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Individualistic patterns of annuals and biennials in early successional oldfields

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Abstract

The importance of Gleasonian species individuality, with its relation to life history strategies in succession, has been implied by studies lasting only a few years, or studies relying on chronosequences. Even in long-term studies, it has been addressed without statistical tests. Here, we examine the first six years of succession in permanent plots on ten contrasting oldfields to statistically determine the role of species individuality in early oldfield succession.

Percent cover data were collected each summer in 48 permanent plots in ten oldfields as part of the Buell Succession Study at the Hutcheson Memorial Forest on the New Jersey Piedmont, USA. Congruent patterns of mean percent cover over time clearly reflect life history strategies of annuals and biennials. Kendall's coefficient of concordance, calculated for population patterns of annuals or biennials in each oldfield, confirms that population patterns within life form groups are similar and supports the contention that life history strategies are important in determining successional pattern once species become established in an oldfield.

Profile analysis, a statistical test for parallelism among species patterns, performed on all population patterns in each oldfield, confirms that these patterns are individualistic. The individualistic pattern implies that succession may be driven by the different strategies of dispersal, growth, and resource use of the species involved.

Nomenclature: Gleason & Cronquist (1963).

Introduction

One of the oldest debates in successional theory is between those who maintain that succession does not proceed in discernable stages (Gleason 1926), and those who contend that there are close obligate associations between species (Clements 1916) or supraindividual levels of organization (Margalef 1968) during succession. Succession is generally considered to be a function of population processes as reflected in individualistic population patterns (Noble & Slatyer 1980; Pickett 1982); however, there is little statistical evidence supporting this view.

During secondary succession, species most often appear or dominate in order of life-form: first annuals, then biennials, then herbaceous perennials and last, woody perennials (Oosting 1942; Bard 1952; Grime 1979; Bornkamm 1981; Jukola-Sulonen

1983). This order of dominance supports the contention that life history strategies of species are of primary importance in explaining patterns of vegetation dynamics (Pickett 1976; Horn 1981; Huston & Smith 1987). The order of species life forms may even suggest that concepts such as succession and facilitation are really statements about the comparative life histories of species that are found in association with each other (Horn 1981). Indeed, one of the models of Connell & Slatyer (1977) recognizes this possibility. However, it is impossible to discriminate among the three models of successional mechanisms proposed by Connell & Slatyer (1977) by reference to patterns alone (Connell *et al.* 1987; Pickett *et al.* 1987a, b; Walker & Chapin 1987). Therefore, we restrict our analysis to questions that can be answered using species pattern during a period of rapid community change.

This paper will examine population patterns of dominant species through succession in permanent plots on ten oldfields. Similar patterns among species of similar life-history strategy would imply the importance of life-history strategy in determining successional patterns. To approach the issue of similarity of population patterns, this paper will answer the following questions: (1) What are the population patterns of species through early oldfield succession? (2) How do the conditions at the time of abandonment of an oldfield from agriculture relate to the observed population patterns? (3) Are there general trends for annuals or biennials through succession in different oldfields? (4) Is oldfield succession an individualistic process or do species form groups during early succession?

Methods

The study site, William L. Hutcheson Memorial Forest Center (HMF) on the New Jersey Piedmont, includes ten oldfields (the Buell Succession Study) which have been sampled in late July every year since abandonment. Oldfields vary in size between 0.35 – 0.87 ha. These oldfields differ in five characteristics (Table 1). HMF is located approximately 1/2 mile east of East Millstone, Somerset County, New Jersey, U.S.A. (40° 30′N, 74° 34′W). The oldfields occupy the Penn soil series, developed from the Triassic red shales of the Brunswick Formation (Ugolini 1964). Soil texture, drainage, and depth vary only slightly among the ten abandoned oldfields (Ugolini 1964). Texture is classified as either loam or silty loam. Bard (1952) found no decisive correlation between physical and chemical soil characters and age of fields in the region of HMF. No significant differences in nitrate, ammonium, nitrogen mineralization potential, phosphorous, calcium, potassium, soil structure, soil texture, or organic matter were found in three oldfields at HMF of ages 1, 4 and 19 years (Robertson & Vitousek 1981; Robertson 1982). Soil differences have therefore been assumed to be small among the ten oldfields in this study.

