THE INFLUENCE OF LANDSCAPE POSITION ON TEMPORAL VARIABILITY IN FOUR NORTH AMERICAN ECOSYSTEMS

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Abstract.—The spatial setting of an ecosystem within a landscape influences many of the ecosystem's properties. Here, we ask whether there is a relation between the spatial positioning of different locations in a landscape and the annual variability exhibited at each location. We include data from four biome types represented in the Long-Term Ecological Research (LTER) network: northern Wisconsin lakes, Hubbard Brook Experimental Forest, the Jornada Desert, and the North Inlet estuary. At each LTER site, data on 26–68 ecological parameters have been collected at three to seven locations along an elevational gradient for at least 5 yr. We tested whether at each LTER site the annual variability exhibited by parameters at each location within the landscape was related to the location's relative elevation, that is, landscape position. Specific mechanisms relating spatial positioning to variability differed at the four LTER sites, but at each LTER site, (1) locations differed in the annual variability exhibited by ecological parameters, (2) for at least a subset of the parameters, this variability was related to the locations' spatial positions, and (3) water movement across the landscape was the important underlying factor determining variability patterns. We conclude that landscape position influences the annual variability that ecosystems exhibit.

A basic tenet of landscape ecology (Naveh and Lieberman 1984; Forman and Godron 1986; Turner 1989) is that the spatial position of an ecosystem within the surrounding landscape influences properties of that ecosystem. For example, the presence of a riparian forest can greatly reduce the average nutrient loading to streams draining agricultural land (Peterjohn and Correll 1984). Or, the average concentration of dissolved solids in a lake is a direct function of the lake's hydrologic regime, which, in turn, is determined partly by the lake's relative elevation and the presence or absence of streams (Eilers et al. 1983; Swanson et al. 1988). The mechanisms by which landscapes can influence specific ecosystems are diverse and not always well understood, but there is little doubt that landscape influences are important in governing the average conditions occurring in an ecosystem.

Here, we consider the extent to which the annual variability exhibited by an

ecosystem is also a function of its landscape position. Understanding the factors controlling temporal variability in ecosystems is important for a number of reasons. First, nonequilibrium concepts are often more useful in studying ecosystems than equilibrium constructs (O'Neill et al. 1986; DeAngelis and Waterhouse 1987). Unlike equilibrium models, which emphasize understanding central tendencies of a system, nonequilibrium concepts focus on understanding the constraints on ecosystem behavior, that is, factors affecting the range of variation a particular ecosystem exhibits under natural conditions. It follows, then, that an important characterization of an ecosystem is the relative tightness of the constraints, or how temporally variable the ecosystem is. Another reason it is important to understand the controls of variability is that unusual events can be discerned only when the usual is well described. Given a stress, such as acid precipitation or climate change, we might ask whether an ecosystem has responded or will respond by exhibiting behavior outside its usual range (Watras and Frost 1989). Because characterization of an ecosystem's variability prior to a stress is often unavailable, it is important to develop tools to predict the patterns of variability an ecosystem is likely to exhibit. Finally, to maximize the usefulness of long-term monitoring sites it would be advantageous to locate them at landscape positions within an ecosystem that would minimize annual variability. Identifying low-variability locations requires an understanding of the factors controlling variability.

Temporal variability arises through the interplay between internal dynamics and fluctuations in external driving forces. Landscape position might be expected to be an important determinant of temporal variability because landscape position can affect both the internal and external processes that generate variability. For example, along a mountainous landscape, variation in weather at a single location may be expected to be a function of altitude, aspect, slope, and other topographic features. These differences in the variability of weather may then lead to differences in the variability of ecosystem processes at different locations in the landscape. However, even in landscapes that receive generally the same weather throughout, we may expect landscape position to be a predictor of the magnitude of temporal variability. For example, geologic processes, such as erosion and deposition, may cause landforms to have soil characteristics that vary as a function of landscape position. These differences in soil characteristics may affect biogeochemical processes such as water retention, chemical buffering capacities, and microbial dynamics.

In this article we use data from four contrasting landscapes represented in the Long-Term Ecological Research (LTER) network (Callahan 1984) to test the hypothesis that landscape position is a predictor of temporal variability in ecosystems. The landscapes include the Northern Highland Lake District in northern Wisconsin (Magnuson et al. 1984; Kratz et al. 1986), the Hubbard Brook Experimental Forest in New Hampshire (Likens et al. 1977; Bormann and Likens 1979), the North Inlet estuary in South Carolina (Dame et al. 1986; Blood et al. 1989), and the Jornada Desert in southern New Mexico (Whitford et al. 1986; Wondzell et al. 1987). All these sites share a few common features. First, sampling locations at each site are arranged by elevation, so in all four sites we can rank landscape

position along a gradient of elevation. Second, although the four landscapes differ in area (range, 0.13–40 km^2), each is large enough to include a number of study locations but small enough that each location within the landscape is affected by the same weather. As a result, patterns in annual variation among locations within a site are not due directly to differences in weather. Third, data from at least three locations within each site (range, three to seven) and at least 5 yr at each location are available for a broad suite of ecological parameters.

Our approach is straightforward. For each landscape we test the null hypothesis that there is no relation between landscape position and annual variability of ecological parameters. If such a relation does exist, we then look for similarities and differences in the way landscapes and temporal variability interact among the four diverse landscapes.

METHODS

Data used in this paper were taken from VARNAE, an LTER network data base on variability in North American ecosystems (Magnuson et al. 1991). Prior to inclusion in VARNAE, the data were summarized by personnel at each LTER site so that a single number represented the value for a particular parameter for a particular year in a particular location. Here, we use the term "site" to desig- nate one of the four LTER sites. We use the term "location" to designate a sampling area within an LTER site. As an example, mean chlorophyll *a* concen- tration in Trout Lake, Wisconsin, for 1985 was described by a single number (derived from many measurements), for 1984 by a different number, and so on. From these numbers we calculated the coefficient of among-year variation for each location. We used the coefficient of variation (cv) as our measure of variance because it possesses a number of advantages (Sokal and Rohlf 1981; Kratz et al. 1987). It describes variability relative to the mean condition, so that the common tendency for larger variances to be associated with larger means is counteracted. The coefficient of variation is also unitless, allowing the variability of diverse kinds of parameters to be compared.

THE STUDY SITES AND PARAMETERS

Northern Temperate Lakes

The Northern Temperate Lakes (NTL) field site is located in the Northern Highland Lake District in northern Wisconsin (46°00′N, 89°40′W) (Magnuson and Frost 1982; Magnuson et al. 1984; Kratz et al. 1986). The seven primary study lakes (five clear-water lakes and two bog lakes) lie within an area of about 40 km^2, share the same groundwater flow system, and are arranged along a subtle, but important, elevational gradient (10 m vertical drop in 6 km). We ranked the landscape positions of the five clear-water lakes by elevation. Because the two bog lakes are effectively isolated from the surrounding landscape, we ranked these two lakes as higher in the landscape than the clear-water lakes. We deter- mined the order of the bog lakes by elevation. The results presented here would be largely unchanged had we deleted the bog lakes.

