

CONVERGENCE AND DIVERGENCE OF OLD-FIELD PLANT COMMUNITIES ALONG EXPERIMENTAL NITROGEN GRADIENTS¹

RICHARD S. INOUE

Department of Biological Sciences, Campus Box 8007, Idaho State University,
Pocatello, Idaho 83209-0009 USA

AND

DAVID TILMAN

Department of Ecology and Behavioral Biology, 318 Church St. SE, University of Minnesota,
Minneapolis, Minnesota 55455 USA

Abstract. Data from experiments in three old fields were analyzed using similarity indices and population trajectories to determine if similarity of resource supply rates influenced the similarity of plant community composition. In two of three fields, similarity indices indicated that experimental plots having different resource supply rates diverged in species composition with time. There was some evidence of convergence both within and between fields on plots with similar resource supply rates; however, divergence was also common, especially at high rates of nutrient supply. Much of the divergence indicated by similarity indices can be explained by plot-to-plot differences in the initial abundances of three dominant species: *Agropyron repens*, *Poa pratensis*, and *Schizachyrium scoparium*. High nitrogen treatments favored *Agropyron repens* if it was present, but led to major increases in *P. pratensis* or *S. scoparium* if *A. repens* was absent. The trajectories through time of these three species suggest that plots will converge at high nitrogen levels.

Key words: community; convergence; divergence; nitrogen; old field; resources; similarity index; trajectory.

INTRODUCTION

Resource-based models of community structure predict that, given adequate time for interspecific interactions to go to equilibrium, the species composition of a plant community should be determined by resource supply rates (Tilman 1982, 1985, 1988). Plots with the same resource supply rate should, then, become more similar in species composition, or converge, while plots with different resource supply rates should become less similar, or diverge, as equilibrium is reached. Even if these models are accurate, however, the short-term dynamics of a plant community that has been experimentally manipulated will not necessarily be consistent with these predictions. If a species that is favored by a particular treatment (i.e., a particular nutrient level) is rare or absent on some plots, replicates of a treatment may initially diverge because other species would likely dominate in the absence of the favored species. Under such conditions, commonly used measures that compare plots at a single point in time, such as a similarity index, may give a misleading picture of the long-term response of vegetation to a treatment, for initial heterogeneity in species composition may at first be magnified. Only after the favored

species had invaded and increased on most or all replicates of a treatment would measures like similarity indices indicate convergence.

A more robust approach for determining if plots are converging or diverging may be provided by trajectories through time of population densities of the dominant species. Such analyses may more clearly illustrate how the response to experimental manipulation depends on initial conditions, and whether plots are likely to converge in the future.

In this paper we examine patterns of vegetation convergence and divergence and trajectories of population densities during the first 4 yr of an experimental study of the effects of different nitrogen supply rates on vegetation in three old fields in Minnesota (Tilman 1987). The analyses presented here address four questions. (1) Do patches that have different resource supply rates imposed on them become less similar, or diverge, in species composition? (2) Do patches that experience the same resource supply rate become more similar, or converge, in species composition? (3) Is convergence or divergence dependent on the past history or initial species composition of the vegetation? (4) Whether or not plots are converging, as estimated by similarity indices, do the dynamics of the dominant species suggest that they will converge or diverge?

Vegetation on these plots was still changing in response to experimental treatments after four years of

¹ Manuscript received 23 December 1986; revised and accepted 29 September 1987; final version received 12 November 1987.

TABLE 1. Amounts of nitrogen added to each treatment. In addition to nitrogen (added as ammonium nitrate) all treatments except I received the same background mix of other nutrients.

Treatment	Nitrogen ($\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$)
I	0
A	0
B	1.0
C	2.0
D	3.5
E	5.4
F	9.5
G	17.0
J	27.2

manipulation. For this reason we do not consider these analyses to be a definitive test of the assumptions of resource-based models of community structure. The results presented here are useful in that they provide insights into the dynamics of vegetation in response to fertilization over a period of 4 yr, and they give some indication of the length of time required for such experiments.

METHODS

Because the experimental methods are described in detail in Tilman (1987) they are only summarized here. Cedar Creek Natural History Area, Minnesota, has well-sorted sandy soils (Grigal et al. 1974) that are poor in nitrogen, with nitrogen limiting primary productivity in each of five fields that have been tested (Tilman 1983, 1984, 1985, 1987, Inouye et al. 1987a). In 1982, Tilman (1987) established two experimental grids in each of three old fields, one on an undisturbed area and the second on an adjacent area that was thoroughly disked in the spring of 1982. Each grid consisted of 54 4×4 m plots. Six replicates of each of 9 treatments (Table 1) were randomly assigned to each grid. The nine treatments included an unmanipulated control and eight treatments that received different amounts of nitrogen as well as the same mix of P, K, Ca, Mg, S, and trace metals. Nutrients were added in equal amounts twice each year, in mid-May and late June from 1982 through 1985. The youngest field (Field A) was last cultivated in 1968. The intermediate-age field (Field B) was last cultivated in 1957, and the oldest field (Field C) was last cultivated in 1934. While average soil nitrogen tends to increase with field age at Cedar Creek (Inouye et al. 1987a, b), average total nitrogen on these grids was highest in Field C (637.8 mg/kg), intermediate in Field A (582.6 mg/kg), and lowest in Field B (377.6 mg/kg). Pretreatment soil chemistry and vegetational composition of these fields are reported in Tilman (1987). Vegetation was sampled each year by clipping a 10×300 cm strip at ground level in the same relative position on each plot. Different locations were clipped each year. Clipped samples were sorted to species, dried, and weighed.

We used two methods to look at changes in species composition through time. First, we used a similarity index to compare vegetation on pairs of plots. This index (percentage similarity, PS, Gauch 1982, Pielou 1984) measures the proportion of vegetational biomass that two sample units have distributed among the same species. The formula for the index is

$$\text{PS} = \sum_{i=1}^m \min(x_{i1}, x_{i2}),$$

where x_{i1} is the relative biomass of species i on plot 1, x_{i2} is the relative biomass of species i on plot 2, $\min(X, Y)$ is the smaller of X or Y , and m is the number of species in common for the two plots. We did not include litter in these analyses. To estimate the average similarity of a group of plots, we calculated PS for all pairwise comparisons within the group and took the average of those values.

