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SPATIOTEMPORAL DIFFERENCES IN ^{15}N UPTAKE AND THE ORGANIZATION OF AN OLD-FIELD PLANT COMMUNITY¹

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Abstract. We investigated the hypothesis that spatial and temporal differences in nitrogen uptake facilitate species' coexistence in a nitrogen-limited, old-field plant community at Cedar Creek Natural History Area, Minnesota. Differences among the six most abundant species were assessed by measuring aboveground uptake of ^{15}N injected at two soil depths at each of three times during the growing season.

As described by ^{15}N uptake, species were spatially and, to a greater extent, temporally differentiated into three groups. Differences in species' abundance between and within these groups suggest that spatiotemporal partitioning of nitrogen is a major determinant of community organization. Dominant species (*Schizachyrium scoparium* and *Poa pratensis*) were well differentiated and the abundances of subordinate species (*Artemisia ludoviciana*, *Solidago nemoralis*, *Ambrosia coronopifolia*, and *Panicum oligosanthos*) were positively related to the degree of differentiation from dominant species. A discriminant analysis of the data showed that subordinate species occupy "peripheral" spatiotemporal niches relative to *Schizachyrium* and *Poa*. This may promote coexistence by reducing diffuse competition.

These results suggest that spatiotemporal resource partitioning slows the rate of competitive displacement among co-occurring plant species. Other research at Cedar Creek corroborates that this is an effective mechanism for coexistence on a successional time scale.

Key words: coexistence; competition; diversity; ^{15}N ; niche diversification; old field; resource partitioning; soil nitrogen.

INTRODUCTION

The importance of resource partitioning, or niche diversification, in maintaining species diversity in plant communities has been intensely debated. According to many of the theories of resource competition, the number of species in a spatially and temporally homogeneous, equilibrium environment cannot exceed the number of limiting resources (Volterra 1931, MacArthur and Levins 1964, Stewart and Levin 1973, Armstrong and McGehee 1980). Plants have nothing comparable to the "food niche" of animals; on the global level, the 300 000 terrestrial plant species may have only 20 different limiting resources (light, water, CO_2 , and the same set of mineral nutrients), and field work indicates that at most three or four resources are limiting in any plant community (Tilman 1982). On this basis, many ecologists assert that the "niche diversification hypothesis" is not applicable to plant communities and suggest, instead, that only nonequilibrium theories can explain the patterns of species richness observed in plant communities (Grubb 1977, Connell 1978, Huston 1979).

Alternatively, spatial and temporal resource partitioning has often been proposed as an equilibrium solution to the paradox of n plant species coexisting on fewer than n limiting resources. Berendse (1979), for example, has shown that stable equilibria in homogeneous environments are theoretically possible merely because of differentiation in rooting depths; logically, the same principle should also apply to temporal differentiation in resource use. There is, in fact, abundant evidence that co-occurring plant species often differ in rooting depth (Weaver and Darland 1949, Harris 1967, Parrish and Bazzaz 1976, Yeaton et al. 1977, Berendse 1981), phenology (Gimingham 1978; Rogers and Westman 1979, Turkington and Harper 1979, Kemp and Williams 1980), or both depth and time of root activity (Veresoglou and Fitter 1984, Fitter 1986). However, these studies have not demonstrated whether such differences allow co-occurring species to "sufficiently" subdivide specific limiting resources. Thus, serious doubts persist over the importance of spatiotemporal niche differentiation as a mechanism for coexistence in species-rich plant communities (Aarssen 1983, Fitter 1986).

In this paper, we explore the hypothesis that spatial and temporal differences in the use of a single limiting

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resource (soil nitrogen) facilitate species' coexistence in an old-field plant community. Our approach was to determine if such niche differences or similarities are consistent with community organization. That is, are codominant species well separated in niche space? Do subordinate species occupy niches similar to those of dominant species?

