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## Sampling spatial and temporal variation in soil nitrogen availability

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**Abstract** There are few studies in natural ecosystems on how spatial maps of soil attributes change within a growing season. In part, this is due to methodological difficulties associated with sampling the same spatial locations repeatedly over time. We describe the use of ion exchange membrane spikes, a relatively nondestructive way to measure how soil resources at a given point in space fluctuate over time. We used this method to examine spatial patterns of soil ammonium ( $\text{NH}_4^+$ ) and nitrate ( $\text{NO}_3^-$ ) availability in a mid-successional coastal dune for four periods of time during the growing season. For a single point in time, we also measured soil  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations from soil cores collected from the mid-successional dune and from an early and a late successional dune. Soil nitrogen concentrations were low and highly variable in dunes of all ages. Mean  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations increased with the age of the dune, whereas coefficients of variation for  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations decreased with the age of the dune. Soil  $\text{NO}_3^-$  concentration showed strong spatial structure, but soil  $\text{NH}_4^+$  concentration was not spatially structured. Plant-available  $\text{NH}_4^+$  and  $\text{NO}_3^-$  showed relatively little spatial structure: only  $\text{NO}_3^-$  availability in the second sampling period had significant patch structure. Spatial maps of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  availability changed greatly over time, and there were few significant correlations

among soil nitrogen availability at different points in time.  $\text{NO}_3^-$  availability in the second sampling period was highly correlated ( $r = 0.90$ ) with the initial soil  $\text{NO}_3^-$  concentrations, providing some evidence that patches of plant-available  $\text{NO}_3^-$  may reappear at the same spatial locations at irregular points in time.

**Key words** Coastal dune ecosystems · Ion exchange membrane spikes · Soil nitrogen availability · Soil resource heterogeneity · Spatial statistics

### Introduction

Variation in soil resource levels is common and is important to plants. At relatively large spatial scales, the resources available to plants change as the soil type changes, and this variation has well-known effects on the distribution of plant species. At smaller spatial scales, soil resources continue to show considerable spatial heterogeneity, often down to the smallest scale at which measurements are taken (e.g., Robertson et al. 1988; Lechowicz and Bell 1991; Jackson and Caldwell 1993). Small-scale heterogeneity can have a large impact on the performance of individual plants (Antonovics et al. 1987; Miller et al. 1995), and hence, on the structure and dynamics of plant populations and communities.

Over the past several decades, studies on the spatial heterogeneity faced by plants have progressed from purely descriptive accounts to detailed spatial-statistical analyses. The latter approach has proven to be a valuable tool to characterize resource level variation across space. However, most spatial-statistical analyses of soil resources are for a single time period only. For soil resources that show a high level of temporal variation, data from a single time period may not provide an adequate view of the resource environment experienced by plants during a growing season. For example, forms of soil nitrogen accessible to plants ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) are released with each rain event, then taken up and

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depleted locally by plants and, hence, they are highly dynamic over time (Lee et al. 1981). Although it is known that nitrogen availability varies over time, virtually nothing is known about how this variation affects the spatial distribution of soil nitrogen (but see Ryel et al. 1996). The situation is similar for other soil attributes. Thus, we know little about how spatial maps of soil attributes change over time.

Because soil resources can have large effects on plants, it is important to have a detailed understanding of how the resources available to plants change over both space and time. However, the methods most commonly used to sample soil resources (e.g., soil cores and resin-filled bags) are not well-suited for repeated sampling from a single spatial location (Subler et al. 1995). Thus, when using these methods, it can be difficult to measure how resources at a given point in space fluctuate over time. In this report, we describe a simple method for sampling soil resources that does relatively little damage to the soil substrate. The minimally intrusive nature of our method allows intensive spatial data on soil resources to be collected from the same sampling points over multiple time periods.

We used this method to survey spatial and temporal variation in soil nitrogen availability in a coastal fore-dune community. We focused on soil nitrogen because it is the primary limiting nutrient in fore-dune communities (Ehrenfeld 1990 and references therein). While other nutrients are supplied adequately in a homogenous fashion by salt spray deposition (van der Valk 1974), most soil nitrogen in coastal fore-dunes is contained within sparse pockets of particulate organic matter that mineralize gradually (Evans 1988). In addition, because of extremely low clay mineral and organic matter concentrations, coastal dune soils have a low capacity to retain  $\text{NH}_4^+$  and  $\text{NO}_3^-$  ions. Thus, given the nature of both nitrogen inputs and coastal dune soils, we hypothesize that surface soil pools of inorganic nitrogen are likely to be small and to fluctuate rapidly over time. We also hypothesize that soil nitrogen levels should increase during succession due to the temporal accumulation of soil organic matter.