The second method of examining changes in composition used trajectories of the three grass species that were dominant at the high end of the nitrogen gradient. In these analyses we located individual plots in a three-dimensional space defined by the relative abundances of the three grasses. These graphs were then examined to see whether there was consistency in the trajectories of replicate plots, which we interpret as convergence, or inconsistency in the trajectories, which we interpret as divergence.

We tested for divergence along the nitrogen gradient (question 1) by calculating PS for all possible pairs of plots within each grid ($N = 1431$) for each year. Values of PS were then averaged for all pairs of plots that had the same difference in added nitrogen (this difference ranged from 0 to $27.2 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ of N). These 25 average values were then plotted against the difference in added nitrogen. (Note that two treatments, A and I, received no nitrogen.)

We looked for convergence (question 2) at three levels. First, we tested whether the six replicates of each treatment within each experimental grid became more similar from 1982 to 1985. Data for these comparisons were means of the 15 pairwise comparisons for each treatment, calculated separately for each year and each grid, as well as the trajectories of individual plots in the three-species space. Second, within each field we tested whether the six replicates of each treatment in the undisturbed grid became more similar to the six replicates of the same treatment in the disturbed grid. Data for these comparisons were means of the 36 pairwise comparisons for each treatment in each field. Third, we asked whether the replicates in one field became more similar to replicates of the same treatment in the other two fields. Data for these comparisons were means of the 36 pairwise comparisons for each treatment, comparing similar grids (disturbed or undisturbed) in two fields at a time, as well as the trajectories of the three dominant species. These three levels of compar-

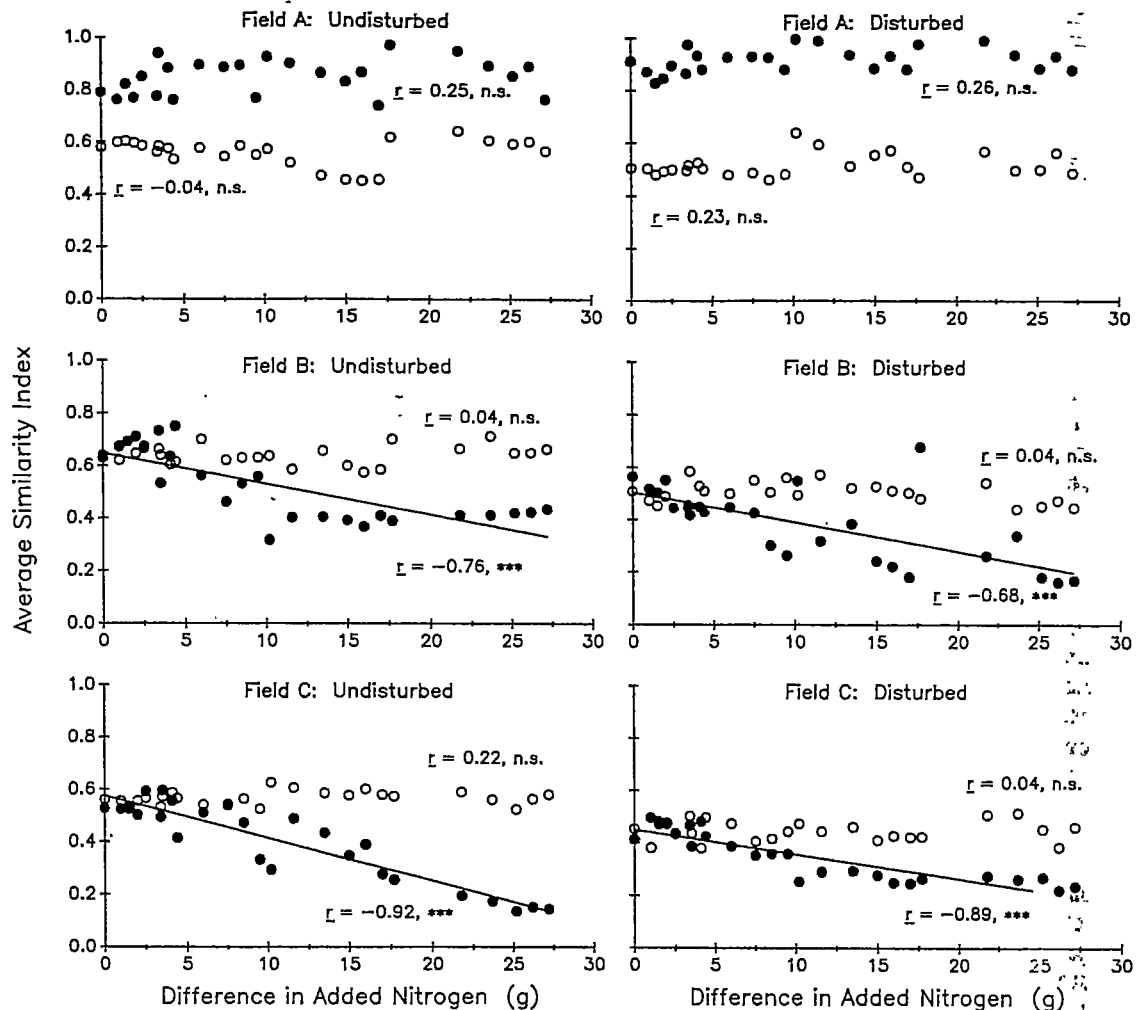


FIG. 1. Average percent similarity (PS, see Methods for definition) of vegetation in pairs of 4×4 m plots in the indicated fields, vs. the difference in nitrogen added each spring, for 1982 (O) and for 1985 (●). Individual points represent the average of various numbers of pairwise plot comparisons. Last year of cultivation for Field A: 1968, Field B: 1957, Field C: 1934. "Disturbed" = thoroughly disked in the spring of 1982. *** $P < .001$.

ison, within grids, between grids in each field, and between fields, all address questions 2 and 3. The second and third levels of comparison can be viewed as increasingly rigorous tests of question 3, due to greater initial differences in species composition of the plots being compared.