METHODS

Study site

This experiment was conducted in a 50-yr-old abandoned agricultural field at Cedar Creek Natural History Area (Cedar Creek) located 45 km north of Minneapolis, Minnesota, USA (45°24'N, 93°12'W). The old-field flora consisted of a mixture of grasses and forbs having a peak living aboveground biomass of 130 g/m². Sixty-eight plant species occurred within the old field, but the six most common species accounted for ≈85% of the total biomass. On a quadrat basis, species richness averaged 12 species/0.5 m² (Inouye et al. 1987). Tree species were virtually absent even though an oak forest borders two sides of this 4-ha field.

The soil is a well-drained, Zimmerman fine sand (Grigal et al. 1974) that developed from well-sorted glacial outwash deposited ≈14 000 yr ago. Agricultural practices begun in the early 1900s sharply reduced soil nitrogen (N) from presettlement levels. Total soil N (0–20 cm) was 170 g/m² (R. McKane et al., *personal observation*), ≈1/3 lower than nearby, undisturbed Zimmerman soils (D. Zak, *personal communication*).

Fertilization experiments have established that available soil N ($\text{NH}_4^+ + \text{NO}_3^-$) is the primary resource limiting production in old fields at Cedar Creek. In the 50-yr-old field, peak aboveground biomass increased by over three times at the highest rate of N addition (28 g·m⁻²·yr⁻¹). Separate and combined additions of other resources (P, K, Ca, Mg, S, trace metals, and H₂O) did not produce any consistent, statistically significant growth response (Tilman 1987).

The patterns of species dominance along experimental and successional N gradients at Cedar Creek indicate that soil N is also a major determinant of species composition. A survey of 22 old fields showed that total and available soil N increased during succession and that major species had individualistic, fairly Gaussian distributions along this successional N gradient. Species distributions along experimental N gradients were generally consistent with the patterns observed in the old-field survey (Tilman 1987). Successional increases in total soil N are slow, ≈0.8 g·m⁻²·yr⁻¹ (Inouye et al. 1987), and old-field succession proceeds more slowly at Cedar Creek than is typical of temperate regions. The species composition of the 50-yr-old field has been relatively stable in the 6 yr since annual surveys were begun (Tilman 1987).

The spatial and temporal ranges of N availability in the 50-yr-old field indicate a potential for spatiotem-

poral niche differentiation. Early- (21 April–24 June), mid- (25 June–9 August), and late-season (10 August–1 October) net N mineralization accounted for 42, 38, and 20%, respectively, of the 4.3 g·m⁻²·yr⁻¹ total net N mineralization (0–20 cm). About 62, 23, and 15% of total net N mineralization occurred between 0 and 5, 5 and 10, and 10 and 20 cm, respectively. Of the 1070 g/m² total root biomass (0–60 cm, live + dead roots), >90% occurred above 20 cm and followed, to within ±5%, the same vertical distribution as net N mineralization (R. McKane et al., *personal observation*).

Experimental design and methods

We used ^{15}N , a stable N isotope, to determine how the six most common species (Table 1) in the 50-yr-old field differed in their timing and location of N uptake. To simulate the spatial and temporal ranges of N availability, we injected ^{15}N into the soil at two depths (2 and 12 cm) at each of three times: 1 May, 25 June, and 10 August (the 25 June and 10 August injections were performed in 1984 and, because of delays in shipping of the ^{15}N , the 1 May injection was performed in 1985). Separate 3 × 3 m plots were used for each of the six combinations of depth and time. The plots were laid out in a randomized block with 2 m wide aisles between plots. The plot area presumably had not been disturbed by human activities since the field was abandoned.

The ^{15}N was injected as a 0.067 mol/L ammonium sulfate solution, 20% of whose N atoms were ^{15}N . A syringe was used to deliver 2.5 mL to the desired depth at each of 961 injection sites per plot. The injection sites were spaced in a 10 × 10 cm grid with sites in alternate rows offset 5 cm to achieve equidistant horizontal spacing. This spacing delivered 0.1 g/m² of ^{15}N .

