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Initial Conditions, History and Successional Pathways in Ten Contrasting Old Fields

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ABSTRACT.—We examined the PCA ordination scores of 10 old fields through 22 yr of succession. Clonal species *Dactylis glomerata* and *Hieracium pratense* had the largest correlation with the first principal component in the 1st 18 yr of succession. After 18 yr, *Rosa multiflora* and *Toxicodendron radicans* had the largest correlation with the first principal component. Successional pathways of the 10 old fields show great variation in early succession but variation of pathway decreases later. Comparison with a null model reveals that the trend of increasing similarity of old fields through time is real and convergence is occurring. Because mechanisms causing convergence might include the effect of initial abandonment conditions, we divided the 10 old fields into groups defined by the last crop, season of abandonment, year of abandonment, and mode of abandonment (plowed or not). Analysis of the minimum spanning tree needed to connect the old fields of the same age in ordination space showed that the greatest difference between groups was in the 1st 8 yr between old fields that had *Dactylis glomerata* (orchard grass) as a last crop and those that did not. Of common abandonment conditions, last crop greatly influences successional pathways and convergence in these old fields.

INTRODUCTION

The history of a community may be important in determining its current organization and structure (Connell, 1980; Schoener, 1986). History includes the order and rate of invasion and colonization of a community (Morin, 1984; Chesson and Case, 1986; Hubbell and Foster, 1986; Robinson and Edgemon, 1988) and its initial conditions (Gleason, 1926). The best examples of initial conditions may be those present at the creation of islands (Simberloff and Wilson, 1969) or at primary succession (Crocker and Major, 1955).

For old-field succession, initial conditions include the soil characteristics and pool of viable propagules, as well as abandonment characteristics such as the year of abandonment, the season of abandonment, the previous crops and whether the field was plowed or left unplowed (Bard, 1952; Beckwith, 1954; Buell *et al.*, 1971). Researchers have pointed to the importance of characteristics at abandonment in determining subsequent organization and successional pathways of old fields (Pickett, 1982; Keever, 1983). We test, using minimum spanning trees, null models and confidence intervals, three hypotheses concerning successional pathways, convergence and the role of initial abandonment conditions using permanent plot data collected through 22 yr of succession in 10 old fields.

Hypothesis 1.—Variation in pathway will decrease with time from abandonment. The old fields will converge in floristic composition. Actual successions exhibit a variety of pathways (Olson, 1958) and may best be represented through the use of time trajectories of samples in ordination space (Austin, 1977). Convergence of stands towards a stable species

composition (Clements, 1916; Margalef, 1968) is a concept that may no longer be viable (Drury and Nisbet, 1973). Some studies have shown convergence at the same time scale of our study, 1–3 decades (Monte, 1973; Collins and Adams, 1983), and at a longer time scale of 5–6 decades (Christensen and Peet, 1984). However, other studies have found no evidence of such a trend (Matthews, 1979).

Hypothesis 2.—Characteristics at abandonment of these old fields greatly affect successional pathway. Old fields with similar abandonment characteristics have similar successional pathways. The relationship between the season of abandonment and the germination requirements of the plants in the seed bank may be critical (Busing and Clebsch, 1983; Keever, 1979, 1983). Previous crops may persist in an old field after abandonment or affect colonists in other ways (Drew, 1942; Bazzaz, 1968). Plowing may reduce or eliminate dominant species (Monte, 1973; Tilman, 1987) or, in concert with other abandonment characteristics, affect successional pathways (Jokola-Sulonen, 1983). The year of abandonment is important if there is significant yearly variation in weather or if different species are available for establishment in different years (Pickett, 1982).

Hypothesis 3.—Clonal grasses grown in agricultural fields will persist after abandonment for many years and affect successional pathways. Persistence of grasses grown for hay has been seen in other old fields after abandonment (Beckwith, 1954). These grasses may inhibit the growth of other old-field species (Myster and Pickett, 1988).

