SPATIO-TEMPORAL PATTERNS OF SOIL RESOURCES FOLLOWING DISTURBANCE IN A 40-YEAR-OLD SLASH PINE (*PINUS ELLIOTTII* ENGELM.) FOREST IN THE COASTAL PLAIN OF SOUTH CAROLINA

by

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Dissertation Submitted to the Faculty of the

Virginia Polytechnic Institute and State University

in Partial Fulfillment of the Requirements for the Degree of

DOCTOR OF PHILOSOPHY

BLACKSBURG, VIRGINIA

OCTOBER 2001

Key words: Geostatistics, girdling, heterogeneity, scale, whole-tree harvesting

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Abstract. There has been an increased interest in characterizing and interpreting ecological heterogeneity over space and time in the past two decades. This is mainly due to the renewed recognition of the significance of heterogeneity in ecological theories. However, studies that have combined both spatial and temporal aspects of heterogeneity have been rare. A unified approach to define and quantify heterogeneity has also been lacking. Designed to overcome these problems, this study was conducted in a 40-year-old *Pinus elliottii* Engelm. forest at the Savannah River Site near Aiken, SC, USA with the following specific objectives: 1) to characterize the spatial patterns of soil and forest floor variables (moisture, pH, soil available nitrogen and phosphate, forest floor and soil carbon and nitrogen), 2) to examine the dynamics of these spatial patterns in response to two types of disturbance: whole-tree harvesting and girdling, and 3) to evaluate some of the current methods for quantifying ecological heterogeneity.

In response to both disturbance treatments, spatial heterogeneity measured by sample variance showed a marked "increase and then decline" temporal pattern in soil moisture, soil available nitrogen and phosphorus. Similar patterns were not found in total soil C and N, and total litter C and N. Harvesting resulted in greater and more drastic changes in the variations of soil nutrients and water than did girdling. Despite the popularity of semivariogram analysis in recent ecological studies, the technique did not provide consistent results on patterns of heterogeneity in our system. A simulation

experiment demonstrated that semivariogram analysis may suffer from many problems when it is used to characterize patchiness, one form of heterogeneity.

The results from this study have a number of implications. First, spatial patterns of soil resources are high dynamic. The dynamics of patterns in soil resources may partly account for the weak correlation between vegetation and soil observed in ecological literature. Second, heterogeneity may be most effectively quantified by first identifying quantifiable components and then quantifying these components individually. A common pattern can be sought by comparing patterns of different components of heterogeneity for a given ecological property and by comparing patterns of different ecological variables for a given component of heterogeneity. Third, compared to surveys, field manipulative experiments can provide information that link patterns with ecological processes. As such, this study adds to ecological literature valuable information on temporal changes of soil heterogeneity following disturbance and conceptual advances in the quantification of ecological heterogeneity.

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CHAPTER 1

ADVANCES IN THE STUDY OF HETEROGENEITY IN

TERRESTRIAL ECOSYSTEMS: A LITERATURE REVIEW

1. Introduction

The development and maintenance of spatial and temporal pattern and the consequences of that pattern for the dynamics of populations and ecosystems are two fundamental and related themes in ecology (Levin 1992). Patterns can exist at various scales in time and space (Allen and Starr 1982, Urban et al. 1987, Pickett and Cadenasso 1995). In nature, these patterns can appear as patches, gradients, or other kinds of spatial structures at spatial scales ranging from ecosystems to the area occupied by an individual organism (Webster 1985, Trangmar et al. 1987, Robertson et al. 1988, Jackson and Caldwell 1993 a&b, Levin 1992, Gross et al. 1995, Miller et al. 1995), and at temporal scales ranging from seconds to hundreds of thousands of years (Urban et al. 1987). Though heterogeneous patterns in vegetation and soils are ubiquitous in nature and have been observed for a long time, ecologists did not give sufficient early recognition to their importance. Instead, homogeneity and equilibrium were assumed for convenience and simplicity in much of the history of ecology (McIntosh 1991, Pickett and Cadenasso 1995). Not until recent years, the 1980s and 1990s in particular, has the significance of spatial and temporal heterogeneity received attention from a broad range of ecologists.

Heterogeneity in the broadest sense encompasses all patterns in nature because patterns imply differences in space and time. To address the heterogeneity in nature, one needs to describe heterogeneity both qualitatively and quantitatively (Li and Reynolds 1995). Heterogeneity has been frequently referred to as spatial and temporal variation in environment or distribution and dynamics of species and populations. However, variation alone cannot fully explain heterogeneity. Heterogeneity may also mean

complexity of patterns in nature, which may be difficult to recognize and quantify (Li and Reynolds 1995, Wiens 2000).

To fully appreciate heterogeneity, the importance of scale should also be recognized (Li and Reynolds 1995). There may be an innate scale in nature for a given pattern, but the scale ecologists frequently refer to is the scale of observation and analysis (Allen and Starr 1982). Heterogeneity therefore is essentially based on the spatial and temporal scales at which it is measured and is specific to the questions of interest and the organisms in consideration (Addicott et al.1987, Antonovics et al. 1987, Miller et al. 1995). Traditionally, ecologists, especially those in the field of landscape ecology, have focused on the spatial patterns and their ecological impacts at the scale of kilometers (Forman 1994, 1995, Pickett and Cadenasso 1995). Studies at this scale are useful for regional ecosystem management (pollution control, riparian zone design, regional planning, etc.), for recognizing relationships between landscape dynamics and broad-scale ecological processes (i.e. wildlife movement, fire, etc.), and for global issues such as species conservation. The emergence of new techniques in remote sensing, Geographical Information System (GIS), and Global Positioning System (GPS) has lent ecologists greater leverage in developing large-scale ecological studies. However, the information generated by these studies may not directly lead to a better understanding of the processes that occur at the scales of individuals to entire plant communities and with high temporal frequency, such as competitive interactions, species turnover, and succession, yet these processes are cornerstones of basic ecological theories.

Accordingly, many studies have attempted to quantify the patterns of heterogeneity within plant communities. These studies described and tested the effects of

environmental heterogeneity on individual plants and plant-plant interactions at scales of centimeters to dozens of meters (Caldwell et al. 1985, 1991, Robertson et al. 1988, 1993, Jackson & Caldwell 1989, 1993, Halvorson et al. 1994, Ehrenfeld et al. 1997). The results have demonstrated that significant spatial variations exist in soil attributes at finer spatial scales, and that plants appear to respond to these variations. It is possible that the pattern and dynamics of the fine-scale variations in soil resources may hold the key to understand mechanisms of plant-plant interactions. Furthermore, some studies have revealed that plants can modify the spatial variability of soil attributes through litter production and its composition, absorption of moisture, oxygen and nutrients, and the release from roots of organic molecules (Robinson and Van Vuuren 1998), suggesting the significance of plants in creation and maintenance of soil resource heterogeneity. Therefore, there may be dynamic interactions between plant communities and soil resource heterogeneity. But little information is available to understand such interactions and their importance to plant interactions, succession, and nutrient cycling.

In this literature review, I will assess the development of the concepts of heterogeneity and the methodologies in quantifying heterogeneity, discuss the causes and consequences of environmental heterogeneity, and examine the interactions between plants and environmental heterogeneity at various scales. The purpose of this review is to establish a theoretical basis and empirical evidence for my dissertation research which aims at quantifying patterns of spatial and temporal heterogeneity in a forest ecosystem following disturbance to gain a better understanding of the heterogeneous environment in which competitive interactions and succession occur.

2. Concept of Heterogeneity and Its Quantification

1) Definition of Environmental Heterogeneity

The disagreement on the definition of heterogeneity has been recognized as the biggest obstacle to a thorough understanding of heterogeneity and its importance in ecology (Kolasa and Pickett 1991, Li and Reynolds 1994, 1995). Definitions of heterogeneity often vary from one ecological study to another, thus has made comparisons among studies difficult and has caused great confusion in both theory and practice (Dutilleul and Legendre 1993, Li and Reynolds 1995). A clear, statistically sound, ecologically relevant definition of heterogeneity is needed. In this section, I will review the historical development of the concept of heterogeneity, and address strengths and weaknesses of the most up-to-date definitions in the light of field ecological studies.

About a hundred years ago, Clements (1905) pioneered the use of quadrats and simple quantitative methods in the study of communities and addressed the issue of homogeneity (McIntosh 1991). He stated that in a "homogeneous community" the quadrat is representative in the same way a type specimen represents a species. In a less "uniform" community, the quadrat sample is less representative, and additional quadrats must be used in marked different zones or patches to sample its heterogeneity. Despite this early awareness of the existence of heterogeneity in nature, ecological thinking in the decades that followed was dominated by the assumptions of homogeneity and equilibrium. The view that ecological systems are internally homogeneous is parallel to the typological view of nature that was the foundation of community classification as well as of taxonomy (Wiens 2000). The assumption of equilibrium fit well with a Western worldview of the balance of nature (McIntosh 1991, Wiens 2000). However, as

empirical evidence accumulated, widespread patterns and dynamics in nature became facts that ecologists had to face. At the same time, theoreticians were beginning to introduce temporal and spatial variation into their models and found interesting results (Wiens 2000). The attention to heterogeneity in nature thus was renewed. The last two decades of the twentieth century marked a transition from conceptual recognition and qualitative characterization to the accurate quantification of heterogeneity under the guidance of conceptual development (Kolasa and Rollo 1991, Dutilleul and Legendre 1993, Li and Reynolds 1995). The central goal of these conceptual efforts was to provide an operational definition of heterogeneity for the laboratory and field ecologists to test the theories and hypotheses that address the role of heterogeneity in key ecological functions and processes.

One of the first major conceptual efforts in 1990s was made by Kolasa and Rollo (1991). They distinguished measured heterogeneity, "a product of the observer's arbitrary perspective", from functional heterogeneity, "which ecological entities actually perceive, relate to, and respond to." This distinction emphasizes that heterogeneity measured by an observer may or may not match the heterogeneity perceived by organisms living in a heterogeneous environment. Therefore, the methods used to quantify heterogeneity may directly influence our understanding of heterogeneity in natural systems. At the same time, the authors defined heterogeneity in both spatial and temporal senses. Spatial heterogeneity, they suggested, can be treated as dynamic or static. Temporal heterogeneity, similar to spatial heterogeneity, refers to " one point in space and many points in time." Kolasa and Rollo's definition represents the first major step towards lending the term more operational value.

Followed Kolasa and Rollo's lead, Dutilleul and Legendre (1993) tried to link patterns of ecological heterogeneity with statistical methods. They recognized two types of patterns of heterogeneity - point and surface patterns, and linked each type of patterns to available statistical methods. For example, for a point pattern, spatial heterogeneity could be defined as density variation among sub-regions, and can be quantified by using Poisson process. For a surface pattern, heterogeneity is referred to as the among-sub-region variability, for one or several qualitative or quantitative variables taking values in a spatially continuous manner. Various quantification methods are available, such as trend surface analysis, spectral analysis, semivariance analysis, and Geary's spatial autocorrelation coefficient.

Later, Li and Reynolds (1995) attempted to propose a more operational definition by distinguishing two different attributes of a system property – variability and complexity, and by listing the specific methods to quantify these two attributes. In their definition, heterogeneity is the complexity and/or variability of a system property in space and/or time. They suggested that variability often appears in numerical maps while complexity is frequently seen in categorical maps. They further suggested that each of these two attributes has a number of components and listed the methods to quantify these components. Similar to Kolasa and Rollo's definition, Li and Reynolds (1995) gave separate definitions for structural and functional heterogeneity to distinguish the heterogeneity arbitrarily measured and the heterogeneity that is ecologically responsive. They also emphasized the importance of scale in the definition and quantification of heterogeneity. The definition proposed by Li and Reynolds (1995) is probably the most operational definition so far. However, several key questions remain unanswered.

Among these are how to separate functional heterogeneity from measured (structural) heterogeneity, and how to determine an appropriate scale (or scales) in the quantification of heterogeneity of a system property.

More recently, Wiens (2000) proposed four different forms of heterogeneity. The simplest form is spatial variance, a statistical measure of the aggregate variation among sampling points in a given area. The second form is patterned variance, which describes the patterns of spatial variance, and is usually quantified by autocorrelation and anisotropy. These two forms of heterogeneity correspond to the numerical maps proposed by Li and Reynolds (1995). The third form is compositional variance, which occurs when sample points differ qualitatively as well as quantitatively. When compositional variance is expressed in a spatially explicit way, the heterogeneity can be expressed as locational variance. These two forms of heterogeneity roughly correspond to the categorical maps in Li and Reynolds (1995). Clearly, Wiens (2000) used variance as the cornerstone of the definition of heterogeneity. However, heterogeneity still has different meanings for different patterns.

It is not surprising that the term heterogeneity is defined and used in various ways given the great variety and complexity of patterns in nature. However, to make comparisons and generalizations across different ecosystems and studies possible, a unified and operational definition is necessary. From the discussions given above, it may be said that heterogeneity can not be directly quantified. Components or forms of heterogeneity must be identified and then quantified. Variance is an indispensable component of heterogeneity, as suggested by both Li and Reynolds (1995) and Wiens (2000). Other components include trend, anisotropy, autocorrelation, and patchiness.

Therefore, complex heterogeneity patterns can be reduced to quantitative patterns of each component and/or form of heterogeneity. A common pattern can then be sought on these specific quantitative patterns across different ecosystems and communities.

In this work, we adopt the definition provided by Li and Reynolds (1995) that heterogeneity is variability and/or complexity of a system property. We recognize that to quantify heterogeneity, components of heterogeneity must be identified and quantified, among which we deem sample variance and spatial dependence essential components of heterogeneity for continuous variables such as soil nutrients.

2) Scale

Description of heterogeneity requires the identification of appropriate scales, which depend on the question being addressed and the organisms being considered (Addicott et al. 1987, Antonovics et al. 1987, Miller et al. 1995). For example, Miller et al. (1995) defined spatial heterogeneity at two scales: (1) large scale heterogeneity between sites (i.e. differences between the areas occupied by populations), and (2) smaller-scale heterogeneity between microsites within each site (i.e. heterogeneity between the areas occupied by individuals within a single population). Ehrenfeld *et al.* (1997) discussed the three scales of variation commonly arising in ecological studies. The coarsest scale is a "gradient", which extends up to hundreds of meters. The medium scale is "patches", which extends into the tens of meters, and reflects local changes in physical and chemical attributes of the site. The finest scale, or "meter-scale" variation, occurs at distances of centimeters or meters.

Addressing the problem of scale has both theoretical and practical importance. The gulf between community ecology and ecosystem ecology has been apparent, due to different historical traditions (Levin 1992). In community ecology, generalized patterns are sought in the natural interactions among biota, and general and simple theory is always pursued. By contrast, ecosystem ecology deals with many applied problems, where abiotic and human disturbances as well as biotic interactions influence ecosystem dynamics and transform ecosystem functions. Studies that consider a variety of scales can integrate these and other sub-disciplines in ecology. Scales from the leaf to the ecosystem to the landscape and beyond thread various disciplines together, such as physiological ecology, community ecology, ecosystem ecology, landscape ecology and global ecology.

3) Quantification of Spatial Heterogeneity

Quantification of heterogeneity is ultimately based on the definition of heterogeneity (Li and Reynolds 1994, 1995). With the guidance of an operational definition, one can more efficiently characterize patterns of heterogeneity in nature. However, given the disagreement on the definition of heterogeneity among ecologists, a number of pitfalls should be avoided in the quantification.

First, it should be recognized that heterogeneity might not be directly quantified. It can appear in patches, gradients, hot points, etc. Instead, quantification of heterogeneity may be accomplished by quantitatively characterize different components and forms of heterogeneity. Patchiness, a form of heterogeneity, has been frequently used as a substitute for heterogeneity. Indeed, ecological theory has dealt not so much

with heterogeneity as with patchiness, partly because patchiness refers to a particular spatial pattern with basic structure of patches well defined thus easy to describe and quantify. In comparison, the concept of heterogeneity is diffuse and any form of spatial variation, from an unbounded gradient to a collection of various patch types can be heterogeneous (Weins 1995). Therefore, it is necessary to identify quantifiable components of heterogeneity and qualify each of these components accordingly.

Second, one need choose an appropriate system property to measure (Li and Reynolds 1995). A system property can be anything of ecological interest, such as plant biomass, soil nutrients, or temperature. The choice of a system property depends on the goals of a specific study, but it is also intimately linked to the spatial and temporal scales of the sampling. For example, soil available nitrogen may change at fine spatial and temporal scales, so the sampling scale must be fine enough to capture this variability. In contrast, soil moisture may change at very fine temporal scales but at relative coarse spatial scales if topography is not an important factor at the fine scale. In this case, spatial sampling scales must be large enough to record these coarse-scale changes.

The other challenge in quantification of spatial heterogeneity lies in choosing statistical methods. In many heterogeneity studies, semivariance analysis and krigging are used. However, researchers scarcely address two important points. First, no matter how compelling the result, all statistics cannot prove or disprove. A statistical or geostatistical finding is credible only when it receives support from the data or, at a minimum, from ecological theory (Rossi et al. 1992). Second, an exhaustive exploratory data analysis (EDA) should be performed before computing any of the spatial statistics customarily associated with geostatistics. Such an EDA includes computing traditional

univariate and bivariate statistics, histograms, regression plots, and scattergrams, cluster analysis, principal component analysis, analysis of variance and many others (Rossi *et al.* 1992).

In summary, a rigorous quantification of spatial heterogeneity involves a thorough understanding of the ecological phenomena of interest, a careful selection of the components of heterogeneity to be characterized, considerations of scale, a thorough analysis using conventional statistics, and a careful use of geostatistical methods. Considering the increasing popularity of geostatistics in quantifying spatial heterogeneity, I provide a detailed discussion of geostatistics below.

Geostatistics

Traditional statistical procedures, such as *t*, F, and χ^2 tests and ANOVA are often used in ecology to organize and summarize data and to make meaningful inferences about phenomena of interest (Rossi et al. 1992). These procedures, however, are based on several assumptions: independence of samples, normal distribution of populations under study, and randomization. Often, these assumptions cannot be held in many ecological studies because of spatial and temporal dependence or continuity (autocorrelation) in nature.

To more accurately address spatially dependent patterns in ecology, ecologists began to use geostatisitcal approaches in mid 1980s (Rossi et al. 1992). Two most frequently used geostatistical techniques are semivariogram, which models spatial dependence, and krigging, which uses values from sampled locations to estimate values for unsampled locations. For example, Trangmar *et al.* (1985) discussed the benefits of

using geostatistics in spatial studies of soil properties. Robertson (1988) applied geostatistical techniques to describe: 1) temporal variability of the density of cell counts for a *Rhodomonas* sp. in a lake epilimnion; and 2) spatial variability of soil nitrogen mineralization in a Michigan old-field. Since then, these two geostatistical approaches have been used in numerous studies (Rahman *et al.* 1996, Schlesinger et al. 1996, Kabrick *et al.* 1997, Robertson *et al.* 1997).

The core of geostatistics is to use autocorrelation to describe the pattern of a "regionalized variable", as opposed to that of a "random variable" of conventional statistics. Regionalized variable theory holds that many phenomena are locally autocorrelated in time and/or space. Autocorrelation can be defined as a characteristic of random variables which causes pairs of variables found separated by a given distance to exhibit more or less similarity on average than expected by chance (Legendre and Fortin 1989). Many ecological variables do exhibit spatial autocorrelation due to certain biological properties, such as clumping vegetation, patchiness of seed dispersal, and localized nutrient release (Legendre and Fortin 1989).

Variogram analysis and krigging have allowed ecologists to characterize spatial patterns of autocorrelated phenomena and to conduct spatial interpolation for spatial predictions. The use of these two methods has also assisted soil and vegetation science by bringing out many new techniques for sampling.

Increased interest in these two methods has made geostatistics popular in ecology. But many issues in this field remain unresolved (Rossi et al. 1992). First, a description of the underlying theory and assumptions of geostatistics is missing. Without this, a correct and effective transfer of the techniques from geostatistics to ecology can hardly be

achieved. Second, the semivariogram is sensitive to outliers. The removal of an outlier can greatly affect the interpretation of spatial dependence in semivariograms. Therefore, it is important to be aware of methods for outlier identification, and to understand the circumstances under which the removal of outliers is valid. Finally, semivariograms are strongly affected by fine-scale or local mean and variance differences, thus many of the studies done so far may actually provide an incomplete image of spatial pattern.

To solve these problems, Rossi et al. (1992) suggested that geostatistics should include more than the variogram and krigging techniques. In addition to variograms, *h*-scatterplots, correlograms, and covariance are useful geostatistical tools to describe spatial continuity. According to the questions being addressed, ecologists can also use non-ergodic covariance and correlogram (to more effectively describe lag-to-lag spatial dependence while account for the changing local means and variance), indicator transformations (to capture the spatial patterns of nominal ecological variables like gene frequencies), robust variogram (to deal with outliers more effectively), and cross-variograms/ cross-covariances/cross-correlograms (to define joint spatial dependence between two or more variables).

3. Causes of Belowground Resource Heterogeneity

Heterogeneity in soil resources can be caused by many factors. Among these are soil parent material, micro-climate, micro-topography, soil physical properties, soil organisms, disturbance (Stark 1994), plant activity (Harper 1977, Robinson and Van Vuuren 1998, Gonzalez and Zak 1994, Finzi et al. 1998 a&b), human activities such as grazing (Schlesinger et al. 1996), other agricultural practices (Roberston et al.1993),

forestry practices (Preston 1996), and many others. All these possible sources of heterogeneity operate at different temporal and spatial scales. In this section, I will discuss the factors that most likely to be important to the creation and maintenance of heterogeneity of the belowground resources, which is the focus of this dissertation research. These factors include parent material, soil depth, disturbance, and vegetation dynamics. Many other factors (animal activities etc.) may also contribute to the creation of heterogeneity but will not be discussed here.

