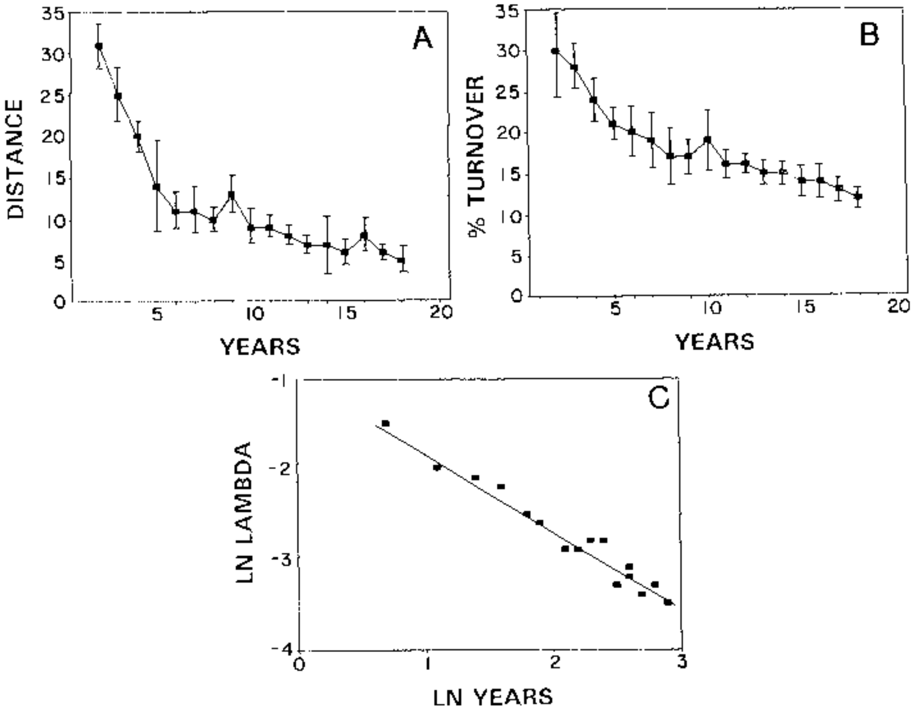

FIG. 1. (A) Euclidean distance (ED) averaged over the 10 Buell–Small Successional Study (BSS) old fields between consecutive years in PCA ordination space through the first 18 yr of succession (mean ± 1 SE). (B) Species turnover (TO, in %) expressed as a percentage of initial species richness for all 10 BSS old fields over the first 18 yr of succession (mean ± 1 SE). (C) Mean log-transformed regression analysis (λ) for all 10 BSS old fields over the first 18 yr of succession. Points represent ln rate of species loss vs. ln years of succession. The regression parameters are y intercept or $a = -0.97$, slope or $b = -0.84$, $R^2 = 0.94$, and $P < .001$.

with time as ED decreased, but years 9 and 16 showed a temporary increase. Coordinates used to compute distances were a combination of all PCA axes. While detrended correspondence analysis (DCA) has also been applied to these data, PCA coordinates were used over DCA coordinates because PCA better separates these old fields by their conditions at abandonment (Myster and Pickett 1990). Turnover (TO) also showed a steady decrease with time (Fig. 1B) with only year 10 showing an increase. λ exhibited a steady decrease during the first 18 yr as shown by the negative slope of the regression line (Fig. 1C). In addition, the P value ($P < .0001$) and the residual pattern both showed that the decrease was close to being negatively exponential because the relationship among the data was linear after ln transformation.