The injection procedure involved several important techniques and precautions. First, the syringe needle (2 mm O.D.) injected the ^{15}N solution horizontally through four holes drilled around and above its sealed tip; this helped restrict the ^{15}N to the targeted depth. Second, a plastic funnel was used to guide the needle from site to site to prevent foliar absorption of any ^{15}N retained on the needle. Third, we minimized plot disturbance by performing the injection procedure from a movable platform bridging the plots. Finally, the plots were covered with a well-supported plastic tarp during rain showers occurring within the 1st wk following ^{15}N injection. We believed that the risk of ^{15}N leaching would be initially high but would decrease rapidly due to microbial immobilization.

Plant samples were collected from plots ≈50 d after ^{15}N injection. This established early-, mid-, and late-season ^{15}N uptake intervals (viz., 1 May–16 June, 25 June–13 August, 10 August–28 September), each interval being represented by a different set of plots. Only the central 2 × 2 m area of each plot was sampled to minimize border effects. This sampling area was di-

TABLE 1. Description of the species analyzed for ^{15}N uptake.

Species	Life form	% of total peak aboveground biomass (Mean \pm SE)*
<i>Schizachyrium scoparium</i>	Perennial grass	42.3 \pm 11.4
<i>Poa pratensis</i>	Perennial grass	20.4 \pm 1.8
<i>Artemisia ludoviciana</i>	Perennial forb	9.4 \pm 1.9
<i>Solidago nemoralis</i>	Perennial forb	8.2 \pm 2.0
<i>Ambrosia coronopifolia</i>	Perennial forb	3.7 \pm 0.5
<i>Panicum oligosanthes</i>	Perennial grass	0.8 \pm 0.4

* Data derived from early-, mid-, and late-season 1-m² plots ($n = 6$ per season) as described in text (*Methods: Experimental design and methods*).

vided into 16 0.5 \times 0.5 m quadrats from which ≈ 10 plants of each species were randomly sampled (one plant per randomly chosen quadrat). Each sample consisted of the entire aboveground portion of a single plant (for the grass species, "single plant" refers to all foliage arising as a discrete bunch; for *Poa*, however, plants from areas of ≈ 20 cm² had to be pooled to make a sufficiently large sample, i.e., >0.25 g dry mass). Roots were not sampled because they could not be quantitatively separated by species.

Each plant sample (≈ 60 per species) was oven-dried at 65°C, ground in a Wiley mill to pass a 0.5-mm mesh, and digested using a micro-Kjeldahl procedure modified to include plant nitrate and nitrite (Bremner and Mulvaney 1982). Steam distillation methods (Bremner and Mulvaney 1982) were used to prepare the digests for total N and isotope ratio analyses. The atom percent ^{15}N (in excess of natural abundance) of each sample was determined on a Varian MAT 250 mass spectrometer operated by the USDA Agricultural Research Service and the University of Minnesota.

We calculated areal uptake of ^{15}N by each species (in grams per square metre) for each of the six treatments as follows:

$$^{15}\text{N uptake} = (^{15}\text{N}/\text{total N}) \times (\text{total N}/\text{biomass per unit area}) \times (\text{biomass per unit area}).$$

The seasonal (early-, mid- and late-season) measures of aboveground biomass used in this formula were determined from a randomized block of 18 1-m² (0.4 \times 2.5 m) plots adjacent to the ^{15}N plot area. At each of the three times corresponding to the ^{15}N plot samplings, six of these non- ^{15}N plots were harvested and sorted to species. For each species, we checked the robustness of our results by substituting the cross-seasonal mean of biomass into the formula when seasonal biomass differences were not statistically significant. This produced only subtle changes in the estimated ^{15}N uptake among treatments and had no effect on our conclusions.

A limitation of our methods is that ^{15}N was used as an analogue for available soil nitrogen. A closer approximation of actual spatiotemporal patterns of N uptake would have been possible if ^{15}N had been injected into the treatments in proportion to the spatial

and temporal patterns of net N mineralization. Logistics prevented this, but the species' observed spatial and temporal patterns of ^{15}N uptake can be normalized according to those patterns of net N mineralization described above. This normalization skews the observed patterns of ^{15}N uptake toward the early-season/2-cm and mid-season/2-cm treatments. However, because normalization produces only minor changes in the species' relative differences, interpretation of the results within a community context is unchanged. We therefore present only the observed ^{15}N uptake data.