1) Parent Material

Parent material, the original geologic material from which the soil is formed, is the first factor influencing soil heterogeneity. Parent material may be composed of hard rock or loose deposits of gravel, sand, silt, clay, or organic material. Its chemical and physical nature determines the rate of weathering, which releases nutrients into the soil solution. Thus, parent material can exert a strong influence on nutrient supply, and on the scale and intensity of soil heterogeneity (Stark 1994). However, the weathering process is relatively slow, occurring over hundreds or even thousands of years, and may have limited influence over dynamic changes in soil resource heterogeneity.

2) Soil Depth

Soil depth is another cause of heterogeneity patterns in soil. Stark (1994) stated that soil depth might be the most quickly recognized source of heterogeneity. Several studies have shown that vertical traits, such as depth to a hardpan or other limiting soil horizon, can have important effects on plant growth and community composition

(Pritchett and Fisher 1987, Ehrenfeld *et al.* 1997). In a study conducted in the Coastal Plain Pine Barrens of New Jersey, Ehrenfeld *et al.* (1997) found that patterns of soil properties vary vertically, i.e., with depth. In another study, Meredieu *et al.* (1996) found that red oak (*Quercus rubra* L.) survivorship and productivity were strongly correlated with spatial patterns of soil depth and depth to a calcareous layer.

Soil depth can cause heterogeneity through several processes (Stark 1994). The activities of organisms can be constrained by soil depth (e.g., litter addition to the surface layer, or root anchorage and nutrient uptake). In a soil profile, different horizons tend to have different organic matter content, pH, moisture levels, and temperatures. Water tables exert different influences on different horizons and the fluctuations of water tables can lead to substantial temporal and spatial heterogeneity in nutrients. Soil depth can also interact with other factors to create heterogeneity. Despite the obvious differences in resources across the soil profile, the vertical dimension is often ignored (Ehrenfeld *et al.* 1997), mainly due to the frequently-made assumption that most dynamic plant activities occur on top layers of soil profile. This assumption may be valid when patterns are pursued at the stand or ecosystem level (variations within a stand are thus averaged out). But when heterogeneity patterns are the focus of a study, the importance of soil depth in causing variations in both soil and plant distribution should receive more attention. Unlike parent material, soil depth can contribute strongly to dynamic changes in soil resource heterogeneity.

3) Disturbances

      The effects of disturbance on ecosystems are obvious and well documented. Even though the literature on how disturbances could influence fine-scale spatial heterogeneity (from the scale of individuals to the community) is scarce, disturbance is probably the most important factor in creating heterogeneity in nature at all spatial and temporal scales. The available information in ecological literature supports this view.

      Gibson (1988) studied the maintenance of plant and soil heterogeneity in dune grassland and found soil heterogeneity did not appear to be controlling the plant patterns in the grassland. Rather, the plants themselves were inducing the soil patterns. Small mammal grazing and low light levels in the hollows controlled plant patterns. Therefore, the disturbances from small mammal grazing led to vegetation patterns, which induced soil heterogeneity patterns.

      Schlesinger et al. (1990) hypothesized that various processes, especially overgrazing, may create spatial heterogeneity in the soils of arid and semiarid grasslands. This heterogeneity in soils may lead to the invasion of desert shrubs. Shrubs may further localize soil nutrients under their canopies, leading to the development of "islands of fertility". In another study, Schlesinger et al. (1996) detected that soil nutrients are autocorrelated in the range comparable to the canopy size of shrubs. By contrast, grassland ecosystems show a finer-scale distribution of soil constituents.

      Additional studies showed the importance of agricultural practices and land-use history in creating spatial patterns in soils and vegetation (Robertson et al. 1993, 1997). However, field experiment tests of the effects of disturbance on soil resource heterogeneity are lacking. By carefully manipulating disturbance experiments in the

field, one may be able to not only catalogue changes in spatial and temporal patterns in soil resources and vegetation after disturbance, but also link these patterns to key ecological processes such as plant competitive interactions, species replacement and coexistence, and succession.

4) Vegetation Dynamics

It is widely recognized that spatial heterogeneity of soil properties and vegetation is ubiquitous (Watt 1947, Greig-Smith 1979, Jackson and Caldwell 1993b). Many studies have quantified the spatial heterogeneity in soil and vegetation in various ecosystems (Robertson et al. 1988, Palmer 1990, Schlesinger et al, 1996, Ehrenfeld 1997, Lister et al. 2000). Some efforts have also been made to correlate patterns in soil with patterns in vegetation.

Experimental studies have shown that plants respond to heterogeneity and that species differ in their abilities to exploit nutrient patches (Caldwell et al. 1985, Campbell et al. 1991, Robinson 1994, Mou et al. 1995, 1997, Robinson & Van Vuuren 1998, Einsmann et al. 1999). This suggests that species can exert a strong influence over spatial distribution of soil nutrient. This influence could happen within a very fine temporal scales (weeks) or over a long period (dozens of years), as suggested in Jackson et al. (1990) and Finzi et al. (1998 a&b). In a recent study, Farley and Fitter (1999) found considerable temporal variation in soil nutrient (ammonia, nitrate and phosphate) concentration and soil moisture levels in a 250-300 year-old woodland site in North Yorkshire in UK. Spatial variation was also detected at various scales (20cm and 2m) and in both the horizontal and vertical dimensions. They concluded that herbaceous

perennial plants are likely to exploit relatively nutrient rich patches at very fine scales thus contribute to changes of the spatial and temporal nutrient patterns at these scales. Similarly, Ryel et al. (1996) and Cain et al. (1999) suggested a strong plant effect on spatial patterns of soil nutrients.

Vegetation dynamics during succession are also believed to be related to the spatial patterns in soil nutrients. Gross et al. (1995) measured spatial variations of soil nitrogen and moisture levels in three plant communities. The study found that, in a mid-late successional field, a larger portion of the variance of nitrogen was spatially dependent than in a newly abandoned field or a second-growth forest. At the same time, the mid-late successional field had a larger range (of spatial dependence) than the other two sites. Although the study did not find any predictable trend in soil resource heterogeneity, the results showed that vegetation dynamics over a successional time scale could have a measurable impact on the scale and magnitude of soil resource heterogeneity.

4. Dynamics of Spatial Heterogeneity and Its Mechanisms

One of the main themes in ecology is how different communities change over time. Changes in species composition and community structure through time have been addressed extensively in the literature of succession. It is also well understood how nutrient availability changes over succession in different ecosystems. However, little information is available to address temporal changes of soil resource heterogeneity during succession.

Succession is a sequence of changes initiated by disturbance (Ricklefs 1997). Forest succession is often characterized as change in species composition or the replacement of the biota of a site by one of a different nature (Barnes et al. 1998). Once succession begins, plant competition is believed to be an important driving force in determining species composition in a community. And competition between plant individuals often occurs through some intermediary such as resources, pollinators, dispersers, herbivores, or microbial symbionts (Goldberg 1990). Therefore, if vegetation dynamics follow predictable trends during succession, we would expect spatial heterogeneity of resources to follow equally predictable temporal patterns. Current ecological theories indeed point to that direction.

Goldberg (1990) separated the plant-plant interaction into two distinct processes: one or both plants have an *effect* on abundance of the intermediary and a *response* to changes in abundance of the intermediary. If we add a spatial component into this theoretical framework, an interaction between substrate heterogeneity and spatial distribution and structure of plants can be assumed: plants have effects on and responses to substrate heterogeneity. Therefore, soil heterogeneity can affect and be affected by plants. In other words, there may a "cause-effect" relationship between plants and substrate, in which both plants and substrate can be either the recipient of an effect or the giver of an effect.

This "cause–effect' relationship can take many forms, depending on the relative strength of *effect* and *response*. The effect of plants on soil heterogeneity can be as important as that of soil heterogeneity on plants. In some cases, however, this balance between plants and substrate can shift towards plants or soil. As suggested by Gibson

(1988), soil heterogeneity did not appear to be controlling the plant patterns in the grassland. Rather, the plants themselves were inducing the soil patterns.

Therefore, by studying the interactions between the heterogeneity in plants and substrate, we could gain a better understanding of plant competition, and ultimately the directions and rates of forest succession. We must recognize that these interactions are highly dynamic. As spatial scales become finer, rates of interactions between plants and substrate will be faster. In this section, I will discuss the interactions between substrate and plants at spatial scales from individual plants to sub-community level.

1) Effects of substrate spatial heterogeneity on plants

Plants acquire resources in patchy environments. They respond to temporal and spatial heterogeneity, exploiting resources from pulses and patches, and competing with neighbors in the face of this variability (Caldwell and Pearcy 1994). There is considerable evidence that many plants respond to this heterogeneity with phenotypic plasticity. Plasticity, a capability of adjusting the size and distribution of shoot canopies and root systems in response to changes of the external supply of resources (Campbell et al. 1991), presumably, can increase the efficiency of resource foraging and allow plants to respond to high nutrient patches through the proliferation of their roots in these patches (Passioura and Wetselaar 1972, Granato and Raper 1989, Campbell et al. 1991, Mou et al. 1997, Einsmann et al. 1999).

Experiments of this root response to enriched nutrient patches began with crops, species that are limited to a small number, and have particular high growth rates and large demands for nutrients (Robinson and Van Vuuren 1998). With non-crop plant species,

the situation may be different. Most species that ecologists encounter in the field are often slow-growing or less responsive to resource enrichment (Robinson and Van Vuuren 1998). However, recent evidence suggests that many species are responsive in both poor (Einsmann et al. 1999), and rich habitats (Bhat and Nye 1973, Robinson and Van Vuuren 1998).

It has been observed that species differ in their capacity to make plastic adjustments to the size and distribution of organs (Jackson and Caldwell 1989). These differences might be important in determining how successfully different species capture resources in heterogeneous habitats (Grime 1979, Tilman 1988). Most wild plants live in an environment with resource patches and pulses. Therefore, the capacity to make these plastic adjustments has been thought to be particularly critical for the growth and dominance of species, especially when competition is important in vegetation dynamics. This line of thought has stimulated hypotheses on the plasticity of plant foraging behavior as related to competition and community structure. The experiments to test these hypotheses were soon followed.

Campbell (1991) hypothesized that in a community, dominant species will be "coarse-grained" in both time and space in their plastic responses and foraging habits, while foraging by subordinate species is comparatively "fine-grained". To assess this hypothesis, a series of light and nutrient foraging experiments were conducted on eight herbaceous plant species that cover a wide variation in morphology, life history, potential growth and ecology. Based on the results from these experiments, the authors suggested that *scale*, *precision* and *rate* are the primary criteria to distinguish dominant species from subordinates of a community. Dominant species are characterized by *"high scale"*

foraging, which refers to the monopoly by dominants in light and nutrient capture. In contrast, subordinate species tend to be "*high precision*" foragers for their ability to make fine adjustments to resources. Therefore, there may be a trade-off between scale and precision.

This trade-off, if it exists, could have important implications in plant foraging traits, nutrient heterogeneity, plant competition, and community structure. Not surprisingly, this hypothesized tradeoff drew a lot of attention from ecologists and eventually lead to a number of studies designed to test the idea.

Mou *et al.* (1997) discovered that competing tree species differ in root responses to fine-scale nutrient patches for scale and precision under sufficient nutrient supply. While sweetgum roots concentrate in the fertilized patch, loblolly pine roots extended more to the unfertilized patches. In contrast, the two species did not differ significantly in root morphology, as rich patches caused increased root interbranch length and smaller root diameter for both species. The difference in foraging traits among different species was also detected in other studies. Robinson (1994) reviewed the responses of 27 wild plants to nutrient patches and concluded that differences exist among different species (fast-growing vs. slow growing in particular) in root plasticity, root growth, root proliferation.

Einsmann et al. (1999) examined nutrient foraging traits for 10 co-occurring plant species. Large differences in scale, precision, and sensitivity between species were observed. No evidence was found to support the negative correlation between scale and precision, as Campbell (1991) previously hypothesized. And interestingly, some sensitive species were found to have very low precision. This might mean that

physiological plasticity and root life span could be important for explaining the mechanisms underlying plant responses to nutrient heterogeneity. Studies showed that even in the absence of plasticity, soil heterogeneity could be potentially important to plants. Using Barber-Cushman nutrient uptake model, Jackson and Caldwell (1996) simulated the importance of soil heterogeneity and root plasticity for nitrate and phosphate uptake. Their results suggested that nutrient uptake can be dramatically greater in an enriched patch of soil without any morphological or physiological adjustment.

It is clear that species with different growth rate and contrasting life forms have different foraging traits. But the underlying mechanisms remain poorly understood. A tradeoff between scale and precision can partly explain the coexistence and dominance of different species during the succession, but evidence that strongly support this tradeoff is still lacking.

Most studies being discussed so far did not consider the temporal scales of plant responses to nutrient patches. However, Jackson et al. (1990) found that plants could respond to patchy distribution of nutrients in a short period time. In a series of field experiments with three perennial species, large and rapid increases were found in the uptake kinetics of plant roots within days after creating nutrient-rich soil patches. This study, combined with the results from others, suggested that the rapid physiological plasticity of roots in fertile soil microsites may be influenced by many factors: a time dependency, rooting density and root length, site nutrient levels, plant tissue nutrient concentrations (which determine plant demand for nutrients), and plant species (fast vs. slow-growing, and those from rich habitats vs. poor habitats).

In summary, one key issue in the effects of soil heterogeneity on plants is the plasticity of root foraging. To fully understand plasticity of plants, more information is needed on how different species (or functional groups) respond to resource patches in nature, and how these resource patches distribute across space and change through time.

2) *Effects of plants on substrate spatial heterogeneity*

Plants are known to affect substrate structure and function. Through root extension, nutrient uptake, litter accumulation, shading, inter and intra-specific competition for resources and space, and many other means. Tilman and Wedin (1991) tested the relationship between plant traits and resource reduction for five grasses growing along a nitrogen gradient. They found that the species differed significantly in the levels to which they reduced soil solution nitrate and ammonium concentrations and light penetration to the soil surface. In an earlier study, Wedin and Tilman (1990) suggested that species effects can be as, or more important than abiotic factors, such as climate, in controlling ecosystem fertility. In a review of effects of plant species on nutrient cycling, Hobbie (1992) suggested that plant species could have positive feedback effects on patterns of nutrient cycling in natural ecosystems. For example, in nutrient-poor ecosystems, plants grow slowly, use nutrients efficiently and produce poor-quality litter that decomposes slowly and deters herbivores. In contrast, plant species from nutrient-rich ecosystems grow rapidly, produce readily degradable litter and sustain high rates of herbivory, further enhancing rates of nutrient cycling. It is interesting to see that species from low-nutrient ecosystems have inherently low relative growth rates, and thus have a low demand for nutrients.

These studies demonstrated the role of plants in nutrient cycling and energy flow but without clear reference to the creation of spatial heterogeneity. A more recent study by Finzi et al. (1998a&b) found that there are strong canopy tree-soil interactions. The contents of soil carbon, nitrogen, pH and cations were influenced by the canopies of individual trees of six different hardwood species dominant in a mid- to late-successional northwestern Connecticut hardwood forests. These patterns suggest that plant activity can create environmental heterogeneity.

An earlier study by Zinke (1962) demonstrated species effects on soil heterogeneity explicitly. The study was conducted in a 45-year-old shore pine (*Pinus contorta* Dougl. ex Loud) system growing on a sand dune area. Soil samples were taken to a depth of 2.5 inches at distances of 4, 8, 12, and 16 ft from the tree on 4 transects at right angles to each other. It was found that pattern of soil properties under single forest trees is generally developed with radial symmetry to the tree, varying with distance from the tree trunk so that there is a systematic change in pH, nitrogen content, exchangeable bases, and exchange capacity and volume weights. The general pattern of this variability is due presumably to the difference between the effects of stem flow, bark litter, leaf litter, and the adjacent opening or neighboring tree. The author suggested that the observed pattern might be predictable in a given forest region.

In a recent experiment, Kleb and Wilson (1997) directly investigated vegetation effects on soil resource heterogeneity (variations in available nitrogen and moisture contents) in prairie and forest by placing soil cores from one system in the rooting zone of another system. Their results showed that: 1) resource heterogeneity tended to be higher in forest than in prairie over the scale of 10 and 90cm; 2) soil resource

heterogeneity is influenced by vegetation; 3) soil resource heterogeneity did not appear to be linked to plant diversity; and 4) resources differed in their heterogeneity. The mechanism by which vegetation influence soil heterogeneity, they suggested, is most likely related to the uptake of resources. They also stated that there might be a general inverse relationship between resource levels and degree of heterogeneity (evaluated by coefficient of variation of a certain resource).

It is worth noting that possible mechanisms of this plant effect are operating on different time scales. Effects from litter input, stem flow, and shading may take long time (years to decades) to be observable and may be relevant only to woody species or dominant herbaceous species (Finizi et al. 1998 a&b). Noises brought in by insects and animals can be both short-term and long-term but hardly be predictable under field conditions. Redistribution of rainfall (creating fine-scale moisture heterogeneity), changes in soil microorganism populations, root exudates, and root foraging may have significant short-term effects. Identification of temporal scales of different processes and the differentiation of species traits as related to these processes would useful in more clearly interpreting the mechanisms through which plants create, maintain, and transform spatial heterogeneity patterns of soil environment.

3) Interactions between substrate and plants as forest succession proceed

While evidence support both the role of plants in creating and maintaining variations in soil resources and the effects of soil heterogeneity on plant growth and species distribution, information is lacking in addressing the dynamic interactions between spatial patterns of plants and soil heterogeneity. Most studies on soil

heterogeneity have considered only a snapshot of the dynamics of either soil or plants. Meanwhile, successional studies have seldom addressed heterogeneity directly (Armesto et al. 1991). Information is particularly lacking on the interactions between substrate and plant as forest succession proceeds.

Nevertheless, conceptual efforts have led the way to a better understanding of the dynamics of spatial heterogeneity of vegetation and soil. Armesto et al. (1991) proposed a model that predicts that resource heterogeneity during secondary succession fluctuates in cycles but has a general decreasing trend in amplitude and an increasing trend in the wavelength of the heterogeneity cycles. This pattern was thought to be driven by changes in the life history and size of species that occur in the communities of interest. But they cautioned that the predicted pattern could be altered by specific conditions such as land-use history, pretreatment of the site, and many other factors. So far, there have not been many studies to test whether the proposed temporal patterns exist in nature.

Using a geostatistical analysis, Gross et al. (1995) determined spatial variability in soil nitrogen and moisture levels three systems: a newly abandoned field, a mid-late successional field and a second-growth forest in south-western Michigan. A more coarse-grained pattern of spatial heterogeneity was found in the mid-successional site for soil nitrogen, particularly in the surface soils (0-5 cm), than in the other two sites. In the same field, a nested pattern of NO3 availability was detected, indicating spatial variation at multiple scales. The results suggest that patterns of spatial variation in soil nitrogen change over time in successional plant communities, perhaps reflecting changes in the species composition or size of individual plants. However, this study assumed that initial

spatial heterogeneity be the same for the three sites that may not be true and thus weakened the predictive value of the findings.

To identify possible trends in temporal changes of spatial heterogeneity of soil and vegetation, a continuous documentation of spatial heterogeneity over succession in various ecosystems is needed (Armesto et al. 1991).

The main objective of this research was to characterize the temporal patterns of spatial heterogeneity in soil and forest floor following different types of site disturbance. I was also interested in evaluating current methods used to quantify heterogeneity in ecological studies. To achieve these goals, two types of disturbance – artificial (i.e., whole-tree harvesting) and natural (i.e., defoliation caused by beetle outbreaks, simulated by girdling and herbiciding trees) were introduced to a 40-year-old slash pine ecosystem. A number of variables were then measured during a 2.5 year period following disturbance. The patterns following disturbance were compared with those prior to disturbance. In Chapters 2 and 3, I present the patterns for all of the variables measured. Chapter 2 deals with soil moisture, which was measured repeatedly at the same sample locations more often than any other variable. The low degree of measurement error resulting from this sampling intensity allowed me to evaluate methods for quantifying heterogeneity. In the majority of heterogeneity literature, measurement error (e.g., mismatch between sampling locations due to destructive sampling, lack of temporal resolution, etc.) often obscured the effectiveness of quantitative methods. After I gained a better understanding of analysis methods (different measures of heterogeneity such as sample variance, coefficient of variation, and parameters of semivariogram), I then

proceeded in Chapter 3 to analyze the patterns of soil available nutrients and other variables such as soil C and N, litter C and N. The wide range of variables offered an opportunity to seek common patterns in ecosystem responses to disturbance.

Initially, I envisioned semivariogram analysis as a cornerstone of spatial analysis for my data, yet while performing analyses for both Chapter 2 and 3, I found many shortcomings in the way that semivariogram analysis has been used in ecology during the past ten years. I therefore designed a simulation experiment in consultation with Andrew Lister and my graduate advisors to test the effectiveness of semivariogram analysis in detecting spatial patterns in ecological data in general, and to uncover the potential pitfalls associated with this method. The results of this simulation experiment pointed out both the usefulness and problems of the current application of semivariogram analysis in ecology. The approach used in this simulation experiment provided a useful tool for improving sample design and analysis when semivariograms are planned for ecological studies.