Hypothesis 2.—Calculating TO within groups of fields based on initial conditions (Figs. 2A–D) implicated final crop in affecting rate because groups defined by final crop showed the largest variation in TO (Fig. 2D). Those old fields that had previously been planted in orchard grass (*Dactylis glomerata*) had a much lower initial TO (Fig. 2D) than fields with other final crops. TO for orchard grass-dominated fields did not decrease as sharply (slope = -1.625) compared to fields abandoned after soybeans (slope = -2.25) or after soybeans and sorghum (slope = -2.625), implying that *Dactylis* reduced new species invasion (Fig. 2D, Myster and Pickett 1988). The pattern of decreasing TO became indistinguishable for all BSS old fields regardless of last crop after 10 yr of succession. The pattern of change in turnover is consistent with other analyses, which imply that *Dactylis* may influence plant successional change (Fig. 2D; Monte 1973, Myster and Pickett 1988). Using regressions of ln λ on ln years, P values of groups defined by initial condition were each significant (Table 1) and, as the patterns of residuals showed, linear. However, the a value was not equal for all 10 BSS old fields (Fig. 3A–D) which had been predicted for habitats in the same geographical area (Shugart and Hett 1973). There were similar slopes between plowed and unplowed fields and between seasons (Monte 1973) but greater variation in y intercept and slope values in groups defined by year of abandonment and final crop (Table 1; Fig. 3A–D). This variation in the regression parameters of λ implies an effect of either year of abandonment or final crop. However, results from the turnover analysis (Fig. 2D) and comparison of the number of species (Myster and Pickett 1988) and the successional pathways (Myster and Pickett 1990) in fields divided by abandonment condition strongly implicate final crop. Fields whose final crop was soybeans and sorghum had the highest initial species richness or largest y intercept value compared to fields with other final

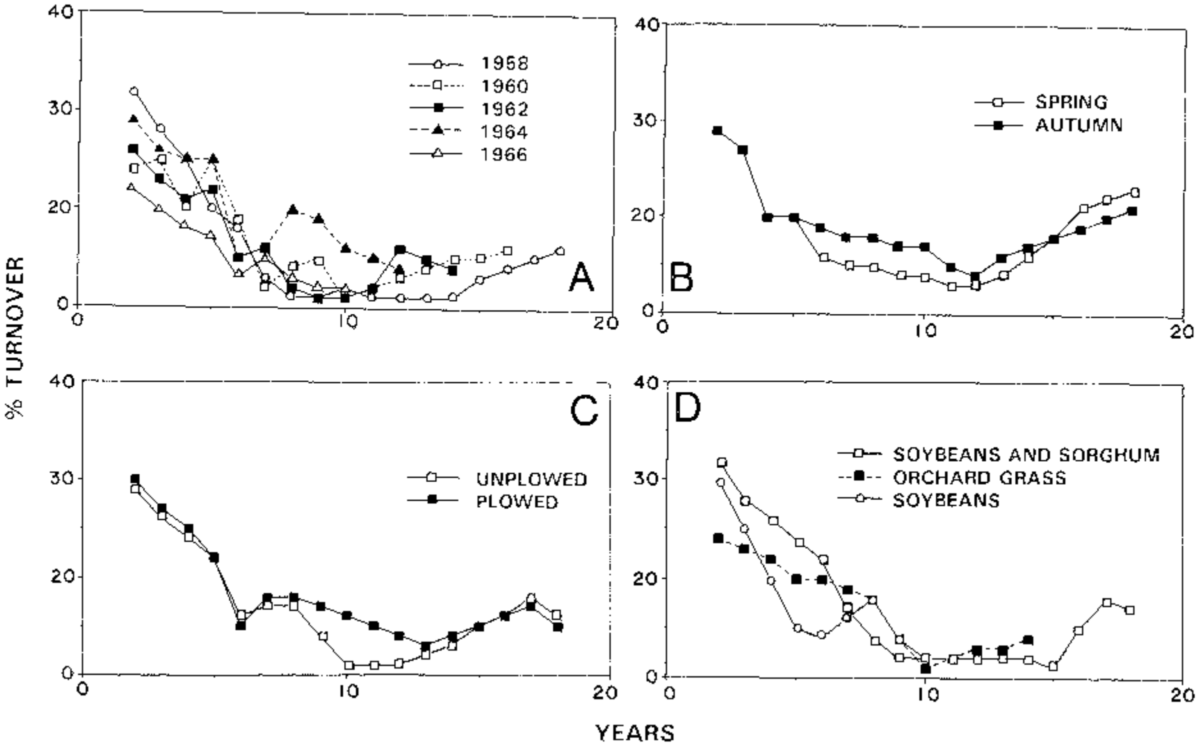

FIG. 2. Species turnover (TO, in %) of the 10 Buell–Small Successional Study old fields averaged over groups based on four initial abandonment conditions calculated as in Fig. 1B: (A) by year of abandonment, (B) by season of abandonment, (C) by mode of abandonment, and (D) by last crop planted before abandonment.