## Materials and methods

### Study site

This study was conducted within the fore-dune system at the southern tip of Matagorda Island, a barrier island along the gulf coast of Texas. The southern end of the island has been prograding over the last 30 years such that the dune ridges represent different geomorphological ages in sequence. Three low dune ridges within this sequence were chosen for study. We refer to these ridges, in order of increasing age, as early, middle, and late, respectively. A  $6 \times 14$  m plot was established in each dune ridge. The early plot was inhabited exclusively by spreading, rhizomatous clonal species such as *Hydrocotyle bonariensis*, *Spartina patens*, *Uniola paniculata*, and *Cyperus esculentus*. In contrast, the late plot was inhabited predominantly by clonal bunch grasses such as *Schizachyrium scoparium*. The middle plot – which was our primary study site –

was inhabited by a mixture of both of these types of clonal growth forms (Table 1).

We collected two types of soil nitrogen data in this study. Soil nitrogen concentrations (with units in mg N/kg soil, or equivalently, ppm) were measured from soil cores collected at one point in time. These soil cores were taken from the early, middle, and late plots, and were used to compare soil nitrogen concentrations in dunes of different successional ages. Available nitrogen (with units  $\mu\text{g N/cm}^2$  membrane) was assessed over four periods of time with ion exchange membrane spikes (see below). It is important to note that ion exchange membranes assess the nitrogen available to plants, not the concentration of nitrogen in the soil. Spatial and temporal patterns of available nitrogen were determined in the middle plot only.

### Soil nitrogen concentrations in early to late successional dunes

On 13 March 1994, we used a 2-cm-diameter corer to sample the surface 7 cm of soil at 20 random points within the early and late plots, and at 112 points within the middle plot. The 112 points in the middle plot were located as described below. Soil samples were stored on ice and transported to the Ohio State University Soil Ecology Laboratory, where they were air-dried within 4 days of collection. At the time of collection, soil moisture was very low (i.e., the samples were essentially already “air-dried”). Thus, it is unlikely that much nitrogen mineralization or volatilization occurred in this 4-day period. After drying, samples were extracted with 2 M KCl (1:5 soil:extractant), filtered through no. 42 Whatman paper, and analyzed on a Lachat flow-injection autoanalyzer to determine ammonium and nitrate concentrations. The gravimetric water content of soil samples was determined by oven-drying ( $60^\circ\text{C}$ ).

### Spatial sampling regime

One hundred twelve sampling points in the middle plot were located to provide a comprehensive, nonbiased determination of the spatial structure, as well as a wide range of distances between sampling points. Thirty-two points were located within the plot to form a single  $8 \times 4$  grid with 2-m spacing; 32 more points were offset 25 cm from the grid points. Additional points were located randomly within nine  $1\text{-m}^2$  quadrats (5 points per quadrat), which were themselves located randomly within the plot. A final 3 points were located randomly within the plot.

Spatial variability in the middle plot was quantified with Geary's  $c$  coefficient (Legendre and Fortin 1989). Geary's  $c$  is structurally comparable to a distance coefficient (e.g., the semivariance in geostatistics; see Rossi et al. 1992) and is standardized to allow comparison among different variables. Geary's  $c$

**Table 1** Occurrence of common plant species in the middle plot, as indicated by the number of the plot's  $84 \times 1 \times 1$  m<sup>2</sup> quadrats in which the indicated species were found

Plant species	Number of quadrats	Growth form
<i>Erigeron myrionactis</i>	82	Spreading clonal
<i>Cassia fasciculata</i>	81	Annual
<i>Sporobolus virginicus</i>	75	Spreading clonal
Bluestems <sup>a</sup>	71	Clump clonal
<i>Spartina patens</i>	60	Spreading clonal
<i>Fimbristylis castanea</i>	51	Clump clonal
<i>Hydrocotyle bonariensis</i>	47	Spreading clonal
<i>Ambrosia psilostachya</i>	40	Spreading clonal
<i>Juncus validus</i>	37	Clump clonal
<i>Heterotheca subaxillaris</i>	36	Aclonal perennial

<sup>a</sup> *Andropogon glomeratus* and *Schizachyrium scoparium* combined

varies from zero, indicating strong positive autocorrelation, to 2 or more, indicating negative autocorrelation. In the absence of spatial autocorrelation, the expected value of Geary's  $c$  equals 1. Statistical significance of Geary's  $c$  was evaluated as in Cliff and Ord (1981). Geary's  $c$  can be computed at several distance classes; a plot of Geary's  $c$  against the distance is called a spatial correlogram. We computed the overall significance of spatial correlograms with a Bonferroni procedure that corrects for the lack of independence among the autocorrelation coefficients computed at various distance classes (Legendre and Fortin 1989). We used the Bonferroni significance levels to provide an overall assessment of whether there is significant spatial structure for each soil attribute.

#### Spatial and temporal variation in available nitrogen

Spatial and temporal dynamics of nitrogen availability were assessed in the middle plot with ion exchange membrane (IEM) spikes. Resin-filled bags or spheres have been used for in situ assessment of soil nutrient availability in dune grasslands (Gibson 1986) and other ecosystems (see references in Subler et al. 1995). More recently, resin-impregnated membranes have been used in situ to measure soil nitrogen, phosphorus, and sulfur availability (Subler et al. 1995).