We used data from these seven lakes from 5 yr (1982–1986). A total of 68 parameters were included. Of these parameters, six were climatic, 49 were edaphic, and 13 were biological. Most of the parameters described below were derived from measurements at many depths on each sampling day. To eliminate depth as a variable, we computed volume-weighted averages for each day. The volume-weighted average estimates the value that would be obtained in a grab sample if the water in the lake were completely mixed.

Each of the six climatic parameters was a different measure of water temperature. Water temperature was measured in each lake every 2–3 wk during the ice-free season (May through November) and every 5–6 wk during ice cover. To calculate the six different measures of water temperature we first computed the average water temperature in each calendar month. Then we picked the largest and smallest of these 12 monthly averages. These values were denoted maximum monthly and minimum monthly, and the difference between them was termed delta monthly. The average summer value was the average of May through October; the average winter value was the average of November through April. Finally, the annual average was the average of the 12 monthly values.

Edaphic parameters included dissolved oxygen, nutrients, major anions, and major cations. With one exception, the same six values described previously for water temperature were computed for dissolved oxygen concentration, oxygen saturation, pH, specific conductance, nitrate, ammonia, and dissolved reactive silica. The exception was that the minimum monthly nitrate values were not included because the mean was zero for several lakes and the coefficient of variation could not be calculated. Dissolved oxygen and oxygen saturation were measured at the same frequency as water temperature; pH, specific conductance, nitrate, ammonia, and dissolved reactive silica were measured at the same frequency as water temperature except for 1986, when ice-free season measurements were made every 4 wk. Major anions (SO_4^{2-}, Cl^-, and alkalinity), major cations (Ca^{2+}, Mg^{2+}, K^+, Na^+), and total dissolved phosphorus (TDP) were measured quarterly, and the average of the four quarterly values was used to estimate the annual average.

The biological parameters included chlorophyll and two zooplankton genera, *Chaoborus* and *Leptodora*. Chlorophyll was measured at the same frequency as water temperature. Again using the monthly means, we calculated the following chlorophyll values: annual average, ice-free average, ice-covered average, mean spring (April–May), maximum spring, mean summer (June–September), maximum summer, mean fall (October–November), and maximum fall. The zooplankton values were from vertical tow samples taken at night in August and were expressed as organisms/m^2 and organisms/m^3.

Hubbard Brook Experimental Forest

The Hubbard Brook Experimental Forest (HBEF) is located in the White Mountains of central New Hampshire (43°56′N, 71°45′W). The soils at HBEF are well-drained haplorthods and fragiorthods developed in shallow glacial drift (mean thickness, 60 cm) overlying bedrock (Littleton formation, schist). The depth of the mineral soil is highly variable but generally increases with decreasing

elevation (Lawrence et al. 1986). The reference watershed (W6) from which the data were collected is completely forested, predominantly with northern hardwood species, *Betula alleghaniensis, Fagus grandifolia,* and *Acer saccharum,* at middle and lower elevations, and small stands of *Abies balsamea* and *Picea rubens* at upper elevations. A summary of the distribution of conifers within the watershed is given by Lawrence et al. (1986).
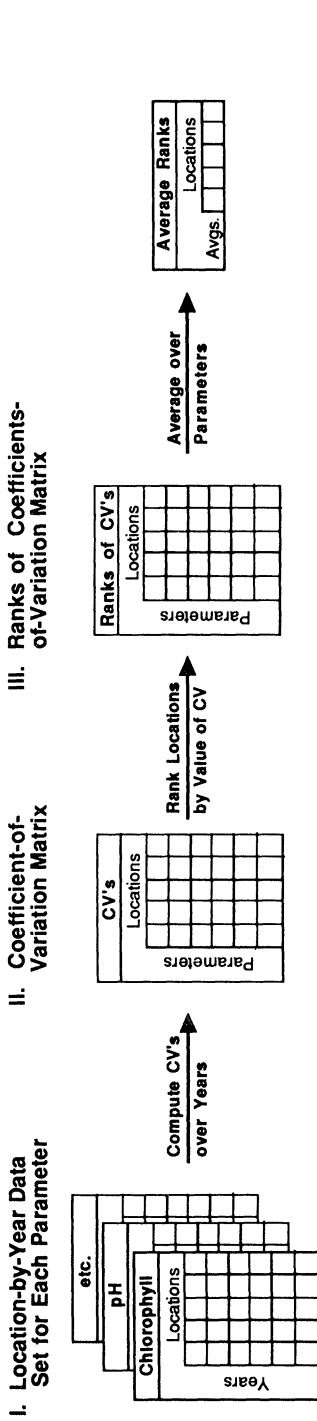
The data used in this study included 44 chemical parameters from samples collected from the major stream in W6 at approximately monthly intervals from June 1982 to May 1987. Samples were collected from six locations along an elevational gradient ranging from 540 to 800 m (Lawrence et al. 1987). Each sample was analyzed according to the analytical methods described by Lawrence et al. (1986). Parameters include pH, base cations (Ca^{2+}, Mg^{2+}, K^+, Na^+), major anions (F^-, Cl^-, SO_4^{2-}, NO_3^-), three forms of aluminum (total Al, total monomeric Al, and nonlabile monomeric Al), silicon, and dissolved organic carbon (DOC). For each of the five hydrologic years (defined as June 1 to May 31), the volume-weighted mean for each parameter was computed for each of the six sampling locations. The minimum and maximum value was also determined for each parameter at each location for each hydrologic year.

North Inlet Estuary

The North Inlet marsh-estuarine-forest system (INLET) is located along the northeast-southwest-oriented Atlantic coastline, 70 km northeast of Charleston, South Carolina (33°30′N, 79°13′W) (Wolaver et al. 1984; Dame et al. 1986; Blood and Vernberg, in press). The North Inlet estuary consists primarily of *Spartina alternaflora* marsh (75%), exposed mud flats (2.5%), and tidal creeks (22%). Water flow and exchanges are dominated by oceanic tidal processes. Freshwater inflow is intermittent and less than 1% of the tidal prism. The three sampling locations are within the 38-km² estuary and lie along an elevational gradient away from the Atlantic Ocean. Situated adjacent to North Inlet, the Town Creek station is the most ocean-dominated location. Clambank is midway between the forest and the ocean. Oyster Landing, which is adjacent to the maritime forest, is the location highest in elevation. We used data from 5 yr (1981–1985). A total of 57 parameters were used, including six climatic, three biological, and 48 edaphic parameters. Samples were collected daily at 10:00 A.M. (EST) at 1 m below the surface. Only one depth was sampled because the North Inlet estuary is a completely mixed system.

