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# Determination of ecological scale

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## Abstract

We suggest that ecological processes and physical characteristics possess an inherent scale at which the processes or characteristics occur over the landscape. We propose a conceptual spatial response model that describes the nature of this ecological scale. Based on the proposed spatial model, we suggest methods for estimating the size of study plots or transects and the distance between replicate plots needed to approach statistical independence. Using data on percent cover for *Agropyron spicatum,* a common arid-land bunchgrass, we demonstrated four relationships that should hold if the spatial response model is appropriate. These relationships are sample variance increases as functions of (1) transect segment length and (2) intersegment length (transect segment dispersal), and correlation decreases as functions of (3) intersegment length and (4) transect segment length. Based on evaluation of these four relationships, cover for *A. spicatum* is correlated over the landscape on a scale of 400 to 700 m, and a segment length of 64 to 128 m is most appropriate for measuring cover for this species.

## Introduction

Early interest in ecological scale was oriented toward determining the appropriate sampling unit size for studying ecological phenomena, particularly those of plants. Species-area curves generated by counting the number of species on increasingly larger plots ‘offered one method (Cain 1943; Cain and Castro 1959; Greig-Smith 1964). This approach emphasized species composition and the inclusion of most of the representative species in the sampling unit. Another method, oriented toward minimizing variance, entailed estimating variances of plant parameters for various plot sizes and choosing the plot size with the minimum acceptable variance (Greig-Smith 1964; Daubenmire 1968; Mueller-Dombois and Ellenberg 1974). This approach has been used frequently to describe pattern in vegetation (Kershaw 1957; Greig-Smith 1961; Usher 1969; Hill 1973; Errington 1973). Other less objective approaches include those of Mueller-Dombois and Ellenberg (1974), who provided ranges of minimal plot-size area for temperate zone vegetation, and of Green (1979), who suggested some rules of thumb regarding minimum plot size based on size and/or mobility of the organisms of interest. These approaches imply that a natural scale exists in ecological phenomena, and that selection of sampling unit sizes approximating that scale will yield the most information about the phenomena.

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More recently, the question of scale in ecological processes has been addressed directly. Morris (1984, 1987) accepts the concept of scale as an inherent attribute of ecological processes and advocates the use of biological attributes of organisms to '... define the organisms' perception of scale' (Morris 1987). Dayton and Tegner (1984) also imply that ecological processes have characteristic scales, both spatially and temporally. In contrast, Allen and Starr (1982) assert that scale in ecological processes is not an inherent attribute of the process, but an artifact of the levels of resolution used to measure the process. Despite the opposing views regarding the nature of ecological scale, both Morris (1987) and Allen and Starr (1982) advocate the study of different ecological communities in order to most clearly define the ecological processes of interest. The concept of inherent and multiple ecological scales has been emphasized in recent studies of avian community dynamics (Maurer 1985), small mammal habitat selection (Morris 1987), herb community associations (Maguire 1985), and kelp forest dynamics (Dayton and Tegner 1984).

We agree with Morris (1987) and others that there are inherent scales in ecological processes. A fundamental principle of ecology is that processes and physical characteristics resulting from those processes are interrelated. We suggest that the strength of those interrelationships can define inherent scales of ecological processes and therefore the most appropriate levels of resolution for further study of the processes. Further, we suggest that the strength of interrelationships, and therefore the inherent scale of ecological processes, can be determined using estimates of spatial variance and correlation. This paper describes a study of the use of variance and spatial correlation estimates for defining ecological scale and determining appropriate levels of resolution for measuring plant distribution and thus, indirectly, the processes that have caused the observed distribution. Thus, this study could be considered in the wider context of landscape ecology (Urban et *al.* 1987).

## Spatial response model

The varying nature and hierarchial complexity of spatial patterns usually precludes data summarization with a few simple metrics. Rather, the dimensionality of spatial patterns usually requires data summaries by one or more graphs. Proper selection of graphical representation depends on underlying assumptions concerning the mechanisms that generated the patterns. We proposed a conceptual model for spatial pattern based on the assumptions of a mosaic of overlapping environmental factors and used this mechanism to predict various data relationships (*i.e.,* deduction) that should exist if the underlying mechanism is correct. Subsequent data presentations and analyses (*i.e.,* induction) are then used to either refute or modify this conceptual model concerning spatial patterns and the scale of ecological processes.

The spatial model we investigated begins with the assertion that plant cover depends on specific local habitat conditions. Further, the particular habitat at a point in the landscape is assumed to be a consequence of a series of concurrent, overlapping environmental factors (Fig. 1). For example, soil texture, nutrient availability, moisture, topography, and slope aspect all contribute to the plant cover. Each of these, as well as other environmental components, may vary either systematically or randomly across the landscape. The scale of this spatial variation also differs between the relevant environmental factors influencing plant density. For example, the spatial scale for soil texture may be smaller than that for soil moisture, or vice versa.