CHAPTER 2

TEMPORAL CHANGES IN SPATIAL PATTERNS OF SOIL

MOISTURE FOLLOWING DISTRUBANCE: AN EXPERIMENTAL

APPROACH

Abstract. The significance of spatial heterogeneity in ecological systems has often been recognized but the studies that characterize both spatial and temporal aspect of heterogeneity in forest ecosystems have been lacking. We quantified heterogeneity using two quantitative components: global (non-spatial) variability and spatial dependence. These were quantified using soil moisture sampled for 2.5 years in the same ecosystem (a *Pinus elliottii* Engelm. forest) following whole-tree harvesting, which is a common anthropogenic disturbance, and tree girdling which simulates a natural disturbance caused by bark beetle outbreaks. We hypothesized that spatial heterogeneity patterns of soil moisture would follow predictable temporal trends.

Global variability increased after disturbance, and then declined, eventually returning to the level of an undisturbed plot. Relative to girdling, whole-tree harvesting resulted in greater, more rapid, and more prolonged changes in both global variability and patterns of spatial dependence.

Geostatistical parameters commonly used to characterize spatial patterns did not show consistent temporal trends; however, the presence and degree of spatial dependence were related to disturbance treatments, spatial sampling scale, and vegetation dynamics. Our results suggest that studies of temporal changes in spatial heterogeneity can be substantially improved if multiple components of heterogeneity are quantified, more than one scale of observation is used, replicate plots are employed, and if sole reliance on geostatistics is avoided. Our results also suggest that in forest ecosystems, global variability of soil moisture increases after a broad-scale disturbance, and then declines.

Introduction

Interest in the role of spatial and temporal heterogeneity in ecological organization and biodiversity has increased considerably (Hutchings *et al.* 2000). Soil resource heterogeneity influences plant growth and competitive interactions (Chapin 1980; Palmer 1994), coexistence of plant species and species diversity (Levin 1974; Grime 1979; Bell *et al.* 2000), and spatial patterns of species distribution within plant communities (Snaydon 1962; Palmer 1990; Nicotra *et al.* 1999). Plants also alter spatial patterns of resources (Hendrickson & Robinson 1984; Breshears *et al.* 1997; Finzi *et al.* 1998a,b), leading to dynamic interactions between spatial patterns of vegetation and soil resources. To describe such interactions and thereby uncover key ecological functions, robust spatial quantification approaches are needed.

Quantification of heterogeneity requires identification of appropriate scales of the questions and the organisms considered (Addicott *et al.* 1987; Wiens 1989; Miller *et al.* 1995). Soil resource heterogeneity has been described at spatial scales ranging from centimeters to broad scale landscape levels (Jackson & Caldwell 1993a,b; Stark 1994; Ehrenfeld *et al.* 1997). Many soil properties vary substantially at scales of meters or less that directly affect plant growth (Antonovics *et al.* 1987; Bell & Lechowicz 1994). Environmental variability may change as spatial scale changes, or show nested patterns (Bell *et al.* 1993; Robertson *et al.* 1997; Pastor *et al.* 1998), because different soil processes may operate at different scales (e.g. individual, community, and landscape levels) (Robertson & Gross 1994). Therefore, soil resource heterogeneity in natural communities should be examined at multiple scales.

Heterogeneity is a complex concept and therefore its quantification should focus on its specific components (Li & Reynolds 1995; Cooper *et al.* 1997). Global variability and spatial dependence are two measures widely used in quantifying spatial heterogeneity (e.g. Jackson & Caldwell 1993a, 1993b; Gross *et al.* 1995; Miller *et al.* 1995; Schlesinger *et al.* 1996; Robertson *et al.* 1997; Pastor *et al.* 1998; Nicotra *et al.* 1999). Global variability is expressed by the variance of an ecological variable within a given sampling area (Bell *et al.* 1993; Li & Reynolds 1995). Spatial dependence of a spatial variable is usually characterized by a semivariogram, and two semivariogram parameters frequently used in ecological studies are SH% and range. SH% is the proportion of the total variability due to spatial factors, and indicates relative structured variability (Robertson & Gross 1994). Range is the distance within which the measured variable is spatially autocorrelated (Journel & Huijbregts 1978; Robertson & Gross 1994; Li & Reynolds 1995). By comparing global and spatial dependence of different variables, researchers have tried to explore causal relationships between plant and soil (Schlesinger *et al.* 1996), herbivore and environment (Pastor *et al.* 1998), light distribution and seedling regeneration (Nicotra *et al.* 1999), and greenhouse gas emissions and soil properties (van den Pol-van Dasselaar *et al.* 1998). However, a widely accepted, effective approach in spatial analyses has not been established in ecology. This has greatly hampered the understanding of ecological heterogeneity. For example, the use of variance and CV in spatial analyses is still confusing ecologists (Downing 1991, Dent & Grimm 1999, Bell *et al.* 2000); the effectiveness of semivariogram range in characterizing patchiness remain unclear (Nicotra *et al.* 1999, Dent & Grimm 1999, Ryel *et al.* 1996, Meisel & Turner 1998).

An adequate understanding of heterogeneity also requires the attention on temporal aspects. Only a few studies have briefly discussed temporal changes in spatial heterogeneity (Bramley & White 1991; Pastor *et al.* 1998; van den Pol-van Dasselaar *et al.* 1998). In most studies, ecological heterogeneity is usually examined with snap-shot data, while spatial distributions of many variables can change over a wide spectrum of temporal scales, from days to years (e.g. Gross *et al.* 1995; Ryel *et al.* 1996; van den Pol-van Dasselaar *et al.* 1998; Cain *et al.* 1999; Farley & Fitter 1999). The short-term temporal variation of soil resources has been cited as a reason for the poor correlation between spatial patterns of vegetation and those of soil properties (Robertson *et al.* 1997; Ehrenfeld *et al.* 1997).

This article is one of the reports of our on-going study on spatio-temporal heterogeneity of a coastal plain forest ecosystem in South Carolina, USA. The main objectives of this study were: 1) to quantify temporal changes of global variability and spatial patterns of soil moisture, and 2) to relate these changes to ecological processes such as vegetation dynamics during early succession. We applied two disturbance treatments, whole-tree harvesting- a common anthropogenic disturbance, and tree girdling-a simulation of defoliation caused by outbreaks of bark beetle or pathogens, to a slash pine (*Pinus elliottii* Engelm.) ecosystem. We took soil moisture samples before the disturbance treatments and during the first 2.5-year period after the disturbances to examine the spatio-temporal changes of soil and vegetation variables in this early successional period when the rapid changes occurred.

In general, we predicted that spatial variation of the dynamic soil variables (available nutrients and water) would greatly increased after the disturbance with greater

change at the harvested sites. We also predicted that this increased availability and heterogeneity of the variables would be transient due to rapid reestablishment of biomass (Canham & Marks 1985, Mou *et al.* 1993).

Specifically, we hypothesized that: (1) global variability of soil moisture would increase after disturbance and then decrease with the reestablishment of vegetation; (2) spatial patterns of soil moisture would become more fine-grained after disturbance due to vegetation removal and increased patchiness of the forest floor, and then become more coarse-grained as revegetation proceeds; and 3) whole-tree harvesting would result in greater, more rapid, and more prolonged changes in both global variability and spatial patterns of soil moisture than would girdling.

Methods

Study Site: This study was conducted in a 40-yr-old slash pine plantation located at the U.S. Department of Energy's Savannah River Site near Aiken, South Carolina. The climate of the study area is typical subtropical. The mean July maximum, January minimum and annual temperatures are 27°, 9° and 24° C, respectively. The mean annual precipitation (113 cm) is relatively evenly distributed throughout the year (South Carolina State Climatology Office, 1998). The soils are well-drained Dothan sandy loam (kaolinitic, thermic Plinthic Kandiudult) with a low nutrient-holding capacity and a low organic matter content (Rogers 1988). The site was a pasture prior to the establishment of the plantation in 1958, and was probably used for row crop production sometime between 1900 and 1950 (Rogers 1988). Prescribed burning was used to control forest floor fuel load in 1988 and 1993; the fires burnt relatively evenly throughout the stand.

We chose a visually homogeneous study site with a low topographic relief and similar understory species composition. The dominant overstory species is slash pine that comprised 82.5% of the pre-disturbance stand with total basal area of 37.3 m^2/ha. Other common overstory species include seve ral oaks (*Quercus* spp.), waxmyrtle (*Myrica cerifera* L.), and black cherry (*Prunus serotina* Ehrh.) (Lister *et al.* 2000).

Plot Establishment: Five one-hectare plots were randomly placed within a 20-ha area. In March 1997, a 50 x 50 m permanent survey plot was established in the central portion of each plot with a 25 m buffer zone on each side. Each survey plot was divided into 100 grid cells of 5 x 5 m. Coarse-scale sampling locations were systematically established at 41 of the grid intersections (Fig. 1) following Halvorson *et al.* (1994). Within each survey plot, two grid cells were randomly chosen and further divided into 100 micro-grids of 0.5 x 0.5 m. An additional 41 sampling points were arranged for each grid cell for fine-scale sampling, with the same sample layout as the coarse scale (Fig. 1). This nested sampling system allowed us to examine spatial variations at scales from 0.5 to 60 m using geostatistics with a relatively balanced distribution of sample pairs at all distance lags. Coarse-scale sampling locations remained unchanged throughout the study period. Fine-scale plots were randomly relocated each year to minimize bias associated with sampling disturbance. Over the entire sampling period, fine-scale plots have been relocated for three times: May 1997, and the beginnings of 1998 and 1999.
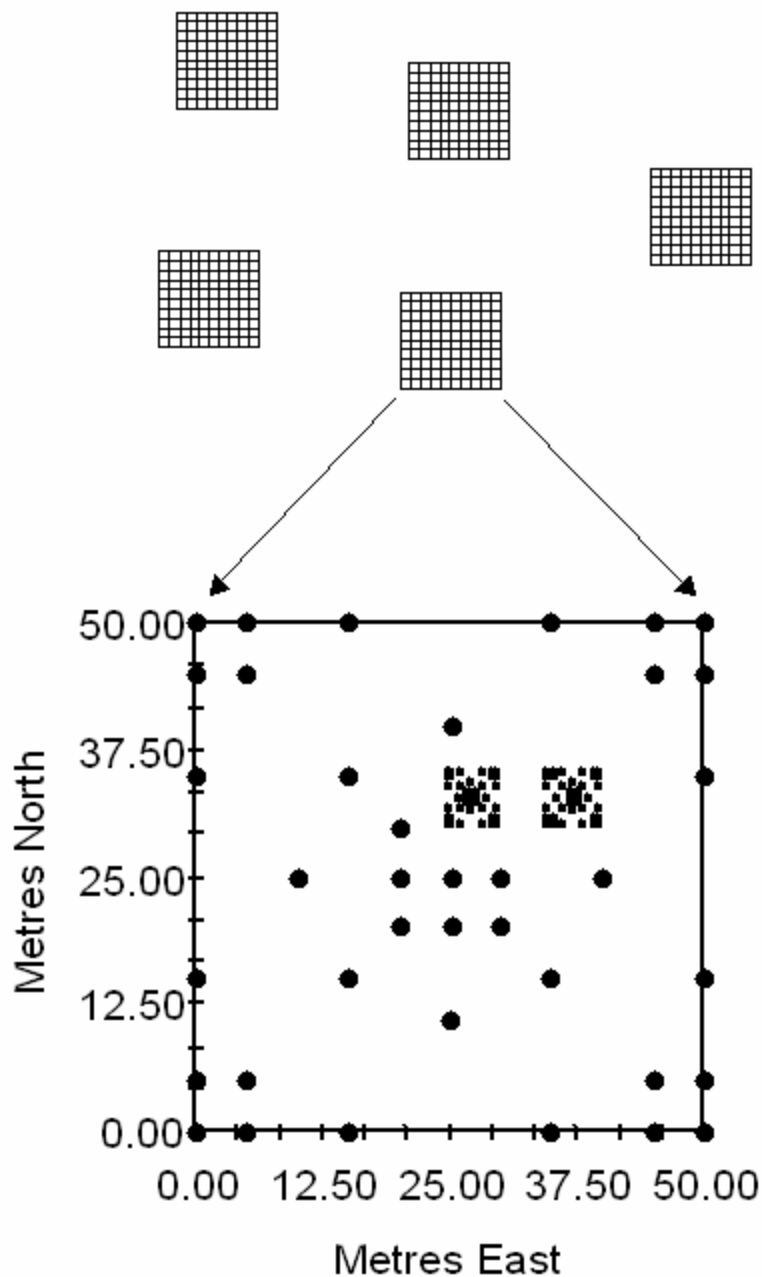
Figure 2.1 Layout of survey plots at Savannah River Site near Aiken, South Carolina, USA. In each of the five plots, 41 points were located on the nodes of a grid partitioned into one hundred 5 x 5 m cells, in a configuration to optimize semivariogram analysis with a minimum sampling interval of 5 m. The same sampling layout was also applied to each of two randomly chosen cells, but with a minimum sampling interval of 0.5 m.

Disturbance Treatment: In late May 1997, a commercial whole-tree harvest was applied to two randomly selected plots (Harvested 1-H1, Harvested 2-H2). Girdling was applied to another two randomly selected plots (Girdled 1-G1, Girdled 2-G2). One plot (Undisturbed) was left undisturbed as a reference. In H1 and H 2 plots, trees of all sizes were cut and removed from the site, but a large amount of slash (branches and needles) was left. In G1 and G2 plots, dominant, co-dominant, and intermediate pines were girdled, and the herbicide triclopyr amine (44% ai in water; Garlon 3A, Dow Chemical Co., Midland, MI, USA) was applied to the girdling cuts; all suppressed pines were felled by chainsaw and left in place, and all hardwoods were left undisturbed.

Soil Moisture Measurement: Soil moisture was measured using time domain reflectometry (TDR; Topp *et al.* 1980; Topp & Davis 1985) with a Tektronix model 1502C cable tester system (Tektronix, Inc., Wilsonville, OR, USA). A pair of stainless steel rods of 21 cm was installed vertically, parallel to each other, in the soil at each sampling location to measure moisture (% by volume) of the top 20 cm soil. TDR trace shapes were visually inspected following the procedure of Gray & Spies (1995). Measurements were obtained once before the disturbance treatments (May 10, 1997) and eight times after the treatments between November 1997 and October 1999. Samples were taken at least two days after a rain event and at approximately similar hours during the day. A TDR calibration curve was constructed in the lab using samples of natural soil following the procedure of Topp *et al.* (1980). We found Topp *et al.*'s (1980) equation underestimated soil moisture in dry conditions and overestimated in wet conditions. The linear equation developed for sandy loam soil (core 7) by Gray & Spies (1995) accurately

predicted soil moisture across the entire range in our study, and was adopted for our TDR estimates of soil moisture.

Statistical Analysis: Parametric statistics were performed using SAS-8 (SAS Institute, Cary, NC, USA). The mean, variance, and CV of soil moisture were calculated for each coarse- and fine-scale plot. For each sampling date, we tested differences among plot means and variances at the coarse scale, and differences in variance between a coarse-scale plot and its two embedded fine-scale plots using ANOVA and simple F-test. Coarse- and fine-scale plots could share some sampling points, we included shared points in the coarse-scale data, and excluded them from the fine-scale data before using F tests. Since our sampling is systematic, the results of the ANOVA and F-tests were used to highlight the patterns of the data, rather than to make cause-effect conclusions.

Spatial patterns of soil moisture were examined using trend surface analysis (TSA) and semivariance analysis. Semivariogram modeling requires the data to be stationarity (without trend) (Journel & Huijbregts 1978; Rossi *et al.* 1992), and TSA was used to detect trends in data and to detrend the data prior to semivariance analysis.   . TSA was conducted for coarse-scale samples following the procedure of Davis (1986).

Semivariograms were modeled using GS+ 3.11.12 software package (Gamma Design, Plainwell, MI, USA). When semivariograms were erratic, data were inspected and spatial outliers were deleted following the procedure of Isaaks & Srivastava (1989). Our data had normal distribution in general with less than 5% of extreme values and spatial outliers for each semivariogram. The choices of lag distance were based on a balance between equal lag distance and equal numbers of pairs for each lag (Zheng &

Silliman 2000). Isotropic semivariograms were computed but not directional

semivariograms due to insufficient sample pars. Semivariance parameters used to

characterize spatial dependence include goodness-of-fit (R^2), nugget (C_0), sill ($C + C_0$)

(C: the variability due to spatial dependence), and range (Isaaks & Srivastava 1989; Rossi

et al. 1992; Robertson & Gross 1994). SH% or $C/(C + C_0)$ x 100%, a proportion of

spatial dependence variance, is usually used to indicate the structural variability in a

spatial data set (Li & Reynolds 1995). Range is used to indicate the spatial pattern of

variability. A smaller range may suggest a more fine-grained spatial pattern. A

semivariogram with a high R^2 and a high SH% indicates a strong spatial structure (or

high degree of spatial dependence). If the samples are completely uncorrelated, the

semivariogram will exhibit a so-called pure nugget effect.

Spearman rank correlation coefficient (CC) between soil moisture values on

different sampling dates was calculated to evaluate temporal persistence. A high CC

indicates a high temporal persistence (Kachanoski & de Jong 1988; Goovaerts & Chiang

1993). Temporal persistence was examined at two scales. At the coarse scale, CCs were

calculated for each plot between all possible pairs of the sampling dates. At the fine

scale, CCs were calculated the same way but only within each year because the locations

of fine-scale plots changed yearly. The fine-scale CCs were not calculated for 1997

because fine-scale plots were relocated after the disturbances in 1997.

Results

Temporal Changes of Mean, Variance, and CV: Prior to disturbance, mean soil moisture was similar in all five plots at the coarse scale, though statistically significant differences were tested among the plots (Table 2.1).

Table 2.1 Mean, variance, and CV% for volumetric soil moisture (%) at nine sampling dates in coarse-scale (5-60 m) plots. n=41 for each value. May 10, 1997 is the pre-disturbance sampling date. Means with different upper-case letters (A, B, C, D) within each column indicate significant differences by Duncan's multiple comparison tests (p<0.05) after significant ANOVA tests (p<0.05). Variances with different lower-case letters within each column indicate significant differences according to F test (p<0.05).

Statistics	Plot	Date								
		5/10/97	11/24/97	3/21/98	7/7/98	7/25/98	11/7/98	3/11/99	7/14/99	10/9/99
Mean	Girdled 1	13.9^A	14.7^C	19.5^C	7.1^D	11.8^B	7.8^C	13.6^C	13.8^D	2.4^D
	Girdled 2	13.1^{AB}	15.5^C	21.3^B	8.7^C	11.9^B	8.8^B	13.8^C	14.4^D	2.6^D
	Harvested 1	13.2^{AB}	23.7^A	27.4^A	13.5^A	16.8^A	13.1^A	21.0^A	24.2^A	7.3^A
	Harvested 2	12.0^C	20.1^B	28.4^A	11.8^B	15.9^A	13.0^A	17.7^B	21.4^B	5.0^B
	Undisturbed	12.6^{BC}	15.6^C	17.1^C	6.1^D	12.0^B	7.9^B	12.3^D	15.6^C	3.1^C
Variance	Girdled 1	2.6^b	2.7^c	9.6^c	1.5^d	2.6^c	1.3^d	3.1^b	2.8^c	0.7^b
	Girdled 2	3.3^b	2.5^c	16.6^b	2.5^c	2.1^c	2.2^c	3.2^b	3.2^c	0.8^b
	Harvested 1	6.9^a	11.6^a	27.6^a	16.3^a	13.2^a	12.8^a	7.7^a	8.4^a	2.1^a
	Harvested 2	2.9^b	4.3^b	14.4^b	7.7^b	9.5^b	4.6^b	2.5^b	5.0^b	0.8^b
	Undisturbed	2.2^b	1.9^c	2.3^d	0.7^e	2.0^c	0.8^d	2.4^b	3.4^c	0.8^b
CV (%)	Girdled 1	11.5	11.2	15.9	17.5	13.5	14.5	12.9	12.1	34.1
	Girdled 2	13.8	10.3	19.1	18.2	12.3	16.7	13.0	12.5	34.8
	Harvested 1	19.9	14.4	19.2	29.9	21.7	27.3	13.2	12.0	20.0
	Harvested 2	14.1	10.3	13.4	23.5	19.3	16.5	8.9	10.5	18.2
	Undisturbed	11.7	8.7	8.9	13.8	12.0	11.5	12.6	11.9	28.2

Soil moisture increased after both treatments, and the increase occurred earlier and were greater in the harvested plots than in the girdled ones (Table 2.1, Fig. 2.2). Mean soil moisture of the girdled plots then rapidly decreased to the level of the undisturbed plot and remained low thereafter. The mean soil moisture of the harvested plots had been high during the entire sampling period. The differences between the two replicate plots of each treatment were small (Table 2.1, Fig. 2.2).

Before disturbance, both variance and CV of soil moisture in Harvested 1 were higher than in the other plots (Table 2.1). After disturbance, variance in the two harvested plots increased, and then decreased, gradually returning to the level of the undisturbed plot (Table 2.1, Fig. 2.2). Variance in the girdled plots also increased and then declined, but the magnitude of increase was smaller and the recovery was faster (Table 2.1, Fig. 2.2). CV increased after both disturbance treatments and then declined. The magnitude of the increase was similar for all four disturbed plots, but the recovery was faster in the girdled plots (Table 2.1, Fig. 2.2). Throughout the study period, variance and CV in the undisturbed plot fluctuated a little (Table 2.1). High CVs were observed across all five plots on the last sampling date (October 9, 1999), due to the extremely low means. The two replicate plots of each treatment had similar temporal changes in variance and CV (Fig. 2.2).

