A MULTIVARIATE ANALYSIS OF TREE SPECIES INFLUENCE ON FOREST FLOOR FERTILITY

by

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ABSTRACT

The objective of this study was to assess tree species influence on forest floor fertility in a mixed forest stand using Redundancy Analysis (RDA). Eighty microsites were located in a [illegible] hemlock-red maple forest. Forest floor was analyzed for thirteen variables; total [illegible] Ca and Mg, extractable Ca, Mg and K, mineralizable N (NH_4+), basal microbial respiration (CO_2), pH, thickness and bulk density. The influence of seven tree species was calculated as a function of tree diameter and distance from each microsite. Spatial patterns were detected by using correlograms and incorporated in a variation-partitioning m[illegible] trend surface analysis. Tree species, microtopography, and spatial structure [illegible] of the total variation in forest floor data. The fraction explained by tree [illegible]) was studied with a RDA ordination biplot. The main source of va[illegible] data was related mainly to the opposite effects of American beech and eastern hemlock on calcium while most of the other species had a beneficial effect on soil fertility. This study showed the potential of RDA as a tool for studying the role of tree species in mixed forests.

RESUME

L'objectif de cette étude est d'évaluer l'influence des espèces d'arbres sur la fertilité des sols de peuplements mixtes en utilisant l'analyse de redondance. Quatre-vingt microsites ont été localisés dans une forêt de hêtre-pruche-érable rouge. Treize variables de la couverture morte ont été mesurées; N, P, K, Ca, et Mg total, K, Ca et Mg extractible, pH, respiration microbienne basale (CO_2), N minéralisable (NH_4), l'épaisseur et la densité apparente. L'influence des essences a été calculée en fonction du diamètre de l'arbre et de sa distance du microsite. Des patrons spatiaux ont été détectés à l'aide de corrélogrammes et intégrés dans un modèle de partition de la variation avec une analyse de tendance de surface. La variation totale de la couverture morte expliquée par les différentes essences, la microtopographie et la structure spatiale fut de 53 %. La fraction expliquée par les essences seulement (16 %) a été étudiée à l'aide de l'ordination d'une analyse de redondance. La source principale de variation dans le sol est associée à un effet contraire du hêtre et de la pruche sur le calcium pendant que la plupart des autres essences semblent avoir un effet bénéfique sur la fertilité du sol. Cette étude a démontré le potentiel de l'analyse de redondance pour étudier le rôle des différentes essences dans les forêts mixtes.

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INTRODUCTION

The fertility of forest soil is controlled by many interacting factors including parent material, topography and drainage, climate, disturbance and biological activities. At the stand level, trees have been recognized to play a major role in influencing properties of surface soils. The nature of this influence is primarily determined by the quantity and the quality of nutrient and organic material inputs in the ecosystem through aboveground litter decomposition, fine root turnover and exudates, and by the interception, alteration and redistribution of precipitation water. This influence of trees on soil fertility varies among species.

Many studies have observed the relationship between the quality of foliage litter and its decomposition rate and nutrient release (Aber and Melillo 1982; Melillo *et al.* 1982; McClaugherty *et al.* 1985). The differences between the litter of different tree species in terms of nutrient content, lignin and polyphenols concentration (Melillo *et al.* 1982; Berg *et al.* 1984) and their acid-base status (Côté and Fyles 1993) can affect the decomposition and thus, the characteristics of the forest floor (Melillo *et al.* 1989; Boerner 1984a; Tappeiner and Alm 1975). The input of carbon and nutrients through exudates and the turnover of fine roots is considerable. Carlyle (1986) indicates that the belowground organic input can be 2-5 times that of aboveground litterfall. Bowden *et al.* (1993) observed that 30 % of the respiration in forest soil can be associated with the decomposition taking place belowground. Berendse *et al.* (1989) suggest that root carbon exudates may affect nutrient mineralization rates in forest floor and that exudation may differ between species. The effect of stemflow and throughfall (Parker 1983) may affect soil characteristics at the base of the trunk and under the canopy of trees. Gersper and Holowaychuk (1971) have observed differences in the quality and quantity of the stemflow among tree species.

In addition, tree uptake of nutrients can alter the fertility status of forest floor. Some studies have demonstrated differences between tree species in terms of their nutrient cycling mechanisms (Boerner 1984b). Tree species also affect a series of other ecological parameters such as understorey density and species composition (Crozier and Boerner

1984; Beatty 1984), mycorrhizal communities (Nantel and Neumann 1992), and soil water content (Mergen and Malcolm 1955) all of which can alter soil nutrient status.

Information about the role of different tree species on forest soil fertility is necessary for appropriate management of forests. Many silvicultural practices involve modification of the species composition of stands, by selectively planting or harvesting certain tree species. Although these practices may also have an effect on other ecological parameters (eg. competition for resources such as light or water), the potential to affect the nutrient cycling and the productivity of the stand is considerable. In plantation the presence of species that can ameliorate soil fertility may improve the productivity. The positive effect of larch on the productivity of Sitka spruce stands (Malcolm 1987), gambel oak in Ponderosa pine stands (Klemmedson 1987; Lefevre and Klemmedson 1980) and big-leaf maple in Douglas-fir stands (Fried *et al.* 1990) illustrate the fact that some tree species may be considered beneficial for the fertility of a stand. These results suggest that a better understanding of the influence of different tree species on soil properties may lead to a more efficient use of mixed-plantations (see Cannel *et al.* 1992) that would not only be more productive and economically profitable, but also more sustainable.

Practices involved in the management of natural and semi-natural woodlot that selectively harvest certain species (shelterwood, thinning) or remove the understorey layer (weeding) may use information about the role of specific tree species on soil properties in order to evaluate the impact of these practices on the long-term fertility and sustainability of the forest stands.

In cold and temperate forests, however, the ability to evaluate a particular management practice is made difficult by the time frame at which tree species can grow and affect site conditions. In order to get information about the effect of tree species on soil fertility it is necessary to study natural and mature forest stands in which trees have been able to influence soil characteristics for a long period of time. Many studies have examined the effect of different tree species on soil characteristics either at the single-tree level (Zinke 1962; Boerner and Koslowsky 1989; Boettcher and Kalisz 1990; Lodhi 1977) or at the stand level (Fyles and Côté 1993; Fyles and McGill 1988; Klemmedson 1987; Carlyle and Malcolm 1986). In general, these studies were able to demonstrate significant differences between tree species. Most of the studies were done however, on stands of relatively low diversity (pure stands or mixtures of two species) and there is very few information about the specific role of different tree species in mixed-stands.

The presence of many co-existing species generates more interactions between the different processes involved in community structuring (see Frelich *et al.* 1993), either through the relationship between the different tree species themselves or the effect of other controlling factors such as parent material or drainage that can be spatially structured over the site. Spatial heterogeneity, where tree species are distributed neither evenly nor randomly, can make the tree species influence on soil properties difficult to isolate from the confounded effect of other controlling factors. In addition, part of the spatial structure observed on the site can be caused by the presence of autocorrelation in which observations cannot be considered independent from each other (Legendre 1993). This non-independence of observations violates the assumption of most parametric statistical models.

In order to isolate tree species influence on forest soil fertility, a statistical model needs to incorporate the spatial component. Legendre and Fortin (1989) stressed the fact that most ecological data is spatially structured and that an analysis of that spatial structure should be the first step of the analysis. A model of variation-partitioning was developed by Borcard *et al.* (1992) in which the spatial structure is incorporated as one of the factors influencing the variation in ecological communities. Trend surface analysis is used to integrate spatial structure by building a polynomial equation with the geographical coordinates of the observations. This model has not yet been tested on soil data but has the potential to address the problem of spatial heterogeneity found in mixed-stands.

The model of Borcard *et al.* (1992) is also adapted for multivariate data, in which the statistical model aims at explaining the variation in the response data taken as a whole instead of the response variable taken individually. Since soil variables have been shown to be intercorrelated and to vary more or less in concert (Norris 1970; Webster 1977), I have decided to examine the variation found in the soil data taken as a whole, in which each variable is considered to be part of a more complex system that is commonly referred as soil fertility, and responds to the same environmental gradients.

The objective of this study is thus, to measure in a mixed-stand the tree species influence on soil properties taken as an ensemble by using the method of Borcard *et al.* (1992) in which spatial structure is integrated in a variation partitioning model. Because this model has not been tested with soil data, a preliminary test of the applicability of the method was necessary before proceeding with the study of tree influence on soil fertility.

In the first chapter, as proposed by Legendre and Fortin (1989), a preliminary study of the spatial structure present in the data set was done with the help of Moran's *I* correlograms and multivariate correlograms in order to detect and visualize the shape of the different spatial patterns. The ability of the trend surface analysis to capture the spatial structure in the data was tested before proceeding with the partitioning of the forest floor variation into four fractions; a) variation related to environmental variables (tree species and microtopography), b) variation related to a shared effect of environmental variables and spatial structure, c) variation related to spatial structure alone and, d) unexplained variation. In the context of this experimental design, the shared effect of environmental variables and spatial structure can also be described as a confounded effect since it is impossible to separate the effect of environmental variables from the influence related to their spatial structure.

In the second chapter, the partitioning involves another step in which the environmental variables are separated into their tree species and microtopographical variables. A more complete study of the relationship between the different tree species and the forest floor variables is conducted.

CHAPTER ONE

ENVIRONMENTAL CONTROL AND SPATIAL STRUCTURE IN FOREST FLOOR DATA.

INTRODUCTION

Any study aimed at examining the factors controlling forest floor fertility must deal with the inherent complexity and heterogeneity of forest ecosystems. Within a forest stand or landscape, controlling factors such as parent material, topography, biological activities, disturbance and climate vary at different scale over time and space (eg Wyant *et al.* 1991; Cox and Larson 1993). Such variation in the ecosystem generates spatial heterogeneity in which phenomena are distributed neither evenly nor randomly. In addition interactions among controlling factors and forest floor variables generates complexity in the system with the results that variables are typically inter-correlated (Norris 1970) and vary more or less in concert (Webster 1977). The statistical methods appropriate to the study of environmental controls on forest floor properties must be capable of addressing both the complexity and the heterogeneity of the ecosystem. Univariate statistical designs may hardly deal with intercorrelated and heterogeneous data and therefore may fail to adequately extract clear information about how these interacting processes influence forest floor characteristics.

Multivariate analytical methods have been developed to address the problems of complex data where dependent variables are known to be intercorrelated (James and McCullough 1990; Norris 1970). The general objective of multivariate statistics is to build statistical models that will represent or explained the main source of variation in an ensemble of many variables rather than as single variables examined individually

A group of multivariate methods called gradient analysis have been used with ecological data (ter Braak and Prentice 1988; ter Braak 1987c). In gradient analysis, the main source of variation in the multivariate response data is expressed by independent linear axes that can be displayed in ordination graphs Gradient analysis can be divided in indirect gradient analysis, where the objective is to measure the intrinsic variation in the response data, and direct gradient analysis, where the goal is to measure the variation in the response data caused by specific explanatory variables (ter Braak and Prentice 1988; ter Braak 1987c).

Principal component analysis (PCA) is a well known example of indirect gradient analysis which has been used with soil data (Norris 1970). PCA has been used to identify the principal source of variation in soil data in order to infer potential controlling processes or treatment effects (Dinel *et al.* 1991), and has also been used to classify or group soil or forest floor units on the basis of certain variables of interest (Fyles *et al.* 1991; Muys and Lust 1992; Seelig *et al.* 1991). Some studies have conducted multiple regression of each PCA ordination axis on a chosen set of explanatory variables to determine the variation in the soil data that could be explained by those variables (Odeh *et al.* 1991; Ross *et al.* 1975).

To measure the effect of specific controlling factors on forest floor properties, however, direct gradient analysis may be more appropriate since the axes are constrained to be linear combination of the explanatory variables (ter Braak 1987c). Canonical correspondence analysis (CCA)(ter Braak 1986) and Redundancy analysis (RDA) (van den Wollenberg 1977) are examples of such techniques which are used when the response along the environmental gradient is expected to be unimodal and monotonic, respectively. Odeh *et al.* (1991) were the first to test these methods on soil data. One of their conclusions was that the assumption of the linear response of the soil data in RDA was more adequate then the more general unimodal-gaussian response assumed in CCA. CCA was developed (ter Braak 1986) to include the concept of an optimum position of species along environmental gradients, but this concept seems more difficult to apply to soil data (Odeh *et al.* 1991).

RDA is a combination of multiple regression and ordination (ter Braak and Prentice 1988; ter Braak 1987c) and can be thought of as a PCA on the estimates of each soil variable obtained by multiple regression on environmental variables (van den Wollenberg 1977; Legendre 1993). Each canonical axes then represents a fraction of the variation explained by specific environmental variables. The sum of the variation explained by all of these 'constrained' axes is thus equal to the total variation explained by the explanatory variables. RDA was proposed by van den Wollenberg (1977) as an alternative to a method named Canonical correlation (COR) which had been used a few times for soil study (Norris 1970; Webster 1977). COR aimed at maximizing the correlation between the linear function of two sets of variables (Webster 1977). It gives, however, no information about the variation of one set explained by the other set (van den Wollenberg 1977). Other inconveniences, such as the high sensitivity of COR to multicollinearity between variables, have demonstrated that RDA may be more appropriate for the analysis of ecological data (ter Braak 1987c).

Although RDA has not been previously applied to forest floor data, it addresses the problem of the complexity and intercorrelation of the variables and consequently may be a useful technique for studying relationships between forest floor fertility and environmental factors. Odeh *et al.* (1991) were able to relate physical properties of soils to landform using this technique. Their study demonstrated the importance of appropriate data transformation in using this method. The applicability of the procedure to forest floor data remains to be determined.

The other problem encountered in working with forest ecosystems, mentioned above, is the heterogeneity of the studied phenomenon. Legendre (1993), Legendre and Fortin (1989) and Dutilleul and Legendre (1993) have indicated that most ecological data is heterogeneous and spatially structured. Many studies demonstrated the importance of spatial heterogeneity in forest ecosystems (Wyant *et al.* 1991; Whitney 1991; Collins and Khlar 1991; Cox and Larson 1993; Frelich *et al.* 1993; McClure and Lee 1993). In the case of forest floors, most of the controlling factors are themselves spatially structured and consequently forest floor characteristics are expected to show spatial dependency This could present difficulty in the analysis of the data for two reasons. First, part of the spatial structure may be caused by autocorrelation, meaning that the value of a variable at a certain sampling station would be influenced by values at surrounding sampling stations (Legendre 1993). This non-independence of the observations violates one of the classical assumptions of the fitting of the multiple linear regression model (Steel and Torrie 1980; ter Braak 1987b) used in RDA. Secondly, the effect of a specific environmental variable on forest floor characteristics can be partly confounded with the effects of other factors that can vary spatially on the study site. In view of the analytical risks inherent in the analysis of spatially structured data, Legendre (1993) and Legendre and Fortin (1989) have stressed the importance of assessing spatial patterns and functions as the first step of ecological data analysis. Recent studies have considered the role of spatial heterogeneity in the analysis of ecological data (Dutilleul 1993; Dutilleul and Legendre 1993; Legendre 1993; Legendre and Fortin 1989; Kolasa and Pickett 1991).