MATERIALS AND METHODS

Hutcheson Memorial Forest Center (HMF) is located approximately 10 km E of New Brunswick, Middlesex County, New Jersey (40°30′N, 74°34′W). The old-growth forest at HMF has been described as having a *Quercus–Carya* canopy and a *Cornus florida* understory (Bard, 1952). During 1989, we analyzed 10 old fields that comprise the Buell-Small Succession Study (BSS; Buell *et al.*, 1971; Myster and Pickett, 1988). Each of the old fields contains 48 permanent plots (2.0 × 0.5 m) arranged in a grid. Each old field was sampled every year between the year of abandonment and 1979, and every other year since then. The percent cover all species in each plot was recorded during each sampling period. These old fields differ in four abandonment characteristics or initial conditions: years of abandonment (1958, 1960, 1962, 1964, 1966), mode of abandonment (plowed, unplowed), season of abandonment (spring, autumn), and last crop [orchard grass (*Dactylis glomerata*); soybeans; soybeans and sorghum; Myster and Pickett, 1988].

Principal components analysis (PCA; Pielou, 1984) is the best ordination method based on variance of the species abundances (Allen, 1987; Wartenberg *et al.*, 1987) and was used to ordinate the 217 samples of the BSS (one sample = data from one old field in 1 yr). In addition, Detrended Correspondence Analysis (Hill and Gauch, 1980) and Bray-Curtis ordination (Bray and Curtis, 1957) were performed on these data (Myster and Pickett, 1988). These other methods showed similar trends but PCA sorted the fields on the basis of conditions known to differ at abandonment more clearly (Myster and Pickett, 1988). Successional pathways of these old fields were represented by plotting the first two principal component scores of the 217 samples and examining trends through time. For the 10 old fields of a given age we computed the centroid of mean coordinates (Calhoon and Aaronson, 1979; Pielou, 1984) and standard errors (Sokal and Rohlf, 1981) on each principal component axis. The 1st 22 yr of successional data were used for analysis because the youngest fields were abandoned 22 yr ago.

Minimum spanning trees (MST; Pielou, 1984; Moulton and Pimm, 1986) were used to describe the similarity or dissimilarity of old fields of the same age. The length of a MST is the shortest euclidean distance needed to connect all 10 old fields of a given age in PCA