Mean, variance, and CV of soil moisture at the fine scale generally followed the temporal patterns at the coarse scale for all treatments (Tables 2.1, 2.2, 2.3 & 2.4). Means were more similar between the two scales than CVs and variances (Tables 2.2, 2.3 & 2.4). Small differences between disturbance treatments were observed. More similar means between the two scales were found in the harvested plots. The differences of

means between the two scales within 10% (based on coarse-scale means) were 13, 16, 8, 6, and 10 out of 18 cases in the H1, H2, G1, G2, and Undisturbed plots, respectively (Table 2.2).

Variances at the coarse scale were greater than that at the fine scale in the harvested plots, especially in the first 18 months after the harvesting, but were more similar, or smaller than that at the fine scale in the girdled/undisturbed plots (Table 2.3). In the disturbed plots, CVs were generally greater at the coarse scale, while marked differences in CV between the two scales were not detected in the undisturbed plot (Table 2.4). The two fine-scale replicate plots were generally similar in their CVs at each sampling date, particularly in the undisturbed plot.
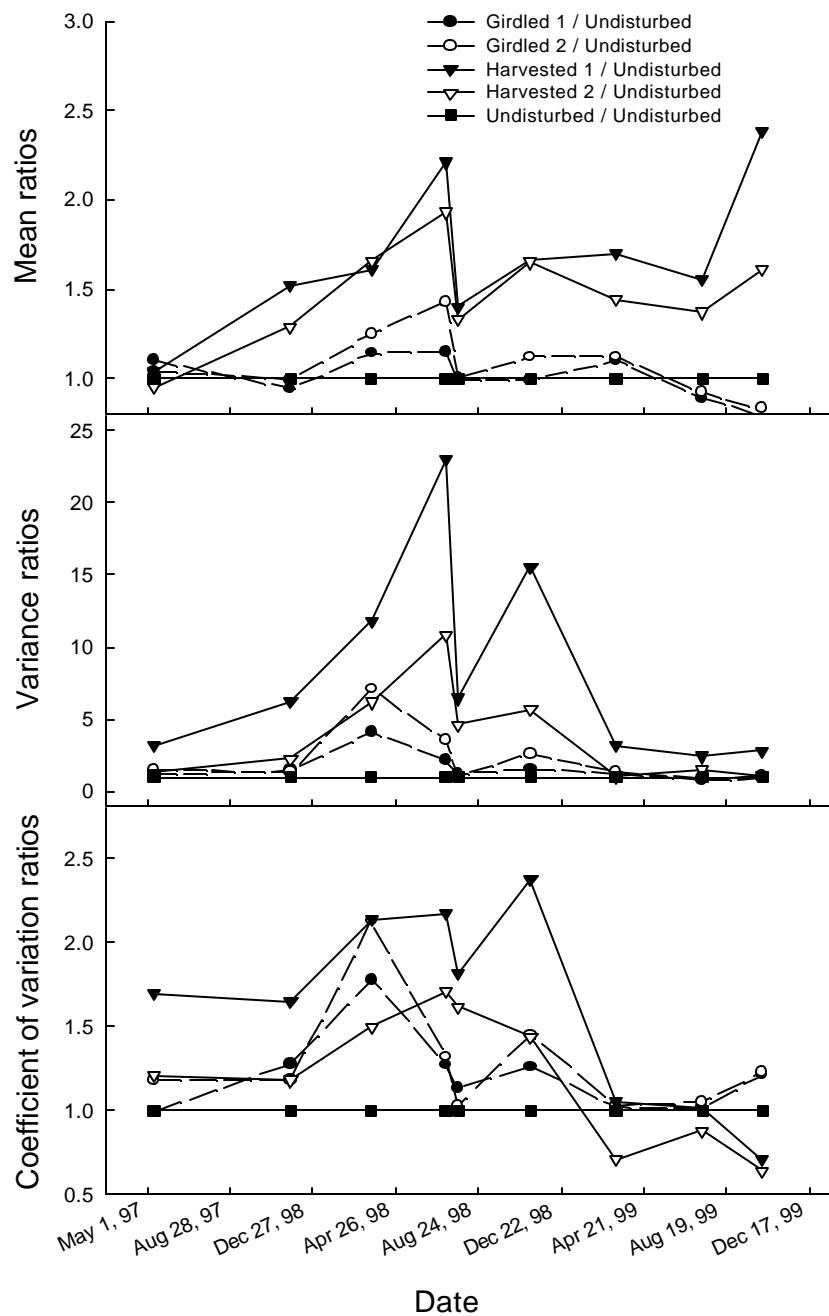
Figure 2.2 Temporal changes in mean, variance, and CV of soil moisture at the coarse scale (5-60 m) expressed by the ratios of mean, variance, and CV of soil moisture in each plot divided by those in the undisturbed plot.

Table 2.2 Ratios of mean soil moisture between a coarse-scale plot and the two nested fine-scale plots (a & b) at each sampling date. May 10, 1997 is the pre-disturbance sampling date, the remaining dates are post-disturbance. An average (Avg.) of all post-disturbance ratios is also indicated.

Plot (coarse/fine)	1997		1998				1999			
	10-May	24-Nov	21-Mar	7-Jul	25-Jul	7-Nov	11-Mar	14-Jul	9-Oct	Avg.
Girdled (1/a)	1.04	0.98	0.73	0.64	0.79	0.72	0.89	0.81	0.70	0.78
Girdled (1/b)	1.05	0.96	0.86	0.94	0.90	0.93	0.92	0.81	0.84	0.89
Girdled (2/a)	0.96	0.88	0.66	0.8	0.77	0.79	0.98	0.85	0.66	0.80
Girdled (2/b)	0.93	0.87	1.13	0.96	0.88	0.81	0.97	0.91	0.64	0.89
Harvested (1/a)	1.01	1.07	1.12	1.07	1.08	1.14	1.07	0.94	0.95	1.06
Harvested (1/b)	1.18	1.17	1.00	1.09	1.07	1.13	1.05	0.98	0.98	1.06
Harvested (2/a)	0.97	1.04	1.05	0.92	0.92	0.95	1.08	1.07	0.97	1.00
Harvested (2/b)	1.08	1.02	0.86	0.91	0.90	1.02	1.02	0.87	0.94	0.94
Undisturbed (/a)	0.96	0.96	0.96	0.81	0.83	0.87	1.08	0.94	0.81	0.91
Undisturbed (/b)	1.03	1.03	0.94	0.71	0.89	0.82	1.02	0.90	0.72	0.88

Temporal Changes in Spatial Patterns: Significant spatial trends in soil moisture were not found before disturbances, but spatial dependence was detected in four of the five plots (Table 2.5 & 2.6). Semivariogram ranges of G1 and G2 were 35 m and 22 m, respectively, with relatively high SH%s (> 75%) (Table 2.6). Semivariogram of H1 showed a relatively weak spatial dependence ($R^2 = 0.39$, SH%= 65%), while that of H2 showed a nugget model (Table 2.6). Spatial dependence in the undisturbed plot was weak with a low R^2, a low SH%, and a short range of 8 m (Table 2.6).

Table 2.3 Ratios of variance of soil moisture between a coarse-scale plot and the two nested fine-scale plots (a & b) at each sampling date. * = variance of the coarse-scale plot is significantly different from that of a nested fine-scale plot (F-tests, α=0.05). May 10, 1997 is the pre-disturbance sampling date, the remaining dates are post-disturbance. An average (Avg.) of all post-disturbance ratios is also indicated.

Plot (coarse/fine)	1997		1998				1999			Avg.
	10-May	24-Nov	21-Mar	7-Jul	25-Jul	7-Nov	11-Mar	14-Jul	9-Oct	
Girdled (1/a)	0.44*	1.37	0.69	0.19*	0.61	0.42*	0.71	1.12	1.20	0.79
Girdled (1/b)	0.89	0.75	1.30	1.19	1.29	1.72	1.38	1.02	1.65	1.29
Girdled (2/a)	0.64	1.05	0.90	0.48*	0.34*	0.74	0.86	1.11	0.83	0.79
Girdled (2/b)	1.02	0.98	3.61*	0.61	0.77	1.20	1.08	2.05*	0.70	1.38
Harvested (1/a)	1.98*	1.81*	4.75*	2.07*	3.33*	3.54*	1.45	1.91*	2.01*	2.61
Harvested (1/b)	3.28*	2.67*	7.74*	1.96*	2.47*	5.36*	2.52*	2.31*	2.97*	3.50
Harvested (2/a)	1.23	1.37	2.36*	1.77	4.12*	2.30*	0.54*	1.44	1.61	1.94
Harvested (2/b)	0.77	0.94	4.01*	1.34	2.49*	1.06	0.91	0.70	1.96*	1.68
Undisturbed (/a)	1.20	0.79	0.44*	0.15*	0.54*	0.88	1.24	0.96	1.60	0.83
Undisturbed (/b)	1.42	0.77	0.78	0.29*	0.60	0.48*	0.89	0.74	1.07	0.70

Table 2.4 Ratios of coefficient of variation of soil moisture between a coarse-scale plot and the two nested fine-scale plots (a & b) at each sampling date for the comparison of the relative global variability between coarse- and fine-scale plots. May 10, 1997 is the pre-disturbance sampling date, the remaining dates are post-disturbance. An average (Avg.) of all post-disturbance ratios is also indicated.

Plot (coarse/fine)	1997		1998				1999			Avg.
	10-May	24-Nov	21-Mar	7-Jul	25-Jul	7-Nov	11-Mar	14-Jul	9-Oct	
Girdled (1/a)	0.64	1.19	1.14	0.68	0.98	0.90	0.94	1.31	1.57	1.09
Girdled (1/b)	0.90	0.90	1.33	1.17	1.26	1.41	1.28	1.25	1.53	1.27
Girdled (2/a)	0.83	1.17	1.44	0.87	0.76	1.09	0.95	1.25	1.38	1.11
Girdled (2/b)	1.08	1.14	1.68	0.81	1.00	1.36	1.08	1.57	1.31	1.24
Harvested (1/a)	1.40	1.26	1.95	1.35	1.69	1.65	1.12	1.47	1.49	1.50
Harvested (1/b)	1.54	1.40	2.79	1.29	1.47	2.04	1.51	1.56	1.75	1.72
Harvested (2/a)	1.14	1.13	1.47	1.45	2.20	1.60	0.68	1.12	1.31	1.37
Harvested (2/b)	0.81	0.95	2.32	1.28	1.75	1.01	0.94	0.97	1.49	1.34
Undisturbed (/a)	1.10	0.92	0.70	0.48	0.89	1.08	1.04	1.04	1.55	0.96
Undisturbed (/b)	1.21	0.85	0.94	0.75	0.87	0.84	0.93	0.95	1.43	0.94

After disturbance, spatial trends were detected in all of the disturbed plots. First- or second-order trends appeared at the first two post-disturbance sampling dates (Nov. 24, 1997, March 21, 1998) in the harvested plots, but only at the second sampling date in the girdled plots (Table 2.5). Spatial trends disappeared after the second sampling date in all disturbed plots except in H1 where spatial trends were found throughout the post-disturbance sampling period, but the trend proportion of the variance (Var %) declined with time (Table 2.5). Weak spatial trends reoccurred in H2 and G1 on March 11, 1999. All semivariograms of detrended data had nugget models. For those data sets with no spatial trends, spatial dependence was not detected except couple occasions in G2 (Table

Table 2.5 Trend surface analysis for soil moisture calculated at the coarse scale (5-60 m). Trends were either first- or second-order. No higher-order surfaces were found significant. Var % indicates the proportion of the total variability that can be explained by a spatial trend. P-values indicate the significance level of a spatial trend. Data with no significant trend is indicated by "--".

Parameter	Date								
	5/10/97	11/24/97	3/21/98	7/7/98	7/25/98	11/7/98	3/11/99	7/14/99	10/9/99
Girdled 1									
Trend	--	--	1st	--	--	--	2nd	--	--
Var%	--	--	57.1	--	--	--	29	--	--
P value	--	--	<0.0001	--	--	--	0.03	--	--
Girdled 2									
Trend	--	--	1st	--	--	--	--	--	--
Var%	--	--	44	--	--	--	--	--	--
P value	--	--	<0.0001	--	--	--	--	--	--
Harvested 1									
Trend	--	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd
Var%	--	44.9	73.6	72.5	53.1	72.9	57.4	31.9	48.3
P value	--	0.0006	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0007	0.0002
Harvested 2									
Trend	--	1st	1st	--	--	--	1st	--	--
Var%	--	17.9	47.4	--	--	--	15.7	--	--
P value	--	0.02	<0.0001	--	--	--	0.04	--	--
Undisturbed									
Trend	--	--	--	--	--	--	--	--	--
Var%	--	--	--	--	--	--	--	--	--
P value	--	--	--	--	--	--	--	--	--

Table 2.6 Coarse-scale (5-60 m) semivariogram parameters for soil moisture. The best model fit to the data based on the least squares is indicated as follows: S = spherical, N = nugget, and L = linear, and is shown after R^2 values. Semivariogram with a pure nugget effect is indicated as nugget model (N), in that case all three parameters (Range, SH%, R^2) are marked with "--". When a trend was identified (see Table 2.5), semivariograms were constructed on residuals after detrending, but we also show in parenthesis the parameters calculated based on the data before detrending.

					Date				
Parameter	5/10/97	11/24/97	3/21/98	7/7/98	7/25/98	11/7/98	3/11/99	7/14/99	10/9/99
Girdled 1									
Range (m)	35	--	-- (88)	--	--	--	-- (60)	--	--
SH%	78	--	-- (89)	--	--	--	-- (54)	--	--
R^2/Model	0.66/S	N	N(0.83/S)	N	N	N	N(0.65/S)	--	--
Girdled 2									
Range (m)	22	--	--(107)	--	--	--	45	--	52
SH%	66	--	-- (92)	--	--	--	95	--	78
R^2/Model	0.33/S	N	N(0.84/S)	N	N	N	0.66/S	N	0.76/S
Harvested 1									
Range (m)	62	-- (81)	-- (53)	-- (56)	-- (52)	-- (53)	-- (37)	-- (10)	-- (42)
SH%	65	-- (73)	-- (100)	-- (100)	-- (86)	-- (100)	-- (82)	-- (97)	-- (78)
R^2/Model	0.39/L	N(0.78/S)	N(0.91/S)	N(0.79/S)	N(0.78/S)	N(0.86/S)	N(0.55/S)	N(0.32/S)	N(0.72/S)
Harvested 2									
Range (m)	--	-- (13)	-- (136)	--	--	--	--	--	--
SH%	--	-- (88)	-- (92)	--	--	--	--	--	--
R^2/Model	N	N(0.31/L)	N(0.90/S)	N	N	N	N	N	N
Undisturbed									
Range (m)	8	--	8	--	--	--	--	--	--
SH%	83	--	89	--	--	--	--	--	--
R^2/Model	0.24/S	--	0.39/S	--	--	--	--	--	--

2.6). Spatial trends did not occur at any sampling date in the undisturbed plot and spatial dependence there was also weak (Table 2.6).

We did not perform TSA with fine-scale data because TSA is usually used at broad scales (Burrough 1987), and stationarity is better approximated at fine scales (Journel & Huijbregts 1978). We found that 7 (of 10) fine-scale plots had various degrees of spatial dependence before disturbance. The semivariograms of these plots had R^2 varying from 0.36 to 0.81, SH%, from 55% to 85%, and range, from 1.4 to 13.4, often with large differences between the two replicates in each large plot (results not shown). After disturbance, soil moisture was still spatially dependent in most of the fine-scale plots at most sampling dates. Temporal patterns corresponding to disturbance treatments were not found.

Temporal Persistence of Spatial Patterning: Soil moisture before disturbance was often significantly correlated with moisture after disturbance in the two girdled plots and the undisturbed plot, but not in the harvested plots (Table 2.7). Temporal trends of CCs were not detected, so that we calculated the mean and the CV of the CCs for each plot to demonstrate the average level and variation of temporal persistence in spatial patterning. High CC means and low CV means indicate high spatial persistence. H1 had cross-year and within-year means of 0.70 and 0.74, and corresponding CVs of 25.1% and 21.3%, of the CCs, respectively (Table 2.8). The other four plots had lower cross-year/within-year means and higher corresponding CVs of the CCs (Table 2.8).

Lower means of the CCs and higher CVs of the CCs were found in the fine-scale plots of H1 and H2 (Table 2.9). In the girdled fine-scale plots, the means and CVs of the

CCs were relatively inconsistent between the replicates, and the values were intermediate

between those of the harvested plots and those of the undisturbed plot.

Table 2.7 Spearman rank correlation coefficients (CC) calculated between the pre-disturbance sampling date (May 10, 1997) and individual post-disturbance sampling date. Significance level: * <0.05, ** <0.01, *** <0.001.

Plot	Pre-11/97	Pre-3/98	Pre-7/7/98	Pre-7/25/98	Pre-11/98	Pre-3/99	Pre-7/99	Pre-10/99
Girdled 1	0.43**	0.39*	0.24	0.69***	0.34*	0.59***	0.55***	0.51***
Girdled 2	0.43**	0.36*	0.07	0.39*	0.29	0.50**	0.39*	0.37*
Harvested 1	0.17	0.04	0.12	0.05	0.05	0.18	-0.1	0.2
Harvested 2	0.23	-0.28	0.14	-0.02	0.31	0.27	-0.05	0.21
Undisturbed	0.49**	0.21	0.35*	0.37*	0.17	0.44**	0.25	0.63***

Table 2.8 Summary statistics of spearman rank correlation coefficients (CC) at the coarse-scale (5-60 m) for post-disturbance sampling dates. Cross-year correlations were calculated using the pairs of sampling dates from the same season but different years (e.g. between March 1998 and March 1999, or November 1998 and October 1999). Within-year correlations were calculated using all possible pairs of sampling dates within each year.

	Cross-year		Within-year	
Plot	Mean	CV	Mean	CV
Girdled 1	0.42	42.1	0.49	33.0
Girdled 2	0.39	53.8	0.31	55.3
Harvested 1	0.70	25.1	0.74	21.3
Harvested 2	0.43	64.3	0.40	62.0
Undisturbed	0.44	45.5	0.32	75.9

Table 2.9 Summary statistics of spearman rank correlation coefficients (CC) at the fine-scale (0.5-6 m) for post-disturbance sampling dates. Only within-year correlations (correlations between all possible pairs of sampling dates within 1998, and within 1999) were used.

Plot	Mean	CV
Girdled (1a)	0.66	16.1
Girdled (1b)	0.43	42.9
Girdled (2a)	0.65	20.8
Girdled (2b)	0.56	28.9
Harvested (1a)	0.54	50.2
Harvested (1b)	0.57	53.7
Harvested (2a)	0.56	40.3
Harvested (2b)	0.56	40.9
Undisturbed (a)	0.66	15.6
Undisturbed (b)	0.63	19.4

Discussion

The two different measures of heterogeneity differed in temporal patterns. Temporal trends in global variability supported our hypotheses but the results of spatial dependence analysis were more ambiguous. We therefore discuss them separately.

Temporal Changes of Global Variability: As predicted, global variability (variance) of soil moisture increased after disturbances and then declined, eventually returning to the pre-disturbance level indicated by the undisturbed plot. Global variability demonstrated little change over time in the undisturbed plot. CV of soil moisture followed the same

patterns. Few studies have explicitly addressed temporal changes in soil moisture global variability after disturbance, though temporal changes in soil moisture global variability (or CV) have been reported. Ehrenfeld *et al.* (1997) found little change in CV of soil moisture over time indicating a relatively consistent spatial pattern in closed-canopy pine forests at sites of low topographic relief and sandy soil. Gross *et al.* (1995) reported different levels of soil moisture variability when three communities in different stages of succession were sampled. They did not identify predictable temporal patterns, possibly due in part to the initial site differences of the communities and a coarse resolution in temporal scale that might obscured significant fine-scale temporal patterns. Ryel *et al.* (1996) showed that CV of soil moisture changed over a growing season. Their data indicated a decreasing trend in global variability of soil moisture over a growing season as mean soil moisture availability declined. Using CV alone, Dent & Grimm (1999) concluded that overall variability of nitrate increased during succession in a stream, but their data suggest both absolute variability (variance) and mean decreased dramatically from early succession to middle succession and slightly increased thereafter. However, CV alone maybe misleading, particularly when mean, variance, and CV change in different directions or in different proportions.

Our data supported the hypothesis that whole-tree harvesting would result in greater, more rapid, and more prolonged changes in global variability. The differences in temporal patterns of global variability between harvesting and girdling because of the different intensities, rates, and spatial patterns of vegetation removal and regrowth, as well as differences in the severity and spatial patterns of forest floor disturbance. Whole-tree harvesting removed all the woody vegetation and introduced substantial amount of

disturbance to forest floor (unpublished data) that would greatly increased spatial variations of forest floor micro-topography (Edwards & Ross-Todd 1983; Pritchett & Fisher 1987; Liechty *et al.* 1992) leading to an increase of spatial variation in soil moisture (Beatty 1984; Fleming *et al.* 1998; Clinton & Baker 2000). Global variability might increase immediately after the harvesting. Unfortunately, we did not record the soil moisture until six months after the disturbance. Vegetation recovery in the harvested plots was initially patchy (when plants were small and scattered); this may have further increased soil moisture spatial variability, or simply maintained soil moisture variability until a more uniform and complete establishment of vegetation cover. As a result, the temporal trend in the harvested plots was characterized as an early and extended increase, followed by a slow decline.