The six climatic variables were measures of water temperature and were computed as described for the NTL site. The edaphic parameters included salinity and various fractions of carbon, nitrogen, phosphorus, and suspended sediments. Carbon fractions included dissolved organic and particulate organic (POC). Nitrogen was separated into nitrate/nitrite, ammonia, total nitrogen, total dissolved nitrogen (TDN), and particulate nitrogen. Phosphorus was fractionated into total phosphorus, dissolved phosphorus, particulate phosphorus, and orthophosphate. Suspended sediments were separated into organic, inorganic, and total. The minimum monthly, maximum monthly, yearly average, and delta monthly values described previously for water temperature were calculated for each of the edaphic

COARSE-RESOLUTION ANALYSIS

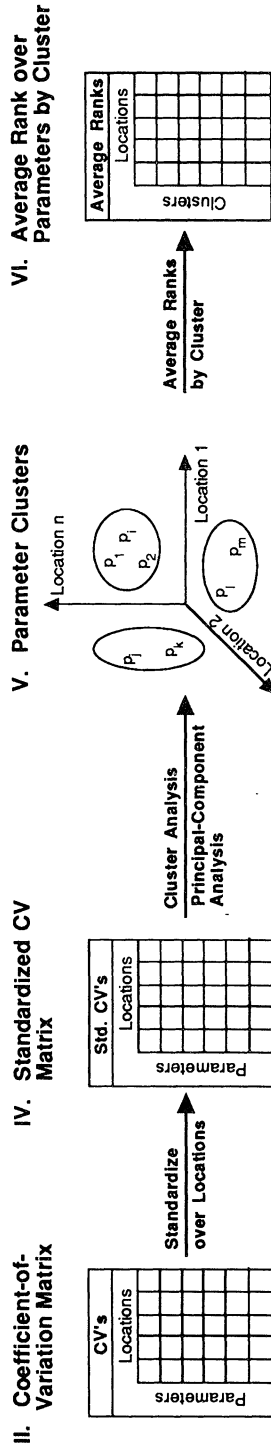**I. Location-by-Year Data Set for Each Parameter**

II. Coefficient-of-Variation Matrix

III. Ranks of Coefficients-of-Variation Matrix

Compute CV's over Years

Rank Locations by Value of CV

Average over Parameters

FINE-RESOLUTION ANALYSIS

II. Coefficient-of-Variation Matrix

IV. Standardized CV Matrix

V. Parameter Clusters

VI. Average Rank over Parameters by Cluster

Standardize over Locations

Cluster Analysis
Principal-Component Analysis

Average Ranks by Cluster

Fig. 1.—Schematic flowchart of data manipulations performed

parameters. The biological parameters were the minimum monthly, maximum monthly, and delta monthly for chlorophyll, calculated as described previously.

Jornada Desert

The Jornada Desert field site (JOR) is located along the northeast aspect of the piedmont slope of Mt. Summerford in the Dona Ana mountains in the northern portion of the Chihuahuan desert in southern New Mexico (32°30′N, 106°45′W) (Wondzell et al. 1987). The landscape is a mosaic of desert grasslands, dominated by the perennial C_4 grass *Bouteloua eriopoda,* and shrub lands. The six locations used in this study are component landforms along a 2.7-km transect running from the base of Mt. Summerford along the piedmont slope to the center of an ephemerally flooded basin or playa. The elevation difference between the top of the transect and the playa is only slightly greater than 100 m. The six component landforms, from highest to lowest in the landscape, are (1) an alluvial fan collar with predominantly perennial grass cover, (2) an erosional fan remnant with predominantly perennial shrub (*Larrea tridentata*) cover, (3) an alluvial fan apron with some *L. tridentata* along drainage channels but with primarily perennial grass, subshrub, and forb cover, (4) a nonburied fan remnant with primarily perennial grass, subshrub, and forb cover, (5) an alluvial plain with vegetation similar to the nonburied fan remnant, and (6) a playa with predominantly perennial grass cover (Wondzell et al. 1987).

Data from 5 yr (1982–1986) on a total of 26 parameters were used. Of these parameters, 10 were climatic, four were edaphic, and 12 were biological. The 10 climatic parameters were all measures of soil water content integrated over various depths and time intervals to reflect water availability at different rooting depths and seasons. These measures provided an ecologically relevant integration of year-to-year variations in timing and amount of precipitation. The edaphic variables were measures of available soil nitrate and ammonia during the two principal growing seasons, spring and summer–fall. Nitrogen has been shown to be the principal limiting nutrient in these ecosystems (Whitford et al. 1987). The biological parameters were all measures of plant cover, species richness, or species diversity measured at the time of peak vegetative standing crop in the spring and summer–fall growing seasons. The cover data were sums for the principal growth-form photosynthetic pathway types at each location (e.g., C_3 perennial forb, C_4 annual forb, etc.). Sampling methods are described by Cornelius and Cunningham (1987).

DATA PRESENTATION

We present results at two levels of resolution (fig. 1). At the coarser level, we did the following calculations for each of the four LTER sites. First, for each parameter, we ordered the locations within a site by cv and assigned a rank of 1 to the location with the lowest cv, 2 to the location with the next lowest cv, and so on. For example, there were 68 parameters measured at each location at the NTL site, resulting in 68 sets of rankings of the locations. Next, for each location, we computed the average of the 68 ranks. Finally, we compared the average

ranks of the locations and, for each site, we looked for correlations between each location's average rank and attributes of the location, such as elevation or soil characteristics.

At the finer level of resolution we identified clusters of parameters at each site that had cv's exhibiting similar patterns across locations. We used multivariate ordination and clustering techniques. Before doing the ordination and clustering we transformed the cv data for each parameter by dividing each cv by the maximum cv for that parameter across locations. This transformation scaled each parameter to a maximum cv of 1, removing differences among parameters due solely to differences in the magnitude of the cv's and allowing us to compare the parameters' relative patterns of variability across locations for each LTER site. For example, consider the cv's arrayed as follows for three parameters across two locations: cv's for the first parameter are 4 and 2 for the two locations, for the second parameter, 0.04 and 0.02, and for the third parameter, 4 and 3. Even though the first and second parameters behave similarly in a relative sense (each has a cv twice as high in the first location as in the second), without the transformation the first and third parameter would be considered the most similar across locations. After the transformation, the first and second would be considered most similar.

To reduce the dimensionality of the data to a workable level we clustered the data into three to five major groups of parameters using principal components analysis (PCA) and average linkage clustering. We performed a PCA on the transformed data and plotted the scores for parameters on the first two principal component axes. To define clusters of parameters objectively, we performed average linkage cluster analysis on the transformed cv data. We were looking for discrete groupings of parameters, particularly for that discrete group whose pattern of variation was related to landscape position.

To interpret the underlying mechanisms for how variability was distributed among locations for each cluster of parameters, we plotted histograms displaying the average cv rank of all parameters in the cluster for each location. The average Spearman rank correlation (r_s) among all pairs of parameters in each cluster was computed as a measure of how similar parameters within a cluster were with respect to the ranking of variability across locations.