Each of the ten oldfields contains 48 permanent, 2.0 × 0.5 m, plots. This paper used the data collected from the first through the sixth years of succession in each oldfield. The percent of the surface area of each plot covered by each species present was estimated with the aid of a sampling frame. This paper deals with only those species that achieved at least five percent mean cover in any sampling year (hereafter ‘dominant species’).

Life-form of each species was defined as in Gleason & Cronquist (1963). For each dominant species, several parameters were calculated: number of oldfields in which the species was dominant, the mean frequency over the oldfields each year, the mean first and last years of nonzero cover, the percent of years in which the species was present, the species maximum cover attained in any oldfield, and the average maximum cover over all the oldfields.

We also determined the distribution of peak cover for each species. The number of peaks, average year of highest peak, and the average gap between peaks were calculated for each dominant species. Each mean includes all oldfields in which the species was dominant. To determine a ‘peak’ of percent cover for a species, standard errors of the mean were calculated for each year. Distinct peaks are defined as those separated by two or more years and low (less than 3% cover), non-overlapping standard errors in peaks and troughs. Only annuals and biennials are analyzed here; perennial population patterns and other aspects of pattern in the Buell Succession Study will be analyzed in subsequent papers.

Both principal components analysis (PCA) and detrended correspondence analysis (DCA) were performed on mean cover of species in each field during the first four years to display the relationship among the ten successions and determine which species best differentiated the early successional communities (Wartenberg *et al.* 1987; Faith *et al.* 1987; Minchin *et al.* 1987).

Kendall's (1975) coefficient of concordance was calculated on the ranks of all annuals and all biennials in each oldfield. Changes in cover were coded as ranks obtained from the population patterns through time. Rank numbers increased when percent cover increased, and decreased when cover decreased. To determine if the population patterns were similar in a life-form group, we calculated Kendall's coefficient of concordance, W, which examines all possible pairs of species ranks, m each of size n. W is defined using the sum of squares of deviations of all ranks from the mean, and varies between 0 and 1. The test is analogous to ANOVA and assumes normality and independence of observations. Significant differences are indicated by W in the $(n!)^m$ possible set of ranks and dissimilarity is limited by the probabilities of m and n. χ^2 is derived from W, and p is read from common χ^2 tables. Significant differences require W to exceed χ^2. Such methods are suggested by Greig-Smith (1983) for the analysis of similarity between species responses along series of samples.

To test whether the population patterns were individualistic or parallel, we applied profile analysis, a statistical test for parallelism (Morrison 1976; Timm 1975; Travis 1980). This test is appropriate for repeated measures (Hand & Taylor 1987). Profile analysis determines if the profiles (the shape and contours) of several lines are significantly different. The test assumes equivalence of units among measurements, and independence of groups (here species) measured repeatedly at p distinct ordered time points. The analysis is based on a general linear model, $Y = Xu' + E$, where Y is the response over time, X is a constant, u' is mean response, and E is the error. The null hypothesis of parallelism is $H_0{:}u_1 = u_2 = \ldots u_n$ where n is the number of profiles. The general multivariate fundamental least-squares theorem is employed in the computations, using Wilks' Λ to test H_0. If $\Lambda < U_\alpha$, where U_α is the table value at a significance level of α, H_0 is rejected. Here, mean cover of a species over all 48 plots in a field was used to generate the profiles for testing. Heterogeneity among plots will be the subject of future work.

Results and discussion

Both ordination techniques sort fields on the first axis by year of abandonment (Fig. 1A, B). Fields abandoned earlier (1958–1960) tend to be associated with lower first axis scores rather than fields