Contrast to harvesting, girdling eliminated the overstory pines but left the patchily distributed hardwoods (Lister *et al.* 2000). Girdling caused little immediate disturbance to forest floor and later added only pine needles and coarse woody debris. In addition, girdling might not kill the trees immediately and cut off the evapotranspiration of pine trees until several months later. This may explain the slower and smaller increase in global variability of soil moisture. Meanwhile, the remaining hardwoods may have rapidly extended their root systems and filled the root gaps left by the demise of the pine trees (Wilcznski & Pickett 1993; Jones *et al.* 1996), resulting in a rapid decrease in soil moisture variability.

Temporal Changes of Spatial Patterns: We hypothesized that soil moisture would become finer-grained after disturbance and then become coarser-grained. It was not

supported by the results of TSA and semivariance analysis: 1) at the coarse scale, spatial

trends were not found before disturbance, but appeared in some post-disturbance data

(Table 2.5); 2) non-nugget semivariograms were detected sporadically in disturbed and

undisturbed plots throughout the study period (Table 2.6); 3) when spatial trends were

removed, spatial dependence appeared to be reduced after disturbance (Table 2.6); 4) no

clear temporal pattern in the semivariogram range emerged; and 5) fine-scale and coarse-

scale spatial dependence often showed conflicting patterns.

Bergstrom *et al.* (1998) observed a spatial soil moisture trend occurring in a 225

m long field of 4% average slope showing increasing soil moisture toward the foot-slope

after removal of crop. In this study, vegetation removal apparently triggered the spatial

trends in soil moisture indicating spatial trends of other substrate variables, such as

topographic variation or other soil factors, might overtake the effect of vegetation on soil

moisture. As vegetation quickly recovered, the spatial trend of soil moisture disappeared

indicating a reestablishment of the vegetation control over soil moisture. The persisting

soil moisture spatial trends in Harvested 1 may be a result of a slower vegetation

recovery there and a more pronounced topographic trend (unpublished data).

Spatial patterns of soil moisture may vary with soil moisture levels. Western *et al.* (1998) found a seasonal variation in semivariograms of surface soil moisture (top 30

cm) at Tarrawarra catchment, southeastern Australia. They related this variation to the

seasonality of mean soil moisture. Wendroth *et al.* (1999) also found that semivariogram

range of surface soil moisture (top 10 cm) was related to dry-wet cycles. Study by Ryel

et al. (1996) indicated that semivariogram range increased as mean soil moisture

declined. We cannot identify relationships between mean soil moisture and spatial patterns because we did not sample soil moisture following its annual cycles.

We recognized some potential pitfalls of using semivariogram parameters to characterize spatial dependence. First, a spatial trend in the data might result in semivariograms with large ranges (Rossi et al. 1992). This might have occurred in our study because we found that the spatial trends often coincide with large semivariogarm ranges (Tables 2.5 & 2.6). Second, sampling and data analysis procedure can greatly affect estimation of semivariogram range (Isaaks & Srivastava1989; Bogaert & Russo 1999; Zhang & Silliman 2000). In our analysis, we found that the choice of lag distance, the number of sample pairs for each lag, and the model used all affected the estimate of semivariogram range. Third, semivariogram analysis may be unlikely to detect the multiple scales of pattern in ecological data (Meisel & Turner 1998). The conflicting spatial dependence patterns at two different scales, and the marked differences in spatial dependence between the replicate fine-scale plots may indicate this. Fourth, the conceptual connection between semivariogram range and an ecologically meaningful patch has not been established convincingly. Lastly, sampling intensity seems affect the reliability of semivariogram analyses. Therefore, more work is needed to determine if a functional connection exists between semivariogram range and patch.

Patterns at Different Spatial Scales: Global variability was greater at the coarse scale than at the fine scale in the harvested plots, similar at both scales in the girdled plots, and less at the coarse scale in the undisturbed plot (Table 2.3). It has been proposed that environmental variance may increase continually with scale (Bell *et al.* 1993), but our

results suggest a more complex relationship at the scales we measured (0.5-60 m), especially under the influence of disturbance.

Estimates of global variability may vary with the extent (coverage), and the grain (minimum sampling distance) of the sampling (O'Neill *et al.* 1986; Wiens 1989; Palmer & White 1994), yet it was difficult to examine the impact of sampling scale on the global variability in this study. Because some fine-scale heterogeneity may be lost in coarse-scale sampling (Wiens 1989), estimated coarse-scale variability sometimes may be smaller than fine-scale variability. This may have occurred in the undisturbed plot, or even in the girdled plots (Table 2.3). The greater coarse-scale variability of harvested plots (Table 2.3) may indicate higher broader scale variation caused by processes different from those at fine scales.

Spatial structure (spatial trend and spatial dependence) was detected at both scales but spatial dependence was more prevalent at the fine scale. Nested spatial structure did not emerge when semivariograms calculated from pooled data of two scales. The fine-scale spatial structures did not appear to respond to disturbance treatments, may be due in part to the yearly change of fine-scale plot locations.

Temporal persistence of spatial patterning of soil moisture also differed with spatial scales. High post-disturbance temporal persistence at the coarse scale in Harvested 1 was partly related to the spatial trends throughout the post-disturbance sampling period. High temporal persistence of soil moisture at the fine scale in the undisturbed plot suggested that local processes with low temporal variation such as soil aggregates and root domains may control soil moisture spatial patterning.

Plot Replication: Patterns of spatial dependence is often considered site-specific (e.g. Kelly & Canham 1992; Harvorson *et al.* 1994; Palmer & White 1994; van den Pol-van Dasselaar *et al.* 1998). Most heterogeneity studies did not consider plot replication. In this study, two coarse-scale replicates and four fine-scale replicates were employed for each disturbance treatment. Patterns of global variability were highly repeatable (Fig. 2.2), while that of spatial dependence were not (Tables 2.5 & 2.6). Differences were also found at the fine scale between replicate plots for both disturbance treatments. These inconsistent patterns among replicated plots, along with the observed temporal changes in spatial patterns, suggest that caution should be taken against making broad generalizations on the ecological significance of spatial patterns based on data from a single plot or at a single sampling date.

Conclusions

We used an experimental approach to study spatio-temporal heterogeneity of soil moisture after disturbance of a pine ecosystem. We employed global variability (sample variance) and spatial dependence to quantify spatial patterns of soil moisture and the temporal variations of these patterns. Global variability is a robust measure in quantifying spatial variability and showed consistent and replicable temporal patterns of spatial variation in soil moisture after both types of disturbance. Spatial dependence characterized by semivariograms, however, did not provide patterns that can be summarized. We do not attribute the ineffectiveness of semivariogram analysis to the approach itself; rather, the current use of semivariogram analysis in ecology may be incomplete and require further examination.

Our study also highlights the usefulness of field experiments in improving the understanding of heterogeneity. Gibson (1988) advocated the use of field experiments in heterogeneity studies, but this approach has not been fully embraced. This study demonstrated the value of an experimental approach that directly relates theory to patterns in nature.

CHAPTER 3

TEMPORAL DYNAMICS OF SPATIAL VARIATIONS IN SOIL AND

FOREST FLOOR PROPERTIES FOLLOWING DISTURBANCE

Abstract.   Although the significance of spatial heterogeneity in ecological systems is well recognized, studies have failed to offer generalizations of the pattern and scale of heterogeneity in natural comminutes. Progress has been hindered by the lack of agreement on the definition and quantification of heterogeneity, the lack of understanding of temporal patterns in spatial heterogeneity, and the inadequate use of controlled field experiments. To overcome these limitations, we used a manipulative field experiment to quantify temporal changes of spatial heterogeneity in soil and forest floor properties in a *Pinus elliottii* Engelm. forest in the first 2.5 years following disturbance. A whole-tree harvest was used to simulate a common anthropogenic disturbance, and girdling with herbicide applied to girdles was used to mimic a natural disturbance caused by pine bark beetle outbreaks. Sample variance, coefficient of variation, and the scale and degree of spatial dependence were adopted as four quantitative measures of heterogeneity.

Sample variance of soil available nutrients (NO_3^-, NH_4^+, HPO_4^-) increased by more than an order of magnitude in the first year following disturbance, and then gradually decreased and approximated the level of the undisturbed forest. Coefficient of variation (CV) showed large intra-year fluctuations with values generally greater in the disturbed plots than in the undisturbed forest. Spatial patterns of available nutrients characterized by semivariogram range and SH% did not show consistent differences between the two disturbance treatments and the undisturbed forest.

Mean and sample variance of soil C and N and litter mass increased after harvesting, while forest floor C and N and soil pH showed no responses to either disturbance treatment. Spatial dependence was found before and after disturbance. No consistent temporal patterns in spatial dependence can be found for two replicated plots

within each disturbance treatment. Therefore it was difficult to evaluate the effects of disturbance on spatial dependence.

Despite the different forest floor disturbance patterns resulted from whole-tree harvesting and girdling, the two disturbances had similar effects on the temporal changes of variability in soil available nutrients. The results of our study suggest that temporal patterns of soil nutrient variability may be predictable following disturbance.

Introduction

The importance of heterogeneity over space and time has been examined in both theoretical and empirical studies (Kolasa and Pickett 1991, Caldwell and Pearcy 1994, Hutchings et al. 2000). Recognizing the existence of widespread heterogeneity in nature, ecologists have begun to modify the fundamental assumptions of homogeneity and equilibrium underlying many ecological concepts (Wiens 2000). With guidance from conceptual efforts (Kolosa & Pickett 1991, Dutilleul and Legendre 1993, Li & Reynolds 1995), and newly available techniques to ecology (e.g., geostatistics), heterogeneity studies in the past two decades have progressed from descriptive to quantitative. As a result, the understanding of the scale and magnitude of heterogeneity in nature has been improved.

However, these quantitative studies have failed to offer any generalizations about the scale and pattern of heterogeneity of resources, and the controls on and consequences of these patterns, for several reasons. The quantification of heterogeneity in natural communities still suffers from the lack of agreement in the way heterogeneity should be defined and described. This makes the comparisons among different studies difficult. It

has been recognized that heterogeneity can be more accurately quantified when different data types (e.g. numerical vs. categorical) are distinguished (Li & Reynolds 1995). However, the search for robust measures of heterogeneity is far from complete (Wiens 2000). Geostatistics has offered ecologists tools to analyze spatial patterns of ecological data, but the usefulness of these tools remains in doubt (Meisel and Turner 1998, Wiens 2000). The study of heterogeneity has also been limited by the experimental design. The description of heterogeneity in nature has been based mainly on surveys. It is difficult in such surveys to establish convincingly a link between patterns observed and underlying ecological processes. A better approach may be to use manipulative experiments in the field. A number of studies have demonstrated the usefulness of this approach (Gibson 1988, Bell et al. 2000).

General patterns of heterogeneity may have also been obscured by a lack of attention to temporal dynamics of spatial heterogeneity. Temporal patterns of spatial heterogeneity are important in at least three ways. First, if spatial patterns of soil resources are highly dynamic, as demonstrated by various studies (Gross et al. 1995, Ryel et al. 1996, Cain et al. 1999, Farley and Fitter1999), spatial patterns observed at one point in time may not provide a full view of resource heterogeneity experienced by plants, and are likely to have limited interpretive value (Bramley and White 1991, Cain et al. 1999). Second, if temporal changes in spatial patterns follow certain trends, these trends may offer insights into ecological processes such as dispersal, competition or succession (Armesto et al. 1991, Gross et al. 1995). Third, resource incongruence over both space and time has emerged as an important issue in recent studies (Stuefer 1996, Charlton and Bazzaz 1998). Plants require adequate levels of various resources (light, nutrients, water

etc.) at the same time, so a certain degree of congruence among plant resources may be necessary for normal plant growth and development (Chapin et al. 1987, Stuefer 1996, Carlton and Bazzaz 1998). At any time, resource levels are often spatially incongruent, but they may be more congruent in time, which could have important impacts on competitive interactions and succession.

Since the 1960s, large efforts have been directed to understand biogeochemical dynamics of numerous elements during the ecosystem development, especially N, P, K, Ca, the nutrients critical to plant growth and ecosystem health (e.g., Bormann and Likens 1979). However, dynamics of the spatial pattern of these elements have rarely been addressed. Several recent studies showed marked temporal dynamics in spatial heterogeneity in soil moisture and available nutrients (NO_3^-, NH_4^+ and HPO_4^-) during a growing season (Ryel et al. 1996, Cain et al. 1999). These patterns may reflect natural fluctuations of spatial heterogeneity due to the changes of plant activities in a growing season, but in general, the underlying causes and the relationships to ecosystem development remain unknown.

In this study, we describe temporal dynamics of spatial heterogeneity of soil and forest floor resources during the early stages of ecosystem development with attempts to overcome the limitations of previous heterogeneity studies. We compare several quantitative measures of heterogeneity, including sample variance, coefficient of variation, and indices of spatial dependence, and use a manipulative disturbance experiment. We introduce two types of disturbance: whole-tree harvesting, a common anthropogenic disturbance, and tree girdling which simulates a natural disturbance caused by bark beetle outbreaks.

In the previous chapter, we found that after disturbance, temporal changes of spatial heterogeneity in soil moisture followed a predictable "increase and then decline" pattern. We expect the same spaio-temporal pattern in soil nutrients because disturbance treatments will cause greater heterogeneity while vegetation regrowth following disturbance will gradually reduce soil nutrient heterogeneity (similar processes have been showed to cause temporal patterns in soil moisture). Specifically we hypothesize that: 1) heterogeneity of soil properties will increase after the disturbances and then decrease; 2) temporal changes in heterogeneity will occur immediately following disturbance for available nutrients, but not for nutrient pools; 3) spatial patterns of available nutrients will become more fine-grained following disturbance; 4) harvesting will have greater impact on nutrient heterogeneity than will girdling.

In addition, we examine the issues related to resource congruence. We expect that resources will become more congruent after disturbance because disturbance stimulates mineralization and reduces plant uptake, and therefore highly disturbed patches within the community should have uniformly high resource levels.

Methods

Study site: This study was conducted in a 40-yr-old slash pine (*Pinus elliottii* Engelm.) plantation located at the U.S. Department of Energy's Savannah River Site near Aiken, South Carolina. The mean July maximum, January minimum and annual temperatures are 27°, 9° and 24° C, respectively. The mean annual precipitation (113 cm) is relatively evenly distributed throughout the year (South Carolina State Climatology Office, 1998). The soils are well-drained Dothan sandy loam (kaolinitic, thermic Plinthic Kandiudult)

with a low nutrient-holding capacity and a low organic matter content (Rogers 1988).

The site was a pasture prior to the establishment of the plantation in 1958, and was

probably used for row crop production sometime between 1900 and 1950 (Rogers 1988).

Prescribed burning was used to control forest floor fuel load in 1988 and 1993; the fires

burnt relatively evenly throughout the stand. We chose a visually homogeneous study

site with a low topographic relief and similar understory species composition. Prior to

disturbance, the dominant overstory species was slash pine, which comprised about

82.5% of total stand basal area of 37.3 m^2/ha. Other common species included several

oaks (*Quercus* spp.), waxmyrtle (*Myrica cerifera* L.), and black cherry (*Prunus serotina*

Ehrh.) (Lister *et al.* 2000).

Plot establishment: Five one-hectare plots were randomly placed within a 20-ha area. In

March 1997, a 50 x 50 m permanent survey plot was established in the center of each plot

with a 25 m buffer zone on each side. Each survey plot was divided into 100 grid cells of

5 x 5 m for coarse-scale sampling. Sampling locations were systematically established at

41 of the grid intersections following Halvorson *et al.* (1994). Within each survey plot,

two grid cells were randomly chosen and further divided into 100 micro-grids of 0.5 x 0.5

m. An additional set of 41 sampling points was arranged for each of the two grid cells

for fine-scale sampling, with the same sample layout used for the coarse scale (more

details of our sampling design can be found in Lister et al. 2000). This nested sampling

system allows for examining spatial variations at scales from 0.5 to 60 m using

geostatistics with a relatively balanced distribution of sample pairs at all distance lags,

and for examining sample variance at two separate scales. Coarse-scale sampling

locations remained unchanged throughout the study period. Fine-scale plots were randomly relocated each year to minimize bias associated with potential sampling disturbance. Over the entire sampling period, fine-scale plots have been relocated three times: after the disturbance treatment in May 1997 and in the beginning of 1998 and 1999.

Disturbance treatment: In late May 1997, a commercial whole-tree harvest was applied to two randomly selected plots. Girdling was applied to another two randomly selected plots. One plot was left undisturbed as a reference. In the harvested plots, all trees with DBH greater than 10 cm were felled using feller-buncher and were removed from the site, smaller trees were cut with chainsaw and left in place along with a large amount of slash (branches and needles). In the girdled plots, the dominant, co-dominant, and intermediate crown classes were girdled with a chainsaw, and the herbicide triclopyr amine (44% ai in water; Garlon 3A, Dow Chemical Co., Midland, MI, USA) was applied to the girdling cuts; all suppressed pines were felled by chainsaw and left in place, and all hardwoods were left undisturbed.

Data collection: In March 1997, a 2 cm diameter soil core of the A horizon was taken from 0-20 cm depth at each sampling location after the uppermost forest floor was removed. The soil samples were dried to a constant weight at room temperature prior to analysis. Forest floor samples were collected at each point using a 9 cm diameter steel pipe with sharpened edges. To minimize the sampling disturbance, forest floor samples were taken 10 cm away from the center of each sampling location. Samples were dried at

65° C to a constant weight prior to analysis. Ion resin membranes (Ionics Corp.,

Watertown, MA, USA) were cut into 2.5 x 5.0 cm rectangles and were vertically inserted

into the A horizon soil between a depth of 5 and 10 cm at each sampling location in order

to obtain indices of bioavailable nitrogen (NO_3^- and NH_4^+), and phosphorous (HPO_4^-)

(Lundell 1989, Abrams and Jarrell 1992, Qian *et al.* 1992, Cain et al. 1999). Membranes

were removed after 14 days and immediately refrigerated at 3° C until extraction. After

the disturbance treatment, all sampling locations were recovered. The entire sampling

effort was repeated in March of 1998 and 1999 for post-disturbance sampling. At the

coarse scale, soil and forest floor samples were taken at a distance of 10cm from the

previous sampling locations to minimize the effects of sampling disturbance. For

available nutrients including NO_3^-, NH_4^+ and HPO_4^-, we collected additional set of

samples during mid or late growing season of each year. Therefore, there are five

samples in total for available nutrients, once before disturbance (1997 March sample),

and four times after disturbance (twice in 1998 and twice in 1999). For all the other

variables, three samples were taken, once before disturbance (March 1997), and twice

after disturbance (March 1998 and 1999).

In the laboratory, dried soil samples were passed through a 2 mm sieve and

analyzed for pH and total soil C and N (% by weight) after removing the coarse

fragments (> 2 mm). Thirty randomly chosen samples were weighed to determine the

percentage of the bulk soil made up of coarse fragments. The pH was determined in a

10:1 slurry of deionized H_2O (McLean 1982). Subsamples of 25 mg of the remaining

soil were ground to less than 0.2 mm and oxidized in a Perkin Elmer Model 2100 CHN

analyzer (Perkin-Elmer Corporation, Norwalk, CT 06859) to determine total C and N.

Dried forest floor samples were weighed and ground (<0.2 mm), and 20 mg subsamples were also oxidized in the CHN analyzer for total C and N determination.

Membrane-bound NO_3^- and NH_4^+ were extracted with 2.0 M KCl, and membrane-bound HPO_4^- was extracted with 0.5 M HCl. The extracts were analyzed with a Lachat Model 4000 autoanalyzer (Lachat Instruments, Inc., Milwaukee, WI, USA). The results can be converted to soil nutrient concentrations, but often with difficulties (Cain et al. 1999). We therefore use the concentrations in extracts to indicate the relative nutrient availability in soil. This approach is justified because we were mainly interested in temporal changes in nutrient levels and spatial variations, and we used exactly the same sampling and analysis procedure for each sampling period. Reliability of resin-membranes has been shown by Cain et al. (1999), particularly for sandy soil. Soil moisture was measured nine times during the entire sampling period using time domain reflectometry (TDR; Topp *et al.* 1980; Topp & Davis 1985) with a Tektronix model 1502C cable tester system (Tektronix, Inc., Wilsonville, OR, USA) and was reported in detail in the previous chapter.

Data analysis: Parametric statistics were performed using SAS-version 8 (SAS Institute, Cary, NC, USA). Mean, variance, and CV of each variable were calculated for each coarse- and fine-scale plot. Patterns at two different scales were compared to assess the effects of sampling scale on the variations of soil nutrients. ANOVA tests were not performed to compare treatments because our study was mainly designed to characterize spatial patterns and the temporal changes of these spatial patterns. As shown by previous studies (e.g., Gross et al. 1995, Robertson et al. 1997), an accurate description of spatial

patterns requires a large number of samples (123 samples per plot in this study). Therefore, our ability to replicate disturbance treatments across space was limited. But we were able to provide two replicates for each disturbance treatment to demonstrate the consistency/or inconsistency of patterns following disturbance over space and time.

Correlations were calculated to quantify the congruence between different variables and between the same variable at different sampling periods. Charlton and Bazzaz (1998) quantified resource congruence using Kendall's coefficient, which is a nonparametric measure of correlation among more than two variables. In this study, we were mainly interested in paired correlations and therefore the Spearman rank correlation coefficient was used. We calculated correlations between all variables sampled, and between all sample periods. The majority of the correlations were not significant. Therefore we only present the correlations that were most frequently significant, i.e., those among available nutrients, and between the nutrients and soil moisture. Mean soil moisture for each year was used in nutrient-moisture correlation because we found in the previous study that soil moisture was highly correlated over time (correlation efficients > 0.5) within each year. The minimum significance level was set at p= 0.001 for correlations because we made multiple comparisons in correlation matrices (Bonferroni correction).