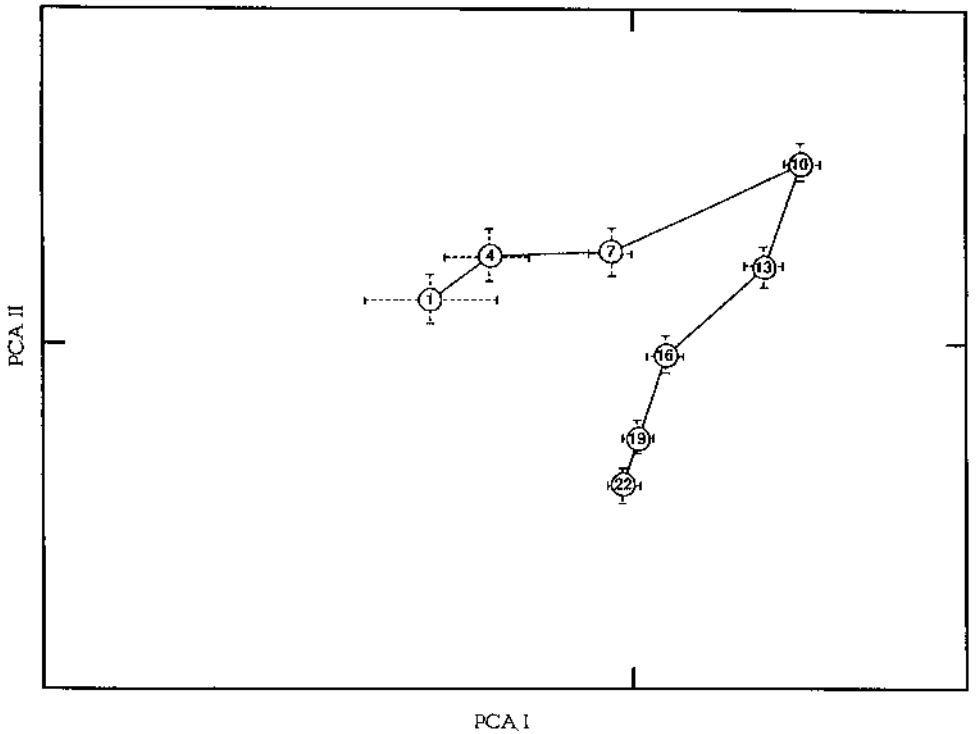

FIG. 1.—The two-dimensional PCA space of the BSS old fields through the 1st 22 yr of succession. There are eight centroids graphed; the location of each is the mean coordinates of the 10 old fields of the age marked: the 1st, 4th, 7th, 10th, 13th, 16th, 19th and 22nd yr of succession. Centroids of intermediate years were not shown for clarity, but have the same trends of variability, directionality and convergence. The dashed lines attached to the centroids are the standard error bars of the 10 old fields

space. MSTs will be used to describe the dispersion of old fields of the same age in ordination space. The length of the MST, the closeness of the 10 old fields in ordination space (Collins and Adams, 1983), will be used as an indicator of convergence. A short MST means that old fields are similar. Other convergence measures are not based on variance of abundance of species as an indicator of convergence; rather they use raw abundances (Monte, 1973), ranks of abundances (Christensen and Peet, 1984) or the rate of species loss (Shugart and Hett, 1973).

A null model of randomly generated points in the PCA space was used to decide if successional pathways and convergence were different from random (May, 1984). We restricted the range of possible random values to between the maximum and minimum PCA values of each of the first five PCA coordinates of year 1. We computed the length of the MST of the 10 points in PCA space representing the 10 BSS old fields in each year and the MST of the randomly generated points. We compared these lengths to investigate significant deviations of the BSS old fields from randomly generated patterns of similarity. We generated 10 null models and randomly generated MSTs for each year to match the 10 old fields. Confidence intervals were computed for the 10 null models (Sokal and Rohlf,

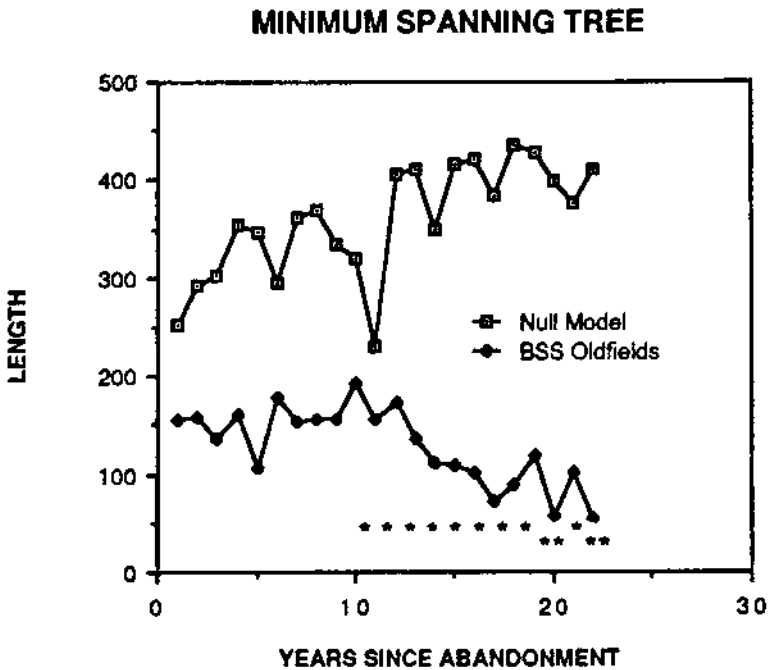

FIG. 2.—Length of minimum spanning trees for the BSS old fields and the randomly generated null model in 5-dimensional PCA space. An asterisk indicates that the BSS old fields are outside the 95% confidence interval for the null model. Two asterisks indicate the BSS old fields are outside the 99% confidence interval

1981, p. 141). If the MST length for the BSS old fields is outside the interval for 95% or 99% confidence, the observed MST is statistically different from the null model. The 10 old fields were than grouped according to the four initial conditions. We computed the MSTs for each of these groups over time. The length of these MSTs was normalized whenever there were unequal sizes of groups.