RESULTS AND DISCUSSION

Spatiotemporal differences in ^{15}N uptake

Each of the six species showed significant differences in the time (season) and depth of ^{15}N uptake (Table 2). A graphical view of these spatiotemporal patterns (Fig. 1) clearly shows that the species are differentiated into three groups: (1) *Poa* and *Panicum*, (2) *Artemisia* and *Solidago*, and (3) *Schizachyrium* and *Ambrosia*. Within each group, the paired species differed ($P < .05$) in no more than one treatment. Between groups, the species differed in three or more of the six treatments. Interpreted another way, the species pairs within the three groups were 88, 91, and 87% similar, respectively, in their patterns of ^{15}N uptake as calculated by

$$\text{PS}_{ij} = 100 - \frac{1}{2} \sum_{h=1}^T |p_{ih} - p_{jh}|,$$

where PS_{ij} is the percent similarity of species i and j , p_{ih} is the percentage of species i 's ^{15}N uptake in treatment h (Fig. 1), p_{jh} is the percentage of species j 's ^{15}N uptake in the same treatment, and $T = 6$ treatments (after Schoener 1970). Percent similarities of between-group species pairs ranged from 55 (*Ambrosia* and *Panicum*) to 84% (*Poa* and *Artemisia*) and averaged 69%.

The species groups are mainly distinguished by temporal differences in ^{15}N uptake, but spatial differences are also important. *Poa* and *Panicum* were characterized by high early-season ^{15}N uptake (52 and 60% of their uptake totals, respectively) and greater uptake from 12 cm than from 2 cm (Fig. 1). *Artemisia* and *Solidago* also had high early-season uptake (54 and 60% of their uptake totals, respectively) but, compared