Statistics

There are two reasons to question the use of simple regression statistics in our tests for divergence. First, regressions of average PS against the difference in added nitrogen (Δ -N) are based on all pairwise comparisons of 54 plots, and hence the individual comparisons are not truly independent. Second, there were different numbers of pairwise comparisons that were averaged for different values of Δ -N. We performed a Monte Carlo simulation as an alternative test of the significance of the slopes of these regressions. In each of 100 such tests, treatments were assigned randomly to the

54 plots in each grid, and a slope and intercept were calculated using a least-squares linear regression. The 100 slopes calculated in this way were compared with the slopes calculated using the correct plot treatments.

RESULTS

Divergence

There were no significant correlations between average PS and the difference in added nitrogen (Δ -N) in 1982. In Field A, the youngest field, average PS increased across the entire range of values of Δ -N between 1982 and 1985. In Fields B and C there were significant negative correlations between average PS and Δ -N for both the disturbed and undisturbed grids in 1985 (Fig. 1). Where these regressions were significant for >1 yr the slopes became more negative with time. Decreasing slopes could result from either an increase in average PS at small values of Δ -N,

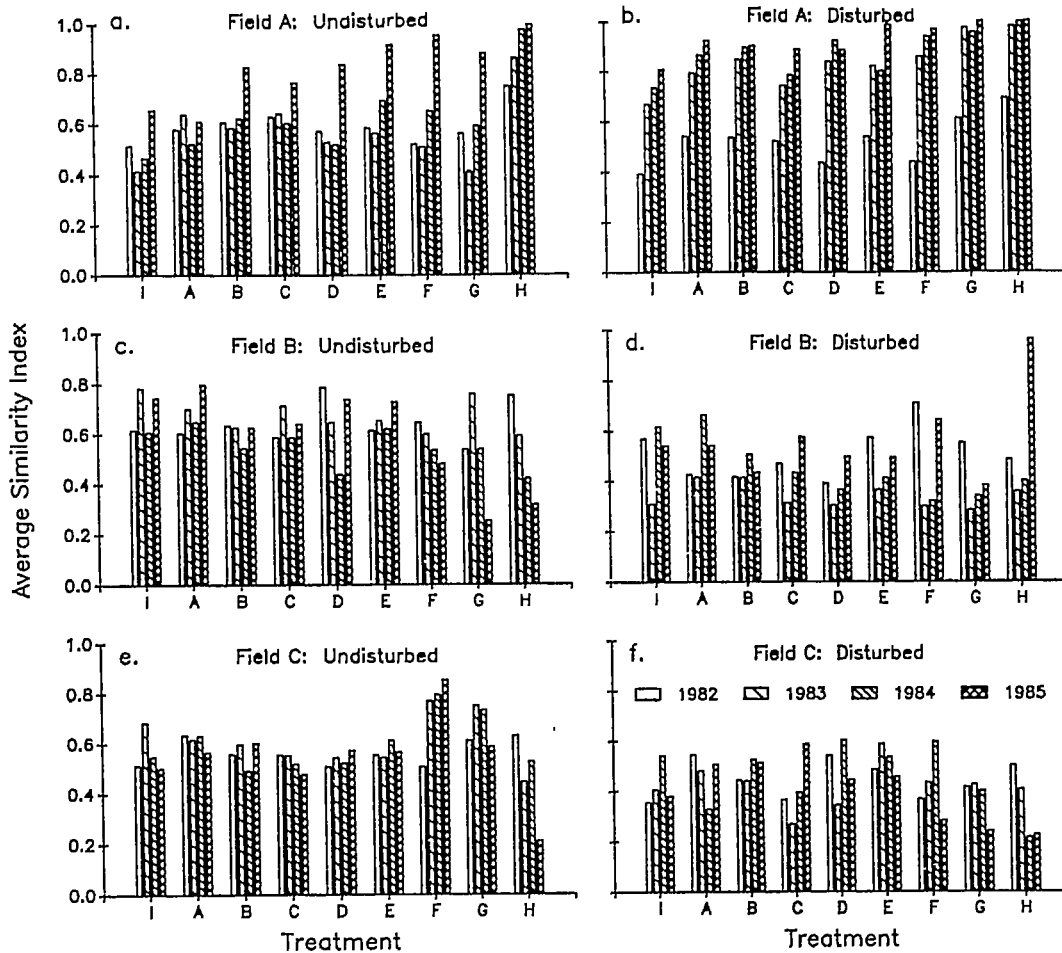


FIG. 2. Average similarity of the six replicates of each treatment within each experimental grid. Each bar represents the mean of 15 pairwise comparisons. Added nitrogen increased from treatments I and A, which received no nitrogen, to treatment H. Standard error did not exceed 0.02 for any of these means.

or from a decrease in average PS at large values of ΔN . It is clear from Fig. 1 that average PS decreased at large values of ΔN in Fields B and C, indicating that plots with different resource supply rates diverged.

For the 1985 data in disturbed and undisturbed grids in Fields B and C, the slopes calculated using the correct treatments were greater in magnitude (more negative) than all 100 slopes generated by the Monte Carlo tests. Thus, while the significance test based on the linear regressions of average PS vs. ΔN may not be precise, the probability that the observed relationships are due to chance is $< .01$.

Convergence within each grid

In the youngest field (Field A), replicates of each treatment became more similar over time at all nitrogen levels on both the disturbed and undisturbed grids (Fig. 2a, b). On the undisturbed grid the rate of increase in similarity was greater for high nitrogen treatments than for treatments that received no nitrogen (A, I).

Average similarity increased very rapidly for all levels of nitrogen addition on the disturbed grid. The rapid increase in similarity at high nitrogen levels (Fig. 2a, b) was due to a very consistent response of *Agropyron repens*, which by 1984 had formed virtual monocultures on many high nitrogen plots on both the disturbed and undisturbed grids (Tilman 1987).