An adaptation of the variation-partitioning method (Whittaker 1984) was recently developed in community analysis to incorporate spatial structure (Borcard *et al.* 1992; Borcard and Legendre 1993). In the model of Borcard *et al.*(1992), the fraction of the variation in the response variable data that can be 'explained' by a third order polynomial equation of the geographical coordinates of the microsites on the site is used to detect the spatial structure in the data set (cf. ter Braak 1987a). A RDA (or CCA), is computed for environmental variables and for significant terms of the polynomial equation to measure the relative contribution of environmental and spatial variables to the explained variation in the response variable data. Partial RDA (or CCA) where the effect of the other group is removed as covariable is used to measure the confounded effect of spatial structure and environmental factors. In the model of Borcard *et al* (1992) the variation in the data can de divided in four fractions; a) variation related to environmental variables, b) variation related to a confounded effect of spatial structure and environmental variables, c) variation related to spatial structure alone , and d) unexplained variation. This approach was developped for ecological communities but to my knowledge, it has not been yet applied to soil or forest floor data. Since this model addresses both the complexity and the heterogeneity inherent in forest soils, it has the potential to generate information that will provide insight into the relationship between forest floor characteristics and the environmental factors.

The objective of this study was thus to test the applicability of RDA, and specifically the variation partitioning model of Borcard *et al* (1992), to forest floor data. The chosen environmental variables are tree species influence and microtopography. This choice is based on many studies that have demonstrated the effect of different tree species (eg.Fyles and McGill 1988; Boettcher and Kalisz 1990; Boerner and Koslowsky 1989; Fried *et al.* 1990) and microtopography (Beatty 1984; Beatty and Stone 1988; Sauvesty *et al.* 1993) on soil and forest floor characteristics. The scale of the study was the microsite, meaning that each forest floor sample was collected from a area of 0.5 m diameter. Since many studies have demonstrated the strong relationship between scale and soil variability (Beckett and Webster 1971; Burrough 1983; Webster and Cualano 1975; Riha *et al.* 1986; Grigal *et al.* 1991; Blyth and Macleod 1978), it will be important to consider scale in interpreting the different fractions obtained in the variation-partitioning model of Borcard *et al* (1992). Assessment of the model assumptions involved several issues, and is discussed in terms of: 1) a initial study of the spatial structure present in the original data; 2) appropriate data transformation of the forest floor data; 3) selection of the spatial polynomial equation; 4) verification of the amount of spatial structure remaining after removing trends with the polynomial equation; and 5) partitioning of the variation in soil data with RDA and partial RDA and ecological interpretation of the fractions obtained.

MATERIALS AND METHODS

Site description.

The study was conducted in the Morgan Arboretum near Montréal, Québec, Canada (45°25'N, 73°57'W). The study site was located in a 20 000 m^2 mixed forest stand dominated by beech, hemlock and red maple. The stand is approximatively 100 years old. The limits of the study site were determined with the help of a pedological map of the Morgan Arboretum to avoid major differences in parent material. The soils have all developed on a fluvial sand deposit and are classified as Ferro-humic podzols. Approximatively 75 % of the study site area is located on Ste-Sophie soil series while the rest, located in the more elevated part of the site, is on Uplands soil-series. The differences between the two series is mainly related to thickness of the deposit and the border between them is not clearly defined at the scale the study was conducted. The humus type is Mor. The general topography was a gentle slope of 2° to the south, the microtopography is moderately mounded and the drainage is good to moderate. The site had been managed as a farm woodlot until 1945 but management practices since that time have been limited to the removal of dead trees.

Field sampling.

Eighty microsites were located on the study site using a 15 m grid. The geographical coordinates x and y and the relative altitude z of each microsite were determined in meters. The altitude was determined by measuring the difference in elevation between neighbouring microsites with the help of a clinometer and a 3 meter ruler. The value of z for each microsite was expressed in meters relative to the lowest microsite, which was given the value zero. Forest floor was sampled at each microsite by cutting around a plastic core of 82 mm diameter. Three forest floor cores sampled in an area of 0.8 m^2 were composited for each microsite. The area of sampling for each microsite was chosen to avoid extreme conditions of microtopography such as distinct mounds developed from recently fallen trees. Thickness of the forest floor was measured at each microsite and used as one of the thirteen forest floor variables in the rest of the analysis. The sampling took place between August 28 and September 12 1992. Forest floor samples were frozen within 3 hours after collection.

Forest floor analyses.

Analyses on sieved forest floor.

Forest floor was thawed, air dried, sieved with a 6.3 mm mesh to remove coarse fragments, and weighed. Bulk density was expressed in mg/cm^3 of forest floor. The following analyses were performed on the sieved forest floor: pH (10:1, H_2O:forest floor), extractable K, Ca, and Mg with the $BaCl_2$ extraction method (Hendershot and Duquette 1986), mineralizable N and basal microbial respiration (CO_2).

Mineralizable N and basal microbial respiration.

The mineralizable N (NH_4^+, NO_3^-) in forest floor was measured using an aerobic incubation technique (adapted from Fyles *et al.* 1990). Five grams of sieved forest floor was brought to a moisture content equal to 20 kPa and incubated aerobically in 30 ml plastic jars at 28°C for 14 days. The available N was then extracted with 1N KCl and determine with a Lachat flow-injection autoanalyser. Since the sampling was done over a period of two weeks, it was necessary to remove the available N that was initially present in the forest floor at the time of the sampling. A KCl extraction was performed on subsamples of forest floor to measure the amount of available N initially present. The amount of N that was mineralized during the incubation is thus equal to the available N measured in the first KCl extraction minus the available N already present in the forest floor and measured in the second extraction. Practically all (>98 %) of the N that was mineralized was in the form of NH_4^+. This laboratory measure of mineralizable N is interpreted as an indication of the inherent quality of the organic matter rather than as an estimate of mineralization in the field.

The microbial basal respiration (CO_2) was measured on the incubated samples used for mineralizable N. After 10 days of incubation the plastic jars were sealed for four hours and CO_2 accumulated in the headspace gas determined by gas chromatography. The basal microbial respiration was computed and expressed in terms of μg of CO_2 produced per gram of air dried soil per hour (μg/g/h).

Analyses on ground forest floor.

Subsamples of forest floor were ground and digested with H_2SO_4 and H_2O_2 (see Parkinson and Allen 1975) prior to analysis for N and P by autoanalyser and K, Ca, Mg by atomic absorption spectrophotometry. The ash content was determined after ignition for 2 hours at 550°C.

Regression of forest floor variables on ash content.

Personal observations and the results obtained for ash content suggested that the presence of mineral soil in the forest floor samples may have been responsible for the variation in ash content. Since there is a possibilty that the amount of sand may be related to the sampling procedure, rather then to some forest floor properties, I decided to remove its effect on the 13 forest floor variables chosen for this experiment. The residuals of the regression of each forest floor variable on ash content were computed and used in the rest of the study. The ash content values used in the previous regression were themselves the residuals of a regression of the initial ash content on the geographical coordinates x, y and z of the microsites, in order to remove the fraction of the variation in ash content that was spatially structured.

Environmental variables.

Tree species influence index.

Tree species influence was expressed as a function of the size and the distance of individual trees from microsite. The index of tree influence used in this study was developed from the procedure normally used in the computation of basal area (c.f. Grosenbaugh 1952).

In effect, when computing the basal area of a particular species on a site, a fixed basal area factor is chosen. The basal area factor can be expressed as follow,

$$B.A.F = 10\,000 / (2 * distance / diameter)^2$$

Where the B.A.F is related to the tree diameter and distance from the center of the site or microsite. The value of 10 000 is used in order to express the B.A.F. in m^2/ha. The usual procedure is to fix a certain B.A.F and to count only the trees that have an equal or a larger individual B.A.F.. The number of trees that meet that condition is multiplied by the fixed B.A.F to get a basal area expressed in m^2/ha. In the field, the fixed B.A.F can be expressed as an angle projection from the center of the site to the tree. If the tree is wider than this projected angle it can be tallied as its B.A.F is equal or larger than the fixed B.A.F..

The method used in this study to calculate tree species influence can be seen as the reverse of the basal area method described above. In effect, instead of counting the trees that are tallied at a fixed B.A.F., I computed the individual B.A.F. of every tree surrounding each microsite. This approach was used because the influence of large trees close to the microsite would have been underestimated with the usual basal area method The measurement of trees was not limited to a specific area around each microsite but rather by a visual approximation of the distance/dbh ratio of each tree (ie the B A.F. of larger trees was computed over a greater distance). The influence of a species on a microsite is thus the summation of the B.A.F. of each individual tree *j*. Since the B.A.F can be seen as a ratio, the geometric mean was considered more appropriate than the arithmetic mean (Steel and Torrie 1980), meaning that the index I_k of the influence of a particular tree species *k* on a microsite was computed as follow:

$$I_k = \sum_{j=1}^{n} ln\ [(B.A.F.)_j]$$

An index of influence was therefore computed at each microsite for the following tree species; eastern hemlock (*Tsuga canadensis* (L.) Carr.), American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), striped maple (*Acer pensylvanicum* L.), red oak (*Quercus rubra* L.), paper birch (*Betula papyrifera* Marsh.), yellow birch (*Betula alleghaniensis* Britton). The influence of uncommon tree species were combined under the variable 'OTHERS' and included species like sugar maple (*Acer saccharum* Marsh.) and amelanchier (*Amelanchier sp.* Med.).

Microtopography.

Three microtopographical variables were determined at each microsite. With each microsite described as being either a mound, a depression or flat. For example, the variable MOUND is equal to one when the microsite is located on a mound, and zero when it is a depression or a flat. The variable FLAT was removed because of the multicollinearity between these three variables. A flat microsite is thus, a site that had a zero value for both MOUND and DEPRESSION variables. The third microtopographical variable (SLOPE) was the greatest slope determined in an area of about half a meter radius from the center of each microsite.

Statistical procedures.

Univariate and multivariate correlograms used in the study of spatial structure were computed with the 'R' package (Legendre and Vaudor 1991). Multiple regressions used for data transformation were computed with SAS (1986). The forward selection of the spatial polynomial terms, the Redundancy Analysis (RDA) and partial RDA's were computed with CANOCO (ter Braak 1987-1992).

RESULTS AND DISCUSSION

Spatial structure in original data set.

Single variables.

As a preliminary study to detect and describe spatial structure in original data, spatial autocorrelation was determined for single variables of both forest floor and environmental data. Autocorrelation is the property of a random variable to take values that are positively or negatively correlated at certain distance classes of observations (microsites) (Legendre 1993; Legendre and Fortin 1989). To determine the distance classes, a matrix is build by computing the euclidian distances (based on geographical coordinates) between each pair of microsites. These distances are then divided into a chosen number of classes for which a coefficient of autocorrelation is computed. The two principal coefficients used to compute autocorrelation are Moran's I and Geary's c. Both coefficients were used to measure autocorrelation in our data set . Since the general conclusions reached with both coefficients were similar, only the results obtained with Moran's *I* will be discussed. Moran's *I* is computed by the following formula:

$$I(d) = [n \Sigma\Sigma w_{ij} (v_i-\bar{v})(v_j-\bar{v})] / [W\Sigma(v_i-\bar{v})^2].$$

The coefficient is computed for each distance class '*d*'. The *v*'s are the values of the chosen variable. The summations are for *i* and *j* varying from 1 to *n*, where *n* is the number of microsites, except when $i = j$. The value of w_{ij} is 1 when the pair (i,j) belongs to the distance class '*d*' for which the coefficient is computed and 0 for all the other pairs. *W* is the number of pairs taken into account when computing the coefficient for the given distance class. Positive values of Moran's *I* correspond to positive autocorrelation, negative values correspond to negative autocorrelation and the value of zero is expected in the absence of autocorrelation.

No statistical tests were computed on the correlation coefficients calculated at each distance class because the assumption of weak-stationarity was not met (Legendre 1993; Dutilleul and Legendre 1993). This has no consequence at this stage, however, because my interest is focused on the general shape of the correlogram (cf.Legendre 1993 and the discussion on trends and autocorrelation presented below).

The shape of the curve of correlogram, in which *I* values are plotted against distance classes, was used as an indication of the general pattern of autocorrelation of each variable over the site. The horizontal and vertical components of the spatial location of microsites were treated separately as I could not assume that the source of variation along the vertical axis was of similar nature to that acting in the two horizontal axes. Consequently, two graphs were plotted for each variable, the first based on the *x* and *y* geographical coordinates, and the second based on *z* coordinates Additional information on the interpretation of correlograms using Moran's *I* and Geary's *c* is given by Legendre and Fortin (1989) and Dutilleul and Legendre (1993), respectively.

Horizontal structure in environmental variables.

Spatial structure in the horizontal dimension was observed for most environmental variables. Figure 1 shows the correlograms of four of the seven tree species considered in the study. The red oak correlogram, in which there is a gradual change in autocorrelation from positive autocorrelation at small distance classes to negative correlation at greater distance classes, is typical of a gradient (Fig. 1a). The spatial pattern of red oak influence is thus either following a gradient or a sharp step between two distinct patches. Beech, hemlock and striped maple correlograms are more typical of a single patch spatial pattern (Fig. 1b,1c and 1d). Despite slight differences, the three curves show a similar pattern where there is positive autocorrelation at small distance classes, negative autocorrelation around classes 8, 9, 10 and positive correlation at greater distances classes. This suggests the presence of an area of different tree association near the centre of the study site. The similarity of these three curves may indicate that there is some underlying spatially structured factor that influences tree species distribution within the study area or that ecological dynamics implicated in forest patch formation and tree species association or exclusion is involved (Frelich *et al.* 1993). The three microtopographical variables did not show clear spatial patterns in the horizontal dimension.

Vertical structure in environmental variables.