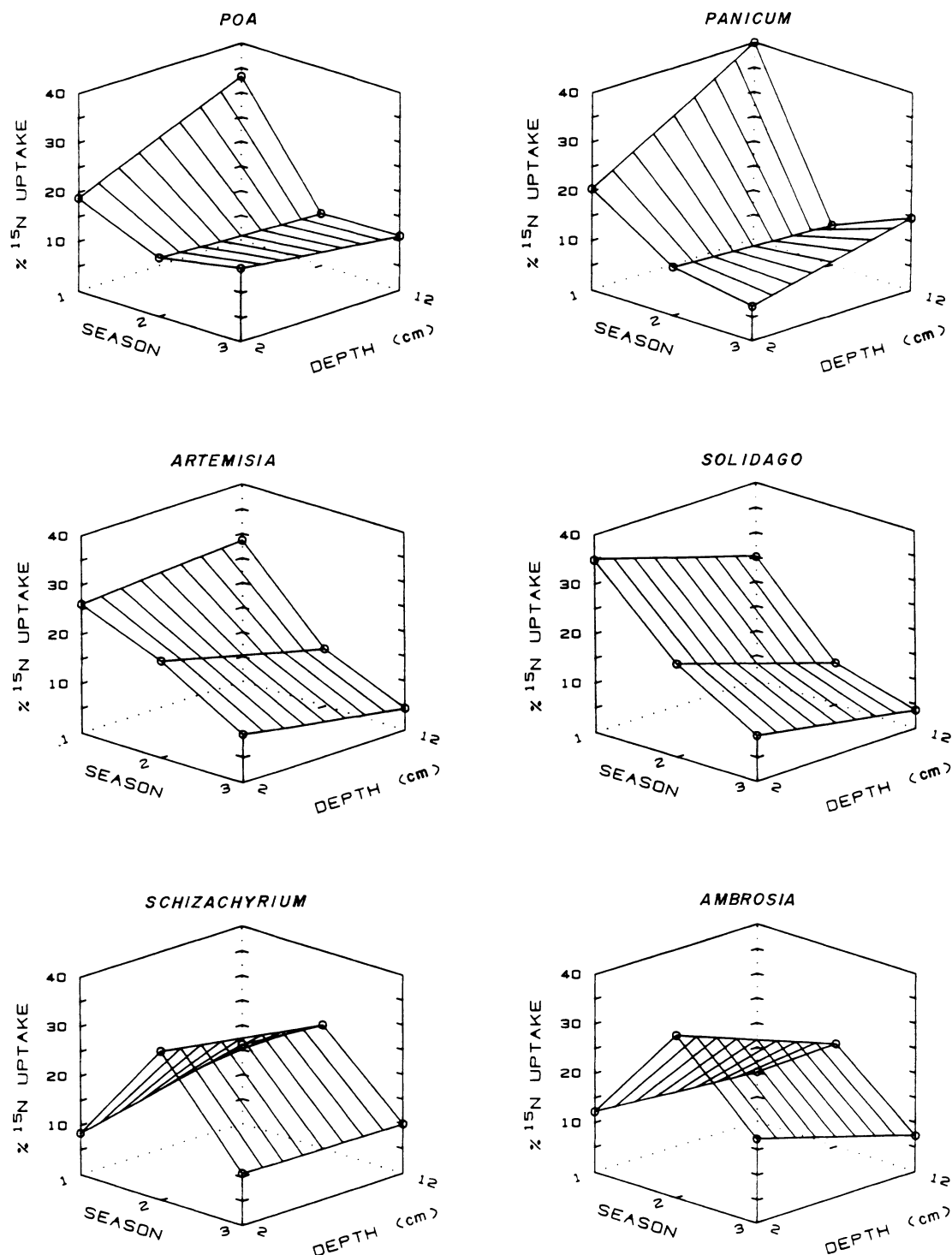


FIG. 1. Spatiotemporal patterns of ^{15}N uptake in the 50-yr-old field. Each figure is a three-dimensional representation of the data in Table 2 (early-season = 1, mid-season = 2, and late-season = 3). To compare all species on the same scale, ^{15}N uptake per treatment is expressed as a percent of each species' total (all six treatments) ^{15}N uptake; lines connecting data points (○) and shading do not indicate a response surface but are included to improve perception of the data. The least significant difference ($P < .05$) for interspecific treatment comparisons is 7.0%.

TABLE 2. Aboveground ^{15}N uptake by depth and season (early = 1 May–15 June, mid = 25 June–15 August, and late = 10 August–28 September). For each of the six treatments, 100 mg/m² of ^{15}N were injected into the soil.

Species	¹⁵ N uptake (mg/m²)						LSD*
	Early		Mid		Late		
	2 cm	12 cm	2 cm	12 cm	2 cm	12 cm	
<i>Poa</i>	9.22	16.33	5.79	5.14	7.29	5.40	2.15
<i>Schizachyrium</i>	1.88	3.62	6.82	5.67	2.37	2.26	1.52
<i>Artemisia</i>	2.45	2.68	1.84	1.08	0.92	0.42	0.67
<i>Solidago</i>	1.70	1.22	0.92	0.41	0.45	0.18	0.44
<i>Ambrosia</i>	0.51	0.42	1.36	0.86	0.70	0.30	0.30
<i>Panicum</i>	0.37	0.73	0.18	0.15	0.13	0.27	0.13

* The least significant difference (LSD, $P < .05$) is given for intraspecific treatment comparisons.

to *Poa* and *Panicum*, were more dependent on mid-season uptake and on uptake from 2 cm. In contrast, *Schizachyrium* and *Ambrosia* peak uptake occurred during the midseason (55 and 53%, respectively); they had relatively low early-season uptake (<25%).

For *Poa* and *Schizachyrium*, the difference in temporal patterns of uptake has a physiological basis. Whereas *Poa* has a C_3 photosynthetic pathway that reaches maximum efficiency at cool, early-season temperatures, *Schizachyrium* has a C_4 , or warm-season, pathway. Kemp and Williams (1980) showed that temporal displacement of growth between co-occurring C_3 and C_4 species was clearly related to the differential temperature responses. Thus, the data for *Poa* and *Schizachyrium* suggest fundamental niche differences.