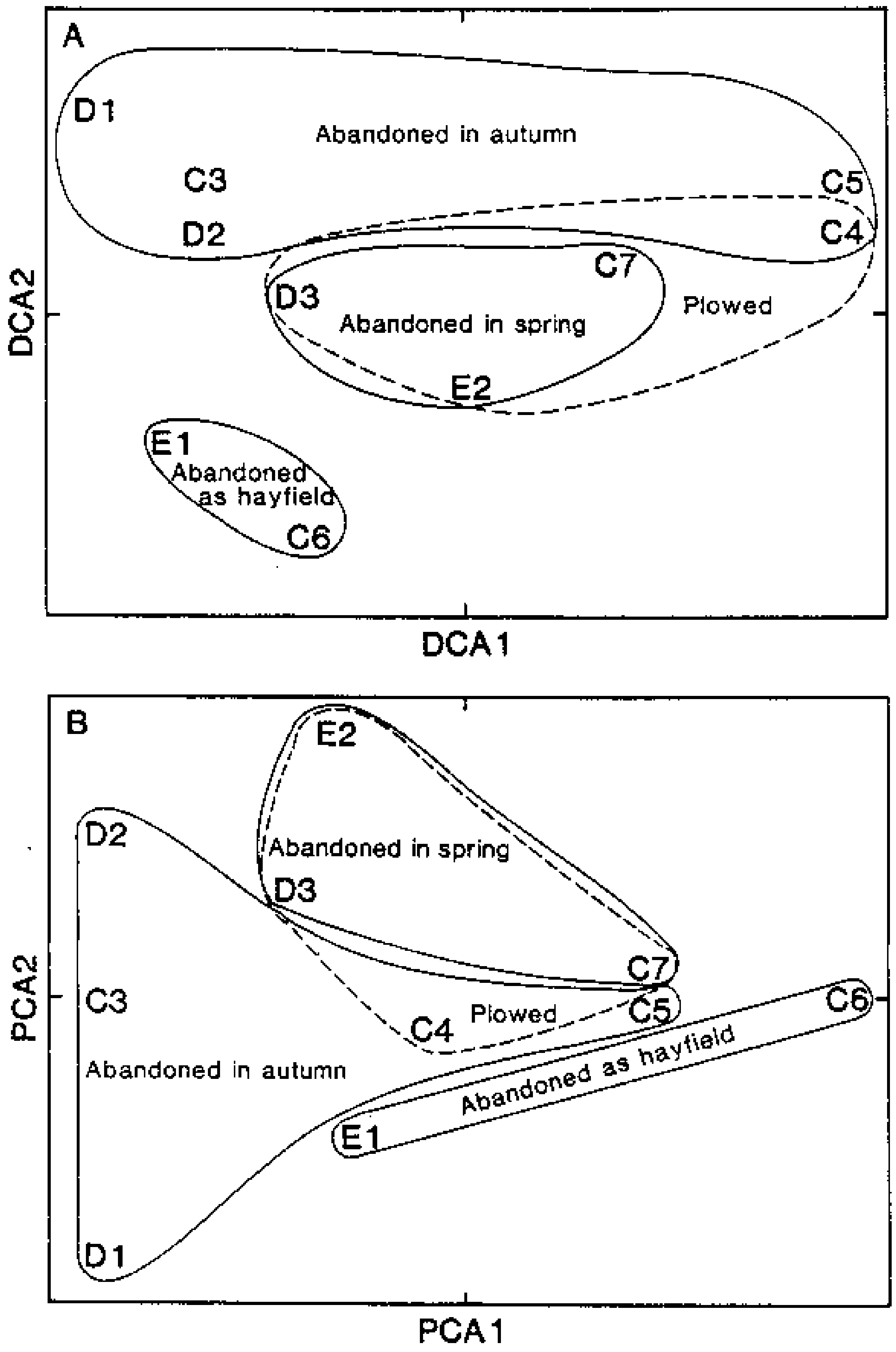

Fig. 1. A. Detrended correspondence analysis of the first four years of succession. B. Principal components analysis of the first four years of succession. Each of ten oldfields is abbreviated as in Table 1. In each panel, fields are grouped according to season and mode of abandonment.

abandoned later (1964–1966; Table 1, Fig. 1). The PCA (Fig. 1B) sorts fields on the basis of conditions known to differ at abandonment more clearly than does DCA (Fig. 1A). The two fields abandoned as hayfield stand out more distinctly, and there is less interspersion of spring-plowed and fall-abandoned fields on the PCA ordination.