crops. Fields whose final crop was soybeans and sorghum or orchard grass had more negative slopes and thus steeper declines in rate of succession. Consequently, fields last in orchard grass were among those with the lowest initial species richness. This supports the previous result for analysis of percent turnover (Fig. 2D) that fields with *Dactylis* as a final crop showed a reduction in initial species richness (12 species compared to 15–16 for other plots) and a reduced rate of succession compared to other fields.

TABLE 1. Regression results (λ) for groups defined by old field initial abandonment conditions.

		y intercept	slope	R^2	*P*
By year	1958	−0.89	−0.90	0.97	.0001
	1960	−0.93	−0.69	0.94	.01
	1962	−1.48	−0.73	0.90	.01
	1964	−1.26	−0.76	0.75	.05
	1966	−1.75	−0.34	0.82	.05
By season	Autumn	−1.30	−0.77	0.99	.0001
	Spring	−0.89	−0.76	0.96	.0001
By mode	Unplowed	−1.33	−0.72	0.98	.001
	Plowed	−1.05	−0.71	0.96	.001
By last crop	Soybeans and sorghum	−0.88	−0.79	0.96	.001
	Orchard grass	−1.42	−0.74	0.87	.05
	Soybeans	−1.75	−0.34	0.82	.05

All three methods showed the same general trend of decrease in the rate of plant successional change with time (Glowacinski and Jarviven 1975, Lewis 1978), as was expected (Shugart and Hett 1973). The commonness, in temperate old fields, or even universality of the decline in successional rate with time (Shugart and Hett 1973), is consistent with a variety of mechanisms known to operate in succession. For example, a closing of invasion windows (Gross 1980, Rankin and Pickett 1989, Myster 1993) and a reduction in safe sites for establishment (Harper 1977) with successional time could cause the decline in rate. Likewise, the net effect of multiple successional mechanisms may exclude species through biotic interactions which strengthen with successional time such as competition (Bazzaz 1979), herbivory (Crawley 1983), or seed predation (Myster and Pickett 1993). Also, the life history traits of established later successional species make them more resistant to invasion (Lepš 1987), and they have longer life cycles (Grime 1979) than earlier successional species. However, we did not find a monotonic decrease in rate (Jassby and Goldman 1974), and the specific years of transient increase differed with method used. Even though old field succession in New Jersey operates on the scale of several decades (Pickett 1982, Myster and Pickett 1990), woody plants begin to dominate after 18 yr of succession (Pickett 1982) and there were 2 yr of increase in the middle of the 18-yr period and

