The spatial heterogeneity of soil invertebrates and edaphic properties in an old growth forest stand in western Oregon

C.E. Torgersen, J.A. Jones[1], A.R. Moldenke and M.P. LeMaster
Department of Geosciences, Wilkinson Hall 104, Oregon State University, Corvallis OR 97331, USA.
[1]*Corresponding author*

Abstract

Geostatistical tools, the semi-variogram and correlogram, were used to compare spatial heterogeneity and patterns of soil microarthropods, O-horizon depth, moisture content, temperature, and pH in two contrasting forest stands near the H.J. Andrews Experimental Forest, Oregon for June of 1992 and 1993. Two adjacent research plots were sampled: one plot consisted of a heterogeneous mix of age classes with a high density of old-growth Douglas-fir (*Pseudotsuga menziesii*); the other plot was dominated by a homogeneous post-fire stand of Douglas-fir regrowth with a low density of old-growth trees. Spatial analysis revealed distinguishable differences between old growth and regrowth forest and between sampled years. In the hot dry spring of 1992, short range variability and patches (0 to 5 m), especially in pH, moisture, O-horizon depth, and faunal census, were more pronounced in the homogeneous regrowth plot, whereas long range patterns (17 to 22 m) were more pronounced in the heterogeneous old growth plot. In the cold wet spring of 1993 both old growth and regrowth forest plots had only short range variation.

Introduction

The forests of the Pacific Northwest are known for their tall stands of moss-covered old-growth Douglas-fir, hemlock and cedar surrounded by an understory of ferns and shrubs that thrive in the maritime climate (Dyrness et al., 1974). The growth of trees, shrubs and other surface vegetation is determined by the biological and chemical characteristics of the soil. Plants rely on bacteria, fungi and invertebrates to break down dead organic material into usable forms through the process of decomposition. With their extensive networks of roots, woody plants have an ecological impact on soil physical structure and chemical content, which, in turn, affects the communities of soil organisms (Moldenke, 1990). In the last several years, scientific and public interest in the ecological significance of old-growth forests of the Pacific Northwest has reached a peak, particularly as a result of the controversy between conservationists and the logging industry concerning the preservation of old-growth timber stands as habitat for the endangered northern spotted owl. Questions have arisen about whether other species and communities exist uniquely in the old-growth envi-

ronment. For example, what ecological components besides trees distinguish an old-growth forest from a younger regrowth stand? How may three-hundred to six-hundred year old trees influence the flora and fauna both in tree canopies and in the soil within the trees' branching root networks?

The most obvious characteristics of old-growth forests in the Pacific Northwest are the trees, shrubs, and plants that grow out of a deceptively nondescript mat of needles and twigs–the forest floor. However, within this rich mixture of decaying matter live vast numbers of arthropods that form the most diverse part of the forest ecosystem. Coniferous forest soils in western Oregon contain some of the richest and most diverse terrestrial complexes of soil-dwelling arthropods in the world (Petersen and Luxton, 1982). Oribatid mites ($150,000\ m^{-2}$) and springtails ($50,000\ m^{-2}$) are the most abundant soil arthropods in Oregon's western forests. One square foot of old-growth forest soil can contain more than 200 species (Moldenke and Lattin, 1990a).

The long-term health of a forest ultimately depends on the biological dynamics in the soil that aid the process of organic matter decomposition and nutri-

ent transformation. Acquisition of nutrients and water through tree roots is influenced by the metabolic activity of fungi and bacteria in the soil (Moldenke, 1990). Symbiotic associations between mycorrhizal fungi and plant roots occur at the interface between root and soil and facilitate uptake of nutrients from the soil into the root (Feldman, 1988). Soil invertebrates such as mites, centipedes, and millipedes contribute to soil production, physical structure, and chemical content. Arthropod faeces make up the bulk of particulate matter in the soil organic layer, while arthropod burrowing activities aerate the soil, making it accessible to root penetration and water absorption (Rusek, 1986). Microcosm experiments by Teuben and Roelofsma (1990) testing the influence of soil arthropods on coniferous litter decomposition found that isopods and collembolla, two very common and abundant soil arthropods, enhanced microbial activity and concentrations of exchangeable nitrate, ammonium, and phosphate. The presence of soil fauna is generally assumed to benefit plants by increasing the amount of available nutrients for root uptake. Setala and Huhta (1991) have shown in laboratory experiments that root biomass of birch seedlings was as much as 70% greater in the presence of nematodes and microarthropods.

Soil invertebrates are integrally tied to their environment. They produce the soil in which they live and are also subject to changes in the forest environment as a whole. Soil ecosystems, and especially their faunal components, are highly sensitive to successional stage changes following forest utilization and management practices, such as logging and burning. Studies by Moldenke and Lattin (1990a) have found that clearcut-and-burn practices reduce total arthropods by approximately 90%. Many species that are characteristic of an old-growth environment do not appear in cut forest stands for 20-40 years following disturbance (McIver et al., 1992; Moldenke and Fichter, 1988). Soil arthropods function as biological indicators of forest type and successional stage (Moldenke, 1990).