We use the first four years to analyze patterns of dominant early successional life histories because it is in these years that annuals and biennials peak in cover and rapidly decline (Frye 1978). The annuals and biennials correlate differentially with the PCA axes. The first axis is defined by correlation with *Ambrosia artemisiifolia* (+0.804), *Chenopodium album* (+0.954), *Hedeoma pulegiodes* (+0.837), *Barbarea vulgaris* (+0.912) and *Convolvulus sepium* (+0.954). *Dactylis glomerata* (−0.838) correlates with the second axis. These then are the species differentiating these early successional communities. Two of these species do not invade these fields by means of sexual propagules. *Dactylis glomerata* (orchard grass) persists mainly in those oldfields where it had been planted to produce pasture; thus, it cannot be strictly considered a colonizing species in these oldfields. *Convolvulus sepium* has an aggressive asexual and twining habit (Quinn 1974) and likely persisted from the last year of tillage. The remaining species correlating with the PCA axes are the invading annuals and biennials (Fig. 2) that best define the early oldfield communities. Annuals and biennials account for 80% of total cover in years 1 and 2, 50% in years 3 and 4, and 10% in years 5 and 6 (Frye 1978).

Species dominant in more than two oldfields (denoted 'common species') also had the greatest percent cover and the greatest mean frequency (Table 2). Therefore, those species that could establish

Table 1. Characteristics of the Buell Succession Study oldfields.

Oldfield code	Year first sampled	Final crop	Mode and season of abandonment	% edge in forest
C3	1958	soybeans & sorghum	unplowed, autumn	44.6
D1	1958	soybeans & sorghum	unplowed, autumn	36.1
D2	1960	soybeans & sorghum	unplowed, spring	37.8
D3	1960	soybeans & sorghum	plowed, spring	27.0
E1	1962	orchard grass	unplowed, autumn	21.4
E2	1962	orchard grass	plowed, autumn	22.9
C6	1964	orchard grass	unplowed, autumn	33.4
C7	1964	orchard grass	plowed, spring	47.4
C4	1966	soybeans	plowed, autumn	28.7
C5	1966	soybeans	unplowed, autumn	31.1

