THE INDIVIDUALISTIC NATURE OF PLANT COMMUNITY DEVELOPMENT*

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Introduction

Most models of plant community development (succession) explicitly or implicitly consider the process to be a series of graded steps culminating in, or converging upon, some relatively stable long-term plant community. Those models which do not proceed by an orderly series of steps nevertheless call for relatively predictable changes in plant communities. Recently, Connell & Slatyer (1977) have seriously questioned the 'facilitation' models of succession, and Olson (1958), Drury & Nisbet (1973), Walker (1970) and Matthews (1979) have questioned the hypothetical convergence of successional pathways. In this paper, I use several sources of evidence to call into question the predictability of plant community change over time. Two of these sources are anecdotal observations, three are reviews of previously published data, and one is research first described here in detail; the quantitative data come from vegetation studies in the north-central United States.

Review of evidence

Anecdotal observations

On the grounds of the Chesapeake Bay Center for Environmental Studies, USA, (a branch of the Smithsonian Institution), which is located on the coastal plain of the Bay, are two parcels of land which, according to Center personnel, were abandoned at the same time and under the same conditions. At present, one of these stands is a young elm (*Ulmus*) forest of pole-sized trees with a typical forest undergrowth. The other parcel is vegetated by a

tangle of poison ivy (*Rhus radicans*) so dense that when traversing the area, one walks across the stems of the plants rather than on the ground. Thus, even though conditions were very similar, plant community development on these two sites has been different.

In the species-rich, old forest of Horseshoe Lake, southern Illinois, USA, (described by Robertson et al 1978), *Sassafras albidum* can be found as large trees sharing the canopy; *S. albidum* is normally thought of as a pioneer species.

Evidence from published studies

Three recent studies of vegetation dynamics in Iowa, USA, bear directly on the question of plant community dynamics. Cahayla-Wynne & Glenn-Lewin (1978) performed a classification and ordination analysis of the upland forest vegetation on the unglaciated area in extreme northeast Iowa. In those communities that were dominated by white pine (*Pinus strobus*), the most significant component of the shorter trees was white oak (*Quercus alba*). It is the normal expectation (e.g. Anderson & Adams 1978) that pine forests succeed to oak forests, but in the forests of northeast Iowa, increment cores show that the tall, large pines were younger than the oaks. In short, the pine and oak do not show the expected successional relationship.

Second, it has been demonstrated recently that plant community dynamics in prairie glacial marshes of the north-central United States are cyclical, rather than convergent (van der Valk & Davis 1978). The apparent explanation for this behavior is found in the interaction between the 'seed bank' in the marsh substrate and water level fluctuations. Mudflat communities, emergent-species communities, and the lake stage of the marsh are all related to the differential germination properties of the seeds of marsh species in response to periodic drought and flooding of the marsh.

Table 1. Average cover and species richness (number of species) for six coal spoil areas of different ages, according to three classes of substrate quality. Southeast Iowa, USA. From Glenn-Lewin (1978).

Area	Age	Per Cent Cover			Richness		
		Non-acid	Intermediate	Acid	Non-acid	Intermediate	Acid
Amsberry	5-7	49.8	13.3	2.7	23.7	11.0	2.5
Fee	13-16	56.0	13.6	3.7	12.0	9.4	3.2
Harrison	17	34.0	17.3	0.5	14.7	7.7	0.8
Wilcox	22-23	144.6	67.7	1.3	32.1	21.6	2.7
Watertor	26-27	77.8	53.9	10.3	27.8	20.9	7.3
Klein	36-38	148.5	42.7	6.0	23.0	15.4	3.9

Third, in southeastern Iowa are found a large number of coal stripmine spoils ('orphan banks') of varying ages. In an analysis of these orphan banks, Glenn-Lewin (1978) found that, aside from the fact that the trees were larger, there appeared to be no relationship between age of the orphan bank and species composition or community structure (interpreted as species diversity and canopy coverage). Instead, substrate conditions, particularly soil acidity due to the oxidation of pyrites, seemed to be the most significant factor in determining the vegetation of these spoils (Table 1). This pattern was confirmed by reciprocal averaging ordination (Glenn-Lewin 1978). Jonescu (1978) in Saskatchewan, Canada, and Chadwick & Hardiman (1976) have also concluded that the normal models of succession are inappropriate for the vegetation of orphan banks.

Natural revegetation of a grazed grassland

It is difficult to find in the rich agricultural region of the central United States, areas of natural grassland in which secondary succession is occurring. Fortunately, in 1946, the State of Iowa preserved Kalsow Prairie, a native tall-grass prairie of approximately 65 ha, of which about 13 ha, in the northwest corner, was a heavily grazed pasture. The pasture was preserved at the same time as the prairie, and the fences around the pasture were removed. The pasture was not analyzed when it was abandoned, but probably contained Poa pratensis, Solidago canadensis, and Cirsium arvense as important species, judging from other heavily grazed pastures in the region.