This research project was designed to examine the spatial pattern of soil arthropods and edaphic variables and assess its relationship to the pattern of trees in an old-growth forest stand. We used geostatistics to compare the spatial patterns of soil organisms, pH, moisture, temperature and O-horizon depth in two contrasting forest stands: a predominantly old-growth stand consisting of a heterogeneous mix of young and old conifers; and a homogeneous, predominantly regrowth stand approximately 80 years of age.
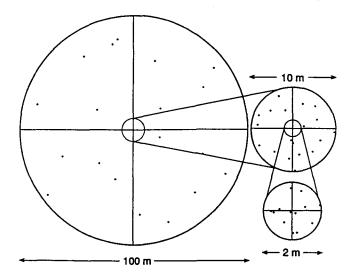

Fig. 1. Sampling design used in the plots showing layout of 52 randomized non-aligned grid sampling points in three concentric nested circular plots with grid cell sizes of 0.5,2, and 20m.

Based on semi-variograms, D. Perry et al. (unpubl. 1991) inferred that soil carbon, nitrogen, canopy cover, and perhaps microbial biomass were spatially autocorrelated over distances of approximately 30 m in old-growth coniferous forest. The research by Perry et al., suggested that trees affect the spatial patterns of soil properties. This research addressed the question of whether two adjacent forest stands of contrasting age have different spatial signatures of soil biota and edaphic properties, and whether these signatures change over time.

Spatial analysis of ecological phenomena

Use of spatial pattern analysis and geostatistics in the field of ecology is rapidly increasing. Statistical tools such as t and F tests and analysis of variance (ANOVA) are commonly applied in ecology but require independent and normally-distributed data. However, spatial and temporal dependence are major ecological factors in dynamic natural systems (Legendre and Fortin, 1989; Rossi et al., 1992). Spatial dependence, also called autocorrelation, refers to the tendency of spatially-distributed phenomena to be more similar the closer they are to one another, and more different as the distance between them, or lag distance, increases.

Spatial pattern analysis has become an accepted method for assessing spatial heterogeneity of chemical and mineral content, moisture, and pH in the soil environment (Goodchild and Mark, 1987; Mausbach and Wilding, 1991; Webster and Oliver, 1990; Yost

et al., 1982). Soils are spatially complex, with discontinuities between homogeneous zones that create patchy gradients and structures (Legendre and Fortin, 1989). Such complexities in heterogeneity are augmented when the spatial structure observed in a given ecological situation is the reflection, not the cause, of different underlying processes that generated it (Borcard et al., 1992). Possible explanations of spatial structure in soils range from large scale associations with surface topography and plant roots (Robertson et al., 1988) to minute spatial scales generated by the interactions between individual microorganisms. Anderson (1988) describes soil biological processes as "a hierarchy of successive levels of organization where macro-, meso- and microfauna influence one another at different scales in the habitat mosaic."

Abundant examples in the current literature describe the theory and application of spatial statistical methods in soil and other ecological data (Burgess and Webster, 1980; Burrough, 1983a; Isaaks and Srivastava, 1989; Legendre and Fortin, 1989; Rossi et al., 1992). The semi-variogram is a plot of sample variance as a function of lag distance (i.e. the distance between paired sample points in a geographical area). It can be used to determine whether the data are spatially autocorrelated and to estimate the fractal dimension of a particular data set (Burrough, 1983a; Webster and Oliver, 1990). Correlograms also display the spatial heterogeneity of data as a function of lag distance, but positive or negative autocorrelation coefficients can be interpreted in terms of spacing and sizes of patches and can be tested for statistical significance (Legendre and Fortin, 1989; Sokal and Oden, 1978). A statistically significant positive autocorrelation coefficient indicates similar paired point values separated by that lag distance, while a negative autocorrelation coefficient indicates contrasting paired point values separated by that lag distance (Legendre and Fortin, 1989). In this study, semi-variograms and correlograms were used to examine the spatial organization of two contrasting forest stands.

Materials and methods

Site description

Research was conducted outside the northwestern edge of the H.J. Andrews Experimental Forest (HJA), in the Blue River Ranger District, in Oregon's western Cascade Mountains (122° 09'46"W, 44° 13'30"N).
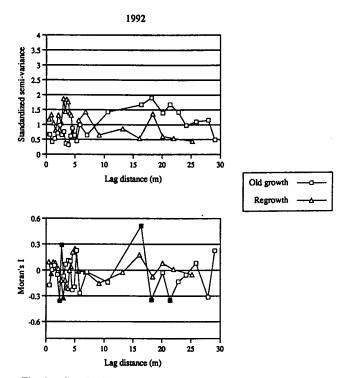

Fig. 2. Standardized semivariograms and correlograms (Moran's I) for O-horizon depth in old growth and regrowth plots in the H.J. Andrews Forest, June 1992. Square symbols represent the old growth plot and triangles represent the regrowth plot; solid symbols indicate autocorrelation coefficients significant at $p < 0.05$.