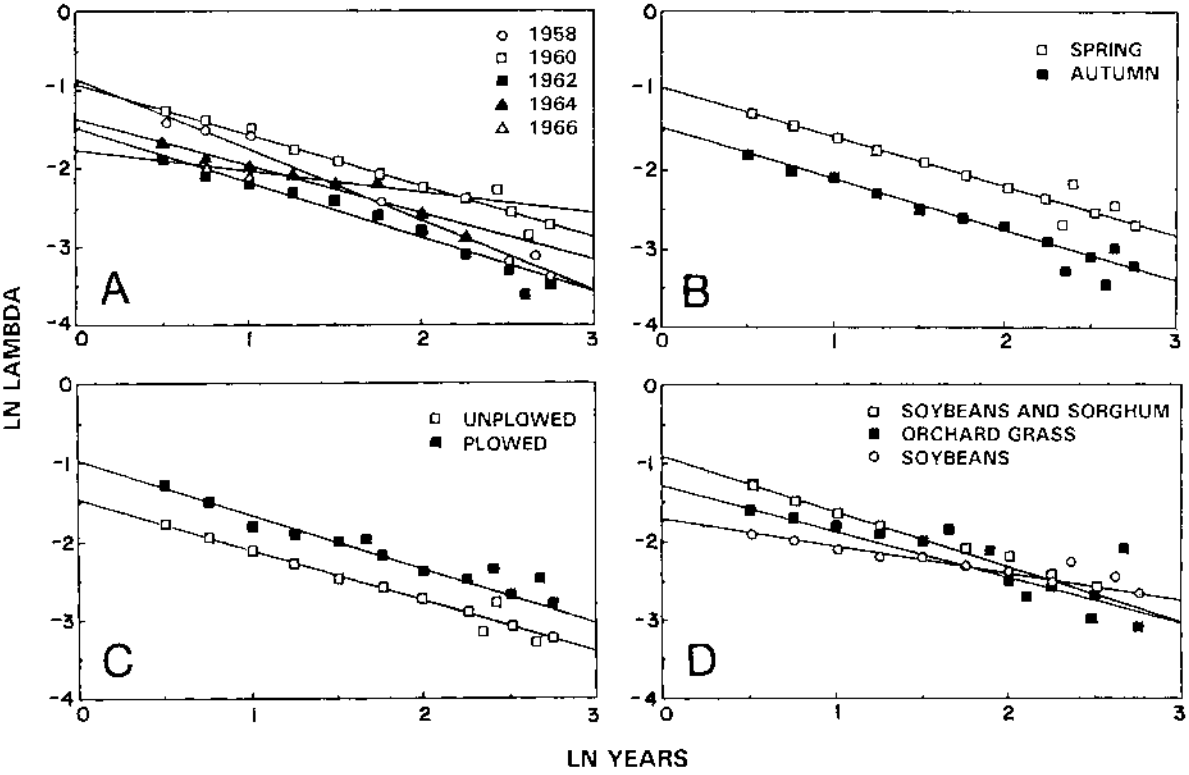

FIG. 3. Log-transformed regression analysis (λ) of the 10 Buell–Small Successional Study old fields averaged over groups based on four initial abandonment conditions calculated as in Fig. 1C: (A) by year of abandonment, (B) by season of abandonment, (C) by mode of abandonment, and (D) by final crop planted before abandonment.

only 1 near the end of our study. The years of increase could refer to stochastic variation, to year-to-year variation in community structure (Helle and Monkkonen 1985), or to the action of important unknown processes.

The effect of last crop on temperate old field successional patterns is again shown (Beckwith 1954, Myster and Pickett 1988, 1990). In the BSS, the grass species grown for hay (*Dactylis glomerata*) persists for at least 5 yr after abandonment, greatly reduces the usual annual or biennial stages (Monte 1973, Myster and Pickett 1988), and alters successional pathways up to 8 yr after abandonment (Myster and Pickett 1990). In addition, *Dactylis* may dominate early successional species by inhibiting other species through the process of competition, which is suggested by a pattern of recurring significant negative species associations involving *Dactylis* during the first 6 yr of BSS succession (Myster and Pickett 1992).

Because Shugart and Hett (1973) examined a variety of successions, we can place our results in a larger context. The b value or slope from the regression on ln λ compares the mesic BSS fields (Fig. 1C; $b = -1.1$; Ugolini 1964) favorably to other mesic successions ($-1.0 < b < -1.3$) and agrees with the general pattern of more rapid rate decrease in mesic successions compared to xeric ($-0.17 < b < -0.24$) successions (Shugart and Hett 1973). Indeed, previous studies have shown that the rate of change is influenced by climatological conditions such as wet and dry cycles and soil type (Major 1974, Bornkamm 1981). The a value or y intercept gives the BSS fields (Fig. 1C; $a = -1.3$) a smaller y intercept than North Carolina old field succession ($a = -2.9$; latitude 35° N; Shugart and Hett 1973) which means that species were retained for a considerably longer time and succession started with a higher initial richness compared to successions in Tennessee, Georgia, Arkansas, and North Carolina (latitude 33°–37° N). Consequently, plant succession in New Jersey (latitude 40° N) corroborates the trend (probably nonlinear) of an increase in retention of species with increasing latitude (Shugart and Hett 1973).

In summary, our results confirm the generality of a decrease in the rate of plant successional change with time, show important relationships between the decrease in rate and abandonment condition, and add a more extreme location to the comparison of old field successional rate and latitude.

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