The vegetation of the Kalsow Prairie grazed area was recorded by Brotherson (1969, 1979), who did his field work in 1967. I restudied the same area in 1977. The purposes of these analyses were to determine:

1. In what fashion was revegetation occurring, i.e., what was the pattern of species replacement?
2. What is the rate of revegetation; how fast was the vegetation returning to the state of the adjacent prairie?

Methods

Brotherson's (1969, 1979) sampling scheme was repeated again in 1977 for comparability between the studies. Thirty plots, each 60 by 78 m, in an arrangement of 5 rows running east and west by 6 rows running north and south, were marked off. Within each of these plots, twenty 0.1 m² (20 × 50 cm) quadrats were placed in a sigmoid fashion and species coverages were estimated in each quadrat. For each plot, coverages were averaged over the 20 small quadrats.

Results and discussion

Brotherson (1969, 1979) noted that the original fenceline between the grazed area and native prairie was still visible in 1967. That fenceline was no longer visible in 1977. Sixty-five species were recorded in 1967, whereas 87 species were recorded in 1977. The coefficient of community (Sørensen 1948) was 0.73.

Brotherson (1969, 1979) stated that there was no pattern of species diversity in the grazed area in 1967. Fig. 1 demonstrates that in 1977, the plots with the greatest species richness were located adjacent to the native prairie, and those with the fewest numbers of species were located farthest away from the prairie. The concentration of dominance, as calculated by Simpson's (1949) index, demonstrates the converse of the richness pattern; the areas of highest dominance are located away from the prairie (Fig. 2).
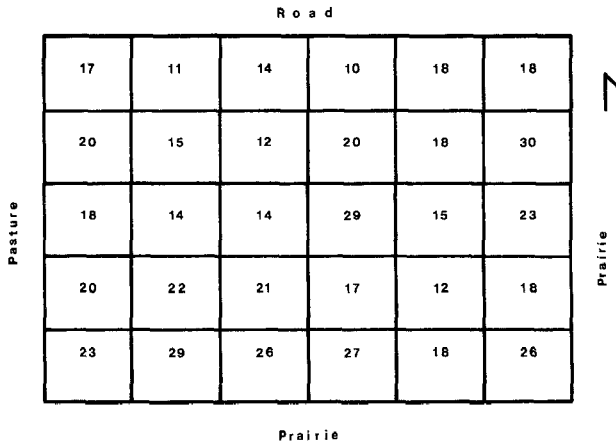
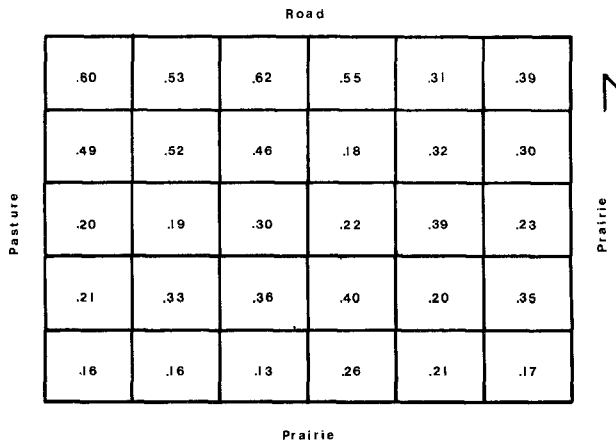Fig. 1. Species richness in the Kalsow Prairie grazed area, 1977.

Fig. 2. Concentration of dominance (Simpson's Index) in the Kalsow Prairie grazed area, 1977.

Table 2. Constancy and average cover of dominant species on the Kalsow Prairie, Iowa, USA, grazed area, 1977.

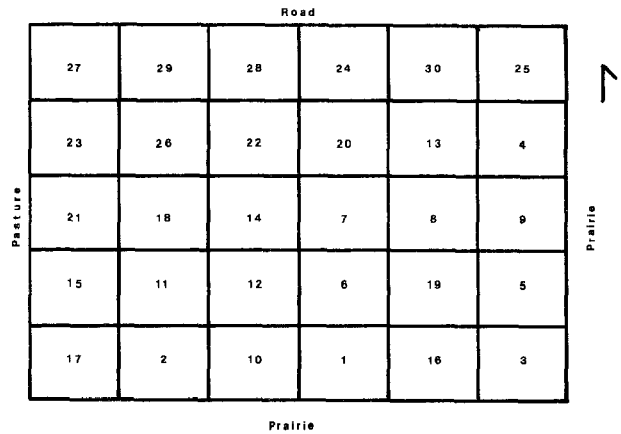| Species	Constancy	Cover
Poa pratensis	1.00	40.73
Andropogon gerardii	.87	39.28
Solidago canadensis	1.00	15.38
Aster ericoides	.97	4.10
Sporobolus heterolepis	.27	3.68
Bromus inermis	.23	2.71
Spartina pectinata	.47	2.60
Carex spp.	.80	2.50
Helianthus grosseserratus	.43	2.17