Semivariograms were modelled using GS+ software package version 3.11.21 (Gamma Design, Plainwell, MI, USA). When data had a skewed frequency distribution, which was the case for all available nutrients, they were log-transformed prior to analysis. The choices of lag distance and number of pairs for each lag were based on a balance between equal lag distance and equal numbers of pairs for each lag (Zheng &

Silliman 2000). Spatial variability of each variable was assumed to be isotropic because

the number of sampling points was insufficient to calculate directional semivariograms.

To characterize spatial dependence, we used several semivariogram parameters including

goodness-of-fit (R^2), nugget (C_0), sill ($C + C_0$) (C is the part of variability that is spatially

dependent), and range (Isaaks & Srivastava 1989; Rossi *et al.* 1992; Robertson & Gross

1994). A proportion of spatially dependent variance SH% or $C/(C + C_0)$ x 100%, is

usually used to indicate the structural variability in a spatial data set (Li & Reynolds

1995). Range is used to indicate the spatial pattern of variability. A smaller range may

suggest a more fine-grained spatial pattern. A semivariogram model with a high R^2 and a

high SH% indicates a strong spatial structure (or high degree of spatial dependence). If

the samples are completely uncorrelated, the experimental semivariogram will exhibit a

so-called pure nugget effect. We have examined in more detail the methodologies of

semivariance analysis as related to sampling scale and plot replication in the previous

chapter. In this study, our main goal is to examine the effects of different disturbance

treatments on spatial patterns of sampled variables. We initially constructed

semivariograms for each plot, and for each scale, but no trends were identified. So the

data within each treatment were combined and used to construct one semivariogram.

Results

Global variability of available nutrients: Prior to disturbance, all plots had similar mean

nutrient availability (Table 3.1). Mean levels of available nutrients sharply increased

following disturbance, with similar magnitude of increase for girdling and harvesting
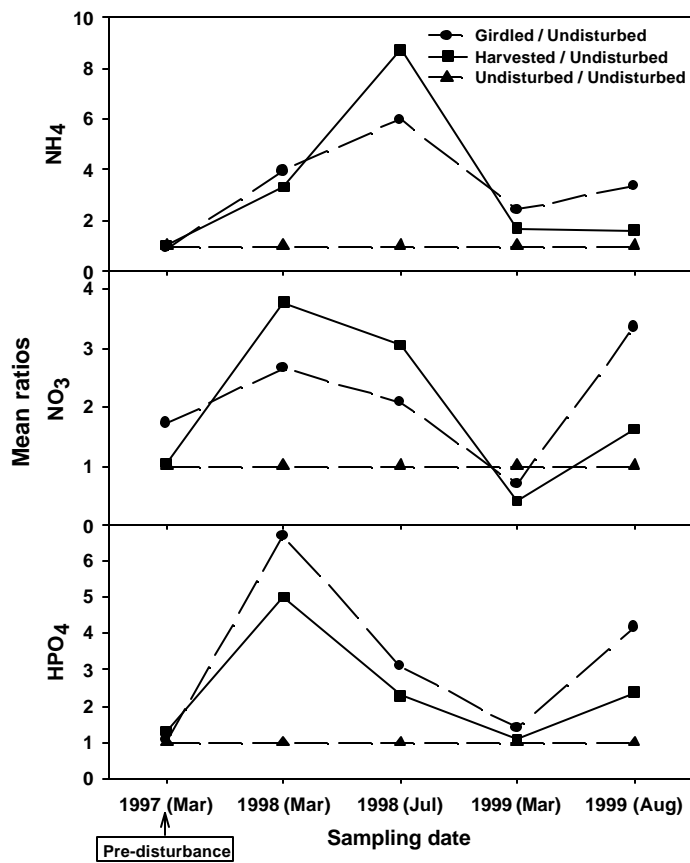
(Table 3.1, Fig. 3.1).

Figure 3.1 Temporal changes in mean of NH_4^+, NO_3^-, and HPO_4^-, expressed by the ratios between mean of NH_4^+, NO_3^-, and HPO_4^-, of each disturbance treatment, and that of the undisturbed.

Table 3.1 Summary statistics of soil available nutrients at Savannah River Site near Aiken, South Carolina, USA. Values shown are means (standard deviation); units are all in ppm.

	NH_4^+	NO_3^-	$NH_4^+ + NO_{3-}$	PO_4^-
March 1997 (prior to disturbance)				
Girdled	0.33 (0.55)	0.22 (0.27)	0.54 (0.61)	0.10 (0.12)
Harvested	0.37 (0.63)	0.14 (0.05)	0.51 (0.64)	0.12 (0.20)
Undisturbed	0.36 (0.58)	0.13 (0.04)	0.49 (0.58)	0.09 (0.14)
March 1998 (12 months after disturbance)				
Girdled	1.19 (1.97)	0.47 (0.94)	1.66 (2.23)	0.49 (0.71)
Harvested	1.00 (2.39)	0.66 (0.73)	1.66 (2.52)	0.37 (0.43)
Undisturbed	0.30 (0.35)	0.18 (0.41)	0.48 (0.63)	0.07 (0.06)
July 1998 (16 months after disturbance)				
Girdled	1.23 (2.05)	1.37 (2.06)	2.60 (3.62)	1.66 (1.17)
Harvested	1.79 (3.50)	2.01 (3.30)	3.80 (5.79)	1.22 (1.09)
Undisturbed	0.21 (0.42)	0.66 (0.52)	0.86 (0.72)	0.53 (0.53)
March 1999 (24 months after disturbance)				
Girdled	1.40 (2.17)	1.01 (1.28)	2.35 (2.59)	0.23 (0.45)
Harvested	0.98 (1.64)	0.61 (0.47)	1.54 (1.65)	0.18 (0.32)
Undisturbed	0.57 (0.44)	1.47 (2.50)	2.04 (2.61)	0.16 (0.21)
August 1999 (29 months after disturbance)				
Girdled	0.91 (2.50)	0.90 (1.19)	1.81 (3.09)	1.07 (1.17)
Harvested	0.62 (1.50)	0.44 (0.55)	1.06 (1.70)	0.61 (0.94)
Undisturbed	0.27 (0.77)	0.27 (0.30)	0.55 (0.81)	0.26 (0.27)

The three nutrients, however, showed slightly different patterns. For both disturbance treatments, NH_4^+ first increased and then decreased as compared to the

undisturbed forest. However, both NO_3^- and HPO_4^- showed a pattern of increase followed by decrease and then a sharp increase again in August 1999 (Fig. 3.1).

Sample variance of the three nutrients also greatly increased following disturbance and then declined (Table 3.1). Compared to the undisturbed forest, sample variance for NH_4^+ and HPO_4^- under both disturbance treatments increased to a peak during the first year after disturbance and then decreased to near the level of the undisturbed forest during the second year. NO_3^-, however, showed more intra-year fluctuation (Fig. 3.2). In March 1997, plots later girdled had markedly higher variability in NO_3^- so that the ratio between the girdled and the undisturbed was much higher than that between the harvested and the undisturbed, but absolute value of pre-disturbance variance of later girdled plots (0.27) was much lower than post-disturbance values (0.94) (Table 3.1). Similarly, in March 1999, NO_3^- of the undisturbed showed particularly high variability, higher than that of the two disturbance treatments, which resulted in variance ratios of less than one for both disturbance treatments. Both NH_4^+ and NO_3^- had greater changes in variance under harvesting treatment while HPO_4^- showed greater changes under girdling (Fig. 3.2). For CV, all three nutrients showed marked temporal fluctuations over time, with post-disturbance values generally higher than those found in the undisturbed forest. There were no marked differences between the two disturbance treatments (Fig 3.3).
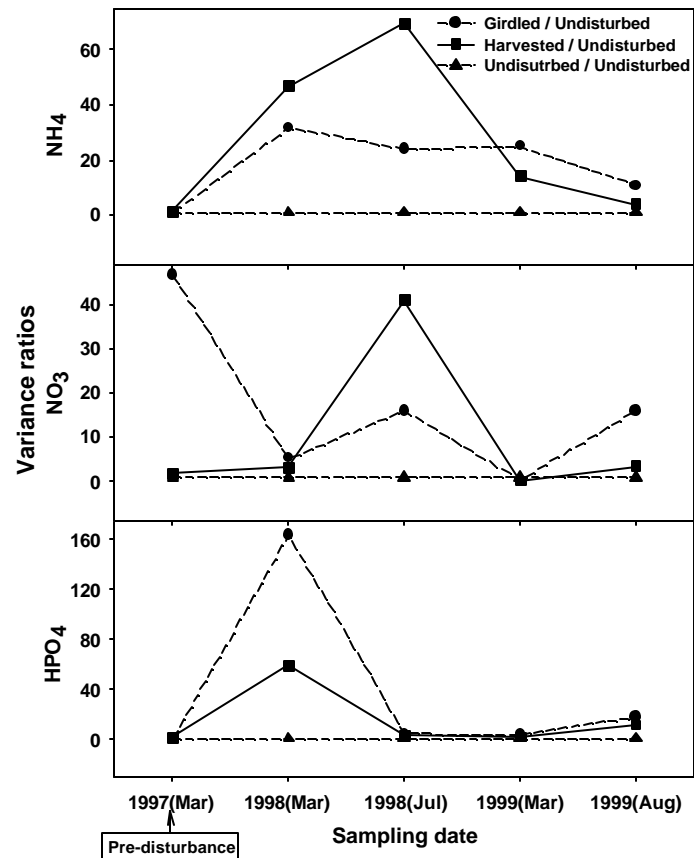
Figure 3.2 Temporal changes in variance of NH_4^+, NO_3^-, and HPO_4^-, expressed by the ratios between variance of NH_4^+, NO_3^-, and HPO_4^-, of each disturbance treatment, and that of the undisturbed.

The effects of sampling scale on the variations of soil nutrients was examined by comparing the coefficient of variation at two different sampling scales (Table 3.3). We found no marked sampling scale effects. Ratios between the CV of a coarse-scale plot (50 x 50m in dimension with minimum sampling distance of 5m) and its two-embedded fine scale plots (each 5 x 5m in demension with minimum sampling distance of 0.5 m) are mostly between 0.5 to 2 for all three nutrients with observable changes over time.
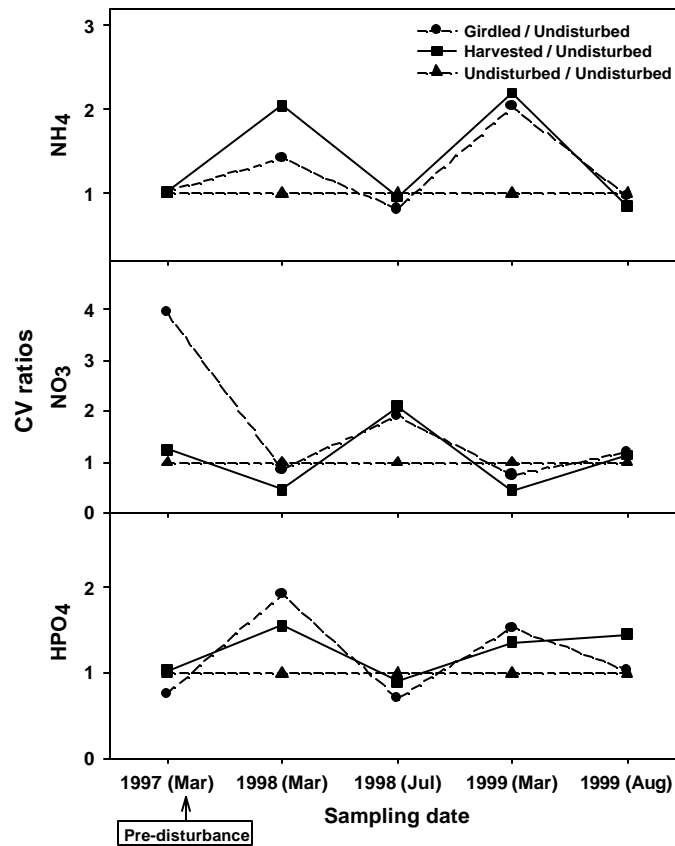
Figure 3.3 Temporal changes in CV of NH_4^+, NO_3^-, and HPO_4^-, expressed by the ratios between CV of NH_4^+, NO_3^-, and HPO_4^-, of each disturbance treatment, and that of the undisturbed.

However, no regular pattern of change in response to disturbance treatment was identified. Following disturbance, in the girdled plots CV appeared to be greater at the fine scale for NH_4^+ and greater at the coarse scale for NO_3^- and HPO_4^-, while in both harvested and undisturbed plots, CVs at the two scales were similar. Differences in CV between two replicate fine-scale plots are sometimes greater than the differences between two different sampling periods of a same plot.

Nutrient pools: Only slight temporal changes in nutrient pools were observed. There are some changes in mean and variance for litter mass, and soil C and N, but not for soil pH and forest floor C and N (Table 3.2). Mean and variance of soil C and N appeared to increase with time, with higher values in both mean and variance associated with harvesting treatment, but these changes were much smaller than those of available nutrients. Forest floor mass for the harvesting treatment was higher than that of the girdling and the undisturbed forest in 1998.

Table 3.2 Summary statistics of soil and forest floor variables. Values shown are means (standard deviation). Units of C, N pools are in %, litter mass in grams.

	Soil C	Soil N	Soil C:N	Soil pH	Litter Mass	Litter C	Litter N	Litter C:N
March 1997 (prior to disturbance)								
Girdled	0.60 (0.14)	0.02 (0.01)	40.0 (15.1)	4.88 (0.21)	36.7 (12.8)	36.2 (6.0)	0.76 (0.17)	48.6 (9.7)
Harvested	0.61 (0.14)	0.02 (0.01)	38.9 (16.2)	4.88 (0.21)	36.5 (14.3)	37.7 (5.6)	0.76 (0.16)	50.5 (9.9)
Undisturbed	0.63 (0.13)	0.02 (0.01)	40.0 (16.8)	4.94 (0.50)	36.9 (10.1)	36.5 (6.1)	0.75 (0.15)	48.4 (6.8)
March 1998 (12 months after disturbance)								
Girdled	0.75 (0.28)	0.03 (0.01)	34.3 (17.9)	4.75 (0.23)	51.0 (19.4)			
Harvested	0.90 (0.31)	0.03 (0.01)	38.9 (19.2)	4.73 (0.32)	76.4 (41.3)			
Undisturbed	0.80 (0.23)	0.03 (0.01)	33.2 (15.5)	4.88 (0.24)	56.2 (16.0)			
March 1999 (24 months after disturbance)								
Girdled	1.31 (0.39)	0.05 (0.02)	30.8 (13.3)	4.71 (0.20)	32.5 (12.0)	45.7 (4.9)	0.91 (0.23)	52.9 (13.4)
Harvested	1.76 (0.72)	0.06 (0.03)	29.3 (7.7)	4.76 (0.23)	37.4 (22.1)	43.3 (5.9)	0.86 (0.22)	53.4 (15.5)
Undisturbed	1.38 (0.36)	0.05 (0.02)	33.4 (17.3)	4.80 (0.23)	36.4 (10.2)	44.5 (5.5)	0.92 (0.19)	49.8 (10.4)

Congruence of available nutrients: Spearman rank correlation tests demonstrated no significant correlations among available nutrients and between available nutrients and soil moisture during the1997 spring pre-disturbance sampling, with the only exception of

Table 3.3 Ratios of CV of soil available nutrients between a coarse-scale plot and the two nested fine-scale plots (a & b) at each sampling date. March 1997 is the pre-disturbance sampling date, the remaining dates are post-disturbance.

Plot (coarse/fine)	NH_4^+					NO_3^-					HPO_4^-				
	Mar-97	Mar-98	Jul-98	Mar-99	Aug-99	Mar-97	Mar-98	Jul-98	Mar-99	Aug-99	Mar-97	Mar-98	Jul-98	Mar-99	Aug-99
Girdled (1/a)	1.87	1.94	1.23	0.84	0.65	1.56	3.21	1.50	1.58	0.41	0.71	1.58	0.77	0.68	1.20
Girdled (1/b)	1.22	0.76	0.84	0.46	0.63	2.81	3.16	1.31	0.77	1.24	0.61	1.06	0.69	1.63	1.26
Girdled (2/a)	0.91	1.35	0.56	0.88	0.96	0.23	2.10	1.47	1.15	1.47	1.05	1.64	1.34	1.48	1.44
Girdled (2/b)	1.80	0.42	0.60	0.86	1.28	0.39	2.11	0.74	3.00	3.64	0.66	2.34	1.64	1.03	1.23
Harvested (1/a)	1.65	1.12	1.10	1.45	1.40	0.57	0.80	1.17	1.94	1.77	1.33	2.05	1.15	0.83	1.02
Harvested (1/b)	1.55	1.84	1.26	0.81	0.66	1.05	0.91	0.59	0.60	0.83	2.03	1.32	0.88	0.56	0.50
Harvested (2/a)	1.72	2.52	0.86	0.71	0.61	0.92	1.49	1.12	1.82	1.06	1.01	1.84	0.83	1.13	0.86
Harvested (2/b)	0.62	2.59	1.26	1.49	0.61	1.10	1.20	1.60	0.95	0.87	0.85		0.88	0.56	1.10
Undisturbed (/a)	0.57	1.65	0.54	1.58	0.26	0.82	0.34	0.91	1.00	0.44	1.81	1.00	0.79	1.14	1.26
Undisturbed (/b)	0.71	1.84	1.55	0.69	0.24	1.04	1.02	0.90	1.85	0.50	4.67	1.09	0.98	1.75	0.97

the correlation between NH_4^+ and NO_3^- (Table 3.4). Correlation patterns changed after disturbance. In 1998, 14 out of 21 correlations were significant within the girdling treatment, but only 2 out of 21 were significant in the harvesting treatment (Table 3.4).

Table 3.4 Spearman rank-correlations between nutrients and water. Soil moisture variable is indicated as 'H$_2$O". Significance levels: bold p< 0.001, bold and italics p< 0.0001.

a. Correlations in1997.

1997	NH4	NO3	PO4
Girdled			
NH4	1		
NO3	0.08	1	
PO4	-0.09	-0.1	1
H2O	0.01	-0.07	-0.03
Harvested			
NH4	1		
NO3	*0.26*	1	
PO4	-0.07	-0.03	1
H2O	0.05	0.01	0.07
Undisturbed			
NH4	1		
NO3	-0.04	1	
PO4	0.02	0.08	1
H2O (1)	-0.07	-0.16	0.05

b. Correlations in 1998.

1998	NH4(1)	NO3(1)	PO4(1)	NH4(2)	NO3(2)	PO4(2)
Girdled						
NH4(1)	1					
NO3(1)	*0.29*	1				
PO4(1)	*0.35*	0.12	1			
NH4(2)	*0.40*	**0.23**	**0.27**	1		
NO3(2)	*0.40*	*0.38*	*0.30*	*0.42*	1	
PO4(2)	0.02	-0.09	0.17	0.09	-0.07	1
H2O	*0.30*	*0.32*	**0.21**	0.13	*0.35*	-0.15
Harvested						
NH4(1)	1					
NO3(1)	0.18	1				
PO4(1)	0.07	0.01	1			
NH4(2)	0.1	0.03	-0.06	1		
NO3(2)	0.08	0.08	-0.01	*0.53*	1	
PO4(2)	0.06	-0.07	0.13	0.12	0.06	1
H2O	0.11	-0.02	0.05	0.18	**0.33**	0.11
Undisturbed						
NH4(1)	1					
NO3(1)	0.08	1				
PO4(1)	**-0.22**	0.18	1			
NH4(2)	-0.06	0.02	-0.03	1		
NO3(2)	0.06	0.13	-0.08	-0.05	1	
PO4(2)	0.15	0.05	0.03	0.01	0.14	1
H2O	**-0.21**	**-0.27**	0.13	0.09	-0.14	0.04

c. Correlations in 1999.

1999	NH4(1)	NO3(1)	PO4(1)	NH4(2)	NO3(2)	PO4(2)
Girdled						
NH4(1)	1					
NO3(1)	0.04	1				
PO4(1)	0.01	-0.01	1			
NH4(2)	-0.01	0.04	-0.03	1		
NO3(2)	-0.07	0.03	-0.02	*0.40*	1	
PO4(2)	-0.05	-0.04	0.23	0.08	0.08	1
H2O	*-0.31*	-0.09	0.09	-0.09	0.09	0.12
Harvested						
NH4(1)	1					
NO3(1)	*0.33*	1				
PO4(1)	*0.31*	*0.31*	1			
NH4(2)	0.05	-0.01	-0.08	1		
NO3(2)	-0.01	0.06	-0.01	*0.35*	1	
PO4(2)	0.12	0.2	*0.26*	-0.03	0.16	1
H2O	*-0.35*	**-0.21**	*-0.41*	0.05	0.04	*-0.29*
Undisturbed						
NH4(1)	1					
NO3(1)	0.01	1				
PO4(1)	0.03	-0.05	1			
NH4(2)	0.13	0.06	-0.1	1		
NO3(2)	0.23	0.2	0.2	0.01	1	
PO4(2)	0.07	0.07	0.15	-0.04	0.09	1
H2O	-0.15	-0.09	-0.11	-0.14	**-0.25**	**-0.23**

For girdling, highest correlations were found between NH_4^+ and NO_3^- sampled at the same time, or between two sampling periods for either NH_4^+ or NO_3^-. Certain correspondence was also found between nutrients and soil moisture. For harvesting, only the correlations between NH_4^+ and NO_3^- and that between NO_3^- and soil moisture in the second sampling period were significant and moderately high. Nutrients and soil moisture were generally positively correlated in the girdled and the harvested treatments

yet were negatively correlated in the undisturbed. In 1999, correlations between nutrients in the girdling treatment became weaker with 2 significant correlations out of 21. But for harvesting, the correlations became stronger with 9 significant correlations, compared to only 2 in 1998. Most significant correlations were found between NH_4^+ and NO_3^- sampled at the same time. For the same nutrient, the correlations between two sampling periods were consistently poor. In addition, the significant correlations between nutrients and water were predominantly negative, regardless of disturbance treatments.