On the undisturbed grid in Field B (Fig. 2c), the most evident pattern was a decrease in similarity among replicates at the three highest nitrogen levels. Average PS did not change in any consistent way on the other six treatments. Plots in Field B were initially dominated by the perennial grass *Schizachyrium scoparium*. Two other grasses, *A. repens* and *Poa pratensis*, increased rapidly on high nitrogen plots where they were present at the start of the experiment. *Poa pratensis* increased rapidly on plots where it was present and *A. repens* was rare or absent. Where *A. repens* was present, it rapidly dominated high nitrogen plots such as it did in Field A. On plots where both *A. repens* and *P. pratensis* were absent, *S. scoparium* remained dominant.

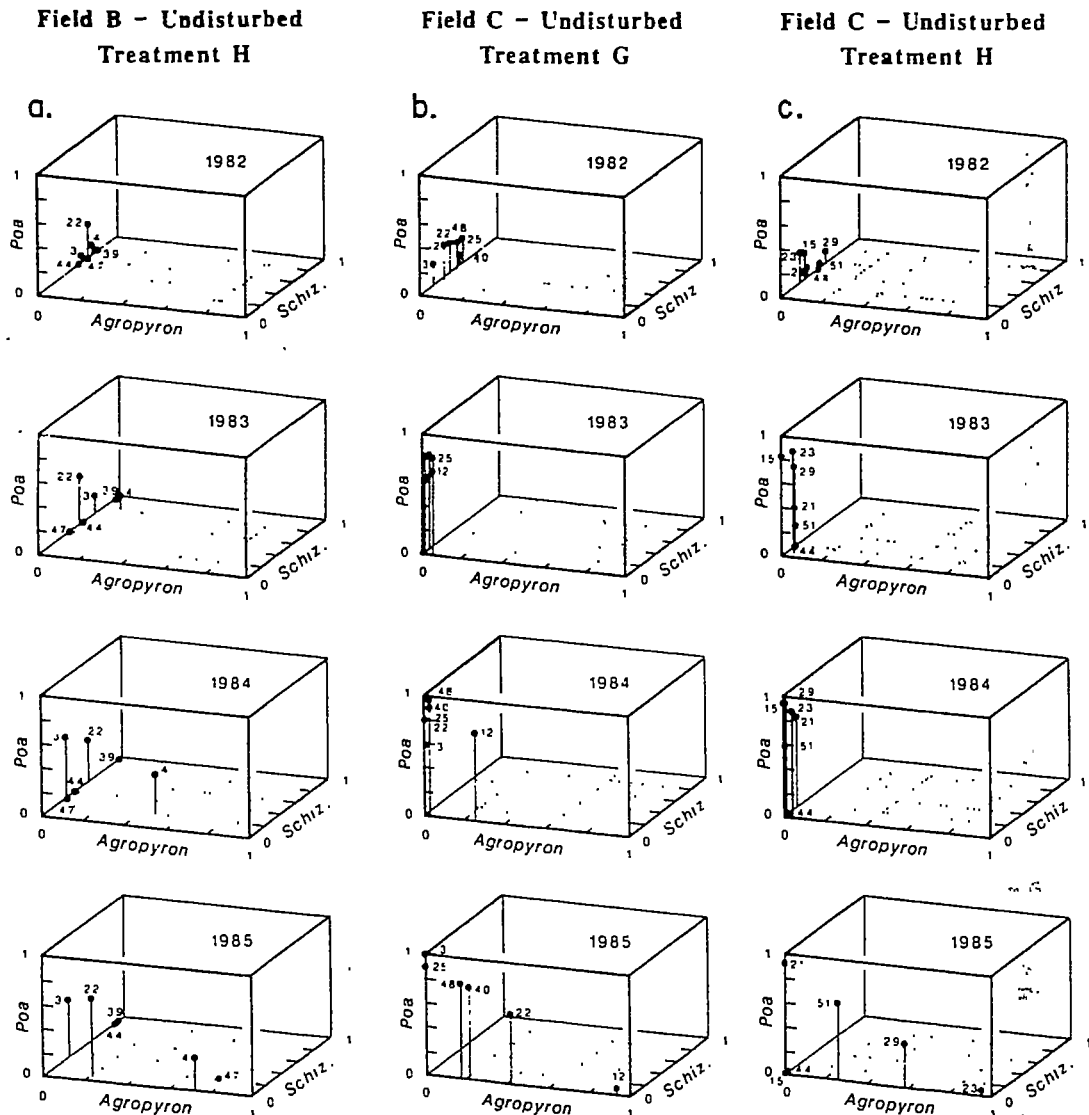


FIG. 3. Proportional abundances of *Agropyron repens*, *Schizachyrium scoparium*, and *Poa pratensis* on the six replicates of the indicated treatment on the specified grid and Field. Numbers next to the points represent plot numbers. Other species were present on most plots in most years; hence proportional abundances of these three species do not usually sum to 1.0.

This pattern can be clearly seen in Fig. 3a, where proportional abundances of *Agropyron*, *Schizachyrium*, and *Poa* are plotted against each other for the six replicates of treatment H on the undisturbed grid in Field B. The six plots were most similar in 1982, when *S. scoparium* constituted > 50% of the biomass on all six plots. By 1985, plots 4 and 47 were dominated by *Agropyron*, plots 39 and 44 were dominated by *Schizachyrium*, and plots 3 and 22 were dominated by *Poa*. Between 1984 and 1985 *Agropyron* increased to > 20% of the biomass on plot 22, suggesting that *Agropyron* can displace high densities of *Poa* as well as at least moderate densities of *Schizachyrium*.

On the disturbed grid in Field B (Fig. 2d) replicates of all but treatment B were less similar in the 2nd yr than the 1st. The lower average PS in the 2nd yr was

due to decreased abundance of a few species that were widespread and abundant immediately after the grid was disturbed (e.g., *Setaria glauca*, *Polygonum convolvulus*) (see Discussion). Average PS generally increased after the 2nd yr. This increase was greatest at the highest nitrogen level: *A. repens* dominated all six replicates of treatment H in 1985.