The HJA, a National Science Foundation Long-Term Ecological Research (LTER) Site, is representative of Northwest coniferous forest habitats with mixed stands of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) with old dominant trees commonly exceeding 400 years in age (Dyrness et al., 1974).

The study area typifies this forest composition and is situated at an elevation of approximately 884 m (2900 feet) on a northwest facing slope of about 10 degrees. Approximately 80 years ago, the forest stand in which the plots are located experienced a natural burn. The fire passed through the stand at varying intensities, leaving higher densities of living old-growth trees in some areas, and lower densities in others. The stand is characterized by two kinds of patches: predominantly regrowth forest with a low density of remnant trees; and primarily old-growth forest with a high density of remnant trees. Regrowth areas are characterized by young trees, close tree-to-tree spacing, low incoming insolation through a relatively closed canopy, and small gaps. In contrast, the old-growth areas are characterized by large gaps and receive direct sunlight and rainfall through a patchy forest canopy. Differences

Table 1. Abundances of soil fauna by guild in old growth and regrowth forest plots near the H.J. Andrews Experimental Forest, Oregon in 1992 and 1993. Arthropod numbers are totals of fifty-two 400 cm³ samples from each plot

	Springtails		Oribatids		Predaceous mites		All arthropods	
	number	biomass (mg)	number	biomass (mg)	number	biomass (mg)	number	biomass (mg)
June 1992								
old growth	3213	40	13052	113	218	18	16483[a]	171
regrowth	2410	33	13688	108	319	25	16417[a]	166
June 1993								
old growth	721	13	2131	55	124	10	2976	78
regrowth	1242	17	3657	70	250	41	5149	128

[a] Total counts in 1992 were 16,747 and 16,683 including fungivorous prostigmatid mites, herbaceous mesoarthropods, predaceous mesoarthropods, and fungivorous mesoarthpropods which did not occur in the 1993 samples.

Table 2. Means and coefficients of variation (CV) of soil properties in old growth and regrowth forest plots near the H.J. Andrews Experimental Forest, Oregon in 1992 and 1993

	1992		1993	
	Old growth	Regrowth	Old growth	Regrowth
O horizon (cm)				
n	51	51	_[a]	–
mean	2.7	3.0	–	–
CV	0.56	0.43	–	–
Soil moisture(%)				
n	52	51	46	52
mean	55	83	189	230
CV	0.52	0.50	0.54	0.45
Soil temperature (°C)				
n	51	50	51	52
mean	15.4	15.6	7.3	5.4
CV	0.10	0.09	0.10	0.13
Soil pH				
n	52	51	46	52
mean	4.9	4.7	5.1	5.2
CV	0.10	0.12	0.10	0.10
Arthropods				
n	52	51	47	51
mean	322	327	63	101
CV	0.56	0.61	0.69	0.59
Biomass(mg)				
n	52	51	47	51
mean	17.8	12.6	1.7	2.5
CV	0.71	0.89	0.63	0.73

[a] O-horizon depth measurements were not reported in 1993.

between the two plots in the spatial organization of soil properties and fauna should be attributable to their contrasting stand compositions.

Field methods

Two 50-m radius circular plots were sampled in the last week of June 1992 and 1993 in adjacent high density and low density forest stands. The first plot, a mixture of old and regrowth conifers with a high density of remnant trees, was centered around one living old-growth Douglas-fir tree. The second plot was centered in 1992 around an old growth stump burned 70+ years before and in 1993 at the base of a young Douglas fir; both are in the same dense stand of regrowth. In each 50-m plot fifty-two random non-aligned sampling points were arranged in three concentric nested circular subplots. The innermost 1-m radius subplot contained 12 points in a randomized 0.5 m grid; the middle 5-m radius subplot contained 20 points in a randomized 2 m grid, and the outermost 50-m radius subplot contained 20 points in a randomized 20 m grid (Fig. 1).

The nested spatial design tests for autocorrelation at three spatial scales: < 1 m, 1 to 5 m and 5 to 50 m. Because plots were centered on living or dead trees, the inner 1-m radius subplot covered an area where bark accumulates in a mound at the base of the central tree, the 5-m radius subplot covered an area of forest floor with shrubs and saplings, and the outermost 50-m radius plot covered an area of several to many tree canopies and root systems. Over two-thirds of the pairs of points in this design include a point in the central 5-m radius area of the plot. Thus semi-variances and autocorrelation coefficients for 0 to 5 m lags describe patterns in this central area, while the semi-variances and autocorrelations for longer lags (10 m or more) compare points in the central subplots to the large outer subplot. This design describes patterns due to the radial influence of the central feature of the plot (in this case a living old-growth tree, a dead old-growth stump, or a living young tree) as a function of distance, rather than the spatial organization of the stand as a whole. When overlaid on artificial landscapes with known spatial patterns, this design can correctly detect random and regular patterns and can discriminate between regular patterns dominated by short-range variation (0 to 5 m frequency) and long range variation (10 to 25 m frequency) (Roberts,1994).