We developed a simple method for the rapid placement, removal, and handling of ion exchange membranes. We cut anion or cation IEMs (types AR204-SZRA and CR67-HMR; Ionics Inc., Watertown, Mass.) into  $2 \times 2$  cm squares, and bonded the squares to short segments of rigid acrylic tubing with methacrylatebase epoxy glue. Bonding of the IEMs in this way did not affect membrane exchange capacity ( $0.07 \text{ mmol}_c \text{ cm}^{-2}$ ) (S. Subler, unpublished data). The segments of tubing bearing the IEMs were secured on threaded metal rods with nuts and washers, using additional segments of tubing as spacers.

The IEM spikes were inserted in the dune soil at each of the 112 sampling locations so that the membranes were at a uniform depth (from 5 to 7 cm). One cation-exchange membrane and one anion-exchange membrane were placed at each sampling location, 2 cm apart. The spikes remained in the soil for 2–4 weeks before being removed and replaced with new spikes. After removal, spikes were transported to the Soil Ecology Laboratory at Ohio State University and stored dry. The segment of tubing bearing the IEM was then brushed free of soil and placed whole into a 125-ml flask for extraction with 25 ml 2 M KCl. The extracts were analyzed for  $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N as above. To recondition the extracted IEMs, we placed them in a saturated solution of KCl for 24 h, then rinsed them with deionized water. After air-drying, the IEMs were replaced on the spikes for reuse in the field. IEM spikes were used to sample soil nitrogen for four time periods in 1994: 13 March to 1 April, 1–15 April, 15 April to May 13, and 13 May to 10 June. See Subler et al. (1995) and the Discussion of this paper for further information on the effects of dry storage, the disturbance to the soil created by IEMs, and the variability of IEM membranes following reuse.

We computed Pearson correlation coefficients to examine whether soil nitrogen availabilities were correlated over time. The presence of spatial autocorrelation in soil nitrogen availability would violate the assumption of independence required by standard parametric tests of the correlation coefficient (Legendre et al. 1990). To ensure that this was not a problem, we corrected the significance level of the correlation coefficient by calculating an effective sample size that is proportional to the intensity of spatial autocorrelation present in the data (Clifford et al. 1989).

Finally, although it is possible to convert results from the analysis of IEM spikes to soil nitrogen concentrations, such conversions are often fraught with difficulties (L. Cooperband, personal communication). Instead, we use the unit  $\mu\text{g N/cm}^2$  membrane, viewing this as an index or relative measure of the nitrogen available to plants. As such, IEM spikes provide similar results to the more commonly used resin bags, which, with units of  $\mu\text{g N/g}$  resin weight, also provide an index of plant-available soil nitrogen. Indices of plant-available soil nitrogen represent a useful complement to measures of soil nitrogen concentration. Although

the latter provide an intuitive measure of soil nitrogen levels, in some cases the concentration of nitrogen that can be extracted from soils is a poor indicator of the nitrogen actually available to plants (e.g., under dry conditions, plants will obtain little nitrogen even when the concentration in the soil is high).

#### Plant cover

We constructed a spatial map of plant cover from photographs of each of the 84  $1\text{-m}^2$  quadrats in the middle plot. The photographs were taken on 13 March 1994, prior to the onset of most plant growth. With one exception, all of the common plant species in the plot were perennials (Table 1). Individuals of the annual species, *Cassia fasciculata*, were seedlings when the photographs were taken; thus, they contributed little to plant cover. Given when the data were collected and given the fact that most plant cover was from perennials, the plant cover data are indicative of growth during the previous year. As such, they are of limited relevance to changes in soil nitrogen that occurred during the 1994 growing season. For this reason, we correlated the vegetation data to soil nitrogen and soil water concentration data only, since data for these soil variables were also collected prior to the growing season on 13 March 1994. To correlate the vegetation data to these three soil variables, we first performed a kriging analysis on the soil variables (Isaaks and Srivastava 1989). We used isotropic spherical models, with different parameters for each soil variable; the interpolation step was 0.5 m. The kriging analysis provided estimates of the soil variables in regions of the plot in which the soil variables were not sampled. We then averaged these estimates within each of the 84  $1\text{-m}^2$  quadrats in the middle plot. Finally, we correlated the average values for the soil variables to the average percent cover for the same  $1 \times 1 \text{ m}^2$  quadrats; the significance level of these correlations was corrected for spatial autocorrelation as described above.