RESULTS

The first three PCA axes account for 52% of the total variance and the first five axes account for 75% of the variance. The species with the strongest correlation with the first PCA component and defining the first axis best are: *Dactylis glomerata* ($r = -0.776$) and *Hieracium pratense* ($r = +0.605$). The species defining the second PCA axis best are *Rosa multiflora* ($r = -0.732$) and *Toxicodendron radicans* ($r = -0.633$), and the species defining the third PCA axis best are *Poa pratensis* ($r = +0.766$) and *Solidago graminifolia* ($r = +0.633$). All are clonal species. The advantage of clonal growth in colonizing disturbed areas has been suggested in other studies of old-field succession (Beckwith, 1954; Bazzaz, 1979). The clonal habit allows species to quickly colonize patches of resources and to dominate easily through aggressive root and lateral growth (Sebens and Thorne, 1985).

The BSS old fields are negatively associated with PCA axis I and have PCA axis II scores close to zero at the beginning of succession (*i.e.*, yr 1, 4 and 7; Fig. 1); the old fields then become positively associated with PCA axes I and II (*i.e.*, yr 10 and 13; Fig. 1), and finally the old fields are negatively associated with PCA axis II and have PCA axis I scores

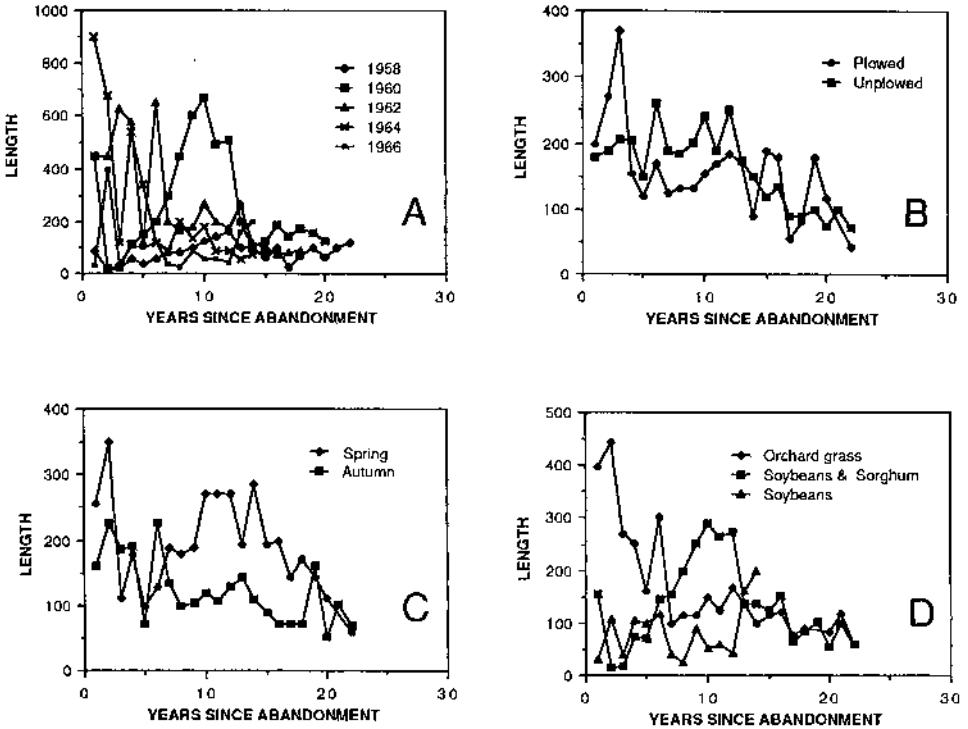

FIG. 3.—Length of minimum spanning trees of old fields divided into groups by initial conditions: (A) by year of abandonment; (B) by mode of abandonment; (C) by season of abandonment, and (D) by last crop before abandonment

close to zero (*i.e.*, yr 16, 19 and 22; Fig. 1). Therefore, the 1st 7 yr of succession reflect the relative abundance of *Dactylis glomerata*, whereas the next 6 yr (yr 8–13) are related to the relative abundance of *Hieracium pratense*. The last 9 yr (yr 14–22) are best described by relative abundances of *Rosa multiflora* and *Toxicodendron radicans*. Through time, the 10 old fields correlate most strongly with different species and the standard errors decrease (Fig. 1). Therefore during the 1st 22 yr, variation in pathway is decreasing and this succession is directional and not cyclic (Fig. 1).