Most environmental variables showed spatial structure in relation to the relative altitude of the microsites. The beech correlogram (Fig. 2a) shows a pattern where beech influence is positively autocorrelated on microsites of the same height and negatively correlated on sites with the farthest difference in altitude. Striped maple correlogram (Fig. 2b) displays a similar pattern until class 11 but is positively autocorrelated on microsites that differ the most in altitude. The general topography of the study site, however, shows a gentle slope going from one end of the site to the other, indicating that the relative altitude of each microsite is itself spatially structured along the horizontal component. The spatial structure observed in the vertical and horizontal component of Figures 1 and 2 are thus partly confounded, meaning that it may be better expressed as a function of the three geographical coordinates.

Horizontal structure in forest floor variables

All forest floor variables except NH_4+ showed some spatial pattern in their distribution over the site. All demonstrate the presence of patches but with differences between them. The different shapes of correlogram curves observed can be summarized by the four examples used in Figure 3. Extractable potassium (Fig. 3a) has a spatial structure relatively similar to Figures 1b,1c, and 1d, suggesting that it is either partly responding to beech, hemlock and striped maple or that it is influenced by a common underlying factor. We can thus predict that the effect of some tree species on extractable potassium will be partly confounded with spatial structure. The same applies to nitrogen (Fig. 3b) which is the most spatially structured of all the forest floor variables. The spatial pattern of nitrogen (phosphorus has a similar shape) does not however fit the tree species curve as well, suggesting the presence of spatial structure unrelated to the environmental variables chosen. Figures 3c and 3d show other type of patchiness found in the forest floor data. Calcium (extractable calcium has a similar shape) exhibited the least spatial structure of the displayed variables (Fig. 3d).

Vertical structure of forest floor variables.

The correlograms in Fig. 4 illustrate that spatial structure was not as evident in forest floor data than in environmental variables. As for the environmental variables, the spatial structure of the vertical component is confounded with the horizontal component.

In general it is clear that my data was spatially structured, since patterns were observed in both environmental and forest floor variables. Although the shape and the strength of spatial structure varied between variables, there was a dominating pattern suggesting a patch present somewhere in the centre of the site (classes 7, 8, 9, 10). This pattern was observed in both forest floor and environmental correlograms, indicating that some confounded effect of spatial structure and environment may be encountered in the further analysis of the data.

The causes of the spatial structure in the data can be of two types, trends (true gradient) or 'real' autocorrelation (false gradient) (Legendre 1993; Dutilleul and Legendre 1993). In trends, the value of a variable at a microsite is a function of its geographical position on the site. This means that the correlation between the values of a variable at certain distance classes is caused by a controlling factor that is spatially structured on the site. Trends can be related to large scale patterns occurring over the site and are potentially removed or captured by trend surface analysis (Burrough 1987). Technically, the observations (microsites) are still considered independent since the error terms are not correlated (Legendre 1993). One consequence of trends is that the assumption of weak-stationarity necessary to compute statistical tests on correlograms is not met since the mean and the variation of variables vary with the geographical position of the microsites (Legendre 1993; Dutilleul and Legendre 1993).

In 'real' autocorrelation the value of a variable at a microsite is a function of the values of that variable at neighbouring microsites (Legendre 1993; Legendre and Fortin 1989). Concretely, this means that forest floor and environmental variables at one microsite influence the variables of surrounding microsites. Some of the autocorrelation in the environmental variables could be caused by inherent biological qualities of the different tree species involved in community structuring (eg. seed dispersion, competition) (Frelich *et al.* 1993; McClure and Lee 1993). For example, the presence of beech at one microsite will have an influence on beech and other species' presence or absence at surrounding microsites. Positive autocorrelation in the small distance classes of Fig. 1 were certainly influenced by the fact that certain trees were large enough and located ina way to influence more than one microsite at a time. The causes of 'real' autocorrelation in forest floor data are more difficult to identify because it is unlikely that a forest floor variable at one microsite could influence variables of another microsite at least 15 m away. We can suppose that it is mostly a consequence of the autocorrelation in controlling factors. One consequence of autocorrelation is that the error terms between neighbouring microsites are correlated, meaning a non-independence of observations that can affect the interpretation of the RDA (Legendre 1993).

The spatial structure detected in Fig 1 to 4 is probably a combination of trends and 'real' autocorrelation. The analysis of the residuals obtained after using a trend surface analysis (see below) was used to gain further insight into the type of spatial structure present in the data.

Multivariate data.

Sokal (1986, cited by Legendre and Fortin 1989) and Oden and Sokal (1986) have developed a method to compute correlograms on multivariate data using two distance or similarity matrices. Since my data is multivariate, I decided to complement the investigation of initial spatial structure with this approach and evaluate the type of information it can generate. Two distance matrices were computed, one for the environmental data and the other for the x and y geographical coordinates data. The euclidian distances based on geographical coordinates and computed for each pair of microsites were divided in ten distance classes (d). For each of these distance classes (d), a binary matrix was constructed where the pairs of observations corresponding to that class d were given the value 1 and all the other the value 0. A mantel statistic (r) (Mantel 1967 cited by Legendre and Fortin 1989) was computed between the environmental distance matrix and each of the binary matrix corresponding to the different distance classes. The results are displayed in a Mantel correlogram. This procedure was repeated for standardized environmental data and for both raw and standardized forest floor data (Fig. 5 and 6). In Figures 5 and 6, a negative r means that microsites close to one another in space (small geographical distances) are more similar (small environmental distances) then microsites far apart (high geographical distances), on the basis of the same set of environmental distances. Positive r means that microsites far apart geographically are also far apart environmentally in the space of the corresponding distances. With this in mind, negative r values may be interpreted as positive multivariate autocorrelation, while the positive r values are translating negative multivariate autocorrelation. Except for figure 6a, the overall shape of these correlograms suggests a gradient or a structure with steps. The positive autocorrelation lasts up to about the fourth distance class, meaning that the zone of multivariate autocorrelation (the size at which forest floor or environmental associations remain similar) is approximatively 105 meters. Figures 5a and 6b show that negative multivariate autocorrelation increases at larger scale as intrinsic association pattern of the variables is becoming increasingly different with increasing geographical distance. The difference between untransformed and standardized correlograms is caused by the fact that variables with greater variance are more likely to influence the correlogram shape in untransformed data. In the environmental data, tree species influence is more spatially structured than microtopography and has a greater influence on the shape of Figure 5a because of its greater variance. By standardizing, the microtopographical variables, which are not spatially structured, contribute more to the shape of the curve and may cause the plateau in large distance class observed in Figure 5b. For forest floor variables, the units of measurement had an influence on relative variation and contribution to the shape of the correlograms. The absence of spatial structure in untransformed data may be caused by the fact that NH_4^+, which was not spatially structured, had the greater variance in forest floor variables.

In summary, Figures 5 and 6 demonstrated that the similarity between the association of variables at each microsites decreases with distance classes suggesting spatial patterns in the data set.

Data transformation.

Maximizing linearity.

RDA is a combination of ordination and multiple regression (ter Braak and Prentice 1988; ter Braak 1987c). Assumptions valid for multiple regression will thus apply to RDA; specifically,independence of observation, normality of distribution, linearity of dependent variable response (Steel and Torrie 1980; ter Braak 1987c). When working with only one dependent variable at the time, data transformation is done so that the variable can be best explained by the chosen statistical model, either by assuring a normal distribution or a linear response. In multivariate data, where the different response variables are expected to respond in a similar way, a unique transformation applied on the ensemble of the data may be adequate. For example, in community analysis, although each species has a different position along the environment gradient, the shape of their response is somewhat similar (c.f ter Braak 1986). In soil and forest floor data, however, the type of response for each variable may vary greatly. Grigal *et al.* (1991) have observed large variability in the shape of forest soil variable response to an environmental gradient. A general data transformation applied to all data may improve linearity for certain variables but decrease it for others. This would arbitrarily increase the explained variation of certain variables at the expense of others. Since RDA uses estimates of single response variables of multiple regression on environmental variables, it was decided to proceed with individual variable data transformation. The objective was thus to maximize the linearity of the response of each forest floor variable to the environmental variable by choosing the transformation that would give the highest coefficient of determination.

Each response variable (v) was thus submitted to the following transformation; e^v, ln(v) and $(v^\tau-1)/\tau$ where τ varies between 0.1 and 5. The $(v^\tau-1)/\tau$ transformation has been used by Box and Cox (1964, cited by Legendre and Legendre 1984) to determine transformation that maximizes the normality of the distribution (Legendre and Legendre, 1984). Table 1 shows the transformation chosen for each variables and the coefficient of determination (R^2) for both transformed and untransformed data. Except for the variable CO_2, the transformations had little effect on the increase of the coefficient of determination. There is, however, differences in the transformation chosen for each variable, indicating that a unique transformation applied to the whole data would have given a lower coefficient of determination overall. The chosen transformations shown in Table 1 were applied and the transformed variables used in the rest of the analysis.

Standardization.

The forest floor variables were centred and standardized so that each variable would have the same weight in their relative contribution to the overall variation in forest floor data (Noy-Meir *et al.* 1975). This procedure was necessary since variables were expressed in units of measurement that are not comparable; for example pH scale vs mg/g or cm.

The environmental variables were also centred and standardized since tree species influence and microtopography were expressed in different units.

Canonical trend surface analysis.

Individual and multivariate correlograms have shown some spatial structure in our data set (Fig. 1 to 6). The procedure used by Borcard *et al* (1992) to incorporate spatial structure in the variation-partitioning model was followed. A polynomial equation was built using geographical coordinates of microsites. Since Figures 2 and 4 have shown the importance of the relative altitude of the microsite in spatial patterns observed, the *z* coordinates were also included in the polynomial equation. The polynomial equation was built to be of third order so as to detect large scale structure on the site while keeping ecological meaningfulness (Burrough 1987). The terms of the polynomial equation were submitted to the forward selection of the explanatory variables using Canoco (ter Braak 1987-1992) in order to select only the terms that contributed significantly to the explained variation in the forest floor data at the 0.1 level of significance. The significant terms chosen were

$$v = b_1x + b_2y + b_3yz + b_4z^3 + b_5y^2z$$

Autocorrelation of residuals.

The objective of this step was to determine the amount of spatial structure remaining in forest floor data after removing the spatial structure expressed by the polynomial equation. Spatial autocorrelation was computed using Moran's *I* coefficient on the residuals of the multiple regression of each forest floor variable on the terms of the polynomial equation.

By removing some of the spatial trends present in the data, weak-stationarity of the forest floor data can be assumed and therefore statistical tests can be computed for each correlograms (Legendre 1993; Dutilleul and Legendre 1993). Since several tests (15) are done at the same time, Legendre and Fortin (1989) recommend that a Bonferoni test be computed on the overall correlogram before interpreting the statistical significance of individual distance classes. The Bonferoni test is done by dividing the chosen level of significance by the number of distance classes (ie. 0.05/15 = 0.003) For the overall correlogram to be significant, some of the distance classes must have a autocorrelation coefficient significant at the 0.003 level. In Figures 7 and 8, although some individual distance classes show significance at the 0.05 level, none of the correlograms contains any coefficient significant at the 0.003 level, meaning that in general, the spatial polynomial equation has extracted the major source of spatial structure in the data and that the remaining spatial structure is not considerable.

It is possible that some of that remaining spatial structure may be caused by undetected trends that could potentially be removed by using more terms in the polynomial equation, by, for example, using the smallest polynomial equation that would include all the terms chosen by forward selection for each forest floor variable taken individually. On the other hand, the remaining spatial structure may also be caused by autocorrelation in the data.

The fact that most spatial structure in forest floor data was captured by the polynomial equation allowed me to proceed with the partitioning of the variation with confidence in terms of the assumptions of RDA.

Partitioning the variation.

The last step in this data analysis was to partition the variation in the forest floor data into the fractions of the model of Borcard *et al.* (1992). The sum of all constrained axes were computed for four RDA's and are equal to the variation explained by the explanatory variables in the forest floor data. The RDA's were computed with CANOCO (ter Braak 1987-1992). The following results were obtained;

1) RDA of the forest floor data constrained by environmental variables. Variation explained= 35.5 % ($p < 0.05$).

2) RDA of the forest floor data, constrained by terms of the polynomial equation. Variation explained= 31.0 % ($p < 0.05$).

3) RDA of the forest floor data constrained by environmental variables, but after removing the effect of the terms of the polynomial equation as covariable. Variation explained = 21.6 % ($p < 0.05$).

4) RDA of the forest floor data constrained by the terms of the polynomial equation, but after removing the effect of environmental variables as covariable. Variation explained= 17.1 % ($p < 0.05$).

The variation explained by environmental variables alone (fraction '*a*') is thus equal to 21.6 % (step 3). The variation explained by spatial structure alone (fraction '*c*') is equal to 17.1%. Finally, the fraction '*b*' which is the variation explained by a confounded effect of both spatial structure and environmental variables, is computed by using step (1) - step (3), or step (2) - step (4): 13.9 %. The relative importance of the different fractions in explaining variation on forest floor data is shown in Figure 9.

Fraction '*a*' (21.6%) is the variation in forest floor data explained after removing the spatial structure expressed by the polynomial equation. The confounded effect of environment and space is thus mostly removed and it can be assumed that the variation in this fraction is primarily due to the tree species influence and the microtopography effect alone. Effects of different tree species on forest soil fertility have been shown by many studies (eg. Fyles and McGill 1988; Fyles and Côté 1993; Boettcher and Kalisz 1990; Boerner and Koslowsky 1984; Xiao *et al.* 1991). Such an effect arises through the combined influence of stemflow and throughfall quality (Parker 1983; Gersper and Holowaychuk 1971), litter quality, (Côté and Fyles 1993;) and root activity (Berendse *et al.* 1989; Bowden *et al.* 1993) all of which may differ between species. Some of these studies have also demonstrated that the tree species effect could be detected at the microsite level at which this study was conducted (Boerner and Koslowsky 1984). Beatty (1984), Beatty and Stone (1988) and Sauvesty *et al.* (1993) have demonstrated that forest soil collected in pits and on mounds have different characteristics.

Fraction '*b*' (13.9%) can be viewed as the variation explained either by spatially structured environmental variables or by underlying spatial factors influencing both environmental variables and forest floor properties independently. On one hand, fraction '*b*' could be caused by tree species influence and microtopography that are unevenly distributed on the site, following distribution of parent material, disturbance or patterns in the general topography or drainage condition of the site. On the other hand, these controlling factors may influence tree distribution , microtopography and the forest floor characteristics independently making the causal effect between environmental variables and forest floor properties impossible to verify.