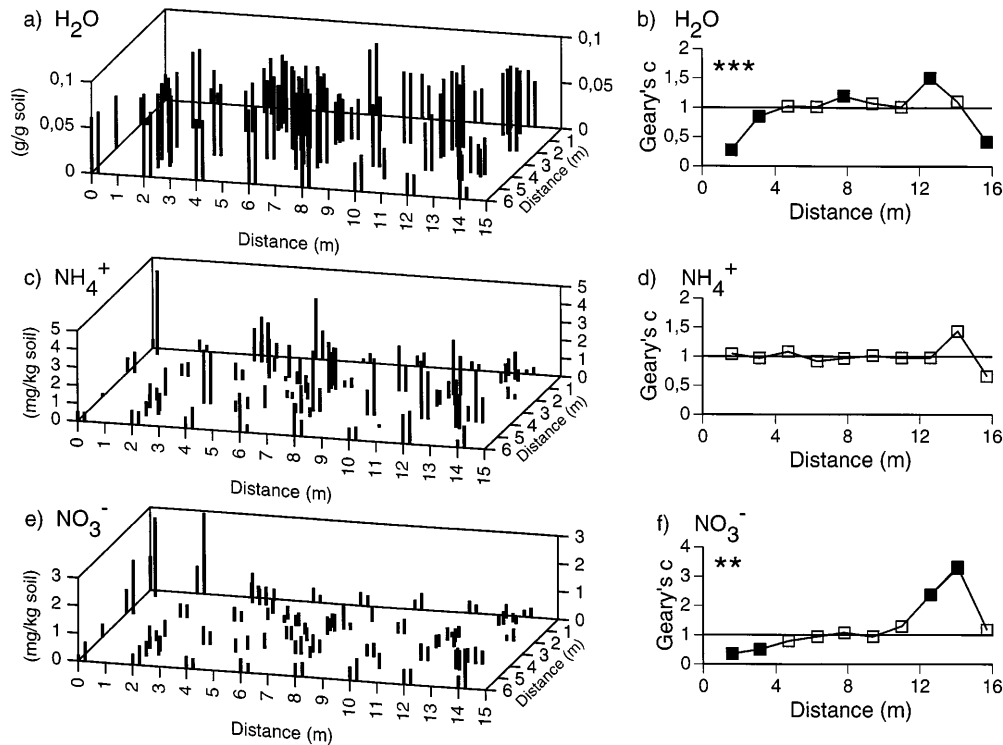
## Results

### Soil nitrogen concentrations in early to late successional dunes

To characterize soil nitrogen concentrations in dunes of different ages, we calculated the mean and coefficient of variation of  $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N for each of the three dune ridges (early, middle, and late successional plots). The mean concentration of  $\text{NH}_4^+$  in the early, middle, and late successional plots was 0.77, 1.21, and 1.39 ppm, respectively. The corresponding coefficients of variation for  $\text{NH}_4^+$  were 387, 74, and 67. The mean concentration of  $\text{NO}_3^-$  in the early, middle, and late successional plots was 0.27, 0.57, and 2.01 ppm, respectively. The corresponding coefficients of variation for  $\text{NO}_3^-$  were 125, 70, and 64.

### Spatial variation in soil water content and soil nitrogen concentration

We constructed spatial maps and spatial correlograms of soil water content and soil nitrogen concentrations for the middle plot (Fig. 1). Both soil water content and soil nitrate concentration showed strong spatial structure (soil water content: Fig. 1b,  $P < 0.001$ ; soil nitrate:



**Fig. 1** Spatial maps of soil water content (a), soil  $\text{NH}_4^+$  concentration (c), and soil  $\text{NO}_3^-$  concentration (e), and Geary's  $c$  spatial correlograms of soil water content (b), soil  $\text{NH}_4^+$  concentration (d), and soil  $\text{NO}_3^-$  concentration (f). For the spatial maps (a, c, e), missing values were set to zero. The  $x$ -axis in the spatial maps runs from north at position zero to south at position 14. Spatial correlograms (b, d, f) were based on ten equidistant classes of 1.6 m each. Significant individual coefficients in the correlograms are indicated by *black squares* ( $P < 0.05$ ). The overall significance of a correlogram, based on a Bonferroni correction, is indicated by two ( $P < 0.01$ ) or three ( $P < 0.001$ ) *asterisks*

Fig. 1f,  $P = 0.004$ ). For these two variables, patches of high internal uniformity were smaller than 4 m in size. Soil ammonium concentration did not exhibit significant patch structure (Fig. 1d).