RESULTS

At each of the four LTER sites there were significant differences in parameter variability among locations (Friedman's rank test: NTL, $P = .0001$; HBEF, $P = .0004$; INLET, $P = .0001$; JOR, $P = .0222$; these probability values should be taken as indicators rather than exact values, because the assumption of independence of parameters is not strictly met). However, the degree to which patterns in variability correlated with landscape position differed among the LTER sites. At the Northern Temperate Lakes site the average rank of the coefficient of variation decreased monotonically with landscape position (fig. 2A). At Hubbard Brook, the location highest in the landscape was significantly more variable than the other five locations, but the other five locations did not differ among them-
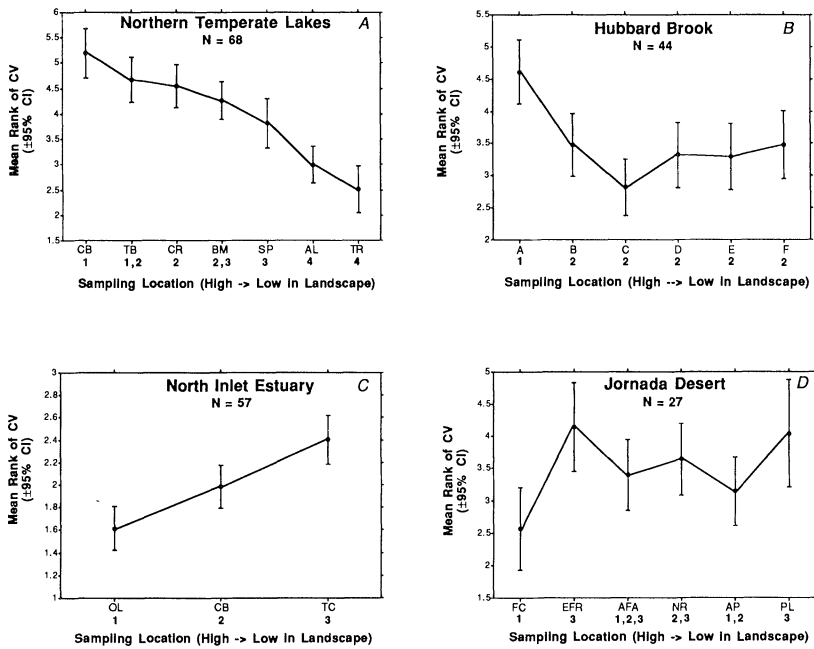
Fig. 2.—Overall average ranks of coefficients of variation by landscape position for the four LTER sites. *A*, North Temperate Lakes. *CB*, Crystal Bog; *TB*, Trout Bog; *CR*, Crystal Lake; *BM*, Big Muskellunge Lake; *SP*, Sparkling Lake; *AL*, Allequash Lake; *TR*, Trout Lake. *B*, Hubbard Brook. *A–F*, Locations 1–6, respectively, in Lawrence et al. (1986). *C*, North Inlet estuary. *OL*, Oyster Landing; *CB*, Clambank; *TC*, Town Creek. *D*, Jornada Desert. *FC*, Alluvial fan collar; *EFR*, erosional fan remnant; *AFA*, alluvial fan apron; *NR*, nonburied fan remnant; *AP*, alluvial plain; *PL*, playa. Larger-numbered ranks indicate larger cv's. Locations having the same number below the identification are not significantly different ($P > .05$, Fischer's least significant difference).

selves (fig. 2*B*). North Inlet, in contrast to the trend seen strongly at Northern Temperate Lakes and weakly at Hubbard Brook, showed an increase in variability at locations lower in the landscape (fig. 2*C*). Finally, although variability patterns at Jornada showed little relation to elevational gradients, certain locations did differ from each other in among-year variability (fig. 2*D*). For example, the erosional fan remnant and the playa were significantly more variable than the fan collar or the alluvial plain (Fischer's least significant difference, $P < .05$, again assuming independence of parameters).

At the Northern Temperate Lakes site, principal component analysis and average linkage clustering identified four major clusters of parameters (fig. 3; table 1). These four clusters contained 63 of the 68 parameters. The other five parameters occurred as two single-parameter clusters and a cluster of three parameters.

One of the four clusters contained parameters whose cv's were correlated with the lakes' landscape positions (fig. 4, cluster 1). Lakes relatively high in the landscape had higher cv's than those lower in the landscape. It was interesting

TABLE 1

PARAMETERS IN THE MAJOR CLUSTERS AT THE FOUR LTER SITES

Cluster	Northern Temperate Lakes	Hubbard Brook	North Inlet	Jornada
1	Maximum NO_3, delta NO_3, winter NO_3, maximum pH, annual pH, winter pH, minimum pH, winter conductance, summer conductance, maximum conductance, annual conductance, summer SiO_2, minimum SiO_2, winter SiO_2, annual SiO_2, maximum SiO_2, annual SO_4, annual Ca, annual Na, annual Mg	Mean base cations, minimum base cations, mean Ca, maximum Ca, minimum Ca, mean Mg, mean K, minimum K, mean Na, mean Si, maximum Si, maximum DOC, minimum DOC, mean pH, minimum monomeric Al, minimum nonlabile monomeric Al	Maximum chlorophyll, minimum chlorophyll, delta chlorophyll, annual PO_4, annual particulate P, maximum particulate P, delta particulate P, annual TDP, minimum TDP, maximum total P, annual particulate N, annual NO_3-NO_2, annual POC, maximum POC, delta salinity, annual total sediments	Summer water 0–45 cm, summer water 45–75 cm, summer water 75–100 cm, winter water 0–45 cm, winter water 45–75 cm, winter water 75–100 cm, spring soil moisture, summer–fall NH_4, spring C_3 annuals, diversity of spring annuals, C_3 perennial forbs, C_4 perennial forbs, C_4 perennial grass, subshrubs, shrubs
2	Annual Cl, annual chlorophyll, mean open-water chlorophyll, mean spring chlorophyll, maximum spring chlorophyll, mean summer chlorophyll, maximum summer chlorophyll, mean fall chlorophyll, maximum fall chlorophyll, annual TDP, *Leptodora* (per m²), *Leptodora* (per m³), delta O_2 saturation	Mean total Al, maximum total Al, mean nonlabile monomeric Al, mean monomeric Al, mean SO_4, maximum SO_4, minimum SO_4, mean Cl, maximum Cl, minimum F, minimum Si, mean NO_3, maximum NO_3, mean DOC	Winter water temperature, minimum PO_4, minimum particulate P, maximum NO_3-NO_2, minimum NO_3-NO_2, delta NO_3-NO_2, maximum total N, delta total N, delta TDN	Spring water 0–45 cm, spring water 45–75 cm, spring water 75–100 cm