Based on this spatial model of habitat distribution and juxtaposition, we assume that the resultant plant cover is a random expression of the cover potential provided by these overlapping environmental conditions. The basis for this model comes from a variance structure describing animal abundance examined by Skalski and Robson (in press). Adapting their findings to our model of overlapping ecological processes, we suggest that sample plots become more similar (e.g., identically distributed) the closer they are together and exhibit local chance variation of the Poisson type. Skalski and Robson show that this type of spatial variation can arise from a mixture of Poisson and gamma densities which, for special case, generate a negative binomial distribution, a common model for spatial pattern (Elliott 1971). In essence, our model assumes that plant cover associated with a given plot is a Poisson chance variable with some parameter unique to that plot ($\lambda_i$, for example). Among plots, the Poisson parameters vary according to a gamma frequency distribution. Under this model, the plant cover from plots close together will behave analogous to independent, identically distributed, Poisson random variables. Thus, adjacent plots share the same Poisson mean density parameter, and. exhibit Poisson variation between plots. In turn, distant samples are expected to have differences in the density parameters and exhibit between-sample variation in excess of the Poisson variability.

This model, when used to describe the spatial distribution of plant cover, has implications in density measurements as a function of both plot size or transect segment length (TSL) and plot dispersion or intersegment distance (ISD) across the landscape. Specific consequences of the hypothesized model are discussed in subsequent sections using line-intercept transect data.

## Sample variance as a function of segment length

The consequence of assuming local Poisson variability is that plant cover is independently and identically distributed for sufficiently small adjacent transect segments. An increase in the size of TSL can, therefore, be viewed as a sum of adjacent transect segments. Reported percent cover (C) for TSL equal to T (i.e., composed of T unit lengths, for example, 1 m) is then simply a mean of T independent random variables with variance

$$\mathrm{Var}\ (C,) = \frac{\sigma_C^2}{T} \quad (1)$$

where $\sigma_C^2$ = variance of plant cover based on transect segments of unit size.

As TSL increases sufficiently in size, Poisson variation is supplemented with variation in habitat conditions, and sample variance no longer strictly follows Equation 1. Rather, the simple model of independent, identically distributed Poisson variables breaks down, and the variance and covariance between the gamma distributed Poisson parameters from adjacent transect segments inflate the overall variance in plant cover. Thus, the variance of the percent cover becomes

$$\mathrm{Var}\ \frac{\sum_{i=1}^{T} X_i}{T} = \frac{\sum_{i=1}^{T} \mathrm{Var}\ (X_i) + 2 \sum_{i<j} \mathrm{Cov}\ (X_i, X_j)}{T^2} \quad (2)$$

where $X_i$ = plant cover on the ith transect unit ($i = 1, 2, \ldots . T$).

In order to evaluate the magnitude of the above variance, the variance and covariance elements in Equation 2 must be further defined as functions of the gamma distributed Poisson parameters. We can minimize the complexity of this mixture of distributions by using the special case where all of the $\lambda_i$'s have the same mean ($\mu_\lambda$) and variance ($\sigma_\lambda^2$) (thus, in the independent case, generating a negative binomial distribution). Under this constraint, local heterogeneity is preserved, but all trends are removed from the model landscape. Equation 2 then becomes

$$\mathrm{Var}\ \frac{\sum_{i=1}^{T} X_i}{T} = \frac{(\mu_\lambda + \sigma_\lambda^2) \sum_{i<j} \rho_{ij}}{T} \quad (3)$$

where $\rho_{ij}$ is the correlation between $\lambda_i$ and $\lambda_j$. Allowing the $\rho_{ij}$'s to be a function of distance such that $\rho_{ij} = \rho_{j-i}$ for $j > i$ gives

$$\mathrm{Var}\ \frac{\sum_{i=1}^{T} X_i}{T} = \frac{(\mu_\lambda + \sigma_\lambda^2) + 2\sigma_\lambda^2[(T-1)\rho_1 + (T-2)\rho_2 + \ldots + (T-T+1)\rho_{T-1}]}{T}$$

Under our model, $\rho_1$ is greater than $\rho_2$ which is greater than $\rho_3$ and so on. Thus, for the general case, our model predicts that the variance of the mean of T transect units will increase as a function of the gamma parameters, which are adjusted by the heterogeneity in habitat factors.