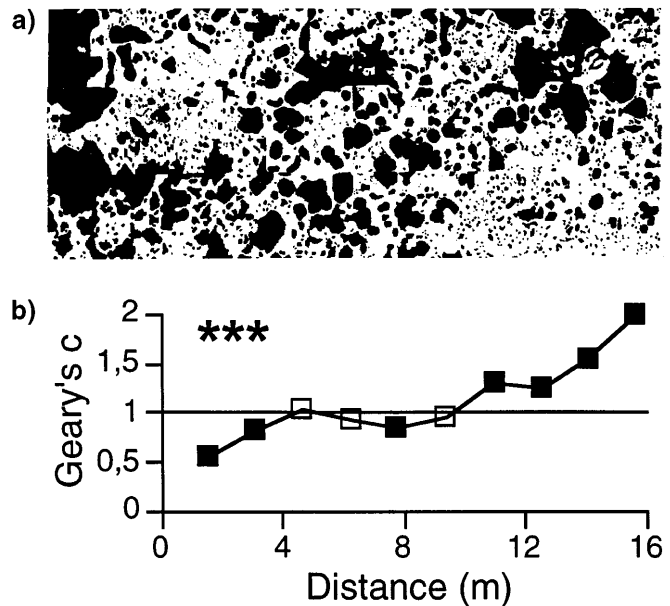
#### Spatial variation in plant cover

We constructed spatial maps and spatial correlograms of plant cover for the middle plot (Fig. 2). Plant cover exhibited strong spatial structure (Fig. 2b,  $P < 0.001$ ), and had patches of high internal uniformity that were less than 4 m in size. Soil water content showed a significant negative correlation with plant cover ( $r = -0.35$ ,  $P = 0.03$ ). The correlations between plant cover and soil ammonium ( $r = -0.09$ ,  $P = 0.51$ ) and nitrate ( $r = 0.04$ ,  $P = 0.85$ ) concentrations were not significant.

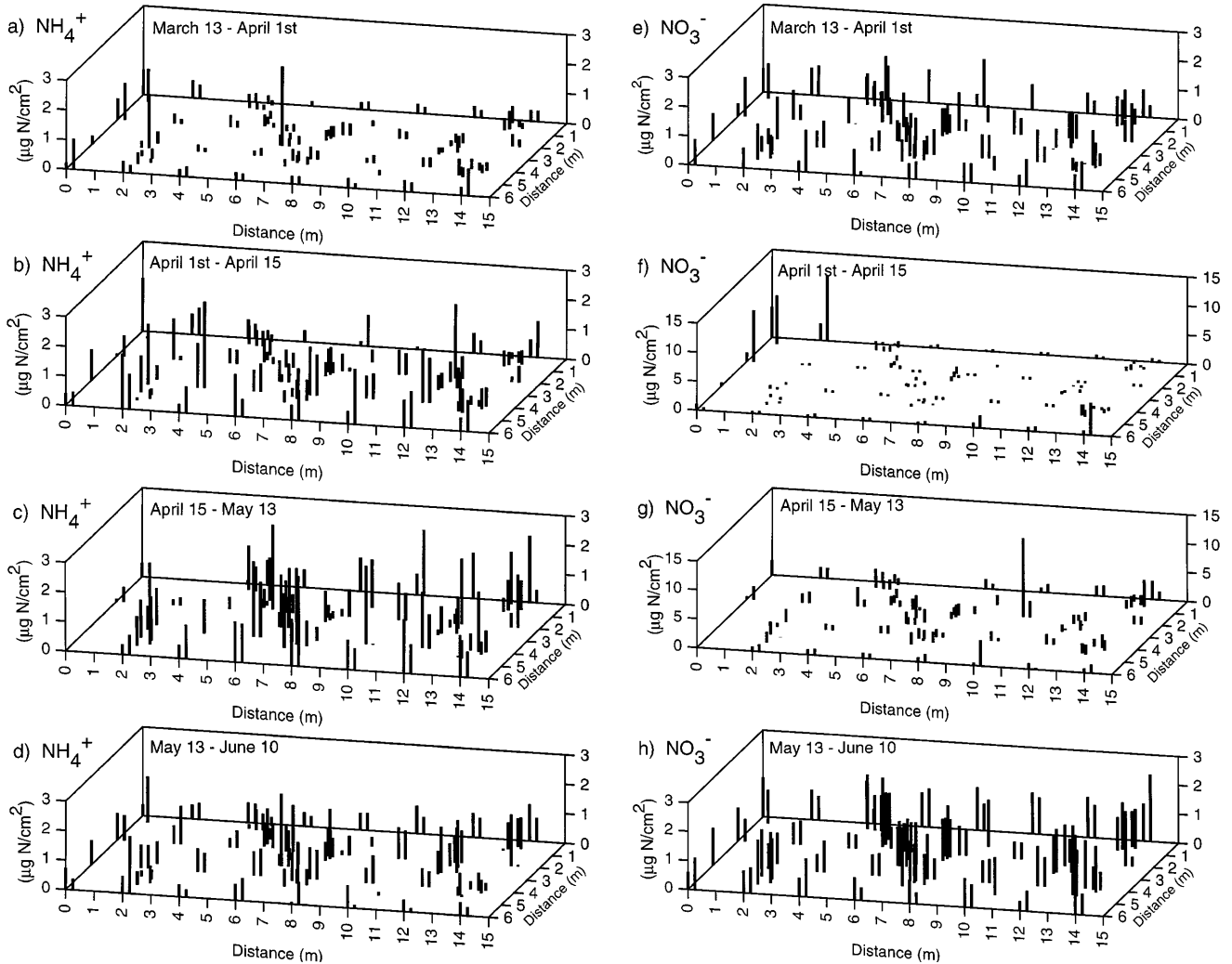
#### Spatial and temporal variation in available nitrogen

The spatial distribution of soil nitrogen availability was assessed with IEM spikes for each of four time periods.