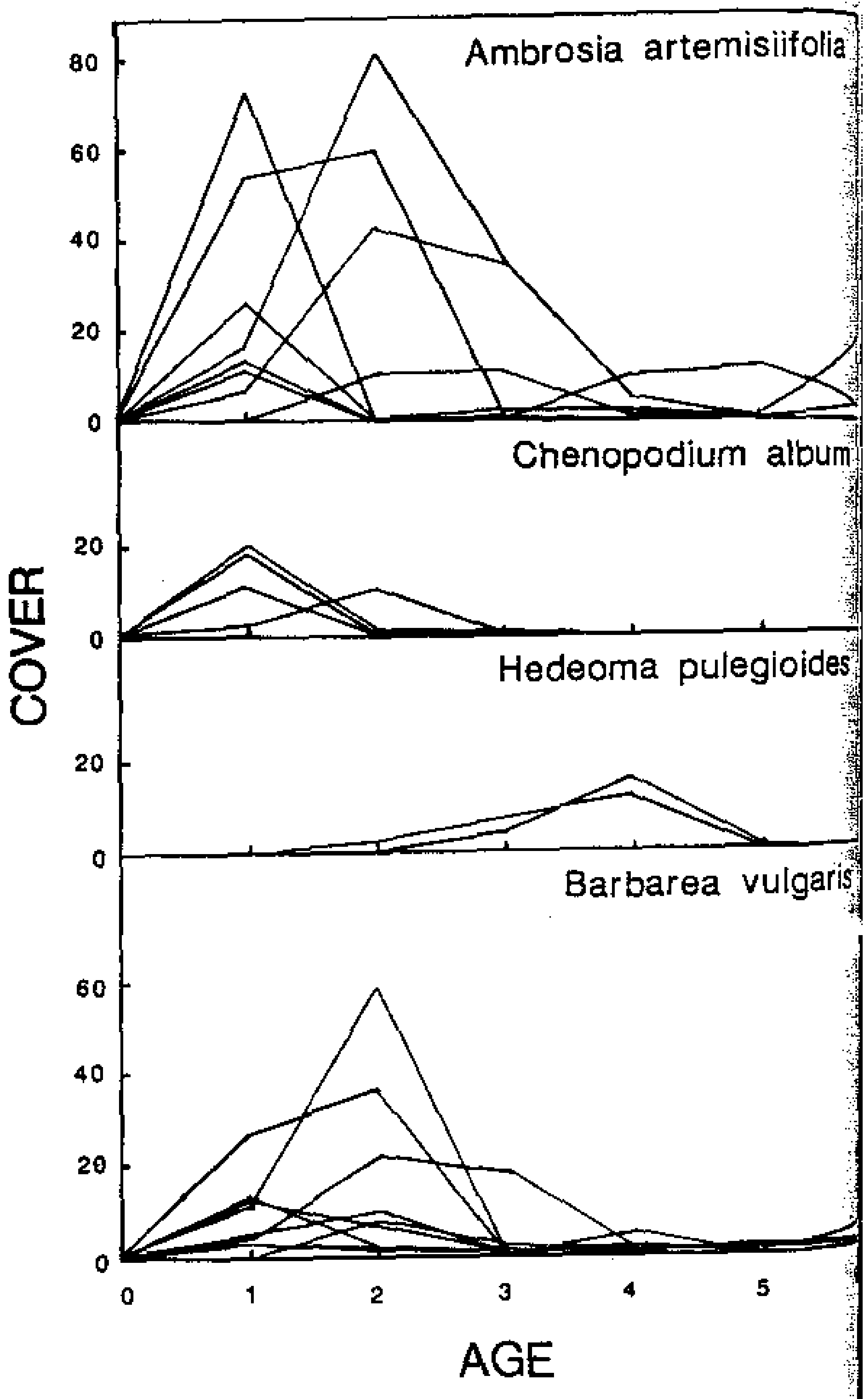

Fig. 2. Population patterns of the four most important species in the early successional community. Mean percent cover is indicated on the ordinate and years since abandonment on the abscissa. Each profile represents the cover attained by a species in one oldfield.

Table 2. Major aspects of temporal and spatial distribution of species during the first 6 years of succession in ten oldfields. Number of fields in which a species exceeds 5% mean cover; mean number of 48 plots a species occupies over all fields; mean first and last years species appears, and the percent of years present; maximum and mean percent cover; number of peaks in cover (as defined in text), year of highest peak, and number of years between peaks exhibited by each dominant species.

Species	Fields	Mean frequency						Mean nonzero years			Maximum cover		Peaks of cover		
		Year 1	2	3	4	5	6	First	Last	Present	Absolute	Mean	Number	Year	Gap
Annuals:															
Acalypha rhomboidea	2	0	22	13	20	10	39	2	6	100%	7	6	2	3	0
Ambrosia artemisiifolia	8	34	32	25	26	17	27	1	6	96%	81	39	11	2	1
Bromus racemosus	1	0	0	0	11	15	19	4	6	40%	5	5	1	4	0
Chenopodium album	4	46	24	13	2	0	1	1	2	73%	20	15	4	1	0
Digitaria sanguinalis	4	45	27	1	4	1	3	1	5	43%	88	34	4	1	0
Erigeron annuus	9	12	37	29	29	26	30	2	6	97%	52	20	24	4	2
Erigeron canadensis	1	3	44	35	0	8	0	2	5	58%	5	5	1	2	0
Lepidium campestre	1	29	0	14	2	15	0	1	5	80%	5	5	1	1	0
Lolium multiflorum	2	31	0	0	0	6	1	1	3	32%	8	7	3	2	2
Mollugo verticillata	2	41	0	0	0	0	0	1	1	14%	30	22	2	1	0
Portulaca oleracea	1	42	6	7	0	0	1	1	2	40%	5	5	1	1	0
Raphanus raphanistrum	6	29	9	6	1	10	2	1	4	60%	37	17	7	2	0
Biennials:															
Barbarea vulgaris	8	35	39	11	15	16	14	1	6	94%	59	21	11	3	3
Daucus carota	8	15	22	25	30	31	29	1	6	100%	40	14	10	4	1
Dianthus armeria	1	0	2	5	20	25	28	2	6	90%	6	6	1	5	0
Oenothera biennis	2	2	3	8	6	12	25	1	6	95%	6	5	2	6	0
Verbascum blattaria	1	13	24	11	5	17	13	1	6	100%	5	5	1	2	0

in many oldfields were the same species that grew well after establishment. All species were present in approximately 87% of years sampled, supporting the initial floristic hypothesis (Egler 1954).