364

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3	Annual O$_2$ concentration, summer O$_2$ concentration, winter O$_2$ concentration, minimum O$_2$ concentration, annual O$_2$ saturation, summer O$_2$ saturation, winter O$_2$ saturation, minimum O$_2$ saturation, delta pH	Maximum monomeric Al, maximum nonlabile monomeric Al, minimum pH, minimum Mg, minimum Na	Maximum water temperature, minimum water temperature, delta water temperature, maximum PO$_4$, delta PO$_4$, maximum TDP, annual total P, annual NH$_4$, annual TDN, maximum TDN, minimum TDN, annual total N, annual DOC, maximum DOC, minimum DOC, delta DOC, maximum POC, maximum salinity, annual organic sediment, annual inorganic sediment	Summer–fall soil moisture, spring NO$_3$, diversity of summer annuals, fall C$_4$ annual forbs, fall C$_4$ annual grass
4	Annual water temperature, summer water temperature, winter water temperature, maximum water temperature, delta water temperature, ice-covered chlorophyll, Chaoborus (per m^3), annual NH$_4$, summer NH$_4$, winter NH$_4$, minimum conductance, delta conductance, delta SiO$_2$, annual NO$_3$, summer pH, annual K, maximum O$_2$ concentration, delta O$_2$ concentration, maximum O$_2$ saturation	Maximum Cl, minimum Cl, maximum K, maximum Na	Annual water temperature, delta TDP, minimum total P, delta NH$_4$, delta DOC, annual salinity, minimum salinity	
5		Maximum base cations, maximum Mg, maximum pH, minimum total Al	Delta total P, maximum NH$_4$, minimum NH$_4$, minimum total N, minimum POC	
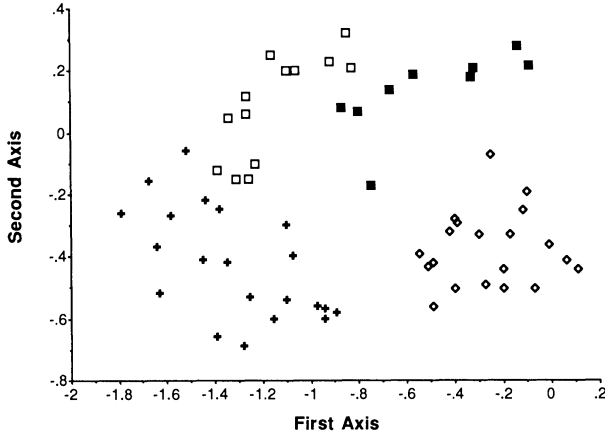
Fig. 3.—Principal components analysis for NTL. *Diamonds,* cluster 1; *open squares,* cluster 2; *closed squares,* cluster 3; *plus signs,* cluster 4.
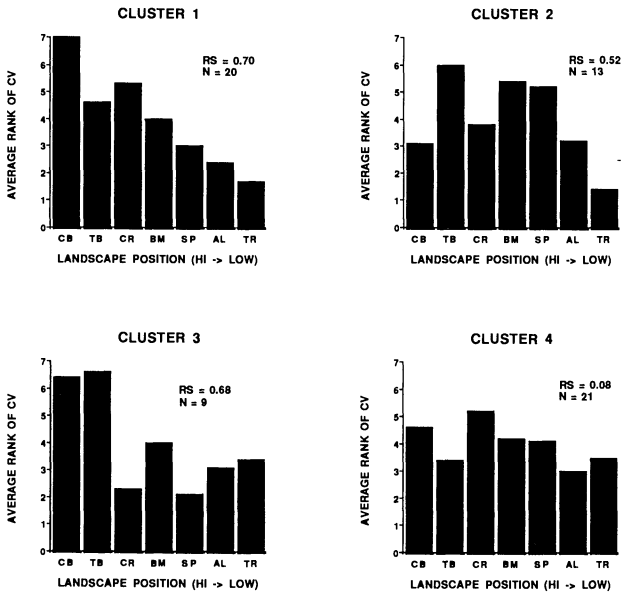

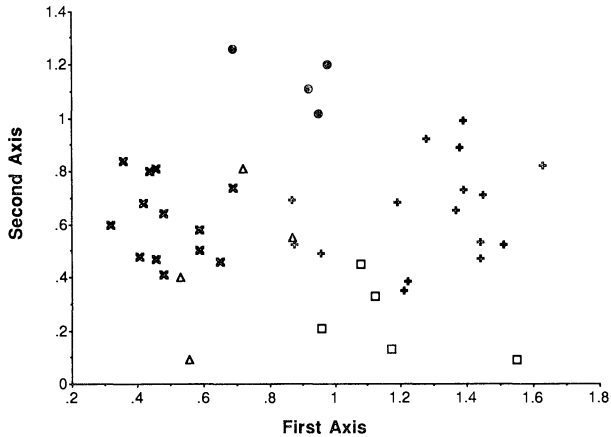Fig. 4.—Average ranks of the coefficients of variation for parameters at each location at NTL.

Fig. 5.—Principal components analysis for HBEF. *Plus signs,* cluster 1; *crosses,* cluster 2; *open squares,* cluster 3; *closed circles,* cluster 4; *diamonds,* cluster 5.

that all of the 20 parameters in this group were edaphic, including measures of SiO_2, conductance, pH, and base cations. The average rank-correlation coefficient, r_s, was 0.70, indicating that the ranking of lakes by cv was similar for parameters in this cluster.

In contrast, the other three clusters did not show a relation between the average rank of cv's and the lakes' landscape positions (fig. 4). Cluster 2 included 13 parameters, 10 of which were biological. Cluster 3 contained nine parameters, all but one of which were measures of dissolved oxygen. Parameters in cluster 3 distinguished the two dystrophic lakes (CB and TB) from the clear-water lakes. Cluster 4 contained 21 parameters and included those parameters whose cv's were nearly the same across the seven lakes. The equitable distribution of cv's in this group is reflected in the low value, 0.08, obtained for r_s. This cluster contained five of the six climatic parameters included in the data set for this site.

At Hubbard Brook, 29 of the 44 parameters occurred in two clusters (figs. 5, 6; table 1). The other 15 parameters were distributed among three clusters containing five, four, and four parameters and two single-point clusters. The largest cluster, cluster 1, had low cohesion ($r_s = 0.17$) and appeared to contain parameters with an equitable distribution of variation across locations. The parameters found in cluster 1 included the mean values for each of the base cations. The variabilities of the 13 parameters in cluster 2 were related to landscape position, with high variability associated with locations high in the landscape. The parameters found in cluster 2 included the mean values for all three Al parameters, DOC, and SO_4^{2-}. Parameters in cluster 3 included measures of water temperature and exhibited low cohesion ($r_s = 0.34$). Parameters in cluster 4 and, to a lesser extent, cluster 5 tended to have higher variability at locations high in the landscape. Parameters in these clusters contained maximum values for base cations.

We identified five major clusters of parameters in the North Inlet data set (fig. 7; table 1). There was one single-point cluster. The first and second cluster together
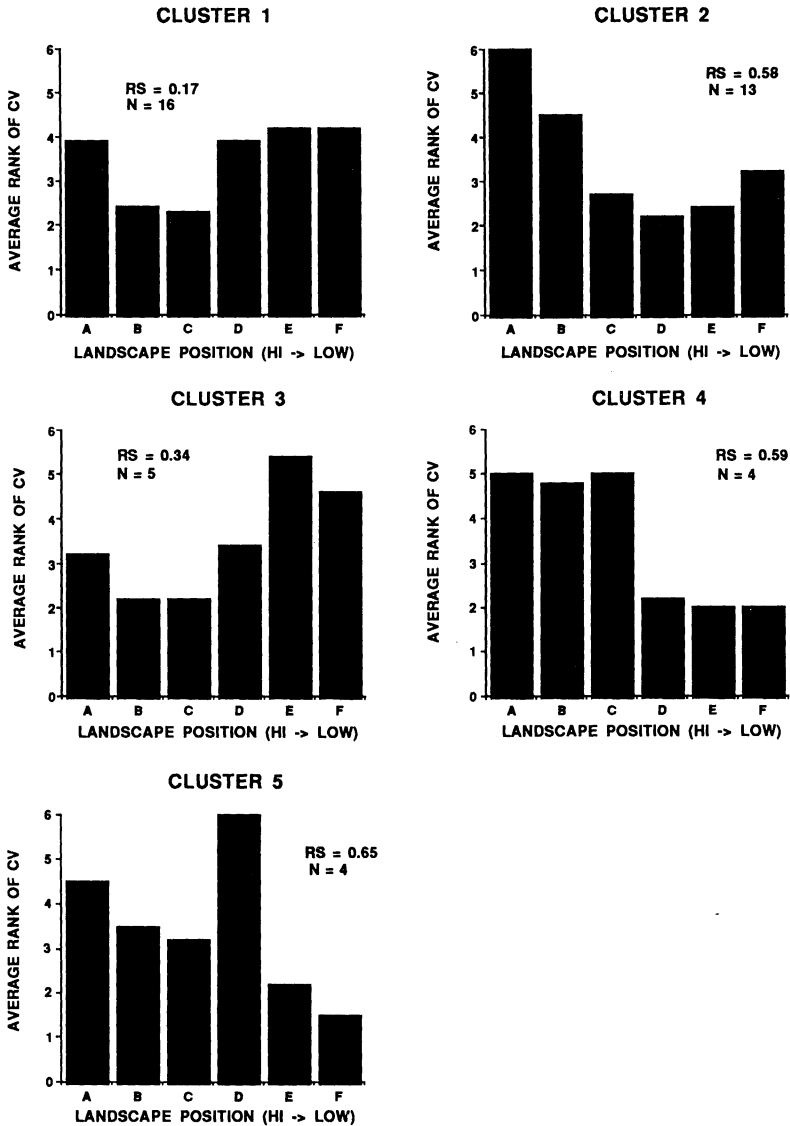
Fig. 6.—Average ranks of the coefficients of variation for parameters at each location at HBEF.