Although we found no reference describing photosynthetic pathways of the other species, *Artemisia*, *Solidago* and *Panicum* were phenologically similar to *Poa*, increasing to >70% of their peak aboveground biomasses by mid-June. In contrast, *Ambrosia* was very similar to *Schizachyrium*; mid-June biomasses of both

species were only $\approx 35\%$ of their peak, or mid-August, biomasses. For all species, then, ^{15}N uptake had a strong phenological component.

Spatiotemporal differences and community organization

We used discriminant analysis (BMDP 1985), a multivariate statistical technique, to examine the hypothesis that spatiotemporal differences in N (^{15}N) uptake contribute to community organization. The discriminant analysis (Fig. 2) and Fig. 1 interpret the same ^{15}N uptake data, but Fig. 2 provides a simplified definition of species' differences by reducing the six treatment variables to two orthogonal (perpendicular) multivariate axes. The first axis, or canonical variable, explains 70% of the variance between species and is highly correlated with the mid-season/2-cm (standardized canonical correlation coefficient = -0.98), late-season/12-cm (correlation = 0.64), and early-season/2-cm (0.54) treatments. This axis primarily separates "early-season" (*Poa*, *Panicum*, *Artemisia*, and *Soli-*

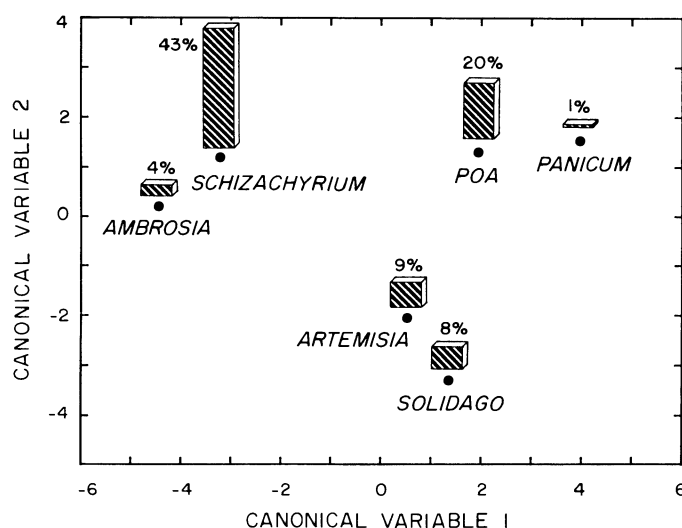


FIG. 2. Discriminant analysis of the same data used to describe the spatiotemporal patterns of ^{15}N uptake shown in Fig. 1. The axes account for 94% of the total variance between species. The columns and percentages adjacent to them represent each species' proportion of total (all species) peak aboveground biomass.

ago) and "mid-season" (*Schizachyrium* and *Ambrosia*) species. The second canonical variable explains an additional 24% of the variance and is highly correlated with the late-season/12-cm (0.98), early-season/2-cm (-0.69), and mid-season/2-cm (-0.29) treatments. This axis primarily separates the "early-season" species into two groups (*Artemisia* and *Solidago* vs. *Poa* and *Panicum*) according to their dependence on mid- vs. late-season uptake and on uptake from 2 cm.

Thus, the canonical space defined by the first and second axes in Fig. 2 explains 94% of the total variance between species. The separation of species in canonical space therefore provides a relative measure of niche specialization with respect to the use of N.

When the species' positions in canonical (niche) space are considered in relation to the species' relative abundances (superimposed over the discriminant analysis, Fig. 2), spatiotemporal differences in N uptake can be seen to be a major determinant of community organization. The two most dominant species (*Schizachyrium* and *Poa*) are well separated in niche space, low-ranking subordinates (*Ambrosia* and *Panicum*) occupy niches similar to dominants, and high-ranking subordinates (*Artemisia* and *Solidago*) show better separation from dominants than do low-ranking subordinates. These observations are consistent with the hypothesis that competitive interactions involving dominant species exert a powerful control on the abundances of other species, and the intensities of such interactions are related to differences in specialization (McNaughton and Wolf 1970). An important implication of this result is that differentiation between dominants is more important than that between subordinates; this is supported by the fact that *Schizachyrium* and *Poa* show more differentiation than do *Artemisia* and *Solidago*. To the extent that equilibria exist between dominant species and rare species, more than one rare species could theoretically occupy the same niche for long periods since there is, generally, a low probability of rare species interacting as neighbors.