On the undisturbed grid in Field C (Fig. 2e), only the third highest nitrogen level (treatment F) showed a consistent increase in average similarity from 1982 to 1985. In contrast with Field A, the six treatment F plots in Field C were all dominated by *Poa*, with the result that average PS was relatively high. Treatment G plots were dominated by *Poa* in 1984; however, by 1985, *Agropyron* was abundant on four plots and had increased to as much as 90% on one plot (Fig. 3b). The

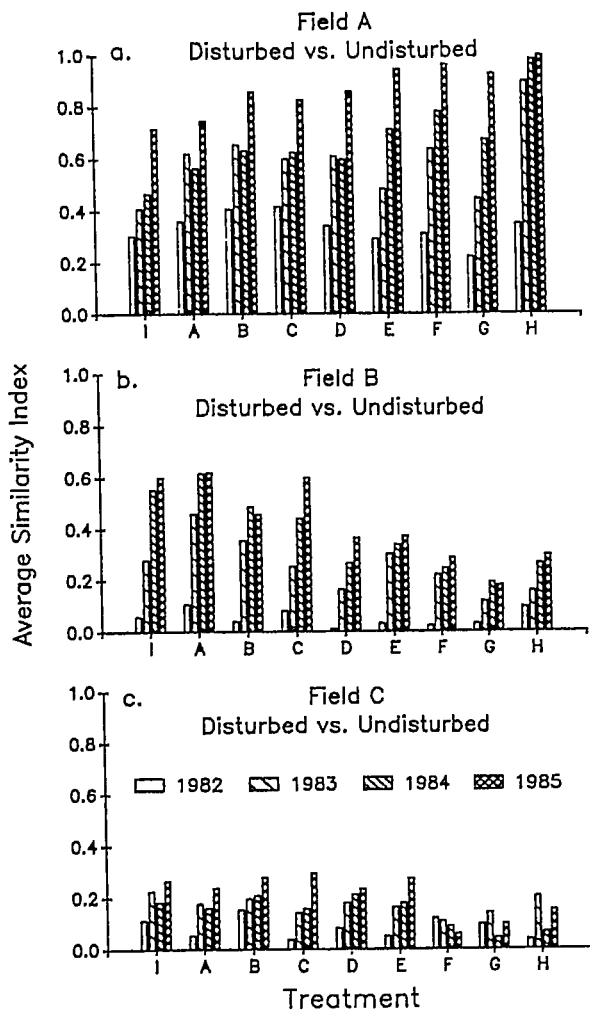


FIG. 4. Average similarity of plots on disturbed and undisturbed grids within each field. Each bar represents the mean of 36 pairwise comparisons of six replicates on the disturbed grid with six replicates of the same treatment on the undisturbed grid. Standard error was >0.09 for two means; other standard errors did not exceed 0.02 and most were <0.01 .

precipitous decline in similarity among replicates of treatment H in 1985 was due only in part to the replacement of *Schizachyrium* by *Poa* or *Agropyron*. Vegetation on two plots that were dominated by *Poa* in 1983 and 1984 (Fig. 3c, plots 15 and 29) lodged late in 1984, forming a dense litter layer. Total live plant biomass on both plots was lower in 1985 than in any of the three previous years. While *A. repens* increased in proportional abundance on plot 29, only a few large individuals of the annuals *Polygonum convolvulus* and *Chenopodium album*, as well as scattered individuals of *Poa pratensis*, successfully penetrated the thick layer of litter that covered plot 15 in 1985. As a result, plot 15 was very different in species composition from virtually all other plots in the undisturbed grid in Field C. Two other plots showed large increases in *A. repens* between 1984 and 1985 (Fig. 3c, plots 23 and 51),

suggesting that *Agropyron* will dominate high nitrogen treatments in Field C much as it has in Field A and appears to be doing in Field B.

On the disturbed grid in Field C (Fig. 2f), replicates at the three highest nitrogen levels decreased in similarity from 1982 to 1985, although average similarity increased initially for treatment F. *Agropyron* had begun to increase on many of the higher nitrogen plots by 1985 (Tilman 1987), indicating that average PS on these plots will probably increase in the next few years.

Convergence of disturbed and undisturbed vegetation

With a few exceptions (treatments F, G, and H in Field C), replicates of all treatments on disked and undisked grids in all three fields showed consistent increases in similarity from 1982 to 1985 (Fig. 4). Initial similarities were highest in Field A, where they increased most rapidly; the rate of increase was greatest at high nitrogen levels. The predominance of *A. repens* on both grids was responsible for the rapid increase in similarity in Field A. In contrast, the rate of increase in average similarity was greatest at low nitrogen levels in Field B. In Field C there was no obvious correlation between the amount of added nitrogen and the rate at which average similarity increased.

The increases in average similarity for treatment I in Fig. 4 demonstrate the response after disturbance of otherwise unmanipulated vegetation. We can contrast this response with field age in two ways. First, average similarity of disturbed and undisturbed plots in 1985 decreased with field age (Fig. 4). A slightly different way of contrasting similarity of disturbed and undisturbed areas with field age is to compare the 1985 between-grid average similarity for treatment I (Fig. 4) with the 1985 average similarity for treatment I on undisturbed plots (Fig. 2). This contrasts the average similarity between disturbed and undisturbed plots with the average similarity among undisturbed plots in each field. In Field A, average similarity of disturbed and undisturbed plots in 1985 (0.72, Fig. 4a) exceeded the average similarity among undisturbed plots (0.66, Fig. 2a). In Field B, average similarity of disturbed and undisturbed plots in 1985 (0.60, Fig. 4b) was $\approx 80\%$ that among undisturbed plots (0.74, Fig. 2c). In Field C, the oldest field, average similarity of disturbed and undisturbed plots in 1985 (0.27, Fig. 4c) was $<55\%$ of that among undisturbed plots (0.50, Fig. 2e).

Convergence among fields

The most consistent pattern in these comparisons was the decrease from 1982 to 1983 in average PS of disturbed grids. The relatively high values of average PS in 1982 were due to the widespread abundance of species characteristic of disturbances in these old fields.