Spatial patterns of available nutrients: Temporal changes were also found in spatial patterns of available nutrients. Before disturbance, NH_4^+ had no spatial dependence but NO_3^- showed a spatial dependence with a range of 16.4 m and SH% of 63% in the plots that were later girdled (Table 3.5). After disturbance, NH_4^+ had stronger spatial dependence in the girdled plots, with three out of four post-girdling samples showing certain degree of spatial dependence. No such spatial dependence was noted in the harvested plots. In comparison, NO_3^- had stronger spatial dependence for both disturbance treatments. NO_3^- was spatially dependent for all four post-girdling samples, for three out of four post-harvesting samples, and for two out four samples taken from the undisturbed forest. Semivariogram ranges varied from 16.4 m prior to girdling to mostly less than 10 m after girdling, and SH% fluctuated around 0.50. More variations over time in both semivariogram range and SH% were found for harvesting treatment. HPO_4^- showed more pronounced spatial dependence thoughout the post-girdling sampling period, with semivariogram ranges consistently lower than 6m, and SH% fluctuating around 50%.

Table 3.5 Semivariogram parameters for soil moisture. The best model fit to the data based on the least squares is indicated as follows: S = spherical, N = nugget, and E = exponential, and is shown after R2 values. Semivariogram with a pure nugget effect is indicated as nugget model (N), in that case all three parameters (Range, SH%, R^2) are marked with "--".

Variable	Disturbance	Parameter	Date				
			97(Mar)	98(Mar)	98(Jul)	99(Mar)	99(Aug)
NH_4^+	Girdled	Range (m)	--	5.2	2.7	--	5.3
		SH%	--	0.55	0.66	--	0.51
		R^2/Model	N	0.72/E	0.32/S	N	0.34/S
	Harvested	Range (m)	--	--	–	--	--
		SH%	--	--	–	--	--
		R^2/Model	N	N	N	N	N
	Undisturbed	Range (m)	--	15.1	–	--	--
		SH%	--	0.73	–	--	--
		R^2/Model	N	0.78/S	N	N	N
NO_3^-	Girdled	Range (m)	16.4	4.1	10.3	6.5	5.6
		SH%	0.63	0.63	0.55	0.49	0.5
		R^2/Model	0.76/S	0.69/E	0.72/S	0.50/S	0.77/E
	Harvested	Range (m)	--	2.9	–	22	3.1
		SH%	--	0.5	–	0.59	0.5
		R^2/Model	N	0.41/E	N	0.88/S	0.22/E
	Undisturbed	Range (m)	--	16.8	–	8.3	--
		SH%	--	0.69	–	0.5	--
		R^2/Model	N	0.76/S	N	0.55/S	N
HPO_4^-	Girdled	Range (m)	--	5.6	4.3	3.4	0.7
		SH%	--	0.5	0.51	0.5	0.55
		R^2/Model	N	0.55/E	0.43/E	0.78/E	0.24/E
	Harvested	Range (m)	27.5	23.4	–	--	2
		SH%	0.5	0.73	–	--	0.56
		R^2/Model	0.86/S	0.91/S	N	N	0.71/E
	Undisturbed	Range (m)	46.9	6.9	–	18.4	--
		SH%	0.64	0.5	–	0.6	--
		R^2/Model	0.57/E	0.65/S	N	0.87/E	N

Discussion

Temporal changes in means and variations of available nutrients: Temporal changes in means of available nutrients followed patterns identified in the previous disturbance studies (Bormann and Likens 1979, Pickett and White 1985). Nutrient availability sharply increased after disturbances and then declined, eventually approximating the levels of the undisturbed forest. Variance of all available nutrients also increased after disturbance, and then gradually decreased. This result supports our first hypothesis that heterogeneity of soil properties would increase after disturbance and then decrease, at least for available nutrients. Temporal patterns in spatial variations of soil nutrients following site disturbance have rarely been addressed. Charlton and Bazzaz (1998) examined soil resource heterogeneity three years after a simulated blowdown in Harvard Forest. They found small differences of variability (CV) in soil water and net nitrogen mineralization rate between the blowdown and understory sites. Only light was much more heterogeneous (with higher CV) at the blowdown sites than undisturbed sites. Our study differed in the types of disturbance simulated, the variables measured, and the temporal resolution of the measurements. During the 2.5-year period following a whole-tree harvesting and a girdling, we took four measurements on available nutrients. Sample variance of NH_4^+, NO_3^-, and HPO_4^- increased by more than an order of magnitude in the first year after both disturbance treatments. Variability of soil moisture also increased markedly after the two disturbances (see the previous chapter). These results suggest a large influence that disturbance had on spatial variations of the resources critical to plant growth. The variations of both soil nutrients and soil moisture then gradually declined and approximated the level of the undisturbed forest. Changes in CV were characterized

by temporal fluctuations with generally higher values under both disturbance treatments as compared to the undisturbed forest. Therefore, the variability of soil nutrients can change fairly quickly following disturbance in southern pine forests, as compared to the more gradual changes found in Charlton and Bazzaz (1998). It should also be noted that sample variance and CV might provide different patterns.

Increases in nutrient availability after disturbances are thought to be due mainly to increased soil temperature and moisture and decreased competition and plant uptake (Matson and Vitousek 1981). As vegetation recovers, soil temperature and moisture is reduced, and more closed nitrogen and phosphorus cycles become reestablished (Marks and Bormann 1972). With the reduced decomposition and increased plant uptake, nutrient availability generally decreases (Bormann and Likens 1979, Vitousek 1985, Waide et al. 1988). Similar processes, operating under a spatially explicit framework, may also be responsible for changes in variability of available nutrients. We have shown in the previous chapter that both the mean level and the variance of soil moisture increased after disturbance. Higher and more dynamic soil temperature and moisture following disturbance have been reported in other studies, mainly as a result of the vegetation removal, the exposure of soil surface, and the reduced plant uptake (Liechty et al. 1992, Fleming et al. 1998). Furthermore, due to the highly heterogeneous forest floor pattern after harvesting, i.e., patches of bare soil coexisting with piles of slash, both soil temperature and moisture are likely to be more heterogeneous following harvesting (Liechty et al. 1992). Girdling and harvesting drastically reduced plant uptake through the removal of vegetation, but the initial patchy revegetation patterns in the harvested plots, and the patchily distributed hardwoods remaining in the girdled plots are likely to

contribute to a more a heterogeneous plant uptake pattern across the plot. The decomposition of fine roots associated with tree mortality can create pulse inputs of nutrients to soil (Silver and Vogt 1993, Lodge et al. 1994, Denslow et al. 1998), and these inputs may also be spatially heterogeneous due to the scattered distribution of severed roots, the increased heterogeneity in soil moisture and temperature and the patchy distribution of plants. Litter input may also be spatially more variable with various early successional species replacing pine monoculture. Greater spatial heterogeneity in these underlying processes led to greater heterogeneity in available nutrients. However, it remains difficult to evaluate the contributions of each process individually.

Temporal changes in means and variations of nutrient pools: In contrast to available nutrients, changes in the size and variability of nutrient pools were small or nil. This supports our second hypothesis that pools are less responsive to disturbance. Or, it takes longer time for these nutrient pools to respond. No differences between disturbance treatments and the undisturbed forest were found in litter C and N, suggesting no substantial amount of new organic material with different N and C content was added to the litter layer in the first two years after disturbance. This result is expected because the study site was a pine plantation before disturbance, and in the first two years after disturbance, pine litter still dominated the forest floor despite the rapid revegetation (personal observation). Soil C and N appeared to have increased slightly after harvesting while few changes were found after girdling, possibly reflecting more and faster incorporation of organic matter into mineral soil in harvested plots. Harvesting can churn some organic matter in forest floor into the mineral soil and can increase soil

moisture and temperature more than girdling. Similarly, Waide et al. (1988) observed 74% increases in soil organic matter in the 0 to 10 cm depth and 17% increase in the 10 to 30 cm depth in the first year following forest clearcutting, probably due to organic matter inputs from mortality and turnover of fine roots, and from the decay and leaching of surface litter layers following forest removal. These results are in contrast with the findings of Silver et al. (1996) that soil organic matter did not change during the entire 6 year-sampling period following a hurricane to a subtropical wet forest in Puerto Rico, and those of Charlton and Bazzaz (1998) that soil organic matter was actually slightly greater in undisturbed sites than in blowdown sites.

Temporal changes in spatial patterns: We hypothesized that spatial patterns of soil nutrients would be more fine-grained following disturbance. This hypothesis was not convincingly supported by the analysis of semivariance. Neither range nor SH % showed consistent changes after disturbance treatments. However, higher post-disturbance variability at both coarse and fine-scale plots (Tables 3.1 and 3.3) does suggest more fine-grained pattern in spatial distribution of nutrients. Therefore, the analysis of semivariance may have failed to provide reliable information on the changes in spatial patterns. We found that semivariogram indices changed over time (Table 3.5). This is consistent with previous findings (e.g. Ryel et al. 1996). However, no changes in spatial dependence that correspond to disturbance treatments were found. Neither range nor SH % showed consistent differences between disturbance treatments. Girdled plots had a higher degree of spatial dependence, but this pattern may be more site-related, rather than treatment-related.

Temporal changes in spatial patterns, especially for available nutrients, have been demonstrated in previous studies using semivariance analysis. Gross et al. (1995) found that semivarioram parameters such as range and SH% varied among three communities at different successional stages. Ryel et al. (1996) reported changes in semivariogarm parameters of NH_4^+ and NO_3^- over a growing season and those changes were more pronounced than what we found in our study, though no disturbance was involved in Ryel et al. (1996). Cain et al. (1999) quantified temporal changes of spatial maps of soil water content, soil NH_4^+ and NO_3^- over a three-month period from March to June. They found regions of high resource availability did not persist. Semivariance analysis was not used in the study, but given the pronounced changes of spatial maps over time, changes in semivariogram indices are likely to have occurred had the procedure been used.

These studies suggested that marked temporal changes in spatial patterns of nutrients are common. However, no clear temporal trends have been found with semivariance analysis. The lack of temporal trends in the results of semivariance analysis is in contrast with the relatively clear and consistent temporal trend (increase and then decrease) in sample variance. This suggests either that no clear patterns exist in our system, or that the common use of semivariance analysis may not be appropriate, and a closer examination of this approach may be needed, or both. A number of studies have pointed out the problems associated semivariance analysis in ecology and have suggested that the results of semivariance analysis can not be unreliable or comparable if variables of interest are highly dynamic (Bramley and White 1991, van den Pol-van Dasselaar et al. 1998), if the scale of sampling does not match the scale of the pattern (Meisel and Turner

1998), or if different sampling configurations and modeling procedures were used (Gross et al. 1995).

Differences in the effects of disturbances on variability of available nutrients: The differences in the effects of girdling and harvesting on the variability and availability of soil available nutrients were not as large as expected. We had hypothesized harvesting would have much greater impact than girdling. It appears that temporal changes in NH_4^+ and NO_3^- were greater following harvesting, which may be explained by the greater forest floor disturbance under harvesting than girdling, while temporal changes in HPO_4^- were greater after girdling, possibly due to greater and more variable microbial activities in girdled plots. Both mean and variability of soil C were also higher in harvested plots than the girdled plots, which may be caused by dramatic forest floor disturbance in the harvested plots, as compared to little disturbance to forest floor in the girdled plots during the sampling period. Despite these differences, the overall effects of these two disturbances were relatively similar, possibly reflecting an overwhelming influence of vegetation removal, a process involved in both disturbances.

Resource congruence: Correlation analysis and spatial maps suggest low spatial congruence among nutrients and between nutrients and water for pre-disturbance pine forest, and for the undisturbed reference forest throughout the study period, and changes in spatial and temporal congruence following disturbance. There are two types of resource congruence, spatial and temporal (Stuefer 1996, Charlton and Bazzaz 1998). Spatial congruence is high when patches rich in one nutrient also rich in other nutrients.

Temporal congruence is high if patches of different nutrients change in the same direction through time (from rich to poor, or vice versa). Spatial congruence interacts with temporal congruence. Charlton and Bazzaz (1998) used Kendall's coefficient to characterize resource congruence among soil water, soil organic matter, net mineralization rate, and net nitrification rate. They found for most combinations of soil resources, congruence was greater on the blowdown sites than the undisturbed (forest understory) sites, but the congruence between soil nutrients and light was lower on the blowdown sites. They concluded that blowdown reduced the congruence between light and soil resources. In our study, correlation among nutrients and water before disturbance was weak. After disturbance, a number of significant correlations emerged in the first year after girdling, particular for NH_4^+ and NO_3^-. Spatial congruence between NH_4^+ and NO_3^- for the same sampling period was moderately high, so was the temporal congruence of NH_4^+ and NO_3^-. There were also a number of positive correlations between nutrients and soil moisture, indicating certain degree of congruence between them. These patterns suggest that girdling increased resource congruence, probably caused by changes in plant uptake and microbial activity that favored congruence among nutrients, e.g., reduced spatial variation in production and uptake of different nutrients in the absence of activities of dominant pines. These significant correlations disappeared in the second year after girdling, probably corresponding to the substantial vegetation regrowth of remaining hardwoods. Cain et al. (1999) suggested that through the nutrient recycling and uptake process, plants could modify the level of resource heterogeneity during a sand dune succession. Ryel et al. (1996) suggested that differences in plant uptake rates and microbial activity, as affected by temperature and soil moisture, were

responsible for highly dynamic N pools and resulted in poor temporal correlations in the concentrations of NH_4^+ and NO_3^-. In our study, rapid species turnover and vegetation regrowth of new colonizers and spouts may be responsible for the rapid turnover of nutrients, low patch longevity, and thus low temporal congruence at the harvested plots. We also found that the correlations between nutrients and water were negative in the second year after harvesting, possibly reflecting negative effects of roots and rhizosphere on soil water coupled with positive effects on nutrients.

Conclusions

We had proposed that quantification of spatial heterogeneity might be problematic if heterogeneity changes unpredictably over time. The results of this study suggest spatial heterogeneity of soil resources is to some degree predictable. Combining the results from the soil moisture and those from this study, we conclude that sample variance is a useful component of heterogeneity. Since sample variance doe not give indication of spatial patterns, and since semivariogram analysis has not provided consistent patterns about spatial distributions of soil nutrients and water, a more thorough study on methods that can characterize spatial patterns of soil resources is needed. Our results also demonstrated that disturbances might increase resource congruence, but resources then quickly became incongruent. Finally, our results provide further evidence for the effectiveness of field experiments in linking patterns found in nature and the possible controlling processes.

CHAPTER 4

CAN SEMIVARIOGRAM ANALYSIS INDICATE PATCHINESS?

Abstract. Semivariogram analysis has become an important tool in spatial analysis of ecological data, yet the understanding of the method is incomplete. This study used a simulation approach to test the effectiveness of semivariogram analysis in detecting patchiness, a form of spatial pattern found in nature. We tested how two parameters of semivariogram – range and SH%- respond to patch size and the proportion of the total patch area in a given landscape. Our results suggest that semivariogram range cannot reliably indicate patch size, due to its responses to total patch area and sampling methods. Our results also suggest that semivariogram analysis is yet fully understood and general conclusions based solely on the results of semivariogram analysis should be avoided. The simulation approach adopted in this study may be useful to improve experimental design when semivariogram analysis is used for a specific ecological study.

Introduction

Geostatistical tools such as semivariograms have been widely used to describe spatial patterns of ecosystem structure (Robertson et al. 1993, 1997, Gross et al. 1995, Dent and Grimm 1999, Lister et al. 2000), temporal changes of the spatial patterns (Ryel et al. 1996), and the spatial correlations between organisms and their environment (Schlesinger et al. 1996, 1998, Breshears et al. 1997, Pastor et al. 1998, Nicotra et al. 1999). These studies cover a wide range of systems with different vegetation patterns and biogeochemical processes, including deserts (Schlesinger et al. 1996, 1998), semiarid woodlands (Breshears et al. 1997), old-growth forests (Nicotra et al. 1999), pine plantations (Lister et al. 2000), agricultural fields (Roberston et al. 1997) and streams (Dent and Grimm 1999).

The main purposes of semivariogram analysis in these studies have been: 1) to detect the presence of spatial autocorrelation (e.g., Robertson et al. 1993, 1997, Gross et al. 1995); 2) to identify the scale at which a sampled variable shows maximum variability (Meisel and Turner 1998); and 3) to establish possible causal links between two variables or processes by comparing the scale of autocorrelation of each variable or process (Breshears et al. 1997, Nicotra et al. 1999). These studies have offered valuable hypotheses on the interactions between environment and organisms, and have promoted spatially explicit studies in ecology.

Unfortunately, the understanding of the application of semivariance analysis in ecology is far from complete. Meisel and Turner (1998) evaluated the ability of semivariograms to detect known scales of variability in artificial maps. Their results suggested that semivariogram range accurately reflected the scale of the variability of binary maps composed of a single-scale pattern, but failed to accurately reflect multi-scale pattern (varying patch sizes and shapes), the pattern most common in real ecological data.

Several additional issues related to the application of semivariogram analysis in ecology remain unresolved. First, though semivariogram analysis is a tool used for analyzing the scale and degree of spatial autocorrelation of various ecological variables (e.g., soil properties), most ecological studies have used it to quantitatively describe spatial heterogeneity but not the spatial autocorrelation per se (Jackson and Caldwell 1993, Robertson and Gross 1994, Nicotra et al. 1999, Dent and Grimm 1999, Stoyan et al. 2000). However, autocorrelation is only one way (among many others) of quantifying heterogeneity (Li and Reynolds 1995) and autocorrelation and heterogeneity should not

be confused. Second, it is still unclear what aspect of heterogeneity can be effectively

described by semivariograms because heterogeneity is a composite concept that consists

of many quantifiable and unquantifiable components. Some suggested that patchiness

may be easier to quantify because patchiness refers to a particular spatial pattern with

basic structure of patches that are well defined (Wiens 1995). This is one reason why

ecological theory has dealt more with the study of patches than with the study of

heterogeneity in general (Weins, 1995). Indeed, recent studies have already begun to use

the results of semivariogram analysis to characterize patchiness of nutrients or light (e.g.,

Nicotra et al. 1999, Dent and Grimm 1999). Third, patchiness has also been frequently

used to replace the term environmental heterogeneity in the studies that simulated spatial

distributions of resources in nature and to test plant responses to these spatial

distributions (Caldwell and Pearcy 1994, Wijesinghe and Hutchings 1999, Einsmann et

al. 1999). However, quantitative information about pathiness in natural communities is

still lacking, and even patchiness as a concept has not been fully scrutinized.

Therefore, testing how semivariogram analysis can be used to characterize

patchiness can serve two purposes: 1) to improve the understanding of the application of

semivariogram analysis in describing specific ecological patterns (e.g., patchiness), and

2) to offer the quantitative information about patchiness in natural communities.

Semivariogram analysis generates several parameters that can be potentially used to

characterize patchiness. Semivariogram range has been explicitly used to indicate patch

size (e.g., Nicotra et al. 1999, Dent and Grimm 1999). Another semivariogram parameter

SH%, or the proportion of the total variance accounted for by structural or spatially

dependent variance, has been used as an indication of the degree of patchiness (Robertson

and Gross 1994). To use these semivariogram parameters to characterize patchiness, some of the key components of patchiness must be recognized. Patch size has been an essential component of patchiness. Some other components of patchiness include patch contrast, patch shape, proportions of patches across a landscape (or total patch area in percentage), and spatial arrangement of patches (Kotliar and Wiens 1990, Li and Reynolds 1994, Wijesinghe and Hutchings 1999).

In this study, we attempt to establish relationships between two components of patchiness - patch size and total patch area, and the parameters provided by semivariograms, using simulation approach to create spatial patterns with known patch characteristics, and then constructing semivriograms based on the data sampled from these spatial patterns. We recognize the difficulty and disagreements in defining the patch concept in ecological literature (e.g., Pickett and White 1985, Kotliar and Wiens 1990). To have a definition to work with, we define patches as landscape units with certain size, shape and clear boundary. In the mean time, we realize this definition can be improved as our study proceeds. We use a simulation experiment to test how semivariogram range and SH% respond to changes in patch size and total patch area. The value of simulation studies has been shown in previous studies (e.g., Li and Reynolds 1994). We also investigate how sampling scheme (sampling grain and sampling intensity) influences the estimation of semivariogram parameters. Specific questions to be addressed include: 1) Whether or not semivariogram range can indicate the size of landscape patches; 2) how sampling gain and intensity influence the accuracy of estimation of semivariogram range; and 3) how spatial arrangement of patches, total patch area, and sampling intensity affect SH%.

Methods

Experimental design and data simulation: To evaluate the parameters of semivariogram, we used a factorial experimental design. The factors of the factorial experiment were total patch area, and patch size/patch number combination. We used five levels of total patch area from 10 to 50%, and three levels of patch size (Table 4.1).