Although the preceding observations could also be drawn from Fig. 1, Fig. 2 uniquely suggests the importance of dominant species and diffuse competition (competition from more than one species) in structuring this community. Since dominant species are likely to be included in the neighborhood of any given plant, the effects of diffuse competition should be most severe in the niche space separating *Schizachyrium* and *Poa*. Because the four subordinate species are located peripherally to this space, this gives the appearance of a community in which niche diversification reduces competition for a limiting resource.

It is impossible to ascertain from this analysis the degree to which diffuse competition has shifted subordinates into peripheral utilization patterns; the appearance of niche diversification between subordinates and dominants may be misleading if subordinates occupy the same fundamental niche as either *Schiza-*

chyrium or *Poa*. However, the divergence of subordinates with respect to diffuse competition supports the hypothesis of different fundamental niches; some of these species must differ either in their fundamental utilization patterns or in the plasticity of their spatiotemporal responses to dominants.

Conclusions

Models that predict that the number of species in an equilibrium environment cannot exceed the number of limiting resources implicitly assume that species are spatially and temporally undifferentiated in their use of those resources (e.g., Armstrong and McGehee 1980). Our results not only demonstrate significant spatial and temporal partitioning of a single limiting resource (soil N) among co-occurring plant species, but suggest that such partitioning may reduce interspecific competition and thereby facilitate coexistence. The importance of interspecific competition for N in organizing this community is suggested by the direct relationship of species' abundances to the degree of spatiotemporal separation from dominant (abundant) species.

Because certain processes (e.g., soil nitrogen accumulation and differential rates of dispersal and colonization) promote nonequilibrium conditions in this successional community, it is unclear whether the spatiotemporal differences we found would be sufficient to allow coexistence at equilibrium. Thus, the conclusion that the observed differences facilitate coexistence implies only that the differences prolong the periods of coexistence, or equivalently, slow the rates of competitive displacement. In the successional time frame at Cedar Creek, spatiotemporal differentiation appears to be very effective in promoting coexistence; well-differentiated *Schizachyrium* and *Poa*, for example, coexist as codominants in fields ranging from 25 to 60 yr old (Tilman 1988).

We emphasize that many factors besides spatiotemporal resource partitioning contribute to species diversity within old fields at Cedar Creek. Tilman and coworkers provide evidence that within-field diversity is promoted by (1) horizontal heterogeneity in soil nitrogen availability and differentiation of competitive abilities along such nitrogen gradients (Tilman 1988, D. Wedin and D. Tilman, *unpublished manuscript*), (2) slow rates of competitive displacement due to relatively slow maximal growth rates of late- vs. early-successional species (Tilman 1986, 1988), and (3) small-scale disturbances due to mechanisms such as gopher activity (Tilman 1983, Inouye et al. 1987). By focusing only on the most abundant species in the 50-yr-old field, this study has emphasized factors (viz., competitive interactions involving *Schizachyrium* and *Poa*) that are sufficiently common to have predictable effects on community structure. In contrast, the occurrences of many of the ≈ 60 less abundant species may depend primarily on infrequent or less predictable factors, such as small-scale disturbances, patches of low or high N

availability, random gaps in the horizontal spacing of dominant species, and the occurrence of germination sites. We have also hypothesized that, because of infrequent interspecific contact between rare species, equilibria between such species are achieved more slowly than between rare species and abundant species. This suggests that, even in relatively stable environments, the number of rare species may exceed the number of available niches, e.g., peripheral spatiotemporal niches in Fig. 2.

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