The difference between the BSS old fields and the null model of MST lengths increases through succession (Fig. 2). The BSS old fields are outside the 95% confidence interval from yr 11 to 22, and outside the 99% confidence interval in yr 20 and 22. The length of the MST for the BSS old fields decreases dramatically with a few instances of increase through succession. This is strong evidence of the reality of floristic convergence (Monte, 1973; Glenn-Lewin, 1988).

Causal mechanisms of succession and convergence may include the initial and historical effect of old-field characteristics at abandonment, as well as soil characteristics and pool of viable propagules. The largest difference between MST lengths for old fields grouped by initial condition occurred for fields that differed in last crop (Fig. 3D). The pattern of MST length for the other initial conditions did not show a clear difference (Fig. 3A–C). Those old fields that had *Dactylis glomerata* as their last crop had the longest MST length.

DISCUSSION

Two results show that the presence, absence and abundance of *Dactylis* in these old fields largely determine their early successional pathway and rate of convergence. First, the abundance of *Dactylis* in an old field is highly correlated with an old field's position in PCA space in early succession (Fig. 1), and second, the dispersion of old fields of the age is most similar for old fields that had *Dactylis* as a last crop (Fig. 3D). Initial conditions other than last crop (*e.g.*, time and mode of plowing) may affect the position of old fields along PCA axis I by altering the relative abundance of *Dactylis*. After 8 yr the successional pathways of all old fields become similar (Fig. 3D), which suggests that the historical effect of *Dactylis* persists for at least 8 yr. Mechanisms other than persistence of last crop may play critical roles in determining species composition and abundance after this point (Monte, 1973).

The old-field succession at Hutcheson Memorial Forest is similar to an old-field succession reported in Michigan (Beckwith, 1954). In both cases, last crops included soybeans and sown grasses mowed for hay. Beckwith (1954) found that early years of succession were greatly influenced by the character of the last crop. The growth habit of the hay species, especially their vegetative reproduction, enables them to withstand plowing and still dominate. Woody species were repressed in the Beckwith (1954) old fields and the hay crop is eventually replaced by other perennials such as *Aster* spp. and *Solidago* spp. (Beckwith, 1954).

In the BSS old fields, the hay species is *Dactylis glomerata* and the cultivated crops are soybeans (*Glycine max*) and sorghum (*Sorghum* spp.). After abandonment of the BSS old fields, the hay species *Dactylis* persists for at least 5 yr and greatly reduces the usual annual or biennial stages (Monte, 1973; Myster and Pickett, 1988). *Dactylis* often dominates early succession by inhibiting other species. In the BSS old fields, the hay crop is also (Beckwith, 1954) eventually replaced by clonal perennials, *i.e.*, *Hieracium pratense, Rosa multiflora* and *Toxicodendron radicans*. However, past crops may affect successional pathways in ways other than direct plant-plant interactions. Crops in fields can develop strong positive associations with weed species (Vengris, 1953). After abandonment, these weeds may persist in the seed bank and invade an old field. Some common weed species have been past crops themselves (Martin *et al.*, 1976). Past crops may also affect early old-field vegetation because they dictate the irrigation practices, herbicide and nutrient treatments of agricultural fields.

Contemporary models of succession (Horn, 1975; Facelli and Pickett, 1990) have been sensitive to the role of history in determining successional pathways. The influence of initial conditions as well as boundary conditions, priority effects and historical echoes is well-documented in numerous successions (Garcia-Novo, 1979; Hobbs, 1984; Pickett, 1989). However, quantitative confirmation of effects of initial conditions are rare (Monte, 1973). Our results demonstrate both an effect of an initial condition (Keever, 1979) and give the length of its influence on successional pathways and rates of convergence. We show that clonal crops persist in old fields after abandonment and that successional pathways and rates of convergence are affected.

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