The distance along the transect at which the Poisson variance law no longer holds can be identified graphically by plotting the observed ratio

$$\hat{V}(C_1) / \hat{V}(C_T) \tag{4}$$

against transect segment length T. Under independence, the expected value of Equation 4 is approximately T, resulting in a 1: 1 relationship of T plotted against itself. The point of departure from this identity under Poisson variation indicates the distance at which the positive covariance in plant cover associated with habitat factors comes into play. The value of T at this point of departure suggests an estimate of the measurement scale or transect size appropriate for studying plant cover.

The estimated variance of $C_T$ from Equation 4 can be calculated for different combinations of TSL and the distances between transect segments (*i.e.,* the intersegment distance; ISD). We have chosen to estimate the variance of $C_T$ by the mean of the within sample variation from many (100, say) pairs of observations of a given TSL and separated by a given ISD. Thus, by expanding our notation to allow for both a specific TSL and ISD, $\hat{V}(C_{td})$ is given as:

$$S^2_{td} = \sum_{j=1}^{100} \frac{\sum_{m=1}^{2} (X_{tdjm} - \bar{X}_{tdj})^2}{100} \tag{5}$$

where $S^2_{td}$ = variance in percent cover for TSL = t, and ISD = d, $X_{tdjm}$ = percent cover for TSL = t, ISD = d, segment pair j = 1, 2, 3, . . . , 100, segment m = 1, 2, and $\bar{X}_{tdj}$ = mean percent cover for TSL = t, ISD = d, segment pair j.

**Sample variance as a function of intersegment distance (dispersal)**

Our model stipulates that neighboring transect segments share more similar environmental components and hence similar plant density or cover than distant transects. The local Poisson model for plant density ensures that transect segments close together will have similar Poisson parameters. As such, plant density is expected to be approximately Poisson distributed for small transect segments in proximity. Under the simpler model, where the $\lambda_i$'s are independent and identically distributed, these same unit segments are expected to exhibit negative binomial between-plot (between-segment) variances in plant density when widely dispersed.

Between-plot variances of larger transect segments, being a sum of local Poisson random variables that are mostly independently and identically distributed, will initially follow the variance law (Equation 1). However, as these larger transect segments become dispersed, each unit segment will be contributing not only Poisson variation but an additional variance component of the negative binomial type to the overall variance. Hence, our model predicts that for segment lengths greater than the distance at which the variance law no longer holds, the within-plot variance will increase with dispersion.

**Correlation as a function of intersegment distance**

As the distance between segments of equal length along the line transect increases, the number of environmental components they share tends to decrease. The spatial correlation (product moment) function of plant density along a transect can therefore be expected to decrease with increasing ISD. In order to characterize this expected decrease, we chose a simplistic first-order autoregressive model with an exponential decay in spatial correlation written as

$$\rho_d = \rho^d \tag{6}$$

where d = distance between transect segments, $\rho$ = the spatial correlation ($0 \leq \rho \leq 1$), and $\rho_d$ = correlation when segments are a total of d units apart.

The limit of (Eq. 6) as d increases is zero, *i.e.*,

$$\lim_{d \to \infty} \rho_d = 0 \quad \text{when } \rho < 1.$$

Functionally, the correlation will approach zero quite rapidly, and the shortest distance d where $\rho^d \approx 0$ provides an indication of the ecological scale for the response being measured. This approach to defining inherent ecological scale is used because it emphasizes the interrelationships of many ecological factors and the result of those interrelationships on plant response.

The value of d can be interpreted as a measurement of the average distance between two points in the landscape where the number of common overlap zones approaches zero. Another way of phrasing this definition of d is the distance at which two points in the landscape no longer experience the same habitat conditions. Thus, the value of d can be used to specify how far apart replicate transects should be in order to obtain nearly independent observations.

The spatial correlation from Equation 6 can be estimated by the sample correlation coefficient, Equation 7. The estimated spatial correlation can be viewed then as the correlation between the 100 pairs of observations (X,, X,) used to estimate the variance of $C_{td}$ where

$$r_{td} = \frac{\sum_{j=1}^{100} (X_{tdj1} \quad \bar{X}_{td1})(X_{tdj2} - \bar{X}_{td2})}{\sqrt{\sum_{j=1}^{100} (X_{tdj1} - \bar{X}_{td1})^2 \sum_{j=1}^{100} (X_{tdj2} - \bar{X}_{td2})^2}} \quad (7)$$

is the sample correlation for TSL = t and ISD = d. This approach for estimating spatial correlation is not influenced by any directional trend in plant cover over the landscape if pairs of observations with a given TSL and ISD are randomly selected and if no inherent ordering (e.g., right to left along the transect) is considered. An alternative estimate of the spatial correlation is the autocorrelation from time series analysis.