Soils were sampled in three-hour periods on June 27, 1992 and June 29-30, 1993. Two adjacent volumetric soil cores were taken at each observation point

with a 5 × 10 cm cylindrical corer and placed in zip-sealing plastic bags to be stored at 2°C (35°F) until faunal extraction and analysis. The cores commonly included both O and A soil horizons, depending on the depth of the O-horizon. The first sample was used for chemical analysis and the second for arthropod extraction. Notes on O-horizon depth, litter composition and surrounding vegetation were taken during soil sample collection. Temperatures were measured with a field thermocouple inserted to 10 cm depth at each observation point.

Soil moisture content was determined gravimetrically and expressed on an oven dry basis; soil pH was measured in a 4:1 water to soil solution using a Corning glass electrode using facilities at the Forest Soil Laboratory (OSU). Soil organism extraction, identification and abundance counts of soil fauna from remaining samples took place two to three weeks following collection. Volumetric samples reserved for microarthropod extraction were removed from refrigerated storage and placed in modified MacFadyen high-gradient moisture extraction funnels (Moldenke, 1993). Extracted fauna were identified by species and placed in functional groups at the Forest Insect Laboratory (OSU).

Statistical analysis

Six variables (O-horizon depth, temperature, soil moisture, pH, soil arthropod numbers, and soil arthropod biomass) were entered into a spreadsheet. Data were tested for normality prior to spreadsheet calculations of bivariate correlations and linear regressions. Prior to spatial statistical analysis, data were examined for spatial gradients along north-south and west-east axes following Webster and Oliver (1990) and Legendre and Fortin (1989). Soil moisture microarthropod biomass increased slightly toward the southwest in both plots. Soil pH in the old growth plot also decreased slightly to the west. These trends were weak ($r^2 < 0.1$) and no attempt was made to remove them.

Semi-variograms and correlograms were constructed from semi-variances, autocorrelation coefficients (Moran's I), and 95% confidence intervals for Moran's I calculated from sample sizes of 30 pairs of points using a program in C based on Legendre and Fortin (1989) and Sokal and Oden (1978). The standardized semi-variance (the semi-variance divided by the overall sample variance) was reported to facilitate comparison between soil properties (Rossi et al., 1992). Measurements of variance and correlation at distances
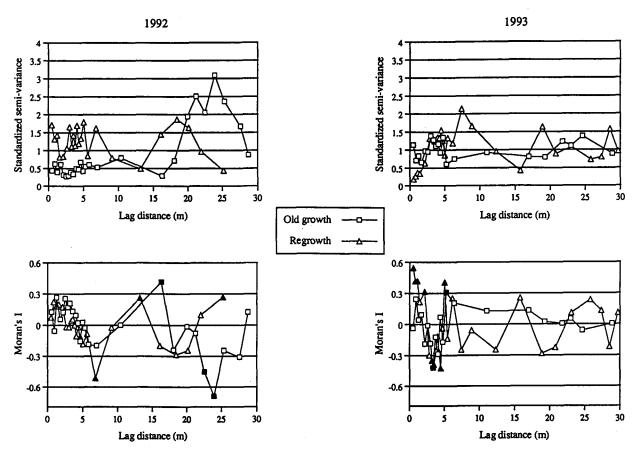
230

Fig. 3. Standardized semivariograms and correlograms (Moran's I) for soil moisture content in old growth and regrowth plots in the J. Andrews Forest, June 1992 and June 1993. Symbols as in Figure 2.

greater than two-thirds of the sampling radius (i.e. 30 m) were disregarded (Legendre and Fortin, 1989). As expected, random spatial data generated significant values of Moran's I about 5% of the time. Thus roughly one significant autocorrelation coefficient could be expected by chance in our correlograms even if underlying patterns were random. However with random data these spurious significant values occur at different lags for every correlogram, and there is a very small chance that random data would produce two or more correlograms with spurious significant values of I at the same or nearly same lag values (Roberts, 1994). In this study we inferred a spatial pattern only when two or more correlograms had significant autocorrelation coefficients at the same lag distance.

Results

A total of 16,747 and 16,683 microarthropods (per 20 liters of soil) were counted in the old and regrowth plots in 1992 and 2,976 and 5,149 in 1993 (Table 1). In 1992, 125 different taxa of microarthropods

were found in both plots: 103 species in the old growth plot and 106 species in the regrowth plot, including 12 species of Collembolla (springtails), 52 oribatid mites, 9 predaceous mites, 2 fungivorous prostigmatid mites, 7 herbaceous mesoarthropods, 25 predaceous mesoarthropods, and 18 kinds of fungivorous mesoarthropods. Oribatids represented over 70% of arthropod numbers and 55 to 70% of arthropod biomass, while springtails represented 15 to 25% of arthropod numbers and biomass in both plots in 1992 and 1993. Predaceous mites represented less than 5% of arthropod numbers and less than 15% of biomass except in the regrowth plot in 1993 (Table 2).