The availability of  $\text{NH}_4^+$  ranged from 0 to approximately  $3 \mu\text{g N/cm}^2$  in all four sampling periods (Fig. 3).  $\text{NO}_3^-$  showed a comparable background range of availability, but had peaks of  $10\text{--}15 \mu\text{g N/cm}^2$  during the middle two sampling periods (Fig. 3).



**Fig. 2** Spatial map (a) and Geary's  $c$  spatial correlogram (b) for plant cover. In a, the bottom-left corner of the spatial map was the northwest corner of the plot. In b, the spatial correlogram was based on ten equidistant classes of 1.6 m each. Significant individual coefficients in the correlogram are indicated by *black squares* ( $P < 0.05$ ). The overall significance of the correlogram, based on a Bonferroni correction, is indicated by the three *asterisks* ( $P < 0.001$ )



**Fig. 3** Spatial maps of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  availability ( $\mu\text{g N}/\text{cm}^2$  membrane) as a function of sampling period: 13 March to 1 April (a, e); 1–15 April (b, f); 15 April to 13 May (c, g); 13 May to 10 June (d, h). Missing values were set to zero. The  $x$ -axis runs from north at position zero to south at position 14

Neither  $\text{NO}_3^-$ -N or  $\text{NH}_4^+$ -N availability maintained a strong patch structure or spatial gradient (Figs. 3, 4). The only spatial correlogram that showed overall significance was that for  $\text{NO}_3^-$  during the second sampling period (Fig. 4f). Nitrate availability in the second sampling period was significantly correlated with the initial soil nitrate concentration ( $r = 0.90$ ,  $P < 0.0001$ ). Significant spatial autocorrelation was identified for  $\text{NH}_4^+$  availability for the second sampling period at scales of up to 1.6 m (Fig. 4b); overall, however, this correlogram was not significant.

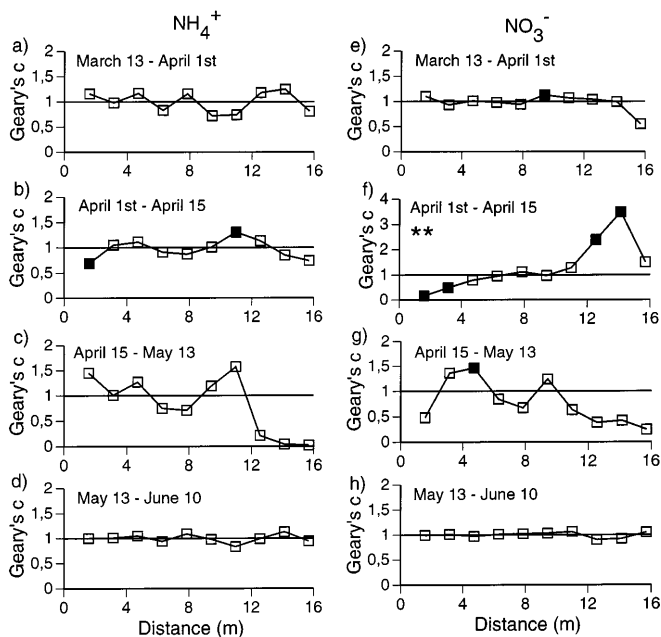
Spatial maps of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  availability indicate that regions of relatively high resource availability do not persist for long (Fig. 3). For example, in the second measurement period, there was a distinct region of relatively high nitrate availability in the northeast corner of the plot, with a steep gradient extending a few meters away (Fig. 3f). In the following time period, there was a

single peak of relatively high nitrate availability near the center of the southern half of the plot, roughly 10 m away from the previous hotspot (Fig. 3g).

Correlation analyses support the impression of rapid turnover in nitrogen availability: only one of six correlations among  $\text{NH}_4^+$  levels over time was significant, and no correlations among  $\text{NO}_3^-$  levels over time were significant (Table 2). Two of the sixteen cross-correlations among  $\text{NH}_4^+$  and  $\text{NO}_3^-$  levels were significant. Soil water content was correlated negatively over space with initial soil nitrate concentration and with soil nitrate availability in the second sampling period (Table 2). One possible explanation for these two significant negative correlations is that where the soil dries out more rapidly (e.g., in areas of greater elevation), nitrate accumulates in the soil because of reduced leaching and/or reduced plant uptake.

## Discussion

For a mid-successional coastal dune site, we assessed spatial and temporal variation in soil nitrogen availability with IEM spikes. This is the first report that we



**Fig. 4** Geary's *c* spatial correlograms of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  availability as a function of sampling period. Correlograms were based on ten equidistant classes of 1.6 m each. Significant individual coefficients are indicated by *black squares* ( $P < 0.05$ ). Only one variable ( $\text{NO}_3^-$  in f) showed an overall significant correlogram, based on a Bonferroni correction, as indicated by two *asterisks* ( $P < 0.01$ )

know of in which IEM spikes were used to measure soil resource availability in a natural ecosystem. Compared to soil resource sampling methods currently in common use (e.g., soil cores or buried resin-filled bags), advantages of IEM spikes include that they inflict minimal damage to the soil, they are simple to use, highly durable and can be recycled, and they allow intensive sampling over multiple time periods at the same spatial locations (see Subler et al. 1995). Narrow tension lysimeters also cause relatively little disturbance to soils, but – unlike IEM spikes – they only work well in mesic soils.