## Correlation as a function of segment length

Envisioning transect segments as a sequence of segments of unit length, the correlation between segments as a function of increasing TSL can be postulated by again using the conceptual model. Assuming for the moment that the adjacent unit segments follow a first-order autoregressive model (Eq. 6), two adjacent unit segments delineated as $X_1$ and Y, have a resulting correlation of

$$\rho_{X_1, Y_1} = \frac{\rho\, \sigma_\lambda^2}{\mu_\lambda + \sigma_\lambda^2} \quad (8)$$

Similarly, for adjoining 2-m transect segments delineated as $X_2$ and $Y_2$, the first-order autocorrelation predicts a correlation of

$$\rho_{X_2, Y_2} = \frac{\rho\, \sigma_\lambda^2\, (1 + \rho)^2}{2\mu_\lambda + 2\sigma_\lambda^2\, (1 + \rho)} \quad (9)$$

For a known mean, variance, and correlation coefficient, one can show that

$$\rho_{X_1, Y_1} \geq \rho_{X_2, Y_2} \geq \rho_{X_3, Y_3} \geq \ldots$$

That is, a first-order autoregressive model predicts decreasing correlation with increased segment length. However, this model neglects the distance in which observations behave like independent random variables for which $\rho = 0$.

An alternative model incorporating the assumption of local Poisson variability (at least for segments of unit length) would result in an autoregressive model where

$$\rho_d = \begin{cases} \rho^{d-1} & \text{for } d \geq 2, \text{ and} \\ 0 & \text{otherwise} \end{cases} \quad (10)$$

Under this new model (Eq. 10), the same calculations as above yield an increase in correlation with increasing segment size up to two units followed by a decrease in correlation for segment lengths g&eater than or equal to three units. In the general case, the correlation will increase with increasing segment length until the distance is reached where observations no longer behave like independent Poisson random variables, and then the correlation will decrease.

Plots of the sample correlation versus the intersegment distance should be consistent with the plots of variance versus transect length.. The ISD where the correlation begins to steadily decrease should be approximately the same TSL where the variance rule of Equation 1 no longer holds.

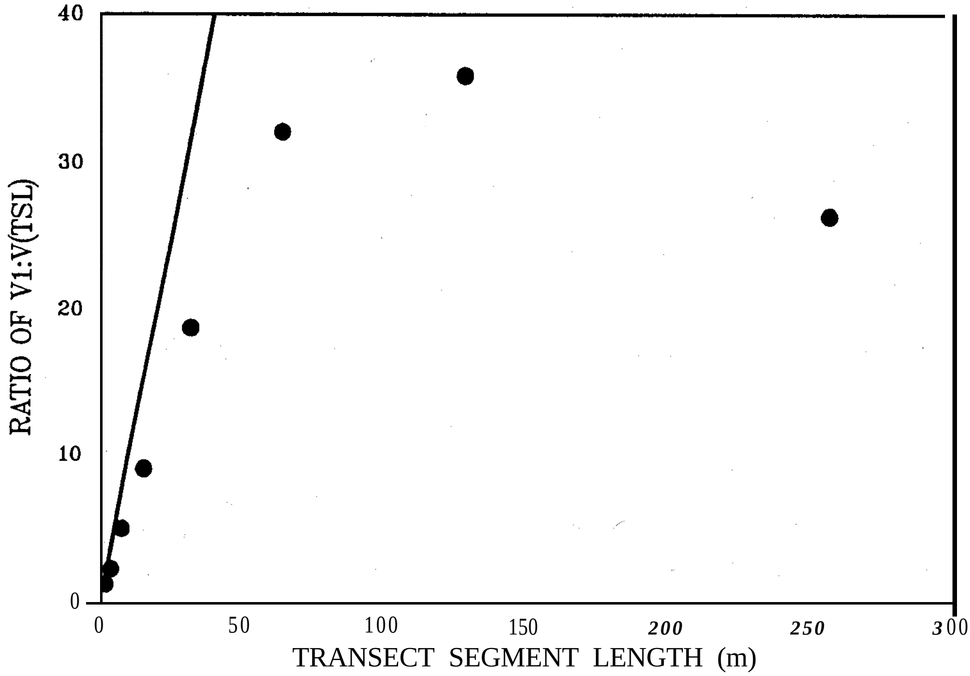


*Fig. 1.* Relative change in betw'een-transect-segment variance (Eq. 5) as a function of transect segment length (TSL). The diagonal line represents the expected ratio under the Poisson variance law.