Fraction '*c*' (17.1%) is described as the variation related to spatial structure alone It could be caused by unmeasured controlling factors that have a spatial structure expressed by the polynomial equation. Different hypothesis can be generated to explain this fraction. First, spatially structured abiotic factors such as parent material and drainage may have an effect on forest floor characteristics that is independent of tree species distribution. In effect, the study site represents a small range of abiotic factors and most tree species present are equally capable of establishing anywhere on that site, suggesting that tree species distribution is not only determined by these abiotic factors but also by biological processes involved in patch formation (Frelich *et al.* 1993) This suggests that the spatial structure of environmental variables and abiotic factors will not be completely confounded and that some of the effects of these spatially structured, but unmeasured, abiotic factors on forest floor will be extracted in fraction '*c*' Secondly, in their interpretation of fraction '*c*', Borcard and Legendre (1993) have considered the time or historical aspect of the studied site. It is possible that natural or man-made disturbances occurring on specific areas of the site have had an effect on forest floor properties and that it was extracted in the fraction '*c*'. Birks (1993) stresses the fact that the spatial alone fraction may be difficult to interpret and that hypotheses could be verified later on

Fraction '*c*' could be described as a part of the unexplained fraction that is spatially structured at the scale of the study.

The unexplained fraction (47.4%) is the variation in the forest floor data that was explained neither by chosen environmental variables nor by the terms of the polynomial equation. The size of the unexplained fraction obtained in this experiment is comparable to results from Borcard *et al.* (1992) measured on different sets of ecological communities It is either related to large scale spatially structured factors that were not captured by the polynomial equation or by undetected factors varying locally at the microsite level or at a smaller scale than the one chosen for this study. Scale has been recognized to have an important effect on the variation of soil properties since their spatial structure and response to environmental variables can vary with the scale of the study (Burrough 1983). Part of this unexplained fraction may thus be a consequence of the chosen scale of study.

In summary, 52.6 % of the total variation in forest floor was explained by the variation partitioning model of Borcard *et al.* (1992). The model demonstrated the importance of spatial structure in the data set (31.0%). More than half of this spatial structure (17.1 %) was not related to the chosen environmental variables, meaning there were important spatially structured factors that were not considered in this study. The model also allowed me to isolate the effects of environmental variables of interest from their confounded effects with spatial structure, indicating that without the incorporation of the spatial structure in the model the interpretation of the influence of tree species influence and microtopography on forest floor fertility could have been biased.

CONCLUSION.

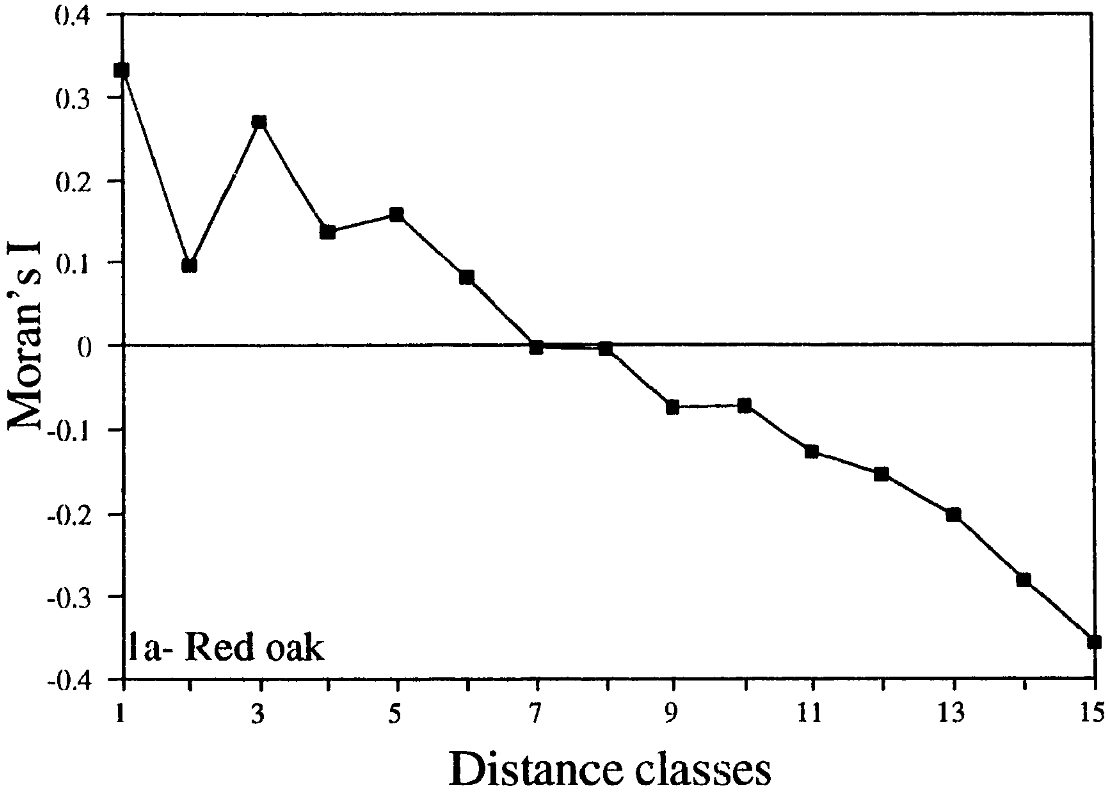
The RDA-variation partitioning model (Borcard *et al.* 1992) was successful in addressing problems of complexity and spatial heterogeneity of our data. The spatial structure detected in the first step of the analysis was incorporated in the model and the effect of a suite of environmental variables on the suite of forest floor properties taken as a whole, was isolated. The study has thus demonstrated the potential of RDA techniques for studying the influence of controlling factors on forest floor properties.

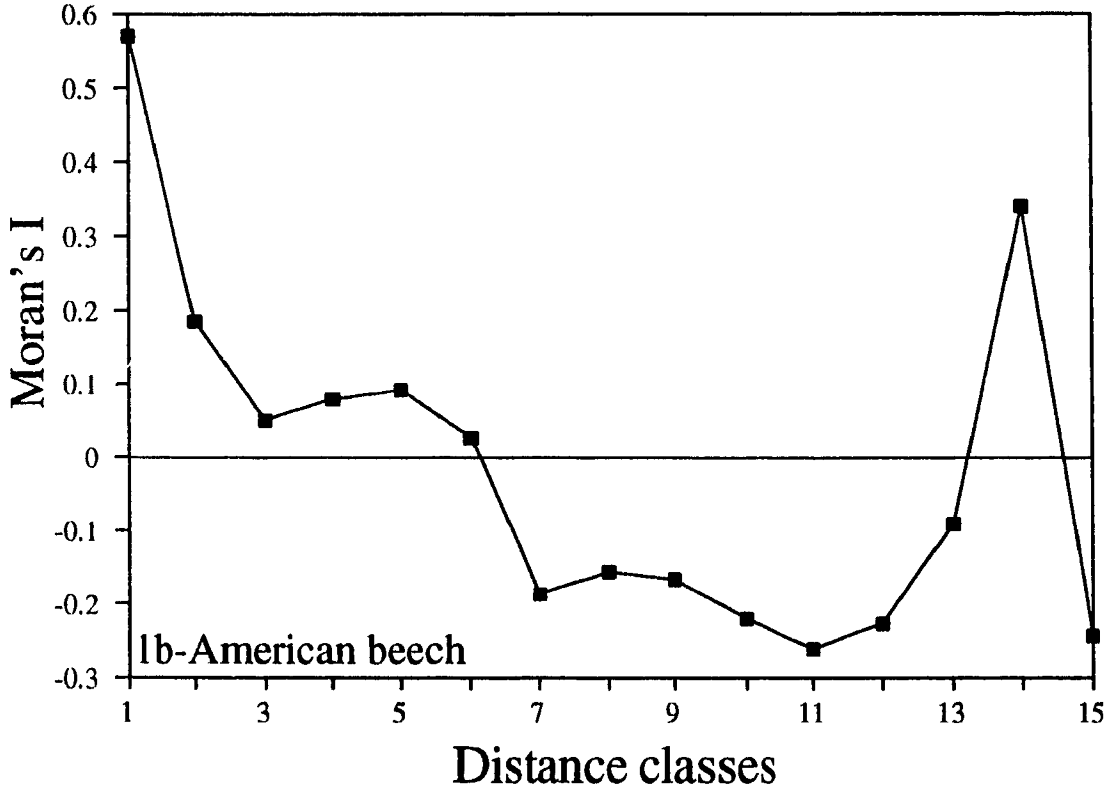
This study examined only one data set and application of this method to other data set is therefore necessary to test its validity as a general method for studying causes of forest floor variation in mixed forests. The ability of the trend surface analysis to capture spatial structure in soil variables should be tested for other forest stands where spatial patterns may be different. The concepts of spatial trends and autocorrelation may have to be addressed in terms of their ecological meaning for forest floor data. Since many soil studies have looked at the importance of spatial pattern and scale it might be possible to find more appropriate techniques to incorporate spatial functions that would integrate different factors and processes involved in controlling forest floor properties.

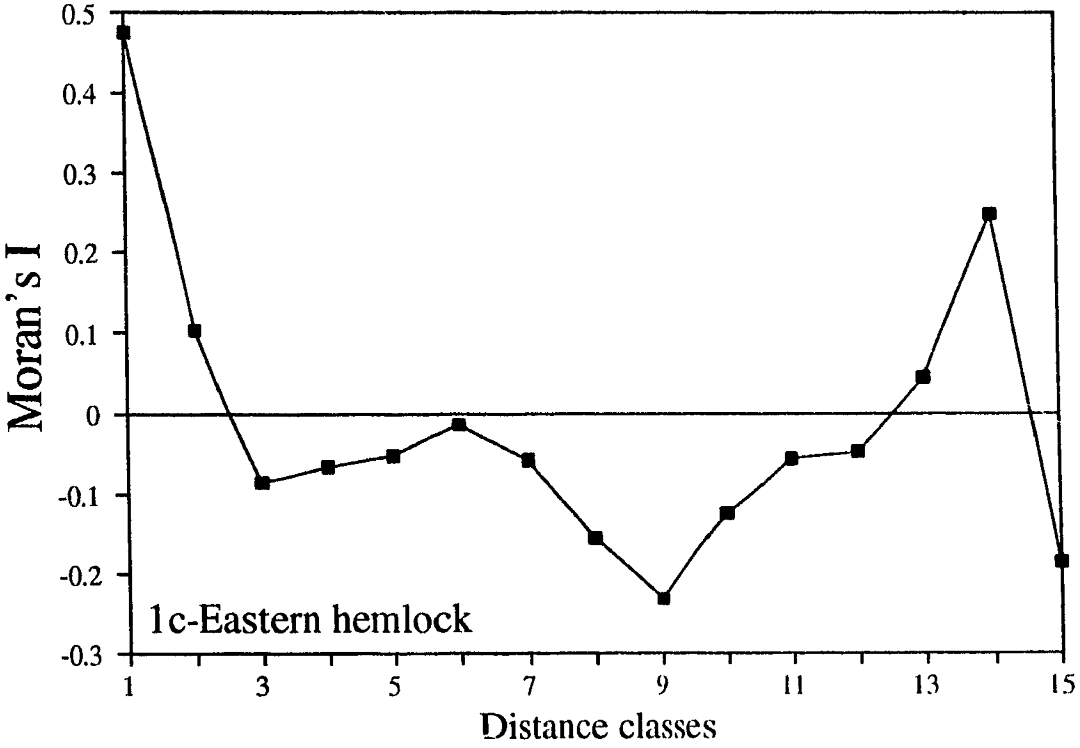
Table 1. Transformation of the forest floor variables that maximizes the coefficient of determination (R^2) of their multiple regression on environmental variables.

		R^2 (%) for	
Variable(v)	Best transformation	transformed variables	untransformed variables
N	$(v^{0.4}-1)/0.4$	46.3	45.3
P	e^v	28.4	27.9
K	e^v	27.5	27.0
Ca	$(v^{0.8}-1)/0.8$	52.5	52.4
Mg	e^v	44.2	40.7
extr.K	ln(v)	28.3	27.9
extr. Ca	$(v^{0.75}-1)/0.75$	52.5	52.3
extr. Mg	e^v	29.9	29.7
pH	$(v^2-1)/2$	30.8	30.6
CO_2	ln(v)	24.3	15.7
NH_4^+	$(v^{1.5}-1)/1.5$	28.7	28.1
THICKNESS	$(v^{0.25}-1)/0.25$	36.6	35.0
BULK DENSITY	$(v^{0.5}-1)/0.5$	30.4	29.9

Figure 1. Moran's correlograms for the horizontal spatial structure of four environmental variables; red oak (1a), American beech (1b), eastern hemlock (1c), and striped maple (1d).


0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
Moran's I
1a- Red oak
1
3
5
7
9
11
13
15
Distance classes


0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
Moran's I
1b-American beech
1
3
5
7
9
11
13
15
Distance classes


1c-Eastern hemlock
Moran's I
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
1
3
5
7
9
11
13
15
Distance classes