Fields A and B.—On the undisturbed grids, the control and the three highest nitrogen treatments increased

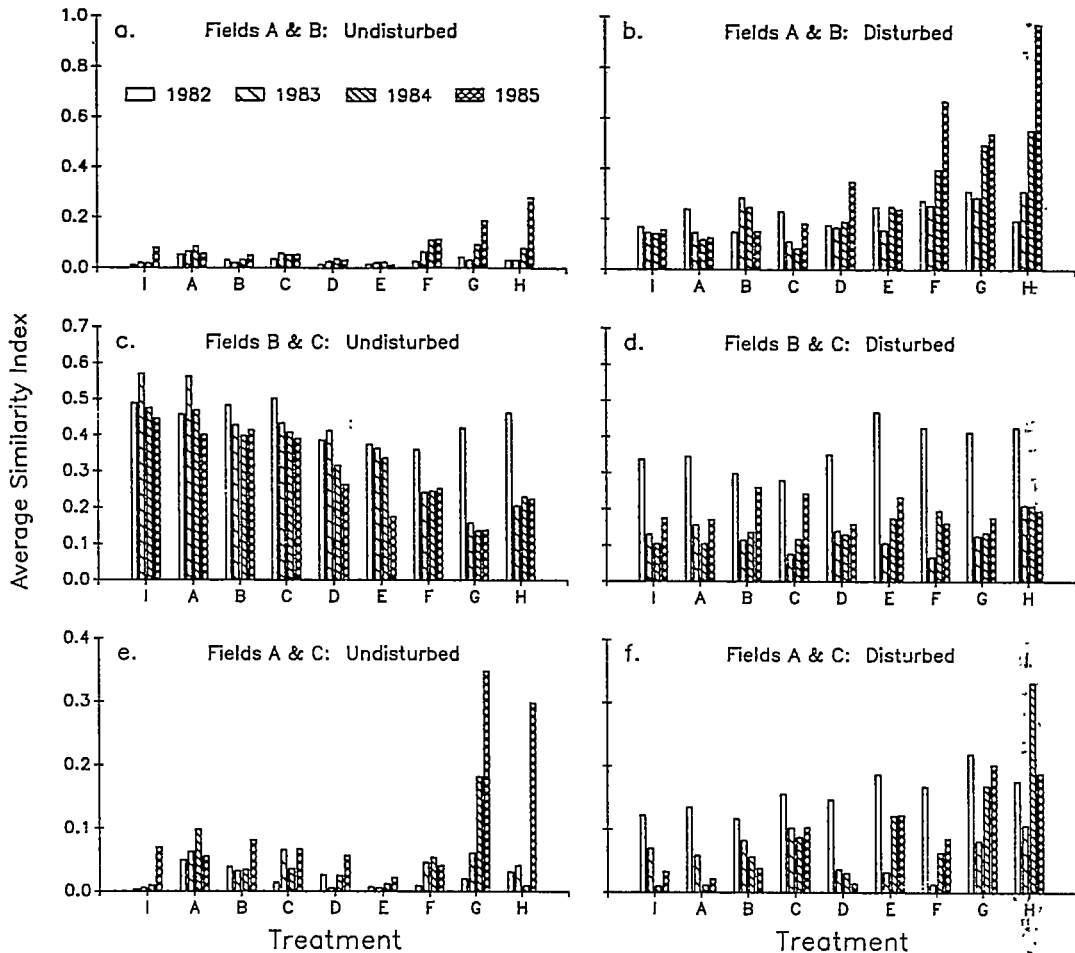


FIG. 5. Average similarity of plots in different fields. Each bar represents the mean of 36 pairwise comparisons of six replicates in one field with six replicates of the same treatment on the analogous grid in another field. Standard errors did not exceed 0.01 PS units for any of these means.

in similarity (Fig. 5). Other treatments showed only minor or inconsistent changes in average similarity. On the disturbed grids the six highest nitrogen treatments increased in similarity after 1983, while average similarity on the other treatments showed no consistent changes.

Fields B and C.—From 1983 to 1985 average similarity on the undisturbed grids decreased on all treatments except the top three nitrogen levels, where it decreased substantially in 1983 and remained low. On the disturbed grids similarity was greatest in the 1st yr. Following the initial decrease in average similarity, plots on the disturbed grids increased in similarity for all treatments except H.

Fields A and C.—Average similarity for the undisturbed grids was initially very low. Similarity increased slightly for all treatments, and quite substantially for the two highest nitrogen levels. On the disturbed grid, average similarity increased on the four highest nitrogen levels after 1983, while at other nitrogen levels similarity remained low or decreased.

DISCUSSION

These analyses were performed to test a hypothesis that underlies any resource-based model of community structure, that species composition is influenced by resource supply rate. While some of the data support the equilibrium predictions of resource-based models, the results are not unequivocal. The vegetation trajectories suggest that this may be because 4 yr is too short a time for this vegetation to attain a new series of resource-controlled equilibria.

In two of three fields there was strong, consistent support for the prediction that plots with different resource supply rates would diverge in species composition. Slopes of regressions of average PS and delta-N became increasingly negative with time, indicating that plots diverged along the nitrogen gradient. Data from the youngest field do not support this prediction of divergence. The increase in average PS across the entire range of delta-N (Fig. 1, top) was due to the increased relative abundance of *Agropyron repens* at all levels of

N addition. While there were significant differences in its absolute abundance along these nitrogen gradients (Tilman 1987), the index we used only compares relative abundances of species. Some species that were most abundant at intermediate levels of N addition in Fields B and C were either absent or extremely rare in Field A (Tilman 1987). The absence of those species may have been partly responsible for the increase in *Agropyron* across the entire N gradient in Field A. Observations of whether such species can invade near monocultures of *Agropyron*, in the absence of disturbances such as gopher mounds or *Microtus* activity, should provide valuable insights about the interaction between small-scale disturbances, establishment, and competitive equilibria in plant communities.

The second prediction we tested is that plots with the same resource supply rates should become more similar in species composition. There were indications of convergence at all three levels we examined: among replicates within each experimental grid, between grids within each field, and among the three fields; however, the data do not all support this prediction. Average similarity among replicates increased across the entire experimental nitrogen gradient only in Field A. Average similarity decreased on some of the high nitrogen plots in Fields B and C (Fig. 2).