## An example

In order to test the above theory, a study of plant cover was conducted at the Arid Lands Ecology (ALE) Reserve, a shrub-steppe grassland on the U.S. Department of Energy's Hanford Site in south central Washington State. The most prominent species are bluebunch wheatgrass ***(Agropyron spica-turn),*** big sagebrush ***(Artemisia tridentata),*** and cheatgrass ***(Bromus tectorum).***

Cover for ***A. spicatum*** was measured along a continuous NW-SE 2050-m line-intercept transect (Mueller-Dombois and Ellenberg **1974),** at an elevation of about 370 m, roughly perpendicular to the drainages from Rattlesnake Mountain, the dominant topographic feature in the area. Points along the transect where a measuring tape intercepted the beginning and end of discrete bunches of ***A. spica-turn*** were recorded. We chose ***A. spicatum*** because it is the dominant plant species on the study site and grows in discrete bunches with well-defined solid crown cover suitable for measurement with **line-**intercept methods.

To explore the influences of sampling unit size and its dispersion on the spatial correlation and variance of ***A. spicatum*** cover, we estimated percent cover $(X_{tj})$ for specified TSL = t and observation (j) along the 2050-m transect. TSLs from 1 to 256 m were considered.

For each combination of TSL and ISD, an estimate of $V(C_{td})$ using Equation 5 was obtained by selecting, from the 2050-m transect, 100 random pairs of segments for a specific TSL and separated by a specific ISD, beginning at a randomly chosen starting location. An average of six replicates of this procedure is reported below. The choice of 100 for the number of pairs was arbitrary. The spatial correlation was also estimated for specific values of TSL and ISD as in Equation 7.

### *Variance as functions of TSL and ISD*

For ***A. spicatum,*** the observed variance ratio as a function of T from Equation 4 departs from the expected 1:1 relationship for t = 10 m (Fig. 1). Be-

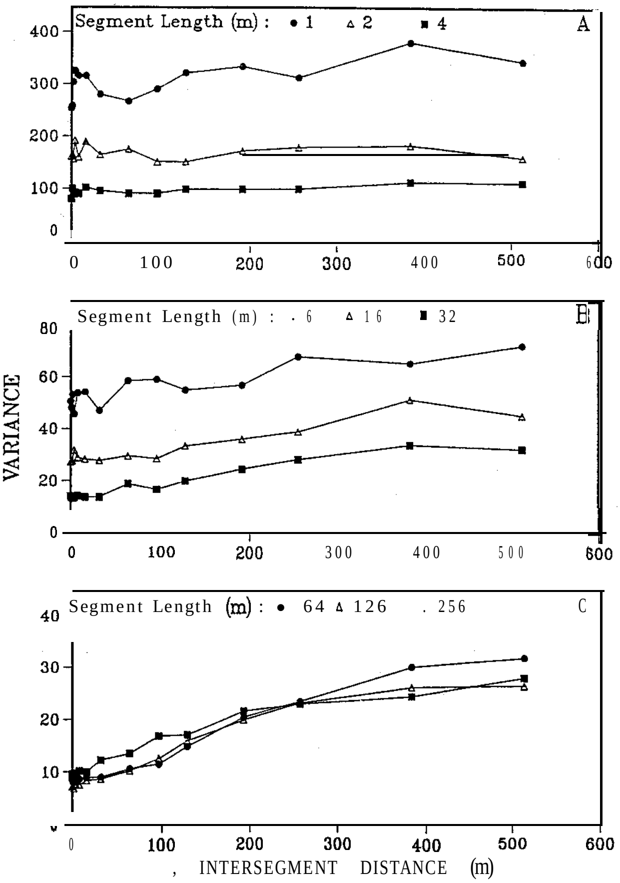


Fig. 2. Variance in percent cover of *Agropyron spicatum* for (A) short, (B) intermediate, and (C)long transect segment lengths as a function of intersegment distance (ISD).

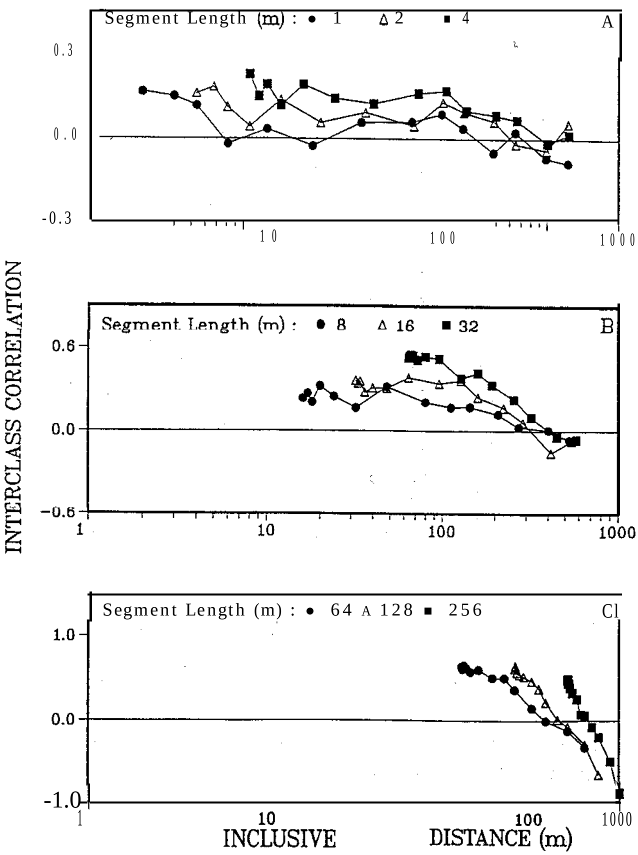


*Fig.* 3. Decay of spatial correlation for ***Agropyron spicatum*** cover as a function of inclusive distance. Inclusive distance includes the length of two separated transect segments and the distance between two segments (*i.e.,* ISD).