We examined population patterns in the aggregate to determine whether there was similarity of species within each life-history group. Kendall's coefficient of concordance (Table 3) showed that the patterns of all annuals taken together are not significantly different (i.e., p values > 0.05). Likewise, the patterns of all biennials are not significantly different (Table 3). Because these groups of species have patterns that are similar, life-history strategies of these species are important in determining the population patterns once they establish. Common annuals peak earlier than common biennials. Annuals have a lower mean frequency over six years and the last year in which they are present is earlier than that of biennials. The population patterns (Fig. 2) reflect these characteristics, showing earlier peaks and a steeper decline in cover after peak years for annuals than biennials.

Differences between oldfields in trends of early peak cover and rapid decline for annuals (Table 2) relate well to oldfield characteristics (Table 1). Oldfields with a final crop of orchard grass have little cover of annual plants (Fig. 3). Oldfields that were unplowed at abandonment also have little cover of annual plants. Those oldfields with the highest cover values for annuals were plowed. Oldfields with the highest annual cover had soybeans as a final crop.

The behavior of biennials as a group was related to oldfield characteristics (Fig. 3). Those oldfields with a past crop of orchard grass had little biennial cover. Oldfields with the most biennial cover had soybeans as a past crop.

To determine whether the species in all ten successions exhibited similar patterns through time, profile analysis was performed. This statistical analysis is focused on the persistent question of species in-

Table 3. Similarity of increase and decrease of cover for annuals or biennials within each of the ten oldfields of the Buell Succession Study, analyzed by Kendall's coefficient of concordance of ranks.

Life-form and oldfield	*W*	Chi-square	*P*-value
Annuals:			
C5	0.0080	1.32	0.923
C4	0.0052	1.58	0.956
C6	0.0049	1.92	0.900
C7	0.0048	1.05	0.895
E1	0.0047	1.12	0.904
E2	0.0075	1.82	0.856
D3	0.0013	1.65	0.833
D2	0.0025	1.72	0.955
D1	0.0052	1.52	0.969
C3	0.0020	1.39	0.998
Biennials:			
C5	0.0081	1.95	0.987
C4	0.0062	1.25	0.992
C6	0.0095	1.03	0.899
C7	0.0092	1.85	0.702
E1	0.0051	1.15	0.888
E2	0.0050	1.82	0.669
D3	0.0045	1.65	0.701
D2	0.0041	1.02	0.995
D1	0.0087	1.31	0.903
C3	0.0082	1.35	0.899