Fig. 3. Reciprocal averaging ordination position of each 60 × 78 m plot in the Kalsow Prairie grazed area, 1977.
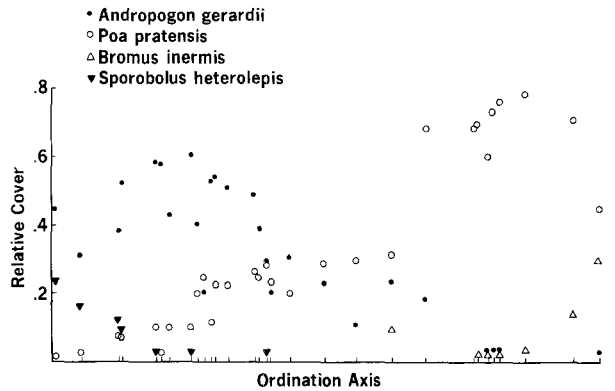
Relative cover of four important grass species along the reciprocal averaging ordination axis, Kalsow Prairie grazed area, 1977.

Fig. 4. Relative cover of four important grass species along the reciprocal averaging ordination axis, Kalsow Prairie grazed area, 1977.

On the whole, the Kalsow Prairie pasture was dominated in 1977 by some species which are characteristic of the native prairie, and some which are characteristic of heavily grazed areas (Table 2). However, these species were unevenly distributed over the grazed area. A reciprocal averaging ordination placed the plots nearest the native prairie at one end of the ordination axis, whereas the plots farthest from the prairie fell toward the other end of the axis (Fig. 3). When the four most important grasses were plotted along the reciprocal averaging ordination axis (Fig. 4), the native prairie species *Andropogon gerardii* and *Sporobolus heterolepis* peaked near the end of the ordination axis having the plots nearest the prairie, while *Poa pratensis* and *Bromus inermis*, species increasing with grazing, had peak abundances at the other end of the ordination axis, which corresponded to the portion of the

grazed area farthest away from the native prairie. By Spearman rank correlation (Steel & Torrie 1960), ordination position near the native prairie was related to higher species richness ($r_s = 0.65$, $p < 0.001$).

Brotherson (1969, 1979) plotted the abundance of *Andropogon gerardii* throughout the grazed area for 1967 (Fig. 5). A similar plot for 1977 is shown in Fig. 6. Brotherson (1969, 1979) was of the opinion that *A. gerardii* had formed an invasion front in 1967. A comparison with 1977, however, indicates *A. gerardii* did not form such a front, since the apparent front had not moved forward. Instead what had happened is that the relative abundance of *A. gerardii* had begun to differentiate from place to place.

It is clear from the facts that: 1) the fenceline was no longer visible, 2) patterns of species diversity had developed, 3) an ordination analysis produced patterns of vegetation related to the geography of the grazed area, and 4) the differentiation of the *Andropogon gerardii* population, that vegetational changes have occurred in the Kalsow Prairie grazed area between 1967 and 1977. However, the changes that have occurred have all done so mainly in those plots adjacent to the native prairie; the farther away from the native prairie, the less change has occurred in the grazed area. Only along the prairie edge were species found such as *Liatris asper, Sporobolus heterolepis, Aster laevis, Gentiana puberula, Phlox pilosa*, all species characteristic of the native prairie.

Rather than changing as a series of different species populations, the vegetation in the Kalsow Prairie grazed area changed by a process of the native prairie encroaching
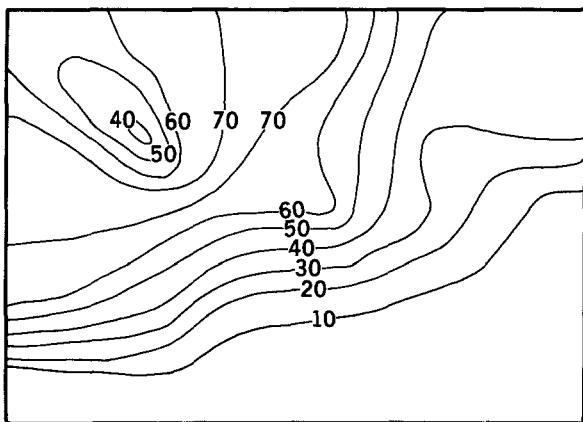
Percent cover of <u>Andropogon gerardii</u>, 1967.
From Brotherson (1968).