tween 64 and 128 m, the observed values of Equation 4 depart markedly from the expected relationship. This indicates that the positive covariance for *A. spicatum,* which begins to contribute to the overall variance in cover estimates at about 10 m, is most apparent at a TSL greater than 128 m. Beyond 128 m, the ratio begins to decline, indicating the increasing influence of the covariance component of the variance estimate (Eq. 2) identified in the conceptual model for patch dynamics.

Sample variance as a function of ISD did not show an increase for TSL's less than 10 m. For shorter TSLs (Fig. 2A), the variances tended to stabilize quickly (particularly for segment lengths of 1 and 2 m), and did not display any marked upward trend. Segments of intermediate length displayed noticeable variance increases with increased intersegment distance (Fig. 2B). Variances for the longest segment lengths, 64, 128, and 256 m, had the most consistent increases with increased intersegment distance (Fig. 2C). Thus, between-plot variance did increase for intermediate and long segment lengths as a function of increased dispersion.

*Correlation as functions of TSL and ISD*

For *A. spicatum,* the point for which $\rho = 0$ occurs at distances between approximately 400 and 700 m (Fig. 3A–C) for the TSLs that show the most consistent decrease in sample correlation (*i.e., 64,* 128, and 256 m). When the 16- and 32-m TSLs are in-

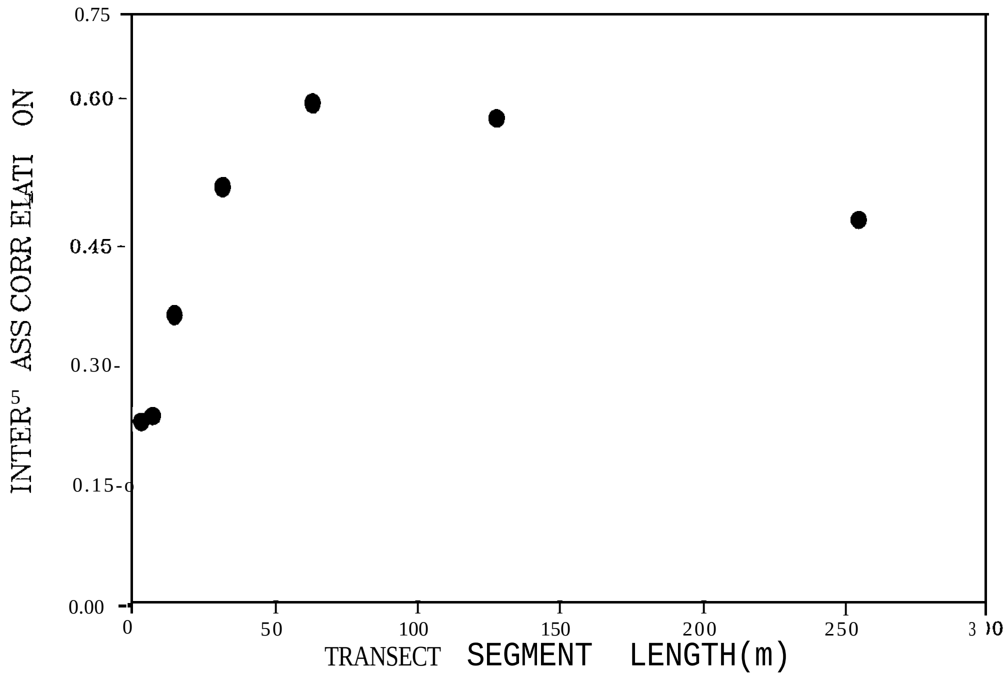


Fig. 4. Spatial correlation for *Agropyron spicatum* cover as a function of transect segment length. Spatial correlations are estimated at lag 1, or ISD = 0.

cluded, the inclusive distance' becomes 300 to 700 m. The distances indicated in Fig. 3A–C include the lengths of the transect segments and the distance between the two transect segments, the 'inclusive distance.' Assuming that the decay of the autocorrelation is the same in every direction from any point on the landscape, the distance where $\rho$ = 0 is the radius of a unit equal in size to the inherent scale of the characteristic being measured. Thus, the scale at which *A. spicatum* cover is expressed is twice 400 to 700 m, or 800 to 1400 m. In reality, the shape of the basic scale unit on the landscape will not be circular. Although the many factors that influence cover for *A. spicatum* probably have scales that differ, collectively they yield a scale of approximately 800 to 1400 m.