contained 25 parameters and were correlated with landscape position (fig. 8). For parameters in these two clusters, variability was higher in locations lower in elevation and closer to the ocean. These two clusters included all four nitrate/nitrite parameters, all four particulate phosphorus parameters, and all three chlorophyll parameters (table 1). The third cluster contained those parameters with an equitable distribution of cv's across the three locations ($r_s = 0.13$) and included three temperature, three dissolved organic carbon, and three total filtered nitrogen (primarily dissolved organic nitrogen) parameters. The fourth cluster, which
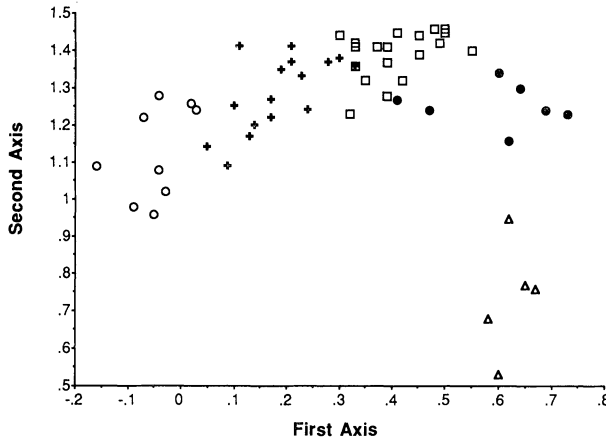
FIG. 7.—Principal components analysis for INLET. *Plus signs,* cluster 1; *open circles,* cluster 2; *open squares,* cluster 3; *closed circles,* cluster 4; *diamonds,* cluster 5.

had the highest cv's at the middle station, included three delta parameters and two salinity parameters. The fifth cluster, which had the largest cv's at the location highest in the landscape, contained the maximum and minimum ammonia parameters.

Three clusters of parameters, containing 23 of the 27 parameters, were identified in the Jornada data set (fig. 9; table 1). The other four parameters occurred as single-point clusters. The first cluster contained 15 parameters and included those parameters that tended to have equitable distributions of cv's ($r_s = 0.05$) across different locations in the landscape (fig. 10). In contrast, clusters 2 and 3 had high r_s values (0.84 and 0.85, respectively), which indicated that, within these clusters, parameters exhibit similar rankings of variability across locations. However, the patterns of variability were quite different between these two clusters.

Cluster 2 was composed of the three parameters measuring soil moisture storage during the winter–spring growing season over three depth intervals (0–45, 45–75, and 75–100 cm). Higher variability of these parameters is observed on the fan collar and playa landform elements. The five parameters in the third cluster showed relatively high variability again in the playa, but also in the erosional fan remnant.

DISCUSSION

We divide this section into two parts: a discussion of mechanism and a discussion of context. In the first part, we explore the site-specific mechanisms that might lead to the patterns of variability seen at each of the four sites. In the second part, we compare patterns at the four sites and look for generalities.

Site-specific Mechanisms

Northern Temperate Lakes.—The clusters of parameters identified for NTL suggest that there are different mechanisms controlling annual variability in differ-
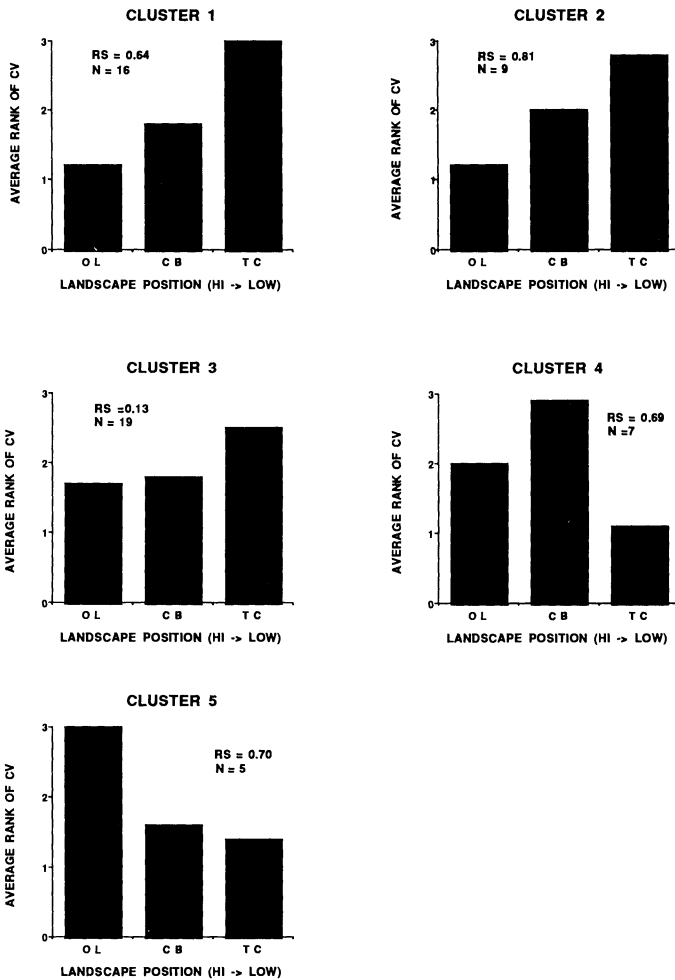
Fig. 8.—Average ranks of the coefficients of variation for parameters at each location at INLET.