Soil properties differed markedly between 1992 and 1993. On average in June 1992, an unusually hot dry spring, soil temperature at 10 cm was 15.5°C, soil moisture content was 69% and soil samples contained 324 invertebrates with a biomass of 15.2 mg. In June 1993, a cold wet spring, average soil temperature was 6.4°C, soil moisture content was 210%, and soil samples contained 82 invertebrates with a biomass of 2.1 mg. The old growth and regrowth plots had similar means and coefficients of variation for all soil proper-
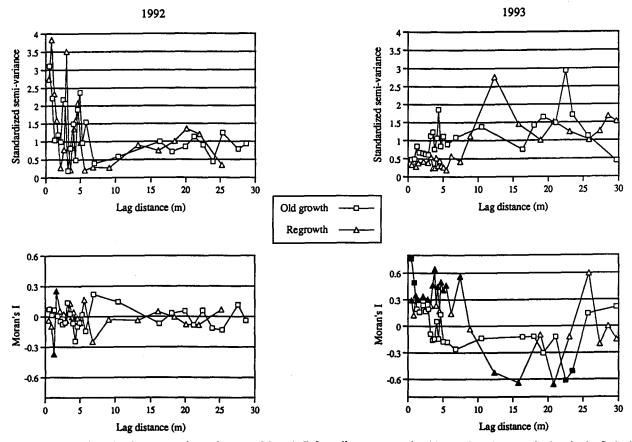
1992

1993

Fig. 4. Standardized semivariograms and correlograms (Moran's I) for soil temperature in old growth and regrowth plots in the J. Andrews Forest, June 1992 and June 1993. Symbols as in Figure 2.

ties in both years (Table 2). There were no significant bivariate correlations between the four soil properties, faunal census, or faunal biomass.

Although average invertebrate numbers and soil properties were quite similar under both vegetation types, spatial patterns differed between old growth and regrowth plots and between 1992 and 1993. In 1992, semi-variograms and correlograms revealed more short range (0 to 7 m) than long range (7 to 25 m) variability in the predominantly regrowth plot, but more long range than short range variability in the plot containing a high density of old-growth conifers. In June 1993 predominantly short-range variation was apparent in both plots (Figs. 2–7).

In 1992, semi-variances of O-horizon depths in the regrowth plot were higher at lags < 5 m than at lags > 10 m, but in the old growth plot they were higher at > 10 m lags than at < 5 m lags. The old growth plot had significant positive and negative values of Moran's I at 16 and 18 m lags whereas the regrowth plot had a significant negative value of I at 3 m (Fig. 2).

Semi-variances of soil moisture in the regrowth plot in 1992 had very high nuggets (a "hypernugget effect"

indicative of spikes or holes in an otherwise uniform field of values, R. Rossi, personal communication) and were considerably higher than those in the high density old-growth plot for lags up to 10 m, but at lags above 20 m, semi-variances in the old growth plot exceeded those in the regrowth plot (Fig. 3). Correlograms show significant negatively autocorrelated soil moisture in the regrowth plot at a 7 m lag with positive autocorrelations at 14 and 26 m, whereas soil moisture in the old growth plot is positively autocorrelated at 17 m and negatively autocorrelated at 22 to 24 m. In 1993 semi-variances of soil moisture did not change consistently from short to long lag distances. The regrowth plot had significantly positively autocorrelated values at 0.5 to 2 m lags and significantly negatively autocorrelated values at 3 to 5 m lags while the old growth plot had significantly negatively autocorrelated values at 3 m and positively autocorrelated values at 6 m (Fig. 3).

Soil temperature in 1992 in both plots had very high nugget semi-variances, high semi-variances at lags up to 6 m, and quite low semi-variances at lags above 6 m (Fig. 4). Values of Moran's I show significant negatively and positively autocorrelated temperatures in
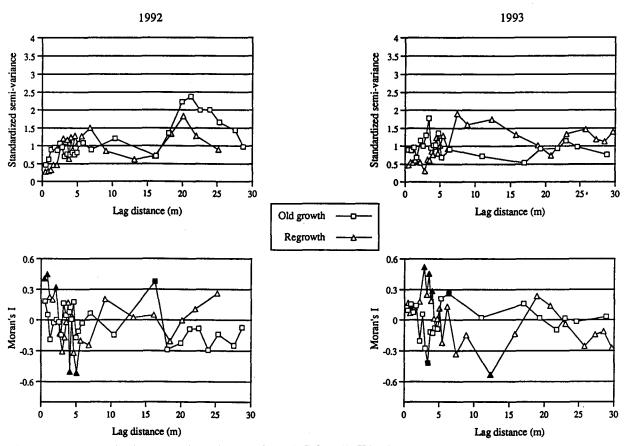
Fig. 5. Standardized semivariograms and correlograms (Moran's I) for soil pH in old growth and regrowth plots in the H.J. Andrews Forest, June 1992 and June 1993. Symbols as in Figure 2.