Spatial correlation (at ISD = *0)* for *A. spicatum* cover did increase with increased segment length up to approximately 64 m and then declined (Fig. 4), suggesting that the minimum transect segment length needed to estimate *A. spicatum* cover is approximately 64 m. As expected, this result is similar to that obtained when examining the variance ratio as a function of TSL (Fig. 1). Based on the conceptual model, measurement at this level of resolution will result, on average, in a segment that includes those habitat factors which combine to determine cover for *A. spicatum.*

## Discussion

Since a fundamental principle of ecology is that components of ecosystems are interrelated, the magnitude (strength) and scale (areal extent) of these interrelationships are inherent attributes by which ecological processes can be characterized. In addition, definition of the inherent scale at which a process occurs may be used to identify this appropriate scale of measurement for additional study of the process. The desirability of determining this appropriate scale has been pointed out by Rotenberry and Wiens (1980), who suggested that incompleteness in the theory relating changes in bird species diversity and habitat structure results partially from an '. . . inability to measure hori-

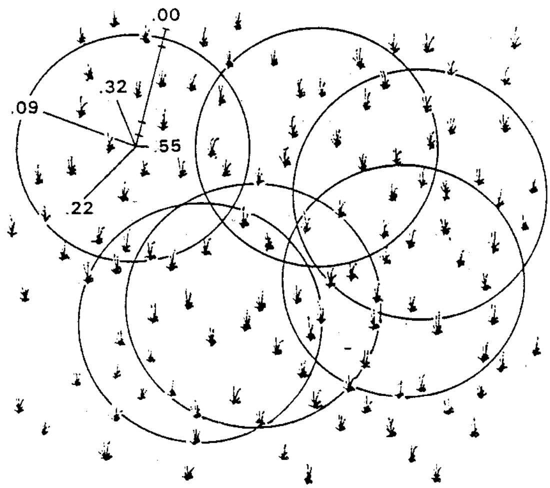


Fig. 5. Schematic of conceptual spatial model of scale for *Agropyron spicatum* cover. Circles represent inherent units of ecological scale. Any point on the landscape is the center of a natural scale unit, and the distance from the center at which spatial correlation declines to zero indicates the bounds of the inherent unit of scale. Numeric values are intraclass correlations for various inclusive distances (see Fig. 3). The apparent scale for *A. spicatum* cover is the result of other overlapping, concurrent environmental components, which determine plant cover and have inherent units of scale that may differ in size and shape.

zontal patch structure . . . on the proper spatial scale . . .'

Several researchers have explored the use of spectral analysis, which incorporates estimates of spatial correlation, for defining pattern in vegetation (Hill 1973; Usher 1975; Ripley 1978). However, Usher (1975) indicated the insensitivity of spectral analysis for defining large-scale heterogeneity of vegetational pattern. Our approach for determining the scale at which ***A. spicatum*** cover was expressed was to identify the distance between points on the landscape at which the spatial correlation in cover declined to zero. Our approach for identifying the minimum sampling unit size was to identify the TSL at which the maximum spatial correlation was attained.

Based on the conceptual model, the reduction of spatial correlation to zero at inclusive distances of approximately 400 to 700 m indicates the distance at which any two points on the landscape no longer share the same habitat conditions that influence cover for ***A. spicatum.*** The results also suggest that a 64-m transect is the appropriate scale of measurement for percent cover, while the decay of the spatial correlation to zero within an inclusive distance of 400 to 700 m suggests the most appropriate dispersion of the transect segments. Since environmental processes influence plant cover, plant cover itself must be characterized by a mosaic of overlapping units (Fig. 5). The size of these units defines the inherent scale for plant cover. Any two points on the landscape that have a non-zero correlation, according to the conceptual spatial model, are part of the same scale unit.

Errington (1973) found that the distance between sampling units (blocks) as well as the size of the sampling units could have a marked effect on the variance of estimates for vegetation parameters. This approach, using the peaks in the variance for particular block ***(i.e.,*** sampling unit) sizes as an indication of the scale of heterogeneity, has been studied extensively (Greig-Smith 1961; Usher 1969; Kershaw 1973; Errington 1973; Hill 1973).