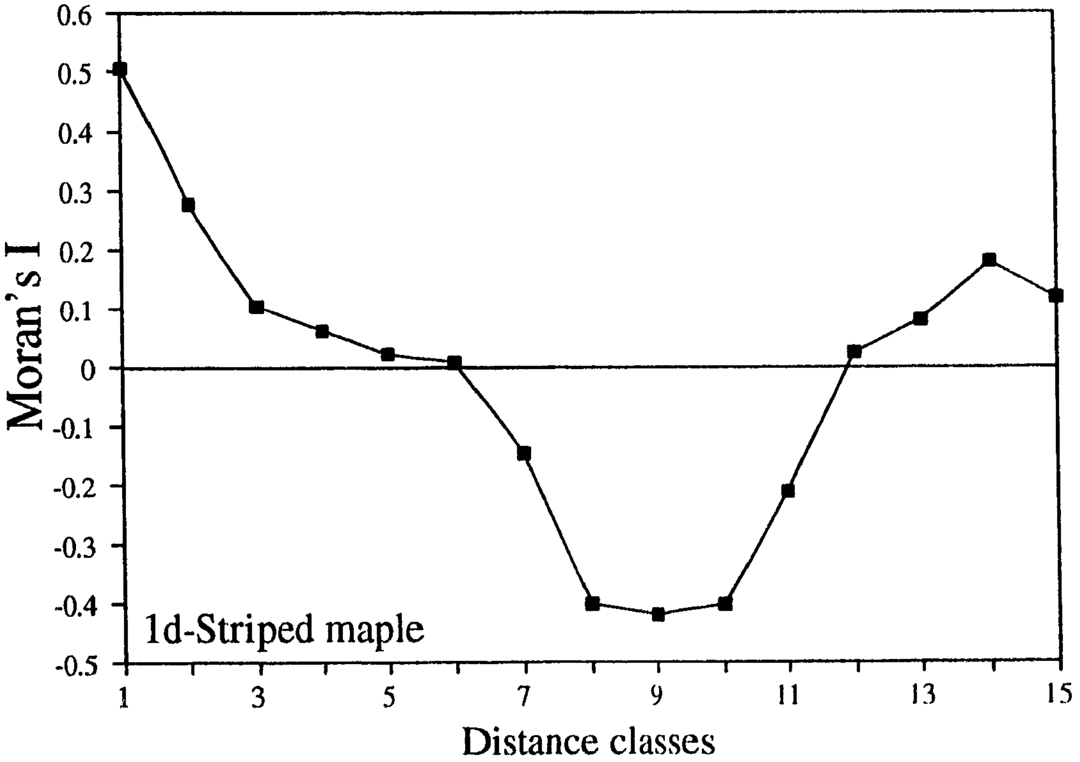
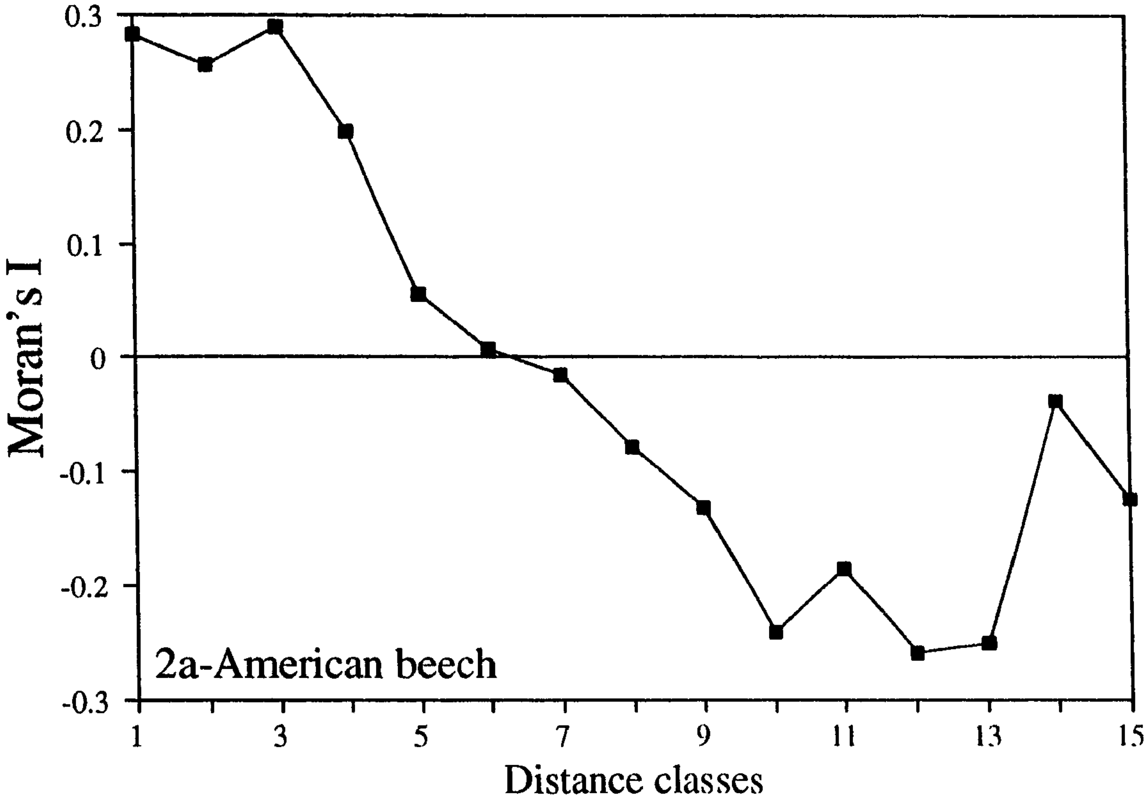

1d-Striped maple
Moran's I
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
1
3
5
7
9
11
13
15
Distance classes

Figure 2. Moran's correlograms for the spatial structure in the vertical component of two environmental variables; American beech (2a), striped maple (2b).


2a-American beech
Moran's I
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
1
3
5
7
9
11
13
15
Distance classes

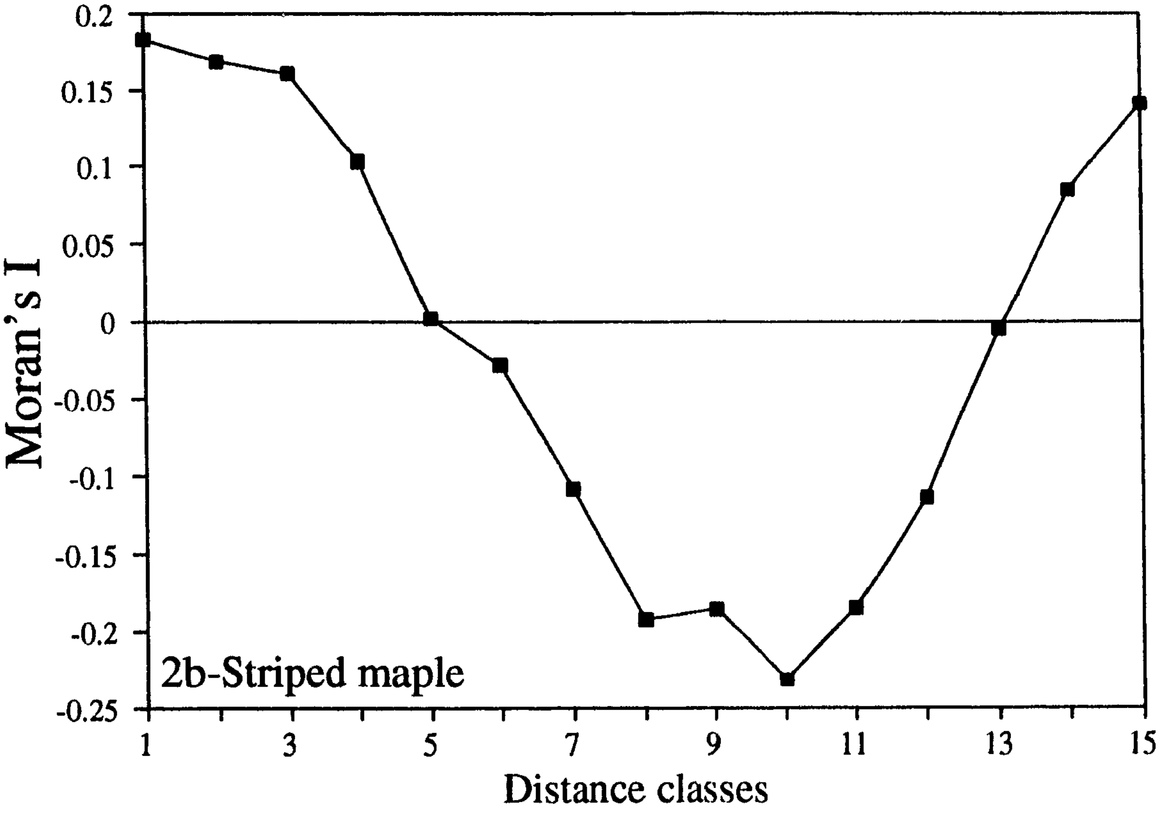
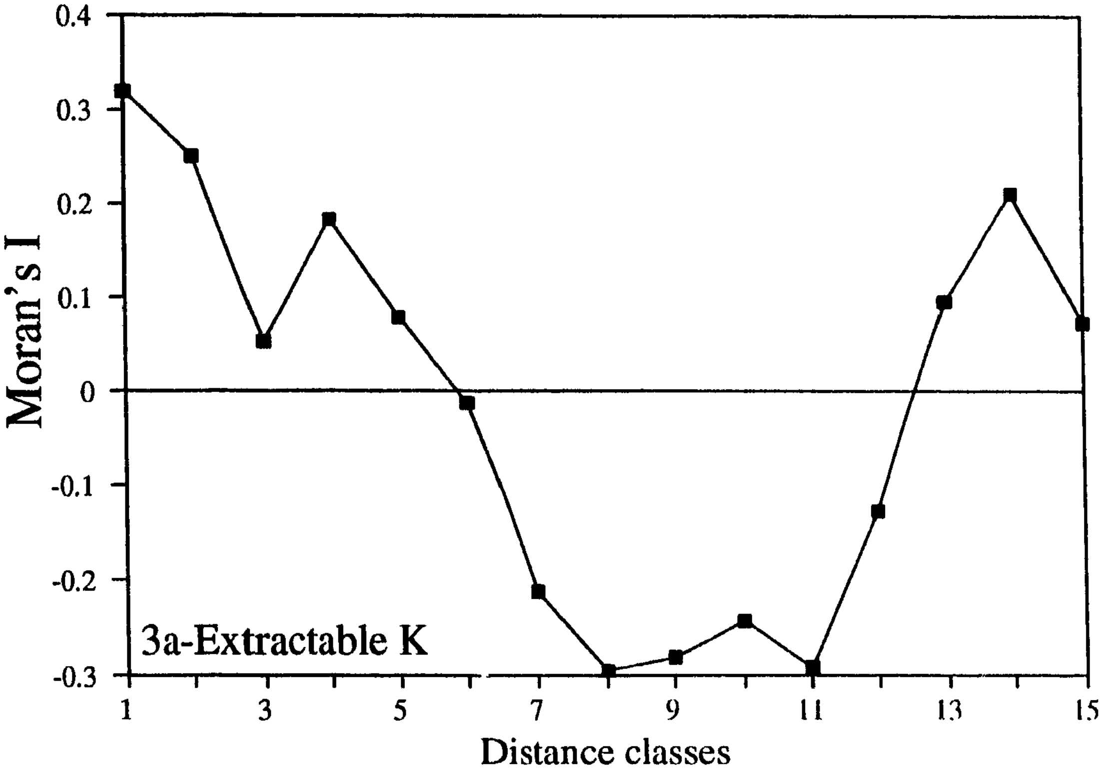
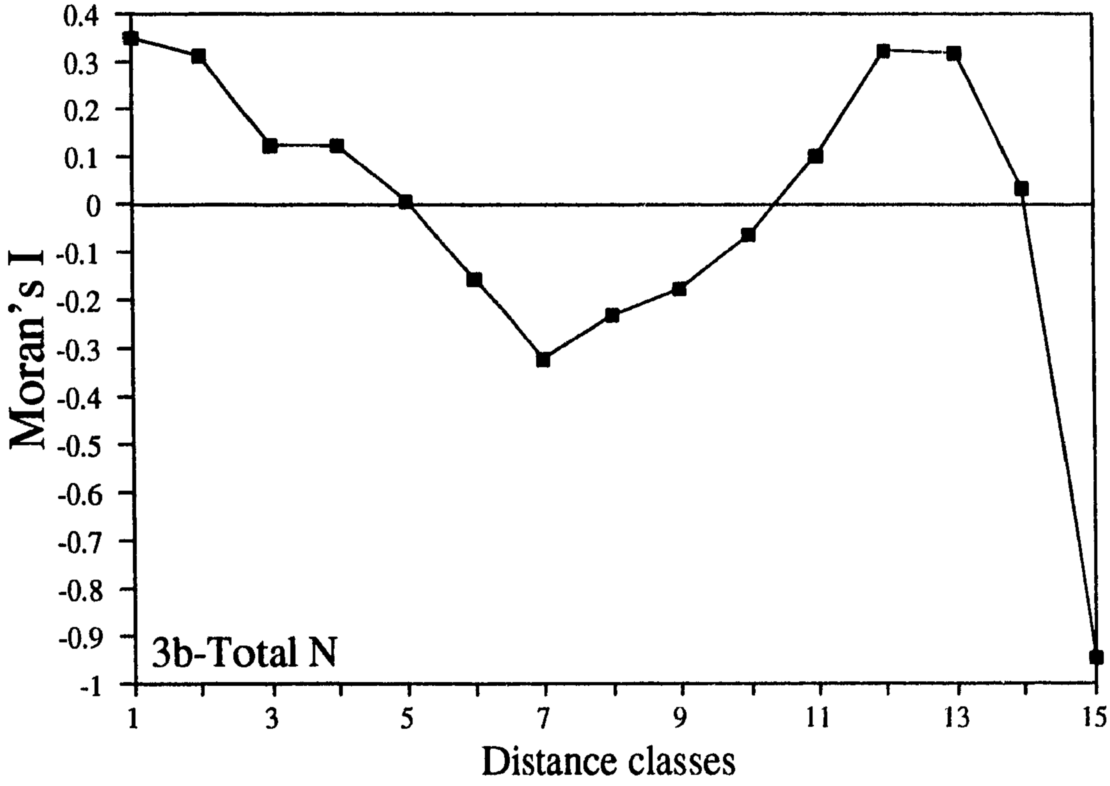
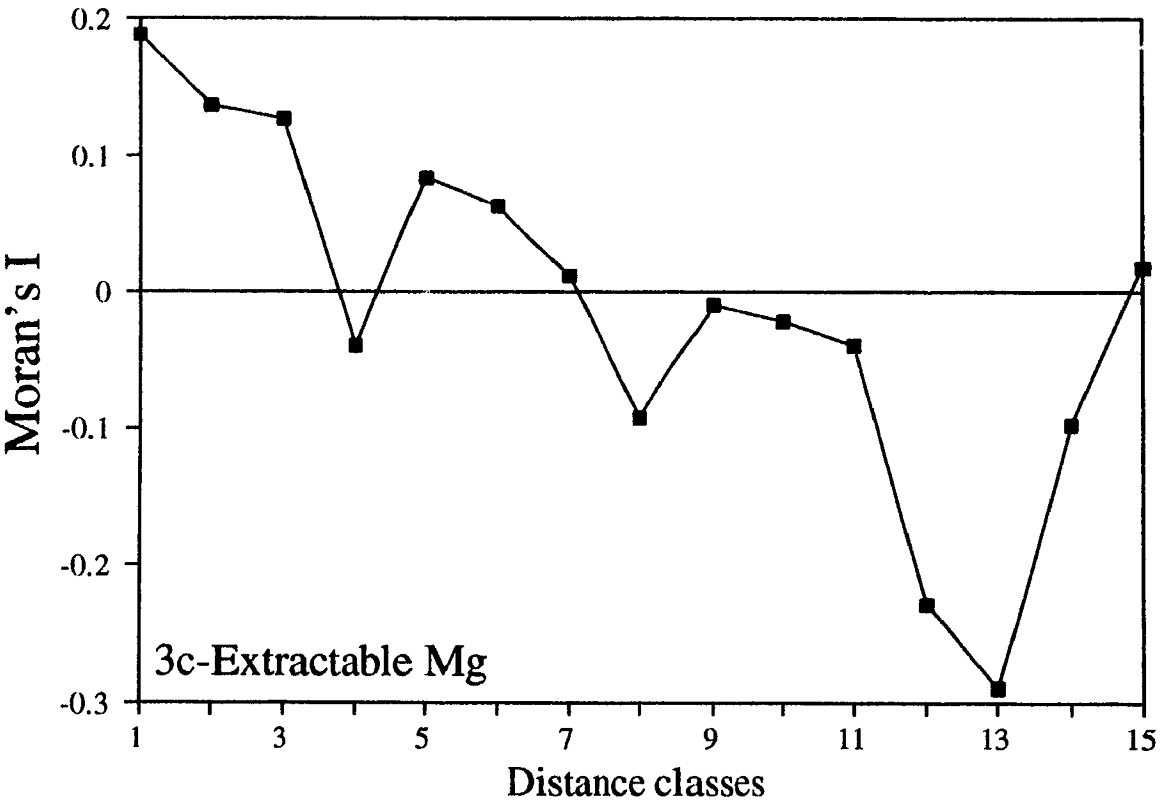

2b-Striped maple
Moran's I
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
-0.2
-0.25
1
3
5
7
9
11
13
15
Distance classes

Figure 3. Moran's correlograms for the horizontal spatial structure of four forest floor variables; extractable K (3a), total N (3b), extractable Mg (3c), and total Ca (3d).