Many of the changes in average similarity that we observed can be understood in light of the dynamics of a small number of plant species. The rapid increase of *Agropyron repens* (Tilman 1987) resulted in increased average PS across all treatments both within and between grids in Field A. The decreases in average PS that we observed at high nitrogen levels in Fields B and C are apparently the result of plot-to-plot differences in the initial abundances of three perennial grasses, *Agropyron*, *Poa*, and *Schizachyrium*. There appears to be a competitive hierarchy among these three species, each of which could potentially dominate high nitrogen plots. *Schizachyrium* was initially abundant and increased in abundance where *Poa* and *Agropyron* were absent or very rare (Fig. 3a, plots 39 and 44). On high nitrogen plots on which *Poa* was present it displaced *Schizachyrium*, provided that *Agropyron* was initially absent or very rare (Fig. 3a, plots 3 and 22; Fig. 3c, plots 15, 23, and 29). Of these three grasses, *Agropyron* appears to be the dominant species at high rates of nitrogen addition: once present on a high nitrogen plot it increased in abundance (Fig. 3a, b, c). Thus the initial effect of nitrogen addition was to magnify pre-existing differences in the abundances of these three species. However, if *Agropyron* continues to increase in abundance where it is present, average PS will increase on high nitrogen plots in Fields B and C. *Agropyron* has increased even where *Poa* represented >90% of the total biomass (Fig. 3b, plots 12, 22, 40, and 48; Fig. 3c, plots 23 and 29), indicating that near-monocultures of *Poa* are invulnerable to *Agropyron*. Although it is not yet clear whether *Agropyron* can invade

high nitrogen plots that are >95% *Schizachyrium* (Fig. 3a, plots 39 and 44), it did invade and come to dominate plots that were initially 70% *Schizachyrium* (Fig. 3a). Even if *Agropyron* could not invade these plots, *Poa* might be able to do so, and *Agropyron* was able to invade plots that were near monocultures of *Poa*. Based on the population trajectories of these three dominant species (Fig. 3a, b, c) we predict that the composition of the high nitrogen plots will converge, despite initial divergence, as *Agropyron* establishes on plots on which it was initially absent.

We do not expect plots at the high end of the nitrogen gradient to remain monocultures of *Agropyron*. As woody species that are characteristic of undisturbed, relatively fertile soils at Cedar Creek establish on these plots they should replace *Agropyron*. Woody shrubs (e.g., *Rubus*) have increased on some high nitrogen plots (Tilman 1987). We predict that, as woody species establish and increase on some plots, average PS will decrease in the same way that it decreased due to initial differences in species composition. Subsequent increases in average PS would then depend on whether the same woody species invade replicate plots, and their rates of invasion and growth. In systems that experience a rapid successional turnover in species composition, or where factors that determine the equilibrium competitive outcome change on a time scale that is rapid relative to those competitive interactions, convergence may be unlikely.

Perhaps the most unexpected dynamics resulted from lodging by *Poa* in two high nitrogen Field C plots (Fig. 3c; plots 15 and 29). Although the changes observed in the abundances of the major species in the other plots for 1984 to 1985 suggest that convergence may occur, it is not yet certain what will happen in these plots. We have not observed such extensive lodging on plots dominated by *Agropyron*. This suggests that once *Agropyron* has invaded high nitrogen plots these unexpected dynamics will disappear.

Comparison of disturbed and undisturbed grids within each field produced the most consistent increases in average PS. With few exceptions there were consistent increases in average PS from 1982 to 1985. Where the short-term effect of nutrient addition is to magnify initial differences in species composition, as was the case at high nitrogen levels in Fields B and C, one might expect to see initial divergence followed by a slower rate of convergence at high levels of nutrient addition. Under these conditions the rate of convergence will be limited by the establishment and increase of species that are absent or rare on some plots (e.g., *Agropyron*). Because other species that are initially abundant are likely to increase in response to nutrient addition (e.g., *Poa*, *Schizachyrium*) it is likely that plots located in heterogeneous vegetation will initially diverge.

Between-field comparisons (Fig. 5) resulted in some of the lowest values of average similarity. These low

values probably reflect the changes in soil nitrogen and plant species abundance that occur during succession at Cedar Creek (Inouye et al. 1987a). The actual nitrogen supply rates experienced by vegetation on our experimental plots were a combination of the fertilizer that we added and in situ mineralization rates. It is at the high end of our gradient that pre-existing differences among fields are most likely overshadowed by the nitrogen we added. Data from comparisons of both the undisturbed and disturbed grids in Fields A and B and Fields A and C are consistent with this hypothesis; in 1985 average PS was greater for the highest nitrogen levels. Data for Fields B and C do not support this hypothesis; in fact the high nitrogen levels of the undisturbed grids showed large decreases in average PS (Fig. 5c).

Comparisons of disturbed plots in Fields B and C (Fig. 7d) and in Fields A and C (Fig. 5f) typically showed that the highest similarities occurred in the 1st yr. The initially high similarities were due to the preponderance of annual plants on these plots immediately after disturbance. In 1982, two common species, *Setaria glauca* and *Polygonum convolvulus*, together accounted for >62% of the total plant biomass on disturbed plots in Field B and in Field C. The lesser importance of these two species on disturbed plots in Field A, where they accounted for <25% of the total plant biomass in 1982, is reflected in the smaller similarities between Fields A and B and between Fields A and C (Fig. 5b, f). The abundance of these two annual species in fields B and C decreased very quickly after the 1st yr. Species that were more representative of undisturbed areas in each field increased in abundance, and the average similarity of plots on disturbed grids in Fields B and C decreased. The gradual increases in average similarity after 1983 reflect increases in the abundance of perennial species such as *A. repens* and *P. pratensis*.

Initial responses to fertilization are measures of short-term growth rates of established vegetation (e.g., Tilman 1985, 1988). Where a species that will become dominant at any particular stage is initially widespread, the rate of convergence is likely to be relatively high, as was the case in Field A. In more patchy communities, where there are greater initial differences in species composition, rates of convergence, and even the initial directions of trajectories in multispecies state space, are more likely to vary. Older fields at Cedar Creek have greater between-plot variability in species composition (Inouye et al. 1987a). It is the relatively short-term, or transient, dynamics that result from greater initial plot-to-plot variability that are responsible for the initial divergence we observed among replicates on the undisturbed grids in our older fields. Despite the initial divergence, the consistent increase in *Agropyron* on nearly all high nitrogen plots suggests that these plots will converge in the near future. The divergence observed during the first 4 yr of this experiment illustrates the need for long-term field ex-

periments. Short-term experiments may give transient results that are more related to growth rate differences and initial composition than to the mechanisms that determine the equilibrium outcome of interspecific interactions (Tilman 1985, 1988). There was a major qualitative difference between the pattern suggested by the similarity index (divergence) and that suggested by the population trajectories through time (convergence). This difference may mean that similarity indices are useful for describing past changes and existing differences in composition, but that population trajectories are more useful for predicting future changes in species composition (see Fig. 3a, b, c). This possibility will be more easily tested when the experiments have proceeded several more years.