the regrowth plot at 1 and 2 m lags. In 1993 these patterns were reversed: soil temperature had low nugget semi-variances, and semi-variance increased with lag. Soil temperatures were significantly positively autocorrelated in the regrowth plot at 0.5 to 8 m lags, and negatively autocorrelated values at 12 to 22 m lags; whereas in the old growth plot temperatures were significantly positively autocorrelated at 0.5 to 1 m lags and negatively autocorrelated at 23 and 24 m lags.

Soil pH in 1992 had slightly higher semi-variances in the regrowth plot compared to the old growth plot at lags of 3 to 7 m but higher semi-variances in the old growth plot compared to the regrowth plot at lags above 10 m (Fig. 5). Soil pH in the regrowth plot in 1992 was significantly positively autocorrelated at 0.5 to 2 m lags and negatively autocorrelated at 4 to 5 m lags, whereas in the old growth plot in 1992 soil pH was positively autocorrelated at a 17 m lag. In 1993 these patterns were reversed: semi-variances of soil pH in the old growth plot exceeded those in the regrowth plot at lags up to 6 m, while semi-variances in the regrowth plot exceeded those in the old growth plot at lags of 8 to 20 m. Soil pH in 1993 in the regrowth plot

was significantly positively autocorrelated at 3 to 5 m lags and negatively autocorrelated at a 13 m lag, while in the old growth plot it was negatively autocorrelated at a 3 m lag and positively autocorrelated at a 7 m lag.

Semi-variances of numbers of soil invertebrates in 1992 did not differ by vegetation type at lags below 8 m but semi-variances in the old growth plot exceeded those in the regrowth plot at lags above 8 m (Fig. 6). Soil invertebrate numbers were significantly positively autocorrelated at 17 m lag in the regrowth plot in 1992 and negatively autocorrelated at 24 m in the old growth plot. In 1993 semi-variances of soil invertebrate numbers had a hypernugget effect in the regrowth plot, while semi-variances in the old growth plot rose from near zero at a lag of 0.5 m to a peak at a 3 m lag; at lags above 3 m semi-variances in the old-growth plot were slightly higher than in the regrowth plot. Soil invertebrate numbers were significantly positively autocorrelated at lags of 0.5 to 1 m and negatively autocorrelated at 2 and 3 m lags in the old growth plot.

Semi-variances of soil arthropod biomass in 1992 in the regrowth plot had a hypernugget effect and semi-variances in the regrowth plot exceeded those in the
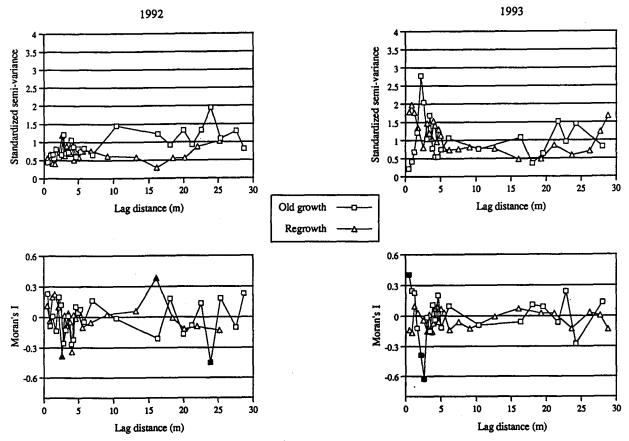
Fig. 6. Standardized semivariograms and correlograms (Moran's I) for soil arthropod numbers in old growth and regrowth plots in the H.J. Andrews Forest, June 1992 and June 1993. Symbols as in Figure 2.

old growth plot at lags up to 6 m (Fig. 7). Arthropod biomass was significantly positively autocorrelated in the regrowth plot at a 2 m lag and significantly negatively autocorrelated at 2 and 4 m lags, whereas arthropod biomass in the old growth plot was significantly negatively autocorrelated at a 6 m lag and positively autocorrelated at 17 and 26 m lags. In 1993 semivariances of arthropod biomass in the regrowth plot also had a hypernugget effect but differed little from those in the old growth plot above a lag of 2 m. Arthropod biomass in the old growth plot was significantly positively autocorrelated at a 0.5 m lag and negatively autocorrelated at 2 and 3 m lags.

Discussion

This study showed spatial patterns in soil O-horizon depth, soil moisture, temperature, pH and soil invertebrate numbers and biomass in 50-m radius plots in a heterogeneous old growth stand in western Oregon. These patterns changed from June 1992 to June 1993 and differed between a high density old-growth stand

and a stand composed of 80-year regrowth and few or no old-growth remnant trees.