0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
Moran's I
3a-Extractable K
1
3
5
7
9
11
13
15
Distance classes


0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.8
-0.9
-1
Moran's I
3b-Total N
1
3
5
7
9
11
13
15
Distance classes


3c-Extractable Mg
Moran's I
0.2
0.1
0
-0.1
-0.2
-0.3
1
3
5
7
9
11
13
15
Distance classes

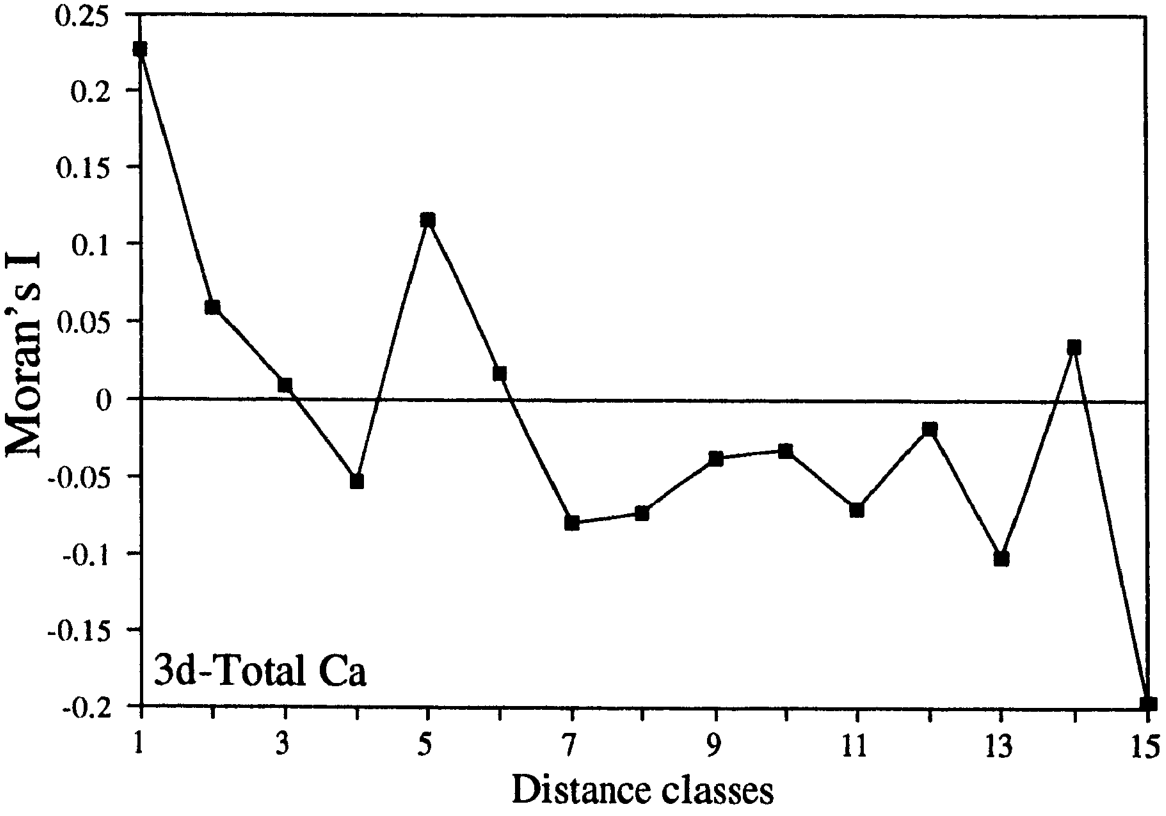
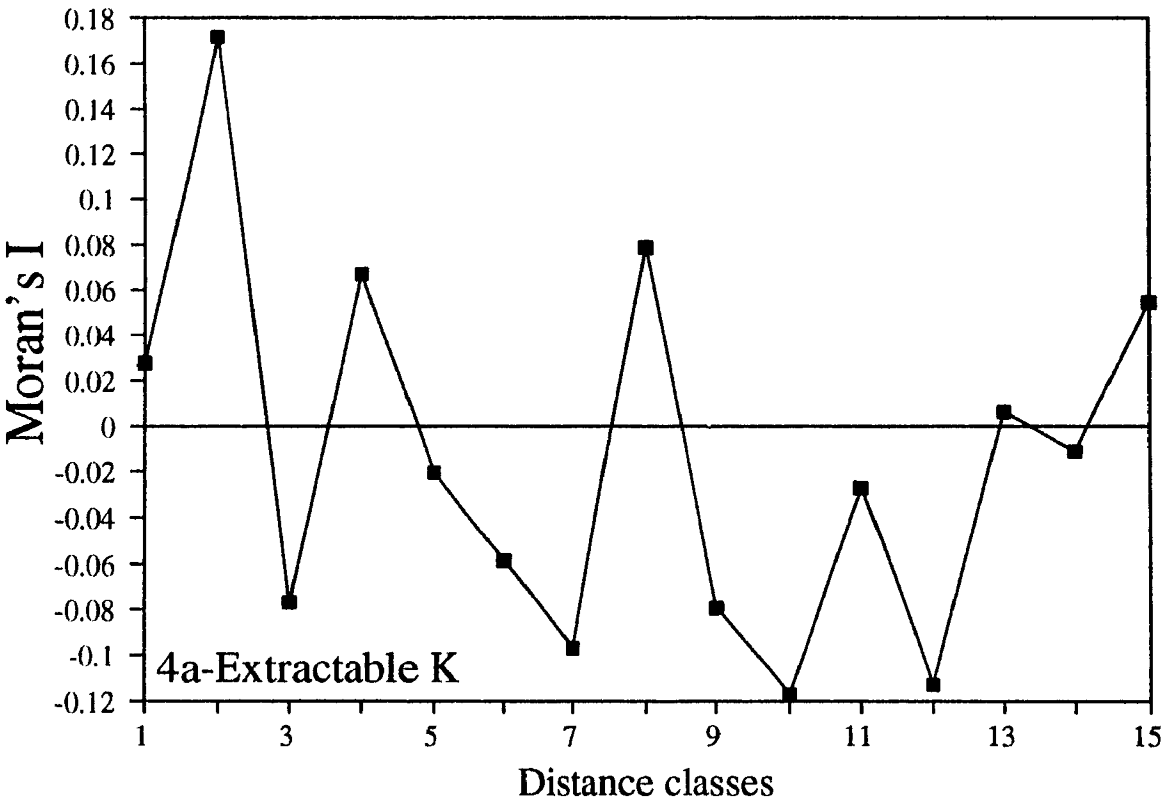

3d-Total Ca
Moran's I
0.25
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
-0.2
1
3
5
7
9
11
13
15
Distance classes

Figure 4. Moran's correlograms for the spatial structure in the vertical component of two forest floor variables; extractable K (4a), CO_2 (4b).


0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
-0.1
-0.12
Moran's I
4a-Extractable K
1
3
5
7
9
11
13
15
Distance classes

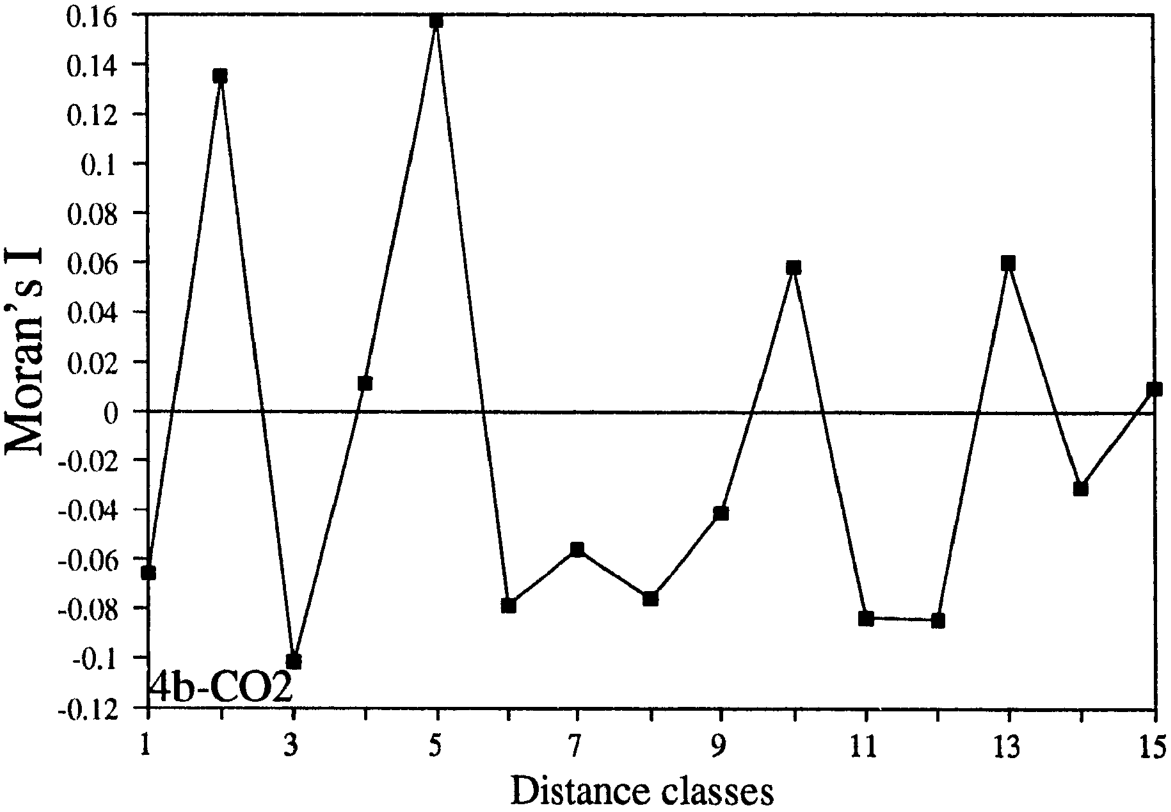
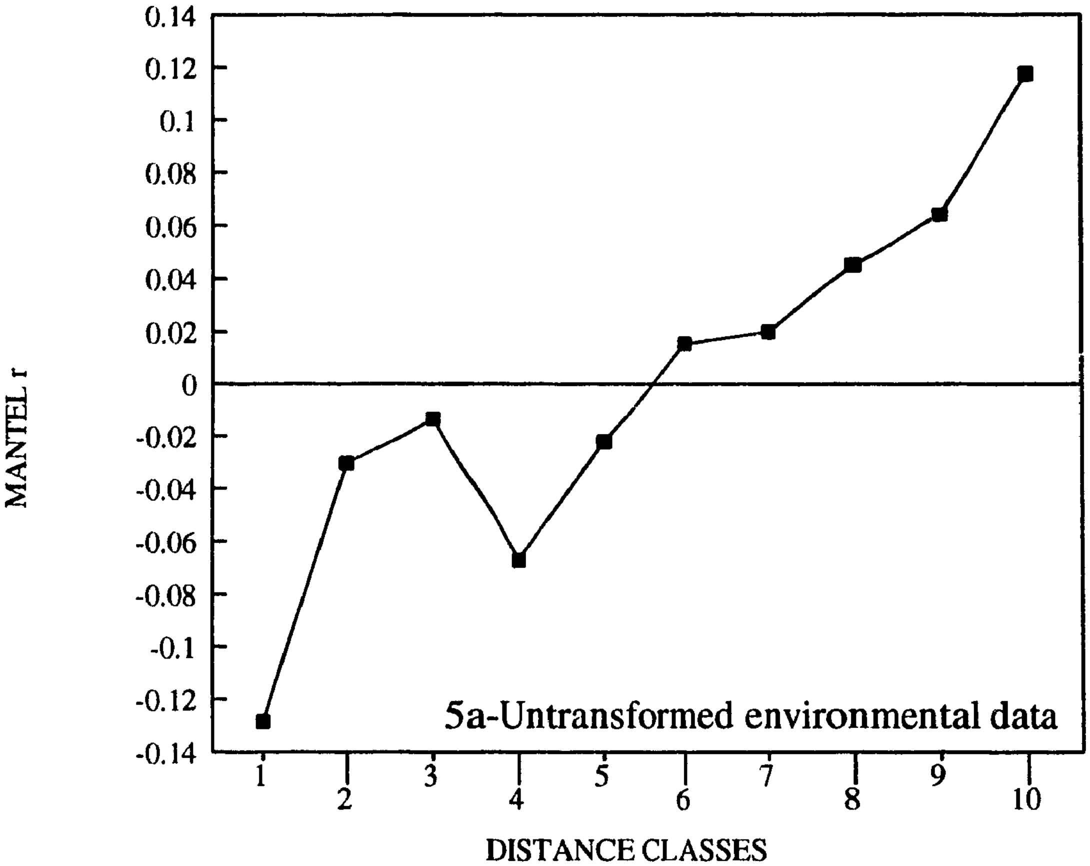

0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
-0.1
-0.12
Moran's I
4b-CO2
1
3
5
7
9
11
13
15
Distance classes

Figure 5. Mantel's multivariate correlograms for the horizontal spatial structure of; the untransformed (5a) and standardized environmental data (5b).