Table 4.1 The factors (patch characteristics) and their levels used to generate landscape maps.

Patch size (dimaeter in meter)	Total patch area (%)				
	10	20	30	40	50
	--------------------Number of patches--------------------				
Small (5.64)	10	20	30	40	50
Medium (10.28)	3	6	9	12	15
Large (17.84)	1	2	3	4	5

For each of the 15 treatment combinations (Table 4.1), 100 landscape maps of 50 x 50 m in dimension were generated. Simulated landscapes were created by first generating randomly distributed points in Arc View GIS (ESRI, Redlands, CA, USA). These points were used as centers of patches circular in shape. Locations of these points were constrained to not occur within a distance equal to the patch diameter of interest in order to avoid spatial interaction of the patches. Points were buffered, and these circular polygon buffers were converted to binary raster datasets. In these datasets, all the area occupied by patches had the value of 1 while the rest of the area had the value of 0. These datasets were then sampled by a 1 x 1 meter sampling grid. An example of landscape maps with three different patch sizes is shown in Figure 4.1. Within each total

patch area and patch size combination, the only landscape characteristic that we varied

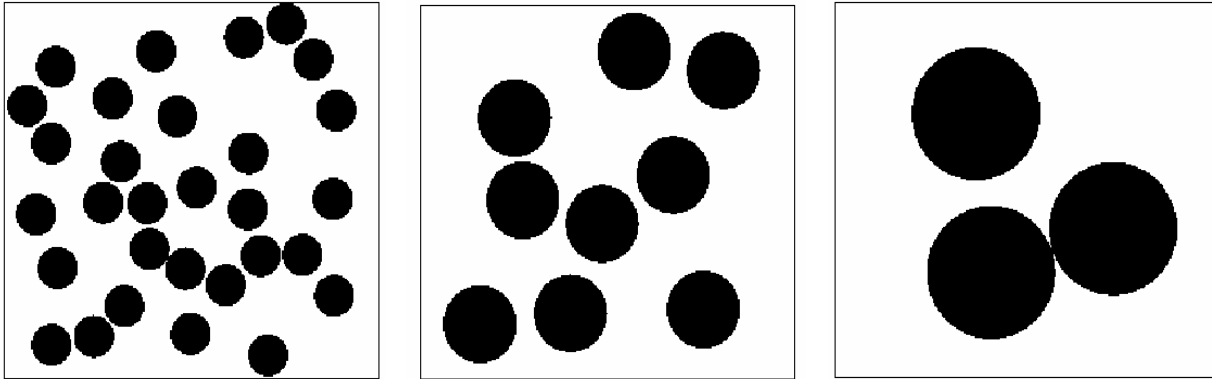was the spatial locations of patches.

Figure 4.1 Examples of simulated landscape maps. All three landscapes are 50 x 50 m in size. On the left is a landscape with 30 randomly located 5.64m (in diameter) patches. In the middle is a landscape with 9 randomly located 10.28m patches. On the right is a landscape with 3 randomly located 17.84m patches.

Semivariogram analysis:

1. Semivariance. The central concept in semivariance analysis is spatial autocorrelation. Assume a certain measurement is taken from a number of points across a two-dimensional surface. If, on average, the measurements taken from points closer to each other are more similar than those from points far apart, there exists spatial autocorrelation. The semivariance, a popular index of autocorrelation, for points that are separated by a distance of h is given by:

$$\Upsilon = \frac{1}{2n} \sum_{i=1}^{N(h)} (x_i - x_{i+h})^2$$

where Υ is the semivariance value for lag class h, x is the value for the variable at point i, h is the distance interval (or lag class) for which the semivariance is being calculated, N

is the number of pairs of points separated by distance h, and n is the number of pairs of

points used to calculate the semivariance for interval h. In other words, the semivariance

is ½ the average squared difference between pairs of values separated by a given

distance.

2. Semivariogram. A semivariogram is a graph in which semivariance is plotted against

distance. Semivariograms were constructed based on the data from each landscape map

using variogram procedure in SAS Version 8 (SAS Institute, Cary, NC, USA). Nugget

(C_0), sill ($C + C_0$), and range (A_0) were estimated (Isaaks & Srivastava 1989; Rossi et al.

1992; Robertson & Gross 1994) for each semivariogram. The range (A_0) is the average

distance over which spatial autocorrelation exists, i.e. the samples are not statistically

independent of one another. The sill, or C_0+C, is the semivariance value around which

the values for lags greater than the range fluctuate. If no spatial trend exists in the data,

the sill should approximately equal the sample variance because at distances beyond the

range, the samples are no longer autocorrelated, and thus their value is independent of

sampling location. The structural variance, or C, is the portion of the model variance

attributed to spatial autocorrelation of the phenomenon under study. The nugget, or C_0,

should theoretically be equal to zero (sample pairs that are 0 distance apart should have

zero variance). However, nonzero nuggets are common, and indicate either spatial

autocorrelation at distances smaller than the smallest lag measured, or experimental error.

Assuming no experimental error, the ratio of structural variance to total model variance

($C/(C+ C_0)$) x 100%, or SH%, has been used as an index of the degree of spatial

autocorrelation measured by one's sampling scheme (Robertson et al. 1997). A ratio of

1.0 would indicate that the sampling scheme measures a high degree of spatial autocorrelation; similarly, a value close to zero would indicate that the phenomenon shows a high degree of spatial dependence at scales smaller than the smallest sampling interval.

Evaluation of sampling effects on semivariogram range estimation: We used the data sets with 20% total patch area to examine how sampling influences the estimation of semivariogram range. In addition to 1 x 1m grid, we used additional eight regular grid systems to sample these datasets: 2 x 2m, 3 x 3m, 4 x 4m, 5 x 5m, 6 x 6m, 7 x 7m, 8 x 8m, and 9 x 9m. The sample sizes corresponded to each of these nine sampling grids are 2601, 676, 306, 169, 121, 81, 64, 49, 36 respectively.

By sampling the same data set in nine different ways, nine new data sets with the same patch characteristics (same total patch area and same patch size) were created. Each new data set had 100 replications (realizations). These new data sets were analyzed using semivariograms and semivariogram range estimates were obtained. Then the mean semivariogram range and the associated standard error were calculated.

Data analysis: The results of the factorial experiment were analyzed by SAS. We used analysis of variance (ANOVA) to examine the effects of each factor (patch size and total patch area) and their interaction to determine the effects of different levels of each factor on semivariogram parameters (range and SH%). Mean and variations of range and SH% estimates were used to assess the accuracy of estimation for these two semivariogram parameters.

Results

Semivariogram range: ANOVA tests showed that the estimates of range responded to changes in both patch size and total patch area (Table 4.2). The interaction between patch size and total patch area was also significant (Table 4.2).

Table 4.2 ANOVA results of the factorial experiment, α=0.05.

Source	Significance probability of F test (P value)	
	Range	SH%
Patch size	0.0001	0.001
Total Patch area	0.0001	0.0781
Patch size x total patch area	0.0025	0.0443

Mean semivariogram ranges were mostly within 30 % of the actual patch size (Table 4.3, Figure 4.2). There was no trend in accuracy of estimation as total patch area increased. However, both lowest total patch area (10%) and highest total patch area (50%) used in this study generated greatest overestimation of patch size, as compared to the other three total patch area levels.

Table 4.3 Estimates of semivariogram range under different total patch areas and patch sizes. Standard deviations of range estimates are shown in parenthesis. Each value is based on 100 realizations.

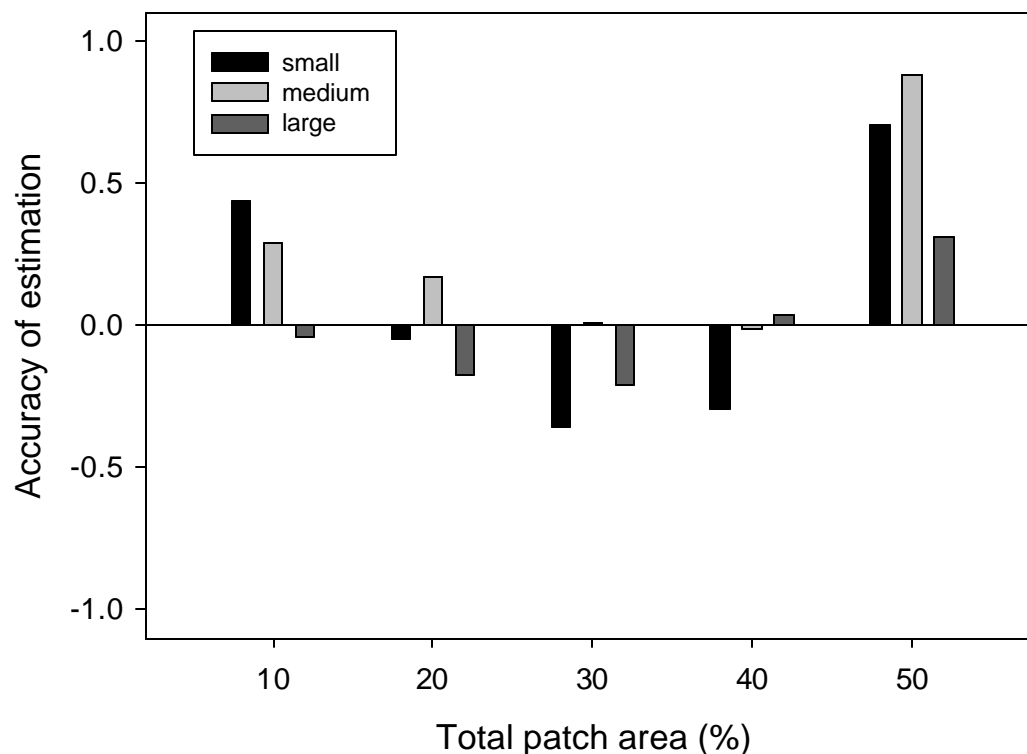| Total patch area (%)	Patch diameter (m)		
	5.64	10.28	17.84
10	8.10 (2.55)	13.21 (3.77)	17.19 (5.36)
20	5.33 (2.56)	12.05 (2.59)	14.88 (4.15)
30	3.59 (2.12)	10.35 (0.61)	14.11 (3.28)
40	4.01 (1.55)	10.13 (0.99)	18.61 (3.77)
50	9.67 (1.27)	19.37 (5.35)	23.35 (6.70)

Figure 4.2 The accuracy of the estimation of patch size using semivariogram range. The accuracy was calculated by the difference between the mean semivariogram range of 100 landscape maps and the actual patch size used to simulated these maps, scaled by the actual patch size. Small, medium, and large indicate three patches sizes (in diameter) simulated: 5.64, 10.28, 17.84m.

At each level of total patch area and patch size combination, the coefficient of variation (CV) of range estimates among 100 landscape maps was generally between 20 and 30%, with the largest value of 59% (based on Table 4.3). We did not find any trend

in CV of semivariogram range estimates as total patch area increased. However, the smallest patches appeared to have greater CVs than the other two patch sizes.

SH%: The estimates of SH% was significantly affected by patch diameter ($p<0.001$) yet not by total patch area ($p>0.05$) (Table 4.2). Estimates of SH% for both small and medium patches were greater than 90%, while those for large patch were mostly lower than 50% (Table 4.4).

Table 4.4 Estimates of SH% under different total patch areas and patch sizes. Standard deviations of SH% estimates are shown in parenthesis. Each value is based on 100 realizations.

Total patch area (%)	Patch diameter (m)		
	5.64	10.28	17.84
10	0.97 (0.13)	0.97 (0.15)	0.26 (0.30)
20	0.99 (0.01)	0.99 (0.07)	0.40 (0.23)
30	0.99 (0.01)	1.00 (0)	0.62 (0.22)
40	0.92 (0.10)	0.99 (0.01)	0.46 (0.22)
50	0.99 (0.01)	0.96 (0.10)	0.48 (0.35)

Effects of sampling: Sampling effects on semivariogram range estimation was significant ($p<0.0001$). However, smallest sampling grain along with greatest sampling intensity (1 x 1 m grid, 2601 sampling points) did not yield the semivariogram range that most closely resembled the actual patch size used in simulation (Figure 4.3). As sampling grid became larger, the degree of resemblance and error of estimation did not change

systematically. However, largest error of estimation was associated with largest

sampling grid (9 x 9 m), which has sample size of 36.

Three different patch sizes showed different responses to sampling. The 5.64m

patch showed largest changes in the estimation of semivariogram range in response to

changes of sampling grid. Once sampling grid surpassed patch size, there appeared to be

a trend that semivariogram range overestimated actual patch size with greater proportions

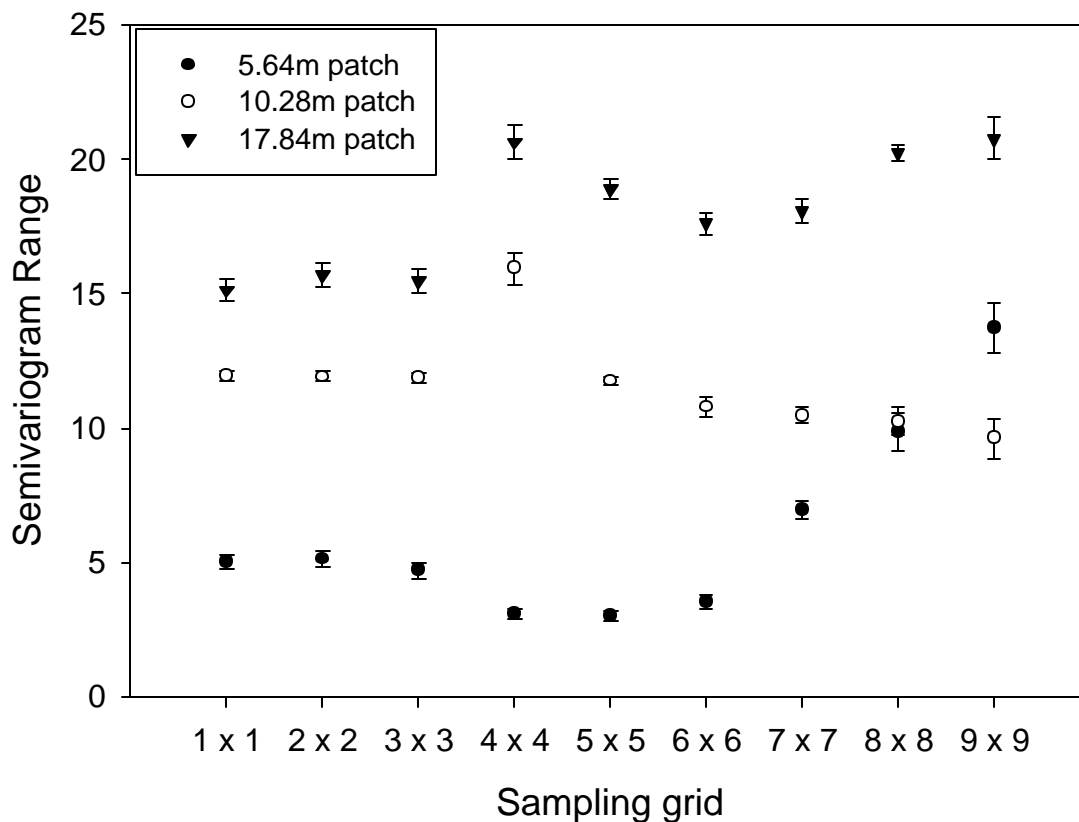as sampling grid increased (5.64m patch in Figure 4.3).

Figure 4.3 Effects of sampling grid on the estimation of patch size using semivariogram
range. Each point represents an averaged semivariogram range of 100 semivariograms
with the same actual patch size using the same sampling grid. Each error bar is 10 times
of the standard error associated with the each point.

Discussion

Semivariogram range as an indication of patch size: Our ANOVA results showed that estimated semivariogram range of the landscape maps consisting of patches with the same size and shape varied with both patch size and the total patch. It is expected that semivariogram range should correspond to patch size if semivariogram range is a useful indicator of patch size. However, the results that semivariogram range also varied with total patch area made semivariogram range an ineffective indicator. Therefore, it is difficult to use semivariogram range to estimate patch size of a landscape even when all patches in this landscape are of same size and shape.

Some studies have interpreted semivariogram range as patch size (e.g., Nicotra et al. 1999). Our results do not offer the evidence to support such an interpretation. In addition to the effects of total patch area on the estimation of semivariogram range, several factors may also influence the estimation of semivariogram range and make it more difficult to use semivariogram range to indicate patch size. First, there is a certain degree of error associated with the estimation of patch size by semivariogram range; the magnitude of error may be associated with the actual spatial pattern. In our simulation experiment, the magnitude of error was around 30 %. Particularly sparse (10% total patch area) or dense patches (50% total patch area) resulted in an overestimation of patch size by as high as 50%.

Second, sampling may be particularly important in generating an estimate of semivariogram range that indicates the actual patch size with high accuracy and small estimation error. As our analysis has indicated, minimum sampling grid (or sampling

grain) should be smaller than patch size. In addition, the largest sample size may not be the best choice if increasing number of sampling does not increase the accuracy of estimation and or reduce the estimation error. However, our results suggest that there appeared to be a minimum of sample size of 50, which is in agreement with the previous study (Webster and Oliver 1992). The simulation approach used in our study may be helpful to determine not only minimum sampling distance and sample size, but also sample arrangement to be used in specific studies.

Third, spatial patterns simulated in this study may be only a special case of ecological patterns in general. All patches simulated for each landscape map were circular and had the same size. Such patches may only appear as even-aged trees in a monoculture forest stand. Other system properties, such as water and soil nutrients, may appear in nature as patches of irregular shapes with different sizes. In such cases, it is even difficult to determine what the patch size is, let alone to use semivariogram range to accurately estimate patch size. One may use average patch size, but whether such an average patch size is ecological meaningful remains to be determined.

Therefore, semivariogram range may not be used to indicate patch size and to make conclusions about ecological processes, even though our results suggest that semivariogram range may give some indication about the underlying spatial patterns of a landscape.

Patterns of SH%: We did not find any predicable changes in SH% as patch size or total patch area changes. We found that SH% was that the lowest when associated with biggest patch size. This may suggest that plot size should be large enough relative to

patch size (or number of patches should be large enough) before accurate measurement of SH% can be obtained. Previous studies have used SH% as a key component of spatial heterogeneity (Li and Reynolds 1994, 1995). Our results suggest that the use of SH% in indicating patchiness remain poorly understood.

Application of semivariogram analysis in quantifying patchiness: Meisel and Turner (1998) have suggested semivariogram analysis is a fairly robust tool in detecting the scales of pattern in artificial landscape maps and in identifying the scale of coarsest spatial pattern in several types of Yellowstone environmental data. However, the authors cautioned that semivariograms should be used only for preliminary analysis of the spatial behavior of many ecological data sets and that the standard use of semivariogram analysis does not lend itself well to the study of multiple scales of pattern. Our results support these previous findings and further suggest the use of semivariogram to indicate patch size suffers from many problems. However, we do not conclude that semivariogram analysis is not a useful tool in characterizing spatial patterns of ecological properties, but that the method remains poorly understood and demand further study, both using field data and simulations.

CHAPTER 5

SUMMARY

The previous three chapters presented the results of several studies aimed at describing patterns and dynamics of spatial heterogeneity of soil resources in a southern pine forest, and evaluating the methods to quantify heterogeneity. Although specific objectives and findings differed in each study, a number of key results emerged from this research as a whole.

1. Spatial heterogeneity of soil available nutrients and water increased markedly following site disturbances that involved a substantial amount of vegetation removal, and then declined towards the level of undisturbed forest.

2. Temporal responses of spatial heterogeneity to disturbances differed with soil and forest floor properties. Available nutrients and water showed drastic and transient changes to disturbance while other variables such as soil C and N, and forest floor C and N had no or only minor responses to disturbances during the first two years after disturbance.

3. Different methods of quantifying heterogeneity may result in different patterns and lead to different conclusions. Our results demonstrated that sample variance may be a measure of heterogeneity that is statistically most consistent (across different variables) and ecologically

most meaningful as compared to other measures such as coefficient of variation, or semivariogram parameters such as range and SH%. Our simulation experiment suggested that semivariogram analysis has potential for accurately describing spatial patterns of ecological variables, yet the current understanding of the method is premature and further studies are required to improve our understanding before any conclusions can be made.

The results presented here point to a number of avenues for future studies. I hypothesize that there is a post-disturbance temporal trend of an "increase and then decline" in the variation of available nutrients and water in forests. This hypothesis can be tested in other ecosystems following different types of disturbance. If a general trend can be found in a number of ecosystems following disturbances that vary in scale and intensity, then new studies should be designed to find the underlying causes of these trends and their impact on biological processes such as species competition and replacement.

The results from this study also suggest that the definition of heterogeneity remains unclear. A key to solve this problem may lie in finding a unified way to quantify heterogeneity. Sample variance emerged in our study as a useful measure of heterogeneity. However, heterogeneity is a diffuse concept and has been used to represent almost all patterns in nature. Therefore, we need conceptual advances such as using patchiness which is more specific and can be more easily defined. We also need a

variety of methods that can quantify different types of patterns in nature rather than rely on a single measure of heterogeneity, and then compare the results generated by different methods before making general conclusions. Among the methods used in quantifying heterogeneity, semivariogram analysis showed some promise but its usefulness in ecological studies demands further study. The simulation approach presented in Chapter 5 can be of great value in testing the effectiveness of semivariograms in characterizing spatial patterns in nature, as well as the effectiveness of other spatial analysis methods.

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VITA

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