The third question posed in the introduction was how past history, or initial species composition, influences divergence or convergence. Our analyses suggest that initial conditions play a very important role. In Field A, where *Agropyron* was widespread and abundant, and where many other species were absent, we did not find evidence for divergence along the nitrogen gradient. All of the analyses, and in particular the trajectories in Fig. 3, illustrate that initial conditions can have a large effect on convergence and divergence in response to experimental manipulations.

Previous studies of convergence have looked at two levels of comparison. The first of these is a very broad comparison of community types. Early ideas about succession and climax communities were based on observations that plant communities in areas of similar climate and substrate were similar. Recent studies have compared physiognomic characteristics and physiology of unrelated species living in areas with similar climates, such as the mediterranean climates of California and Chile (e.g., Mooney et al. 1970, Mooney and Dunn 1970, Sage 1973, Parsons and Moldenke 1975), and found convergence in these characters.

The second level of comparison has been on a much smaller scale, and here convergence has not been a general phenomenon (Glenn-Lewin 1980, 1986). Comparisons of pastures released from grazing (Glenn-Lewin 1980, Pineda et al. 1981), second-growth pine stands (Christensen and Peet 1984), and plots undergoing primary succession after glacial recession (Matthews 1979) all found that convergence in species composition was not occurring at these scales. As suggested by Christensen and Peet (1984), a drawback to this scale of comparison is that individual pastures or pine stands are likely to differ in their soils, topography, and probability of colonization by various species, all of which should lead to divergence.

In these experiments we examined a still smaller scale, and hence there were relatively small differences among plots in soil type, slope, climate, and other edaphic factors. We did, though, have large differences in initial composition. As predicted by resource-based models of community structure, we found evidence

that plots at different points along an experimental resource gradient had diverged. However, we found weak and often contradictory evidence concerning a second prediction: that, at equilibrium, plots receiving similar rates of N addition should converge. While analyses using a similarity index do not provide consistent support for convergence, examination of the dynamics of three abundant grasses does suggest that the degree of convergence will increase, particularly at high nitrogen levels. Our results suggest that trajectories of community change, as shown in Fig. 3, may provide better information on future convergence or divergence than the similarity index. Only at equilibrium, which these plots have not yet reached, would the two approaches necessarily make similar predictions.

ACKNOWLEDGMENTS

This work was supported in part by NSF grant NSF/BSR-8114302 to D. Tilman and J. R. Tester for Long-Term Ecological Research at Cedar Creek Natural History Area. We thank an anonymous reviewer for suggesting the use of a Monte Carlo simulation.

LITERATURE CITED

- Christensen, N. L., and R. K. Peet. 1984. Convergence during secondary forest succession. *Journal of Ecology* 72:25-36.
- Gauch, H. G. 1982. *Multivariate analysis in community ecology*. Cambridge University Press, Cambridge, England.
- Glenn-Lewin, D. C. 1980. The individualistic nature of plant community development. *Vegetatio* 43:141-146.
- . 1986. On the nature of direction and convergence during succession. In J. Downhower, editor. *The biogeography of the island region of western Lake Erie*. Ohio State University Press, Columbus, Ohio, USA, *in press*.
- Grigal, D. F., L. M. Chamberlain, H. R. Finney, D. V. Wriplewski, and E. R. Gross. 1974. *Soils of the Cedar Creek Natural History Area*. Miscellaneous Report 123, University of Minnesota Agricultural Experiment Station, Saint Paul, Minnesota, USA.
- Inouye, R. S., N. J. Huntly, D. Tilman, and J. R. Tester. 1987b. Pocket gophers (*Geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east central Minnesota. *Oecologia* (Berlin) 72:178-184.
- Inouye, R. S., N. J. Huntly, D. Tilman, J. R. Tester, M. Stillwell, and K. C. Zinnel. 1987a. Old-field succession on a Minnesota sand plain. *Ecology* 68:12-26.
- Matthews, J. A. 1979. A study of the variability of some successional and climax plant assemblage-types using multiple discriminant analysis. *Journal of Ecology* 67:255-272.
- Mooney, H. A., and E. L. Dunn. 1970. Convergent evolution of mediterranean climatic evergreen sclerophyll shrubs. *Evolution* 24:292-303.
- Mooney, H. A., E. L. Dunn, F. Shropshire, and L. Song. 1970. Vegetation comparisons between the mediterranean climatic areas of California and Chile. *Flora* 159:480-496.
- Parsons, D. J., and A. R. Moldenke. 1975. Convergence in vegetation structure along analogous climatic gradients in California and Chile. *Ecology* 56:950-957.
- Pielou, E. C. 1984. *The interpretation of ecological data*. John Wiley and Sons, New York, New York, USA.
- Pineda, F. D., J. P. Nicolas, A. Pou, and E. F. Galiana. 1981. Ecological succession in oligotrophic pastures of central Spain. *Vegetatio* 44:165-176.
- Sage, R. D. 1973. Convergence of the lizard faunas of the chaparral habitats in central Chile and California. Pages 339-348 in F. di Castri and H. A. Mooney, editors. *Mediterranean type ecosystems, origin and structure*. Springer-Verlag, Heidelberg, Germany.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey, USA.
- . 1983. Plant succession and gopher disturbance along an experimental gradient. *Oecologia* (Berlin) 60:285-292.
- . 1984. Plant dominance along an experimental nutrient gradient. *Ecology* 65:1445-1453.
- . 1985. The resource ratio hypothesis of succession. *American Naturalist* 125:827-852.
- . 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* 57:189-214.
- . 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, New Jersey, USA.