MANTEL r
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
-0.1
-0.12
-0.14
1
2
3
4
5
6
7
8
9
10
DISTANCE CLASSES
5a-Untransformed environmental data

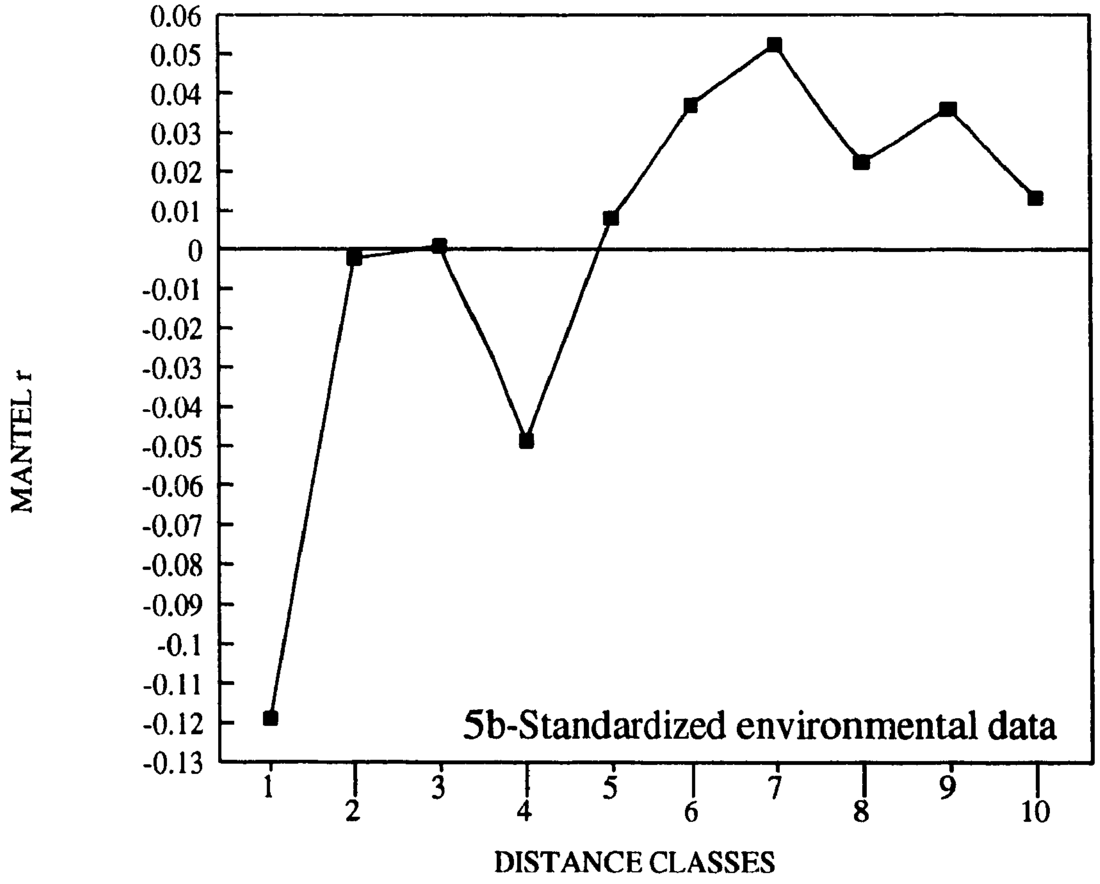
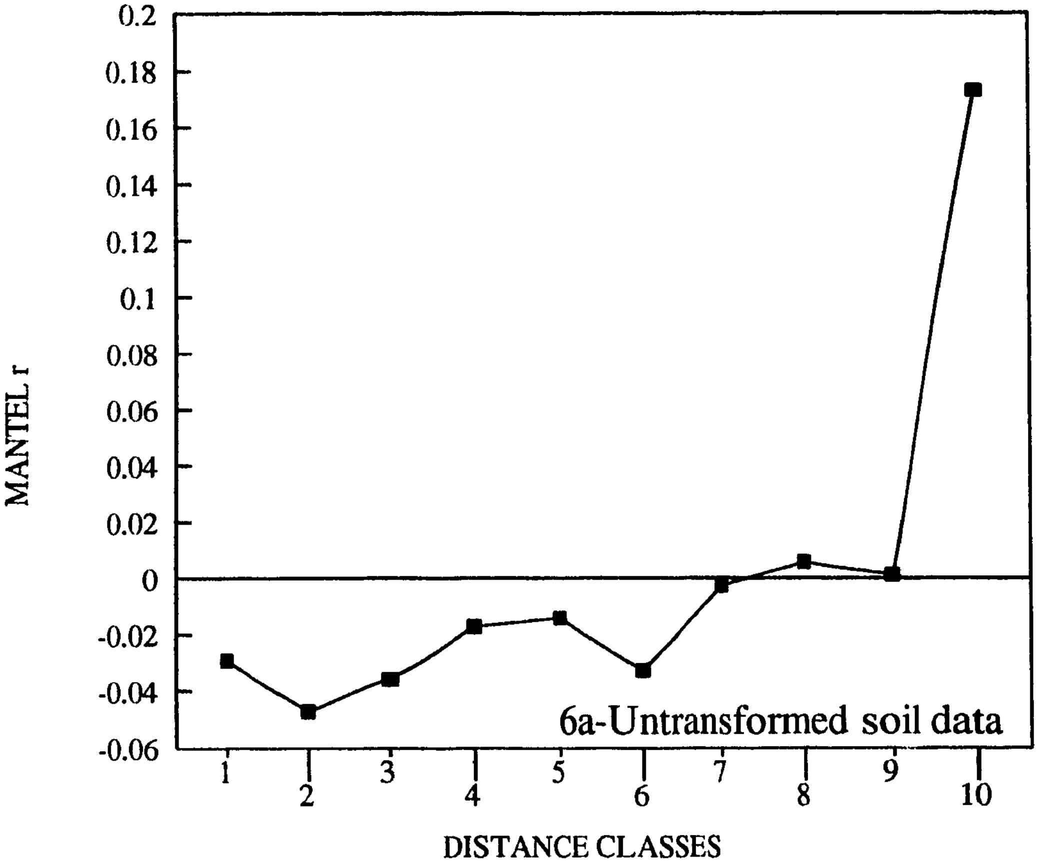

MANTEL r
0.06
0.05
0.04
0.03
0.02
0.01
0
-0.01
-0.02
-0.03
-0.04
-0.05
-0.06
-0.07
-0.08
-0.09
-0.1
-0.11
-0.12
-0.13
1
2
3
4
5
6
7
8
9
10
DISTANCE CLASSES
5b-Standardized environmental data

Figure 6. Mantel's multivariate correlogram of the horizontal spatial structure for; the untransformed (6a) and standardized forest floor data (6b).


MANTEL r
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0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
1
2
3
4
5
6
7
8
9
10
DISTANCE CLASSES
6a-Untransformed soil data

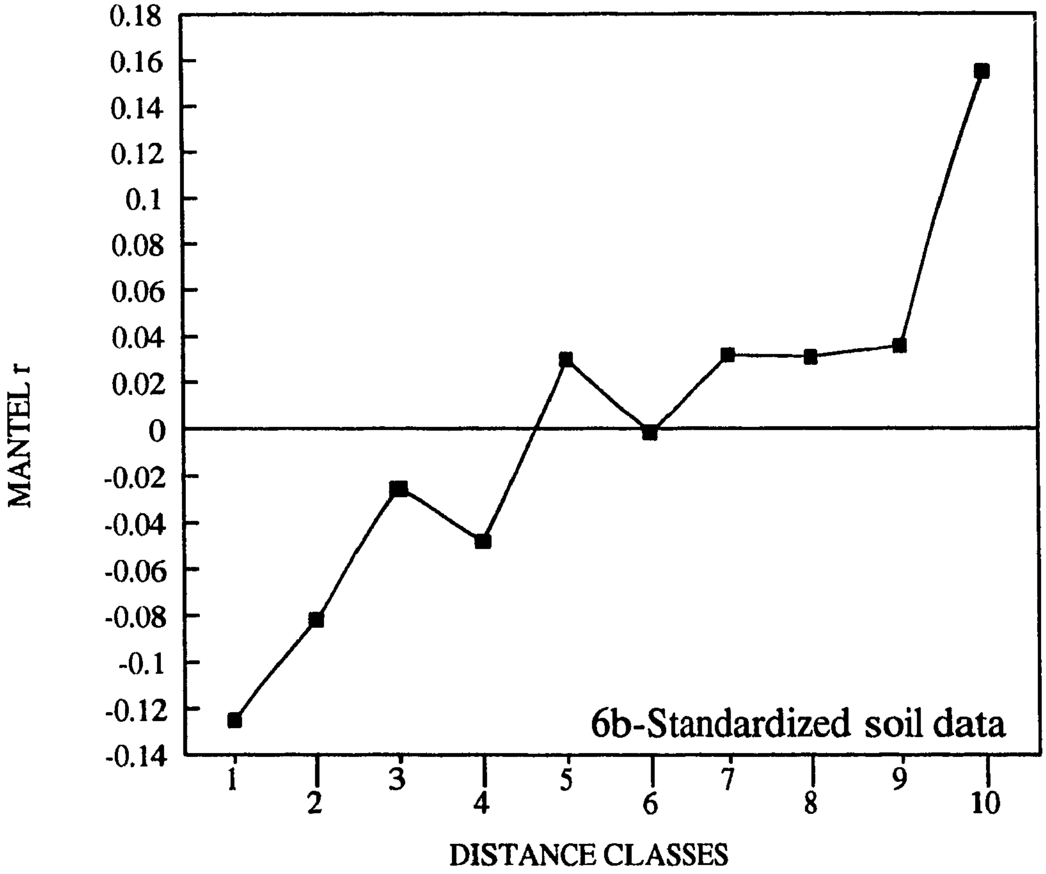
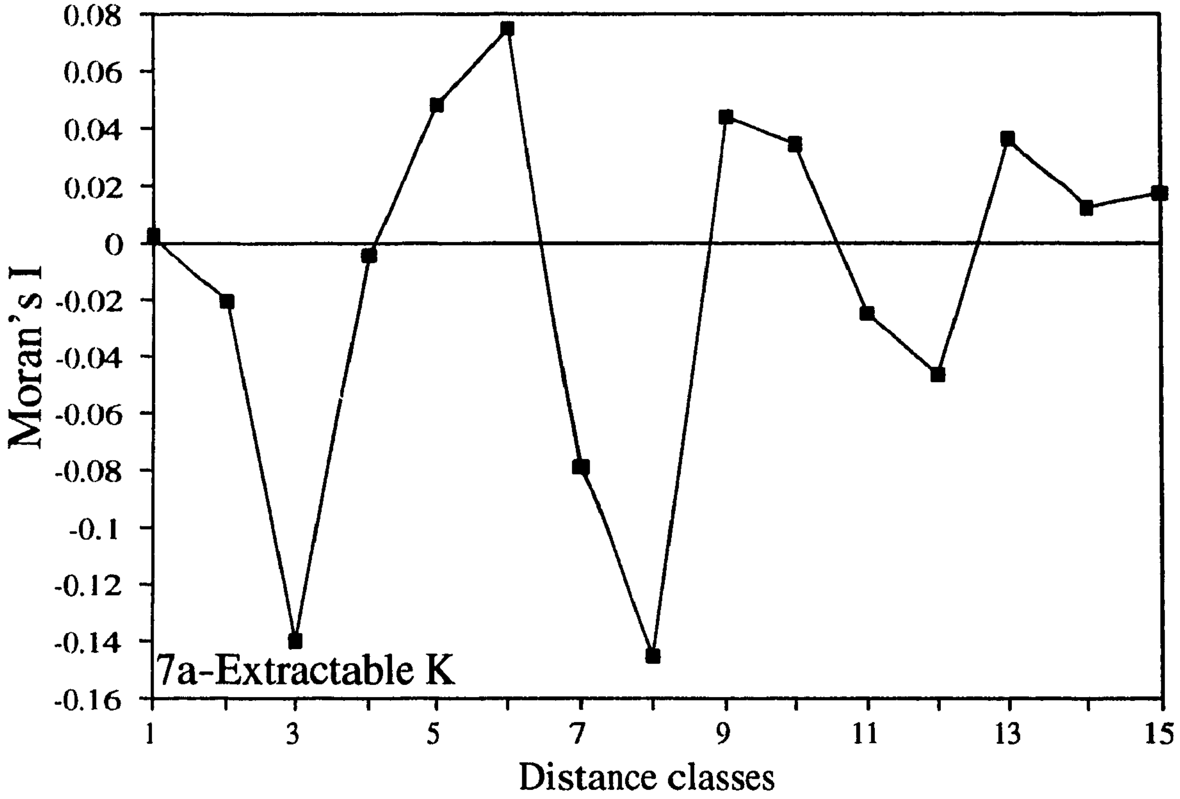
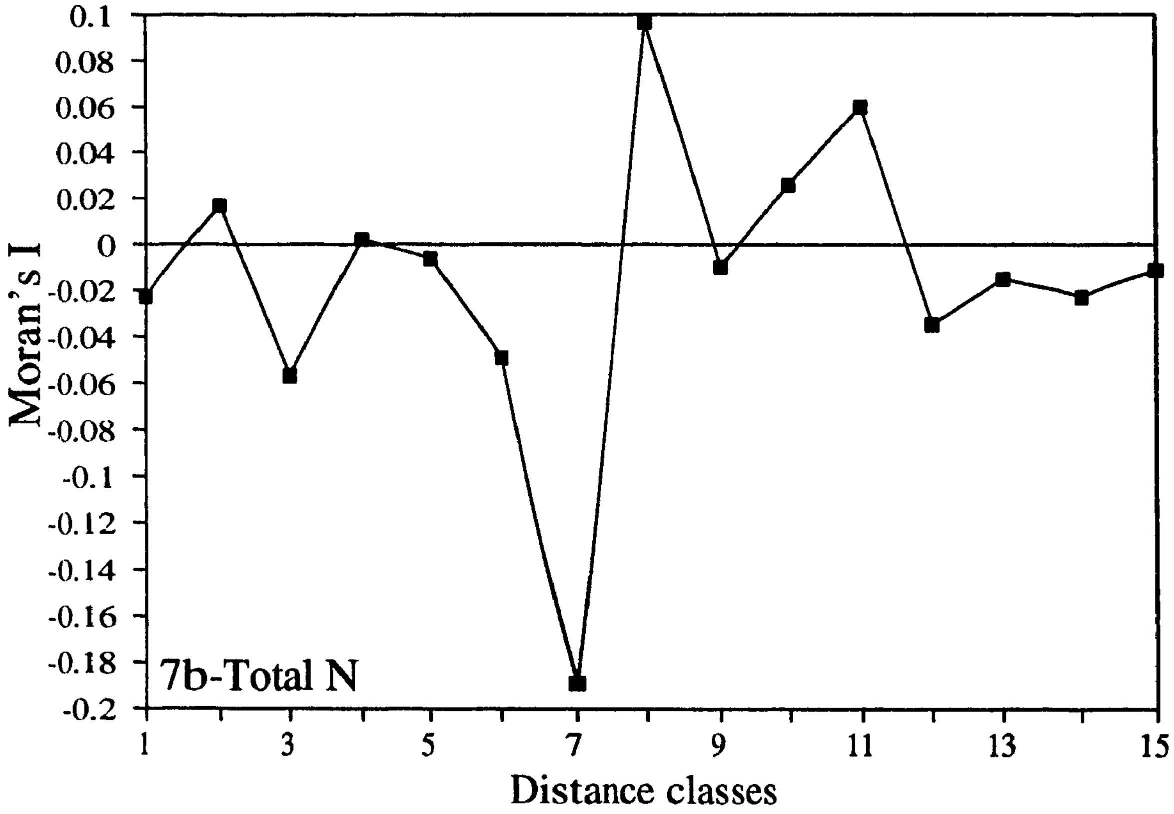
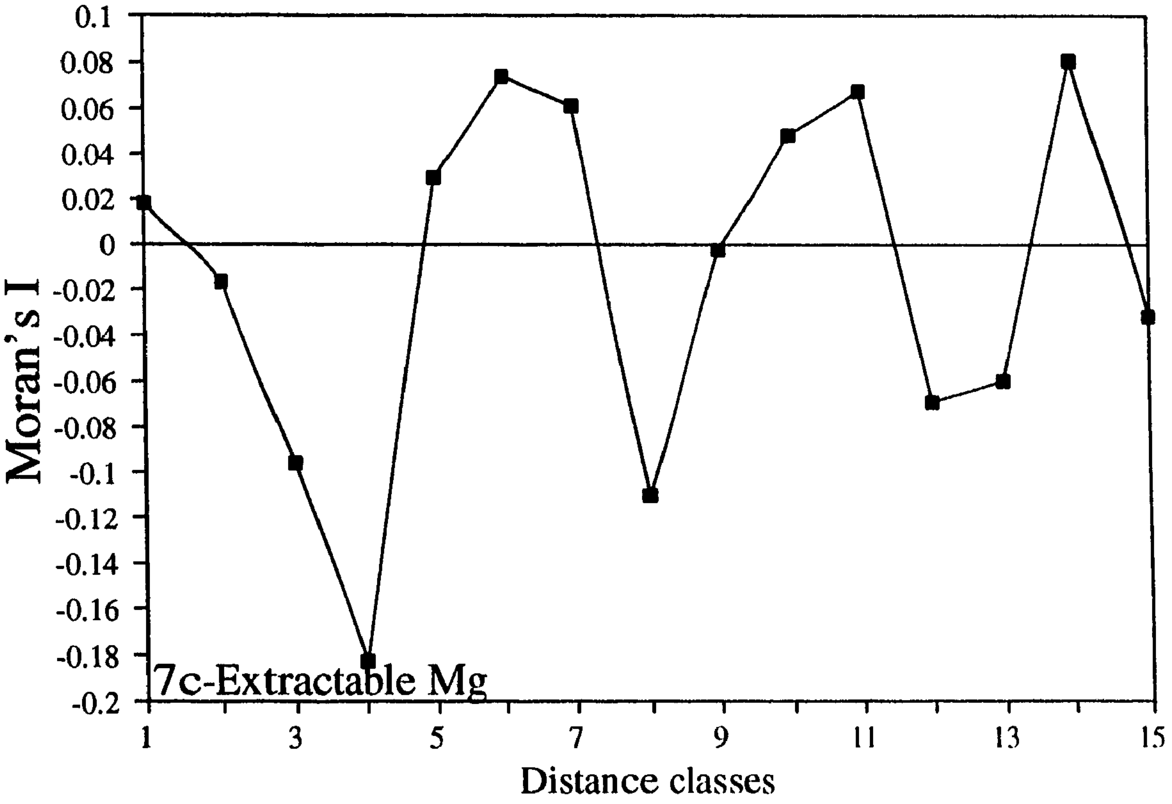