In our study, the maximum spatial correlation attained suggested that the appropriate sampling unit size was approximately 64 m. Further, the appropriate dispersion of those units, to achieve independence of observations, is at least 400 m. Other ecological processes would undoubtedly require different sampling unit sizes and dispersion. It may be inappropriate to interpret the high spatial correlation in cover among contiguous transect segments of 64 m as an indication that cover along one transect segment strongly influences cover along adjacent segments. Rather, the processes or factors that collectively determine plant cover probably exercise their influence such that the result of the processes, canopy cover of ***A. spicatum,*** exhibits high spatial correlation when cover is measured along transect segments. For plant cover, these factors could include edaphic and microclimatic factors. The influencing factors also exhibit spatial correlation just as the response to the factors or processes does. Measured individually, these factors or processes may exhibit spatial correlation at scales other than that exhibited for plant cover. For example, along a 290-m transect, Yeh ***et al.*** (1986) identified a spatial correlation in soil water pressure that declined to close to zero at about 6 m.

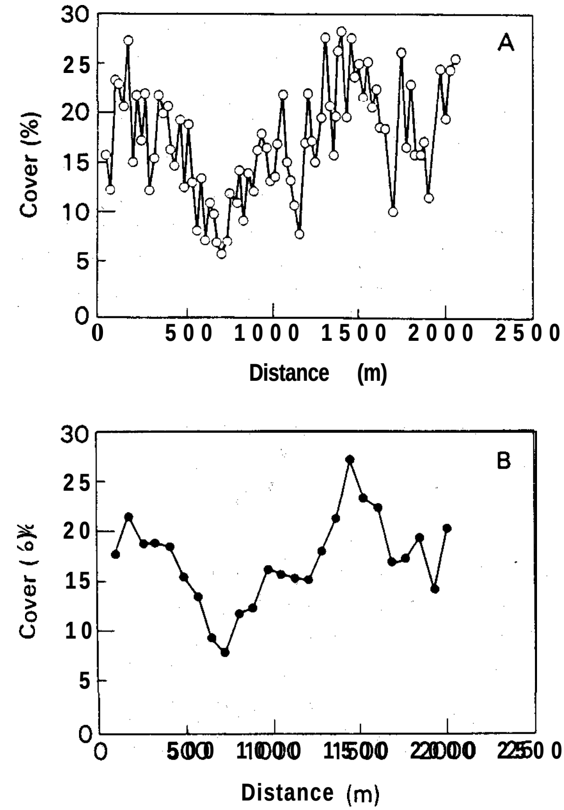


*Fig.* 6. Percent cover for *Agropyron spicatum* along 2050-m line-intercept transect depicting influence of differing scales of measurement. 6A. Percent cover for 25-m transect segments. 6B. Percent cover for 80-m transect segments.

Measurement of ecological processes at an appropriate scale is analogous to viewing a television screen. Viewing the screen closely enough to see individual dots, or measuring on a small scale, may reduce the ability to discern the image formed collectively by the dots. Conversely, viewing the screen from too great a distance or measuring on too large a scale may result in a blurred image. Measurement of *A. spicatum* cover using TSLs of 25 m (Fig. 6A) yielded cover estimates characterized by somewhat erratic fluctuations over the 2050-m distance measured. When TSLs of 80 m were used (Fig. 6B), these fluctuations were damped and the pattern of A. *spicatum* cover over the same distance was clarified.

We recognize that it is necessary to determine the most appropriate measurement scales for different processes or physical properties, e.g., different scales of measurement may be necessary to study the various processes influencing *A. spicatum* in the shrub-steppe habitat. Also, more than a single ecological scale may exist, necessitating measurement at several levels of resolution (Maguire 1985; Maurer 1985; Morris 1987). In his studies of avian community dynamics, Maurer (1985) recognizes the usefulness of studying community responses at more than one scale of observation. Maurer (1985) used three scales of measurement, corresponding to '. . . the community, the average species in the community, and the average individual in the community.' Allen and Star (1982) also emphasize the importance of viewing communities at different levels of resolution or scales of observation. However, they maintain that scale is not an inherent property of the object being measured, but a property of the level of measurement. In contrast, Maguire (1985) refers to characteristic, distinct scales of pattern in the herbaceous strata in a hemlock-hardwood forest.

It may not always be economically or logistically feasible to measure the system of concern at the most ecologically appropriate scale. For certain ecological processes it may be possible to measure on a small scale and then combine the small-scale measurements to yield various scales, as we did using line-intercept transects. This may also be feasible using remote-sensing techniques. For example, a high-resolution visible (HRV) system aboard a recently launched French satellite provides 10-m resolution (Greegor 1986). In order to define an appropriate level of measurement for processes that can be measured with HRV, combinations of the basic 10-m pixels may be formed. Defining the sampling unit size and dispersion on the basis of the ecological scale at which the process or characteristic is manifest can increase sampling efficiency and clarify the nature of ecological phenomena.

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