All properties (soil pH, moisture content, O-horizon depth, temperature, faunal census, biomass and nematode density) were spatially autocorrelated in the study plots. In 1992, short-range variability exceeded long-range variability and autocorrelation coefficients appeared to reflect small (0 to 5 m) patches for all properties in the regrowth plot, whereas long-range variability equaled or exceeded short-range variability and autocorrelation coefficients appeared to reflect large (10 to 30 m) patches for all properties except temperature in the old growth plot. In 1993, short-range variability exceeded long-range variability in soil invertebrate numbers and biomass, while long-range variability exceeded short-range variability in soil temperature, and there were no differences between the two vegetation types. In June of 1992 soil temperatures were twice as high, soil moisture content was one-third as high, and soil invertebrate numbers and faunal biomass were five to ten times higher than in June of 1993. The spatial structures shown in this study appear to reflect the linkages between soil inver-
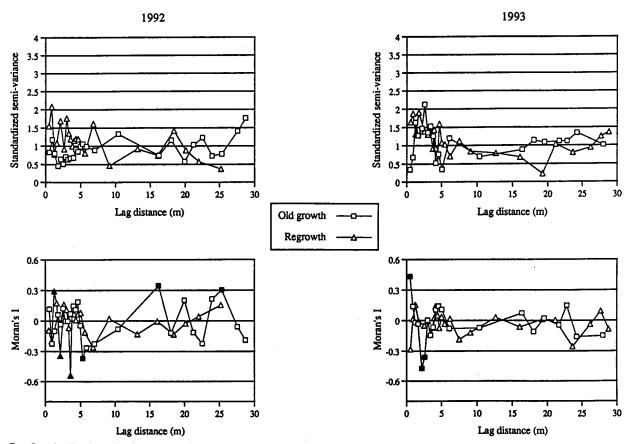
234

1992   1993

Fig. 7. Standardized semivariograms and correlograms (Moran's I) for soil arthropod biomass in old growth and regrowth plots in the J. Andrews Forest, June 1992 and June 1993. Symbols as in Figure 2.

tebrates and their environment (substrate, moisture, temperature and pH) which in turn reflect the spatial organization of the forest floor imposed by different-sized trees. The forest soil is defined by the patchiness of its habitats created by disturbances such as tree falls, root wad tip-ups and refugia of moisture such as subterranean logs left untouched by passing fires (Moldenke and Lattin, 1990b). The biochemical and soil faunal signature of a tree is imprinted on the local soil ecosystem while the tree is living and may persist after the tree burns, blows down or is cut (Anderson, 1988; Moldenke, 1990).

In this study, trees and, more generally, forest stand composition appeared to contribute to the spatial structuring of soil properties. Old growth trees were spaced at approximately 10 m in and around the center of the old growth plot, whereas smaller trees were rare in the old growth plot but common and spaced at 3-5 m in intervals in the regrowth plot. The regrowth homogeneous plot, with its close, relatively even-spaced similar-aged conifers, small scale canopy gap structuring, and low density of remnant trees, displayed well-defined patterns of short patch-to-patch spacing

of soil properties and faunal numbers in 1992. Short between-tree distances and small gap size provide one explanation for the prominent short range patterning observed in 1992 in the regrowth plot.

The plot containing a high density of large old-growth trees intermixed heterogeneously with younger conifers, rhododendron patches, and large gaps had less distinct short range and more pronounced long range spatial structure in 1992. Older, larger trees have wider canopy radii and form stands with larger gaps that affect inputs, such as sunlight, rain, and litter fall (i.e. needles and woody debris), into the soil environment from above. The larger trees' extensive root networks control the uptake of moisture and nutrients from below as well. Longer intervals of tree-to-tree spacing and larger gap size created by large disturbances such as tree falls are very likely related to more significant long range patterning observed in 1992 in the old-growth heterogeneous plot.

The ephemeral nature of the patterns, which differed between old growth and regrowth only in 1992, is attributable to the changing character of the forest floor as a habitat for soil invertebrates. In 1992, after

a hot dry spring, physiologically active trees apparently had extracted available soil moisture and created patches scaled by the size of root crowns, while small-scale temperature variations were created by shading, and soil invertebrates were abundant and appeared to be clustered in the large rooting zone at the center of the old growth plot. In 1993, after a cold wet spring, small-scale soil moisture variations were created by differences in moisture holding capacity in the near-saturated soil, while large-scale temperature variations were created by patches of understory vegetation such as rhododendrons, and soil invertebrates were scarce but clustered in the bark mound at the immediate center of the old growth plot.

In summary, geostatistical tools (semi-variograms and correlograms) revealed spatial patterns of soil microarthropods, moisture, temperature, pH and O-horizons in old growth and regrowth plots in the H.J. Andrews that appeared to be related to the sizes, spacing and physiological ecology of trees. Further examination of such spatial patterns is needed to identify their causes and consequences for coniferous forest ecosystems.