Fig. 5. The distribution of per cent of *Andropogon gerardii*, 1967. From Brotherson (1969).
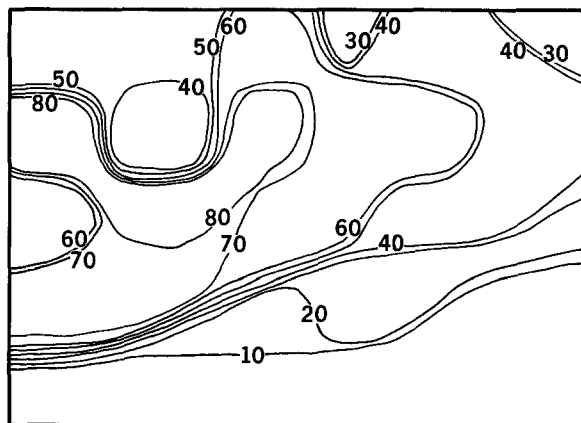
Distribution of <u>Andropogon gerardii</u>, 1977.

Fig. 6. The distribution of per cent cover of *Andropogon gerardii* in 1977.

from the edge as a more-or-less whole prairie vegetation, and it seemed most likely that this encroachment occurred by vegetative reproduction. If this is true, than the rate of revegetation is simply a matter of comparing the total distance to the edge of the grazed area with the distance that the vegetation has moved over the last approximately 30 years. Inspection in the field shows that the majority of the native prairie species have moved perhaps 10 to 20 m since the prairie was preserved. Since, in order to totally revegetate the pasture, the native prairie vegetation must move about 300 m, it appears that it will take roughly 450 to 900 yr for the process to be completed. Such a long time span may be an overestimate, but even if so, replacement of the grazed area species by native prairie species will take a long time.

This analysis of the dynamics of vegetation replacement in a north-central U.S. grazed grassland leads to three conclusions:

1. Revegetation of the grazed area is by encroachment of a whole prairie vegetation from the edge, rather than a series of species replacements as predicted by classical successional models.

2. If 1, above, is accurate, then it is unlikely that abandoned areas will ever get to a native prairie stage unless such an abandoned area is adjacent to a native prairie, or unless the area is intentionally planted.

3. The rate of revegetation in disturbed grasslands is very slow.

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Concluding remarks

The evidence brought to bear on the question of plant community development in this paper comes from simple observation, from studies that compared several sites of differing ages, from studies that examined a site over time, and from citations of others. The evidence indicates that:
1. Species may behave in an anamolous manner, i.e., species may take on different roles in community development than those usually described for them.
2. Vegetation development may be divergent under very similar environmental conditions.
3. Vegetation development may show little or no relationship to time when an environmental factor(s) is very important.
4. Vegetation development may occur by other means than species replacements via seed populations. Such change is very slow.

In the grassland region of Nort America, at least, there may be no such thing as succession in its usual meaning. Rather, plant community development appears to be individualistic in character. Such individualistic plant community development is site-specific and relatively unpredictable, i.e., with a significant random component, at least in terms of species composition.

If this is true, then ecologists perhaps should begin to look in different directions for a better understanding of plant community dynamics. Clearly, vegetation dynamics are related to seed dynamics. In addition, plant life histories are important, and the examples of the orphan banks illustrate the importance of microsite environmental variation. Research in these areas may shed new light on the process of vegetation change.

Summary

A body of anecdotal and experimental evidence raises questions about the common model of plant community succession, in which each temporal vegetation stage facilitates the development of the next stage. Several lines of evidence are discussed which emphasize the individualistic, independent nature of plant community development:
1) There are a number of instances of anamolous behaviour of 'pioneer' or 'early successional' species;
2) In shallow marshes, vegetational change is the result of the interaction between the stored 'seed bank' of the the ecosystem and the fluctuating water regime;
3) On abandoned coal spoils, vegetational composition and structure are almost entirely accounted for by substrate conditions rather than age differences of the spoils;
4) In overgrazed natural grasslands, adjacent to ungrazed areas, revegetation is primarily by vegetative reproduction of the native species creeping in from the edge as a whole vegetation complex, rather than seeding throughout in stages.

Therefore, plant succession can be interpreted as an individualistic result of the interaction of disturbance (both kind and severity) and the predominant reproductive life histories of the plant species.

It is suggested that future research efforts to understand vegetational change should be directed to the interactions between seed dynamics, asexual/sexual life histories, and microsite environmental variation.

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