ent groups of lake parameters. Landscape interactions are most likely to influence hydrologic and chemical inputs to lakes and would therefore be most likely to affect variability of edaphic parameters. Indeed, the group of parameters whose variability was most closely related to landscape position was composed primarily of chemical parameters that are strongly influenced by groundwater inputs to lakes. Lakes low in the watershed tend to receive a higher percentage of their water input from groundwater than lakes higher in the landscape. Yet, because groundwater has a much higher concentration of solutes than precipitation, groundwater is a major source of many chemical constituents even in lakes high in the landscape (Hurley et al. 1985; Kenoyer and Anderson 1989). If the amount of groundwater flow is decreased by a fixed amount in all lakes in a given year,
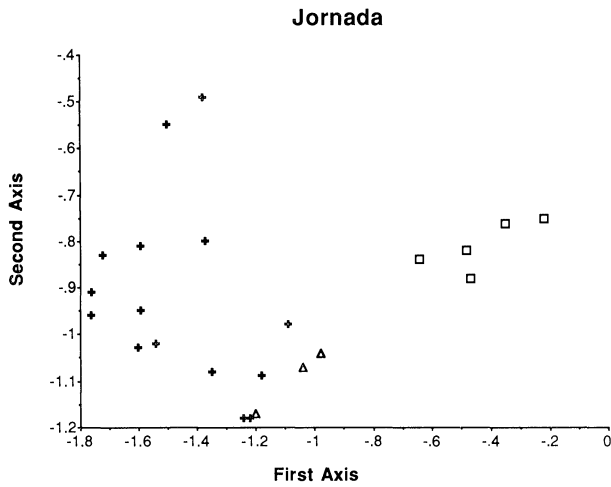
FIG. 9.—Principal components analysis for JOR. *Plus signs*, cluster 1; *diamonds*, cluster 2; *open squares*, cluster 3.
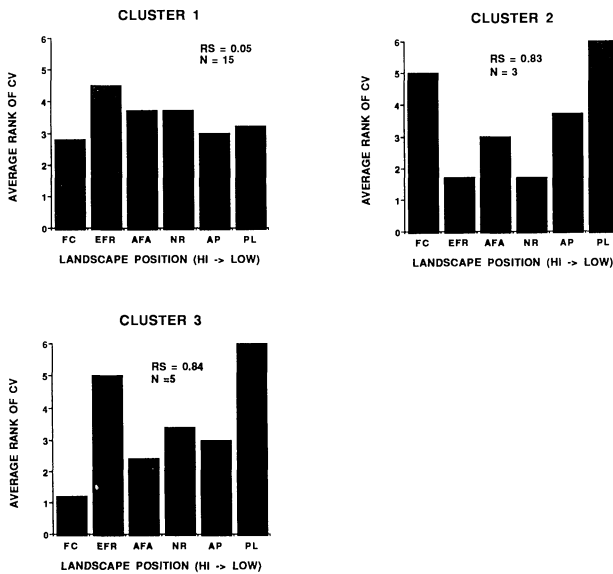

FIG. 10.—Average ranks of the coefficients of variation for parameters at each location at JOR.

it may completely remove any input of groundwater (and corresponding solutes) from lakes high in the watershed but may only reduce by a small amount the loading in lakes lower in the watershed. This difference in groundwater input would cause lakes higher in the landscape to exhibit more temporal variability than lakes lower in the landscape. Another contributing factor to differences in temporal variability may be that lakes lower in the landscape tend to receive their allochthonous inputs from a larger area (because of larger groundwatersheds). This result is consistent with hierarchy theory, which predicts that integration over larger areas damps temporal variability (Allen and Starr 1982; O'Neill et al. 1986).

In contrast to edaphic parameters, biological parameters are influenced more strongly by processes internal to the lake, such as competition and predation, than by landscape interactions. These internal processes may confound any influence landscape position has on biological variability.

The discrimination between bog and clear-water lakes in the variability pattern of oxygen-related parameters is likely due to the lakes' detritus content and morphometry. Bog lakes are small and quickly become oxygen depleted. Variation in the duration of mixing periods in the spring and fall, when oxygen is replenished in deeper waters, can be large and may cause the higher variability observed for these parameters in the bog lakes.

Hubbard Brook Experimental Forest.—Regulation of stream chemistry in W6 at the HBEF appears to be influenced by changes in soil flow paths and variations in source areas (Lawrence et al. 1988). The higher elevations of W6 can be considered a variable source area (Hewlett and Hibbert 1967; Dunne and Black 1970). During conditions of subsurface saturation, continued influx of water causes the depth of soil saturation to move upward into the surface horizons of the soil profile. The lack of a deep mineral soil at upper elevations results in rapid saturation of subsurface horizons and water movement laterally through the upper surface horizons. Water moving laterally does not contact the B horizons before emerging as streamflow. Therefore, during high-flow conditions, the majority of water reaching the stream channel has had little or no contact with the lower soil profile. In contrast, water moving during low-flow conditions (base flow) has had a longer contact time with the lower soil profile prior to reaching the stream channel. Therefore, stream chemistry during low-flow conditions tends to reflect the soil solution chemistry of the lower mineral soil, whereas high-flow stream chemistry tends to be a mixture of upper- and lower-horizon soil solutions (Chen et al. 1984).

The shallow mineral soil at higher elevations in W6 is conducive to producing lateral flow through the upper soil horizons. In contrast, the thicker mineral soil at lower elevations produces greater quantities of base flow. As a result, a greater proportion of the stream waters draining upper elevations results from lateral flow of waters through upper soil horizons, whereas, at lower elevations, waters have generally been in contact with the B horizon before entering the stream. Therefore, for chemical parameters strongly influenced by processes occurring in the B horizon, mean concentrations will be highly dependent on hydrologic conditions that are highly variable, especially in upper elevations. As a result,

concentrations tend to be less variable at low-elevation locations than at high-elevation locations for those parameters that are strongly buffered by processes in the B horizon.

The parameters most strongly influenced by reactions in the B horizon are Al (Dahlgren et al. 1989), SO_4^{2-} (Fuller et al. 1985), and DOC (McDowell and Wood 1984). These parameters all occurred in cluster 2 and showed the greatest variability with respect to landscape position. Mean concentrations for these parameters are all strongly buffered by processes occurring in the B horizon of the soil (mineral precipitation/dissolution, surface adsorption). In contrast, parameters such as base cation concentration are influenced by cation exchange reactions occurring in both the surface and B horizons. The mean concentrations of the base cations were all included in cluster 1, and this cluster did not show differences in variability as a function of landscape position. The distinction between clusters 1 and 2 appeared to be related to the soil horizons that most strongly influence solution concentrations of the particular solute. Whether the solutions pass through the B horizon before emerging as stream water is a function of the hydrologic properties of the watershed, which have been shown to be variable and related to elevation within W6 (Lawrence et al. 1988).

There was also a strong tendency for mean values to fall in different clusters than maximum and minimum values. These differences suggest that the processes regulating mean concentrations of base cations are different from those regulating maximum and minimum values. Hydrology may also be an important factor influencing minimum and maximum values through the dilution of solutes during high flow and the flushing of high concentrations of solutes following periods of low flow (Lawrence et al. 1988). During snowmelt, ions fractionate into the first meltwaters, giving rise to concentrated, often acidic solutions (the so-called acid flush). These pulses of acid may similarly be responsible for producing the maximum and minimum values of certain parameters.