**Table 2** Pearson product-moment correlations among soil water content, soil nitrogen concentrations, and soil nitrogen availability. Soil water content (S1), soil  $\text{NH}_4$  concentration (S2), and soil  $\text{NO}_3$  concentration (S3) were sampled on 13 March 1994. Ammonium ( $\text{NH}_4$ ) and nitrate ( $\text{NO}_3$ ) availability were sampled during four time periods in 1994, as described in the text. A1–A4 denotes ammonium availability during time periods 1–4, respectively. N1–N4 denotes

S1	–											
S2	0.09	–										
S3	–0.50***	0.00	–									
A1	–0.05	–0.07	0.23*	–								
A2	0.12	0.35***	0.10	0.09	–							
A3	–0.04	0.04	–0.07	–0.08	–0.04	–						
A4	0.44**	0.08	–0.18	0.28*	–0.05	–0.03	–					
N1	0.00	0.13	0.19	0.06	0.07	–0.20*	–0.02	–				
N2	–0.55***	–0.13	0.90***	0.28*	0.10	–0.09	–0.16	0.16	–			
N3	0.00	0.04	0.02	–0.04	–0.03	–0.03	0.01	0.07	0.06	–		
N4	–0.07	–0.07	–0.05	0.01	–0.19	–0.12	0.07	0.01	–0.09	–0.08	–	
	S1	S2	S3	A1	A2	A3	A4	N1	N2	N3	N4	

The following portrait of N availability emerges from our study: both  $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N are present in very low amounts, they are highly variable spatially, they show limited evidence of spatial structure, and areas of relatively high resource availability do not persist for long. Thus, the coastal dune ecosystem that we studied presented to plants a highly variable, rapidly changing environment in which the location (but see below), size, and duration of hotspots of available nitrogen were difficult to predict. As is common in dune communities, extractable nitrogen levels were low compared to other ecosystems (see Ehrenfeld 1990). In addition, soil nitrogen concentrations in our early successional site were among the most variable found in ecosystems studied to date (Schlesinger et al. 1990; Jackson and Caldwell 1993; Alpert and Mooney 1996; Ryel et al. 1996).

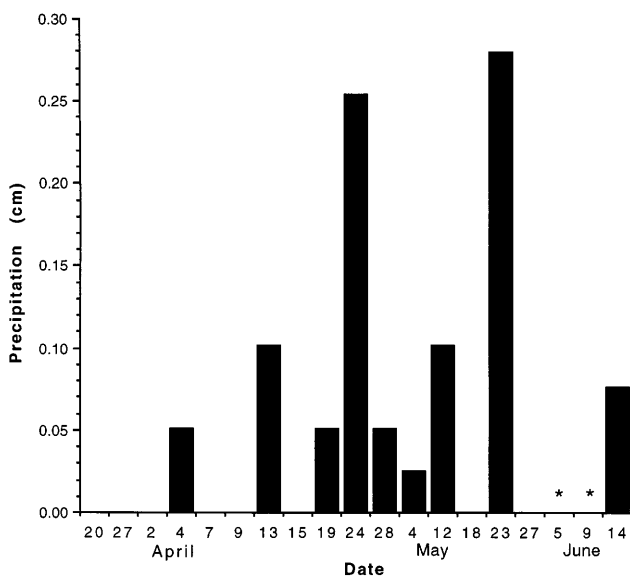
To what extent was the variability in soil nitrogen availability found in this study due to variability introduced by the IEM methodology? In a laboratory study using homogeneous soils, variability in nitrate uptake among individual membranes was generally found to be low ( $\text{CV} < 10\%$ ) (reanalysis of data presented in Subler et al. 1995). Previous work also indicates that storage of air-dried membranes for up to several months does not significantly affect the retention of nutrients on the membranes, and that membranes may be reused several times in the field without appreciable loss of ion exchange capacity (Cooperband and Logan 1994; S. Subler, unpublished data). Although differences in the degree of soil disturbance (and therefore rates of mineralization/immobilization) resulting from the insertion of membrane spikes may represent a potential source of error in some soils, the loose sandy soil in this study allowed easy placement of the membrane spikes with only minimal soil displacement. Overall, then, we think that the variability in membrane uptake of nitrate found in this study was largely due to actual microscale variation in soil nitrogen availability, not to inherent methodological variability. This is supported by the high correlation between membrane nitrate uptake during the

nitrate availability during time periods 1–4, respectively. Significance levels and effective sample sizes were adjusted for the presence of spatial autocorrelation in the data (see text). Actual sample sizes were 106 for the six correlations among  $\text{NH}_4$  availability over time, 93 for correlations involving variables S1–S3, and 98 for all other correlations. Significant correlations are *asterisked*: \* $P < 0.05$ ; \*\* $P < 0.01$ , \*\*\* $P < 0.001$

second sampling period and extractable nitrate concentrations for the same sampling locations.