Acknowledgements

References

Anderson J M 1988 Spatiotemporal effects of invertebrates on soil processes. Biol. Fertil. Soils 216–227.

Baermann G 1917 Eine einfache Methode zur Auffunddung von Ancylostomum (Nematoden) Larven in Erdproben. Geneeskd. Tijdschr. Ned. Indie 57,131–137.

Borcard D, Legendre P and Drapeau P 1992 Partialling out the spatial component of ecological variation. Ecology 73 (3), 1045–1055.

Burgess T M and Webster R 1980 Optimal interpolation and isarithmic mapping of soil properties. I. The semi-variogram and punctual kriging. J. Soil Sci. 31, 315–331.

Burrough P A 1983a Multiscale sources of spatial variation in soil. I. The application of fractal concepts to nested levels of soil variation. J. Soil Sci. 34, 577–597.

Burrough P A 1983b Multiscale sources of spatial variation in soil. II. A non-Brownian fractal model and its application in soil survey. J. Soil Sci. 34, 599–620.

Dyrness C T, Franklin J F and Moir W H 1974 A preliminary classification of forest communities in the central portion of the Western Cascades in Oregon, Bull. #4 Conif. For. Biome. Stud, USIBP.

Feldman L J 1988 The habits of roots. BioScience 38, 612–618.

Goodchild M F and Mark D M 1987 The fractal nature of geographic phenomena. Ann. Assoc. Am. Geogr. 77, 265–278.

Isaaks E H and Srivastava R M 1989 An introduction to applied geostatistics. Oxford University Press, New York.

Legendre P and Fortin M J 1989 Spatial pattern and ecological analysis. Vegetatio 80,107–138.

Mausbach M J and Wilding L P (Ed.) 1991 Spatial variabilities of soils and landforms. Proceedings of an international symposium. Soil Science Society of America Special Publication no. 28. Soil Science Society of America, Madison, WI.

McIver J D, Parsons G L and Moldenke A R 1992 Litter spider succession after clear-cutting in a western coniferous forest. Can. J. For. Res. 22, 984–992.

Moldenke A R and Fichter B L 1988 Invertebrates of the H. J. Andrews Experimental Forest, western Cascade Mountains, Oregon: IV. The oribatid mites (Acari: Cryptostigmata). Gen. Tech. Rep. PNW-GTR-217. Portland, OR: U. S. Dept. of Agriculture, Forest Service, Pacific Northwest Research Station.

Moldenke A R 1990 One hundred twenty thousand little legs. Essays on Invertebrate Conservation, The Xerces Society. Wings, (Summer) pp 11–14.

Moldenke A R and Lattin J D 1990a Density and diversity of soil arthropods as "biological probes" of complex soil phenomena. Northwest Environ. J. 6, 409–410.

Moldenke A R and Lattin J D 1990b Dispersal characteristics of old-growth soil arthropods: The potential for loss of diversity and biological function. Northwest Environ. J. 6, 408–409.

Moldenke A R 1993 Soil arthropods. Chapter 24. In Methods of Soil Analyses: Biochemical and Microbiological Properties. Eds. R Weaver, P J Bottomley and S Angle. Soil Society of America, Madison, Wis.

Peterson H and Luxton M 1982 A comparative analysis of soil fauna population and their role in decomposition processes. In Quantative Ecology of Microfungi and Animals in Soil and Litter. Ed. H Peterson. Oikos 39, 287–335.

Roberts C 1994 Soil spatial heterogeneity in juniper-invaded sagebrush in central Oregon. Masters thesis, Department of Forest Science, Oregon State University.

Robertson G P, Huston M A, Evans F C and Tiedje J M 1988 Spatial variability in a successional plant community: Patterns of nitrogen availability. Ecology 69, 1517–1524.

Rossi R E, Mulla D J, Journel A G and Franz E H 1992 Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecol. Monogr. 62, 277–314.

Rusek J 1986 Soil microstructures: Contributions of specific soil organisms. Quaestiones Entomol. 21, 497–514.

Setala H and Huhta V 1991 Soil fauna increase *Betula pendula* growth: Laboratory experiments with coniferous forest floor. Ecology 72, 665–671.

Sokal R R and Oden N L 1978 Spatial autocorrelation in biology. I. Methodology. Biol. Linn Soc. 10, 199–228.

Teuben A and Roejofsma T A P I 1990 Dynamic interactions between functional groups of soil arthropods and microorganisms during decomposition of coniferous litter in microcosm experiments. Biol. Fert. Soils 9, 145–151.

Webster R and Oliver M A 1990 Statistical methods in soil and land resource survey. Oxford University Press, New York.

Yost RS, Uehara G and Fox R L 1982 Geostatistical analysis of soil chemical properties of large land areas. I. Semi-variograms. Soil Sci. Soc. Am. J. 46, 1028–1032.