North Inlet estuary.—The chemistry and biology of the estuary are highly dependent on the source, movement, and mixing of water. The observed variability patterns reflect the fact that the three locations fall along a gradient of ocean versus upland influence in water flow. The location closest to the ocean is influenced by among-year variation in the composition of ocean waters immediately offshore. Sources of among-year variance in ocean waters include variation in currents, winds, and sea level. The middle location is influenced by the ocean, but also by inputs from a mesohaline bay (Winyah Bay) to the southwest. The location highest in the landscape (farthest from the ocean) is influenced by variation in upland runoff. Because freshwater inflow represents less than 1% of the total water volume exchanged by tides, locations lower in the landscape are buffered from the effects of variation in upland runoff.

Parameters in clusters 1 and 2 showed higher variation at locations lower in the landscape, which suggests that these parameters are highly influenced by interannual variation in ocean processes. These clusters included all three chlorophyll parameters, many particulate parameters (directly correlated with chlorophyll in the estuary), and all four nitrate/nitrite parameters (also related to chlorophyll). The highest total phytoplankton biomass (measured as chlorophyll *a*)

occurs in the North Inlet plume (slightly offshore from the tidal inlet to Town Creek; Zeeman 1982), and exchanges with the coastal ocean indicate a net phytoplankton import to North Inlet from this source (Dame et al. 1986).

In contrast, parameters in cluster 4 showed higher variation at the middle location. Parameters in this cluster are influenced by intrusions of higher-nutrient, low-salinity water from the mesohaline Winyah Bay. Approximately 20% of the water exchanged in North Inlet is through two creeks connecting North Inlet and Winyah Bay. These intrusions are episodic, being driven primarily by winds from the southwest. The occurrence of these winds is highly variable, ranging between 82 and 180 d/yr.

Parameters in cluster 5 were most variable at the highest position in the landscape and were influenced by variation in freshwater inflow. For example, maximum and minimum ammonia are in this cluster. Fresh water draining the uplands has ammonia concentrations 10 to 100 times that of estuarine surface waters. But freshwater stream inflow is intermittent, ranging from 5 to 12 mo/yr, leading to high variability of parameters at the highest location. Parameters in cluster 3 had an equitable distribution of variability across locations and are controlled by processes occurring within the estuary. For example, studies focusing on exchanges of tidal creek water with the *Spartina* marsh indicate that the marsh surface is a major source of dissolved organic nitrogen and dissolved organic carbon in the tidal creeks (Wolaver and Spurrier 1988; Whiting et al. 1989). The relative homogeneity of the marsh surface accounts for the lack of among-location differences in the temporal variability of these parameters.

Jornada Desert.—Although variability patterns among locations at Jornada did not show a simple pattern that could be related directly to the moderate elevational gradient, the variability pattern observed can be related to landscape processes. The landform elements can be ranked along a gradient of decreasing potential for generating runoff and increasing potential for accumulating runon from rain storms. The erosional fan remnant, because of relatively steep slopes and low vegetative cover, has the highest potential for runoff. Runoff potential decreases sharply at the transition from the erosional fan remnant to the alluvial fan apron and, because of decreasing slope and increasing vegetation cover, decreases slightly moving downslope through the alluvial fan apron, nonburied fan remnant, and alluvial plain. Another sharp decrease in runoff potential occurs at the transition from the alluvial plain to the playa. The playa has no potential for runoff and the highest potential for runon. The alluvial fan collar at the base of the mountain and the top of the piedmont slope receives considerable runon from the mountain slope, and, even though slopes are relatively steep, the alluvial fan collar generates little or no runoff, because soils are deep, sandy gravels and perennial grass cover is high. The alluvial fan collar's position in the runoff-runon gradient is thus intermediate between the playa and the alluvial plain and probably somewhat closer to the playa (Wondzell et al. 1987).

Among-year variability was highest for the landform elements at the two ends of this runoff-runon gradient. For example, soil moisture parameters were more variable on the fan collar and playa, locations having high runon and low runoff potential (Wondzell et al. 1987). Because these landforms tend to accumulate

rather than transport or generate runoff, soil moisture storage was high relative to the transect as a whole during years with high-intensity rain events that resulted in runoff. Thus, the high year-to-year variation reflects year-to-year variation in rainfall amounts and storm intensities. The high runoff from the erosional fan remnant and high runon to the playa accentuate among-year variations in rainfall, with the erosional fan remnant retaining less and the playa more water than the mean for the landscape as a whole in years of higher intensity and duration of rainfall. These high potentials for runon and runoff were reflected in the high variability of soil moisture storage during the summer–fall growing season in these landscape positions. As a consequence of this variability in soil moisture during the summer–fall growing season, both the fall C_4 annual grass and C_4 annual forb covers were also most variable, as were their species diversities. The greater variability in fall annual cover and presumably production was the likely cause of the greater variability in soil nitrate in the subsequent spring growing seasons. In addition, during such years, the erosional fan remnant will be a net source and the playa a net sink for nutrients transported with the water moving downslope in sheet flow.

The low among-year variation of parameters in cluster 3 on the alluvial fan collar probably results from a high cover of the original perennial grasses, perhaps owing to reception of runon from the mountain slope and deep, highly permeable soils. Most of the differences in among-year variation observed at Jornada were due to annual plant species. The high perennial grass cover precludes a significant annual component on the alluvial fan collar and thus apparently reduces among-year variation.

General Discussion

There are three important limitations on the scope of this article. First, all four of the landscapes we considered have an important, but not necessarily steep, elevational gradient associated with them. It is an open question whether the general patterns we discuss below are relevant to landscapes lacking an important elevational gradient. Second, the patterns of variability we observed may be only a subset of the possible patterns. We were restricted to the subset of parameters each site chose to measure. Had other parameters been included, other patterns might have been observed. Finally, we restricted our attention to a temporal scale with a grain of years and an extent of 5 yr. Observations made at different grains or extents may or may not follow the same patterns we observed.

Although the specific mechanisms determining patterns of annual variability at each of the four landscapes differed substantially, three general patterns emerged. First, at each of the four sites, individual locations in the landscape differed from one another in the annual variability exhibited by the parameters at each site. Second, at each of the sites, the variability patterns of at least a subset of the parameters were associated with particular landscape processes at that site, demonstrating that landscapes influence temporal dynamics of ecosystems in potentially predictable ways. Finally, water movement was the most important factor determining the variability patterns associated with the landscape position at each of the four sites. The relative amount of groundwater inputs to different lakes at

NTL was correlated with both the landscape position and the annual variability of edaphic parameters at NTL. At HBEF differential water movement through various soil horizons was associated with patterns of variability. At INLET the gradient from upland- to ocean-derived water determined the landscape-level patterns of variability. Finally, at JOR variability patterns were correlated with areas of erosion and deposition by water movement.

We had expected that, because water moves downhill, variability would be correlated in a simple way with the vertical position in the landscape (e.g., the pattern seen at NTL). But the data from INLET and JOR show that this simple conceptual model is not appropriate. Rather, the model requires a consideration of how a particular site responds to water movement. Although the manifestations of water movement were different at the four sites, the context for understanding variability was the same. If we understand variability in water movement and understand how water movement acts in a particular system, we can understand, in principle, which parameters in which parts of a landscape will be more variable than others (at least in the subset of landscapes where ordering by elevation is appropriate).

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