There are very few papers on how spatial maps of soil attributes in natural ecosystems change within the growing season (Ryel et al. 1996; this study). To compare their results to ours, Ryel et al. (1996) found significant patch structure (at a scale of 2 m or less) for two of the three measurements of soil  $\text{NH}_4^+$  concentrations, and for all three measurements of soil  $\text{NO}_3^-$  concentrations. Although they usually found significant patch structure for soil nitrogen concentrations, the size of these patches varied over time. Thus, in both the present study and in Ryel et al. (1996), spatial maps of soil nitrogen changed greatly over time.

We constructed eight spatial maps of soil nitrogen availability. Of these, only nitrate availability in the second sampling period showed significant patch structure. Although nitrate availability lacked persistent patch structure, initial soil nitrate concentrations were highly correlated with nitrate availability in the second sampling period (Table 2; compare Fig. 1e to Fig. 3f), and the spatial correlograms for these two variables were significant and very similar in shape (compare Fig. 1f to Fig. 4f). Mineralization of soil organic matter (most likely particulate materials) and subsequent nitrification may explain this correlation. Prior to the second sampling period, there was little plant growth (personal observations) and no rainfall was observed at a rain gauge located about 200 m from the middle plot (Fig. 5). After the second sampling period, there was abundant plant growth and frequent rainfall. The re-



**Fig. 5** Amount of precipitation (cm) over time as measured from a rain gauge located 200 m from the middle successional study plot. Rainfall data were collected from 13 March to 14 June 1994. Values on the x-axis represent dates on which the rain gauge was emptied. For the two dates marked with an asterisk, data were missing or not collected; other dates without vertical bars indicate periods without rainfall

sulting combination of increased plant uptake, increased leaching, and increased mineralization probably served to remove the correlation between initial soil nitrate concentration and nitrate availability. In addition, initial soil nitrate concentration and soil nitrate availability in the second sampling period were higher in locations that had drier soil (Table 2); these locations corresponded generally to areas of slightly higher elevation (personal observations). Nitrate might be expected to accumulate in areas of dry soil because of reduced leaching and/or reduced plant uptake. Thus, our data suggest that the location of patches with relatively high levels of soil nitrate may be determined by spatial patterns of soil moisture. Overall, our results suggest that hotspots of nitrate – the dominant form of nitrogen available to plants in dune soils – may appear in predictable locations but at irregular points in time (the timing of which would depend on patterns of rainfall and plant uptake).

All four of the spatial correlograms that were significant overall (Figs. 1b,f, 2b, and 4f) had a comparable shape: they indicate that patches occurred at a scale of  $<4$  m, and that there were negative correlations among patches at larger spatial scales (anywhere from 10 to 16 m, depending on the variable). The tendency to have negative correlations at long distances can be an indication that one or more underlying processes govern the spatial structure of the variables. For the coastal dune ecosystem that we studied, we think such underlying effects would most likely be due to topography, via its effect on soil moisture, or to patterns of plant spacing. The spatial correlograms for both of these variables are consistent with this suggestion, whereas the correlation analyses provide stronger support for soil moisture as a factor of underlying importance (soil nitrogen concentrations were not correlated with plant cover but were correlated with soil water content). We do not, however, dismiss the possible importance of the vegetation: our data lack the fine-scale resolution needed to test for the effects of individual plants, and plants have been shown to affect soil resource heterogeneity in coastal sand dunes (Alpert and Mooney 1996), sagebrush-grass steppes (Ryel et al. 1996), and mixed-grass prairie (Kleb and Wilson 1997). In particular, the nitrogen-fixing plant *C. fasciculata*, which was common throughout the middle plot, could have a large impact on soil nitrogen heterogeneity.

The high level of resource heterogeneity found in dunes can be modified by ecological succession. For example, the ability of plants to stabilize dunes and recycle nutrients suggests that nutrient concentrations in older dunes should be higher and less variable than nutrient concentrations in younger dunes; in early, middle, and late successional dunes, this is exactly the pattern that we found for soil nitrogen concentrations. Highly variable environments – such as those found at our early successional site – have been hypothesized to select for spreading clonal plant species because such plants have the capacity to (1) forage for patches of high nutrient availability (de Kroon and Hutchings 1995),

and/or (2) share resources and hence integrate over highly variable conditions (Evans 1988). As succession proceeds and dunes become structurally more stable with higher and less variable concentrations of resources, we expect selection on the ability of plants to cope with heterogeneous conditions to be reduced and selection on competitive ability to be increased. The observed shift from spreading clonal species in the early successional site to the more competitive bunch grasses found in the late successional site was consistent with this scenario.

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