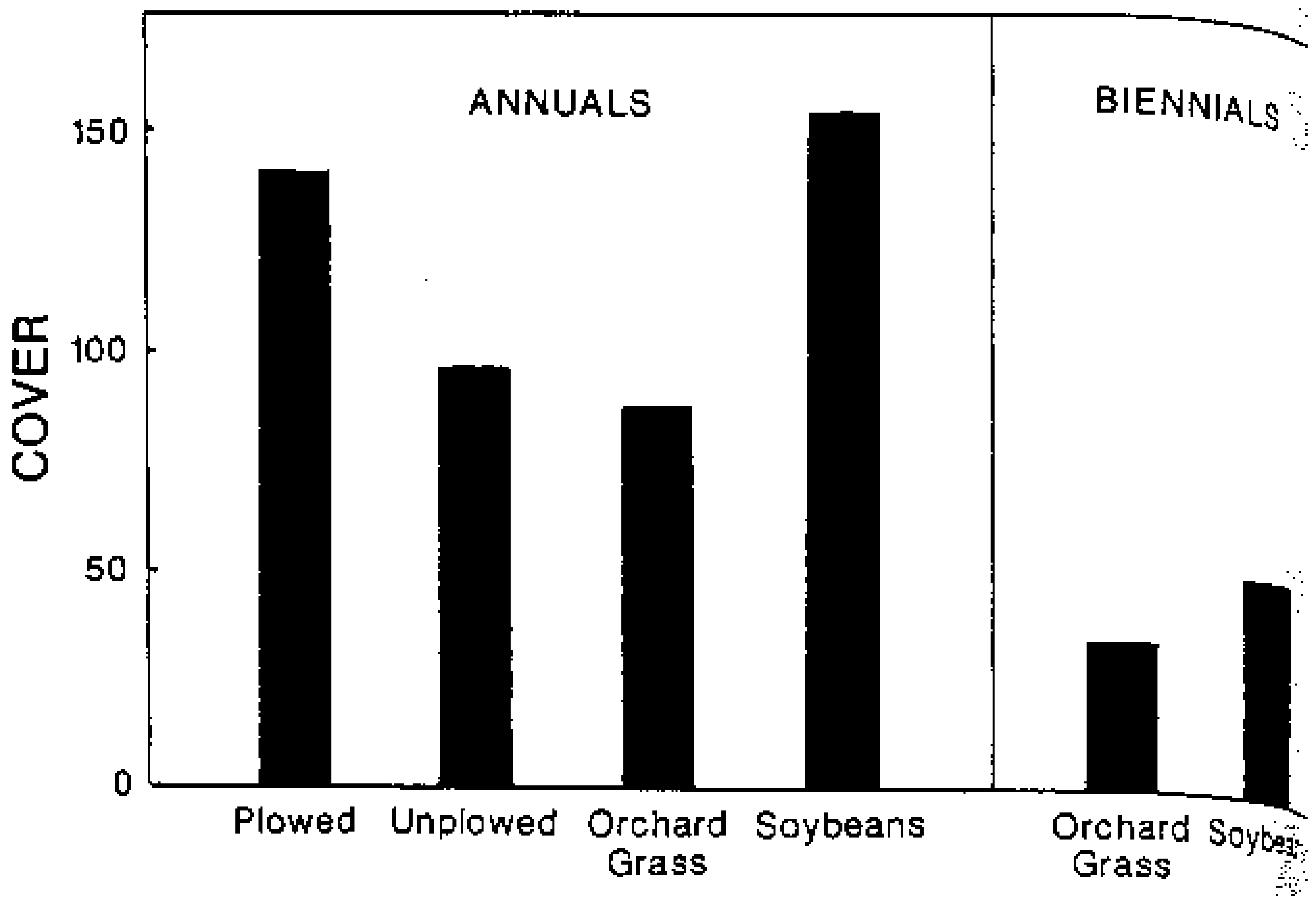

Fig. 3. Mean maximum cover of all annuals or biennials in oldfields abandoned after a row crop (soybean) or pasture (orchard grass), or contrasting abandonment treatment (plowed vs. unplowed).

dividuality. The results of the profile analysis (Table 4) show that when all population patterns are taken together, they are far from parallel (Wilks' Lambda $<<U$, $p>0.05$), and thus show an individualistic pattern. In the ten early successions studied here, successional species do not enter, peak and decline together through time, but enter and go extinct individualistically (Gleason 1927). Individualistic behavior should not be construed as being necessarily random, but rather to reflect the individual dispersal biologies, environmental tolerances, and capacities for interaction of each species.

Conclusions

The problem of species individuality in succession is a fundamental one. Most previous investigations of oldfield succession have had to use chronosequences, with their untested assumptions (Pickett 1988), to piece together population patterns (e.g. Oosting 1942; Bard 1952). Here, actual population patterns through time are presented and the existence of species individuality statistically confirmed. Such a finding increases confidence in the use of life history strategies in explaining patterns of vegetative dynamics (Pickett 1976; Grime 1979; Horn 1981; Huston & Smith 1987).

Our conclusions can be stated in terms of the questions posed in the introduction: (1) The population patterns exhibit early peaks and persistant tails, although few have constantly high levels of cover (Fig. 2). Some species exhibit more than one peak

Table 4. Parallelism of population patterns through time within each of the ten oldfields in the Buell Succession Study, analyzed by means of profile analysis.

Oldfield	Wilks Lambda	*U*	*P*-value
C5	0.182	0.802	0.201
C4	0.201	0.812	0.267
C6	0.106	0.798	0.378
C7	0.212	0.805	0.402
E1	0.152	0.821	0.194
E2	0.143	0.829	0.332
D3	0.162	0.850	0.222
D2	0.178	0.802	0.255
D1	0.121	0.815	0.220
C3	0.125	0.792	0.115

of cover. Taken together, the species overlap widely over time (Fig. 2, Table 2). (2) Oldfields sharing initial conditions at abandonment (Table 1) often exhibit similar species patterns (Fig. 3), although year of abandonment affects community characteristics (Fig. 1). (3) Common trends for annuals as a group and biennials as a group are evident (Table 3). (4) The population patterns are statistically individualistic (Table 4). Community change is not expressed in sudden shifts between discrete compositional communities. These individualistic population patterns and few constantly high levels of species cover suggest differential adaptation or interaction as important mechanisms of succession.

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