MANTEL r
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
-0.1
-0.12
-0.14
1
2
3
4
5
6
7
8
9
10
DISTANCE CLASSES
6b-Standardized soil data

Figure 7. Moran's correlograms for the horizontal spatial structure of residuals of multiple regression of four forest floor variables on the terms of the polynomial equation; a) extractable K, b) total N, c) extractable Mg, and d) total Ca. No autocorrelation coefficients were significant at the Bonferoni level of 0.003.


7a-Extractable K
Moran's I
0.08
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
-0.1
-0.12
-0.14
-0.16
1
3
5
7
9
11
13
15
Distance classes


7b-Total N
Moran's I
0.1
0.08
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
-0.1
-0.12
-0.14
-0.16
-0.18
-0.2
1
3
5
7
9
11
13
15
Distance classes


0.1
0.08
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
-0.1
-0.12
-0.14
-0.16
-0.18
-0.2
Moran's I
7c-Extractable Mg
1
3
5
7
9
11
13
15
Distance classes

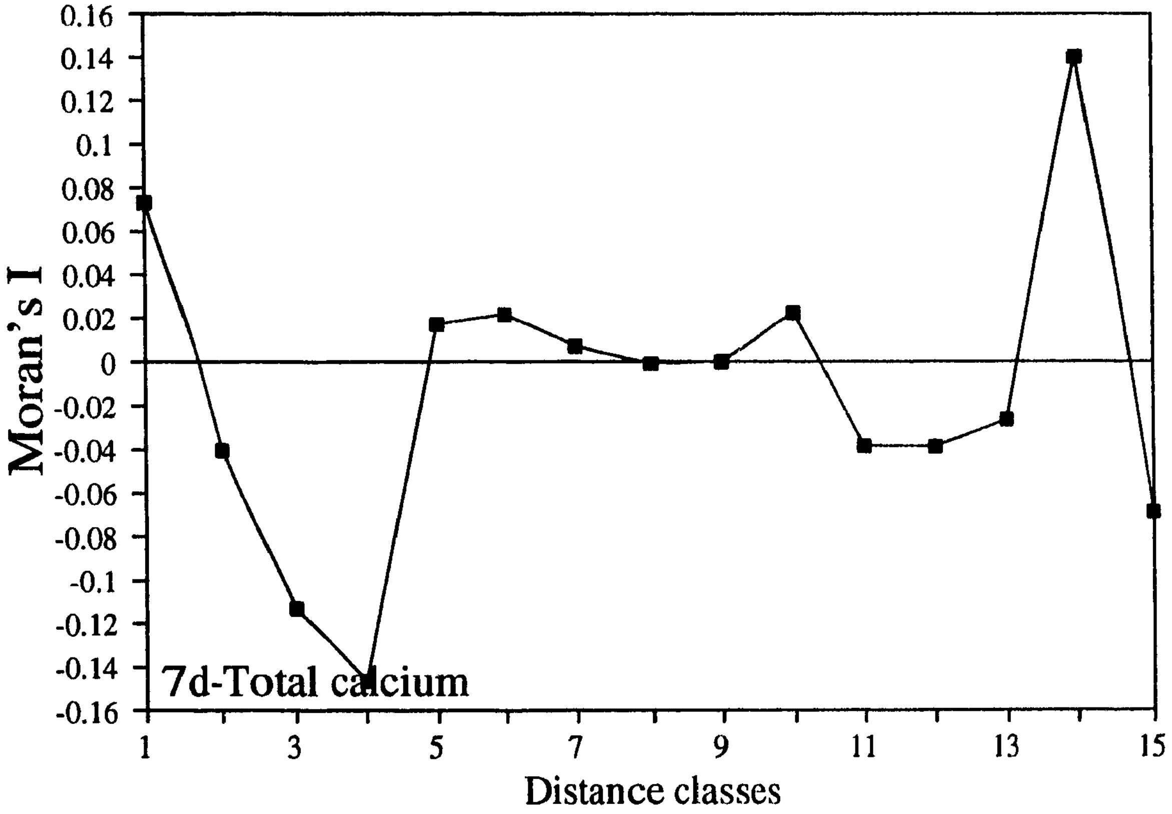
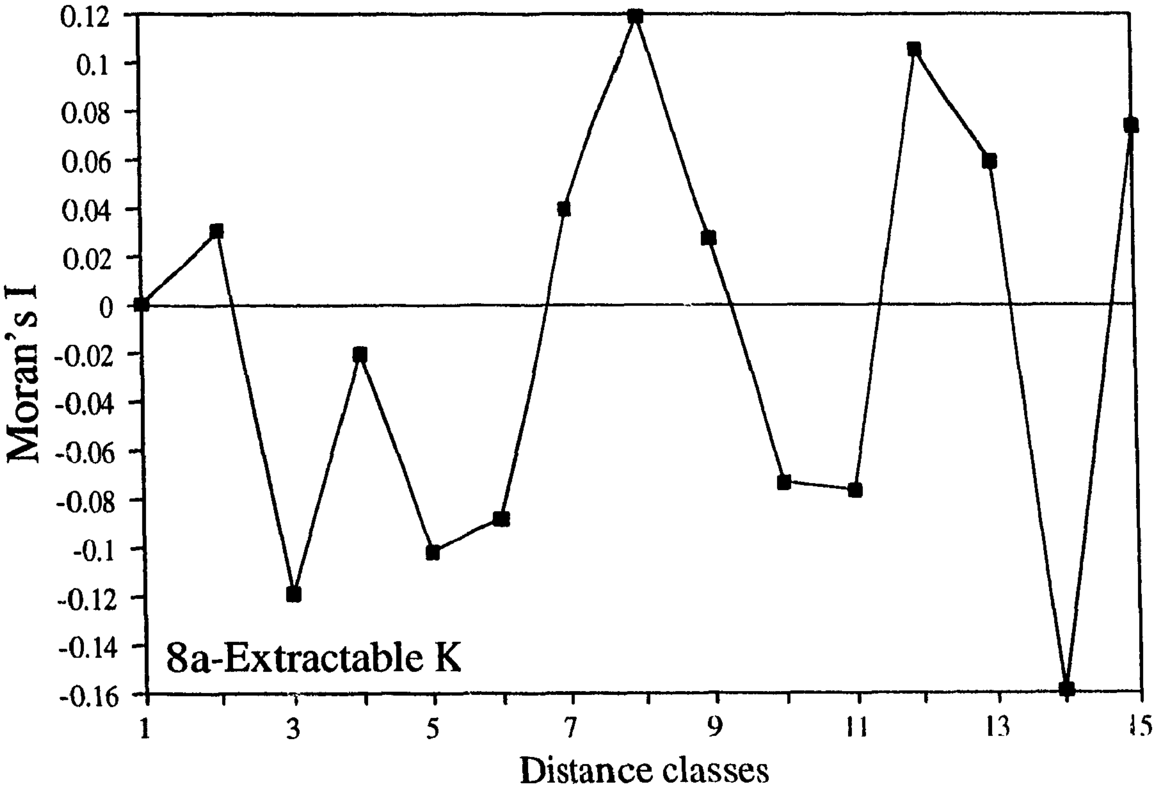
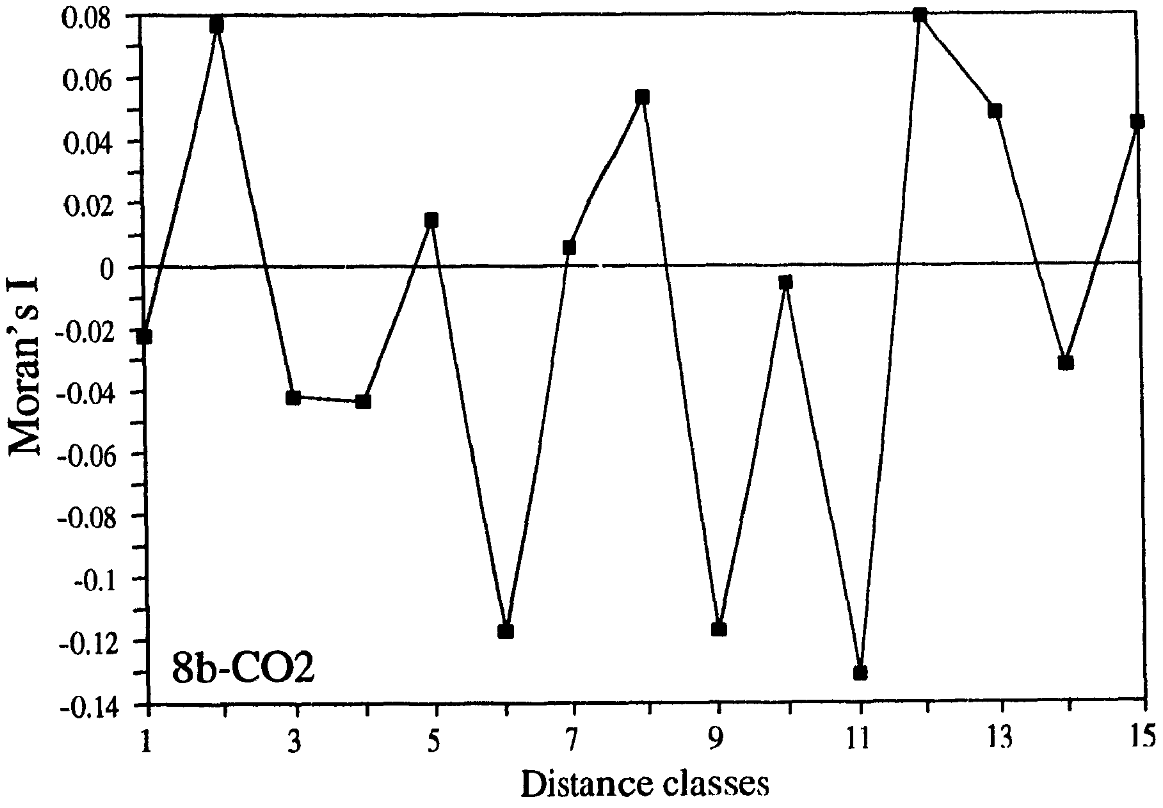

0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
-0.1
-0.12
-0.14
-0.16
Moran's I
7d-Total calcium
1
3
5
7
9
11
13
15
Distance classes

Figure 8. Moran's correlogram for the vertical spatial structure of residuals of multiple regression of two forest floor variables on the terms of the polynomial equation; a) extractable K and b) CO_2. No autocorrelation coefficients were significant at the Bonferoni level of 0.003.


8a-Extractable K
Moran's I
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
-0.1
-0.12
-0.14
-0.16
1
3
5
7
9
11
13
15
Distance classes


8b-CO2
Moran's I
0.08
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
-0.1
-0.12
-0.14
1
3
5
7
9
11
13
15
Distance classes

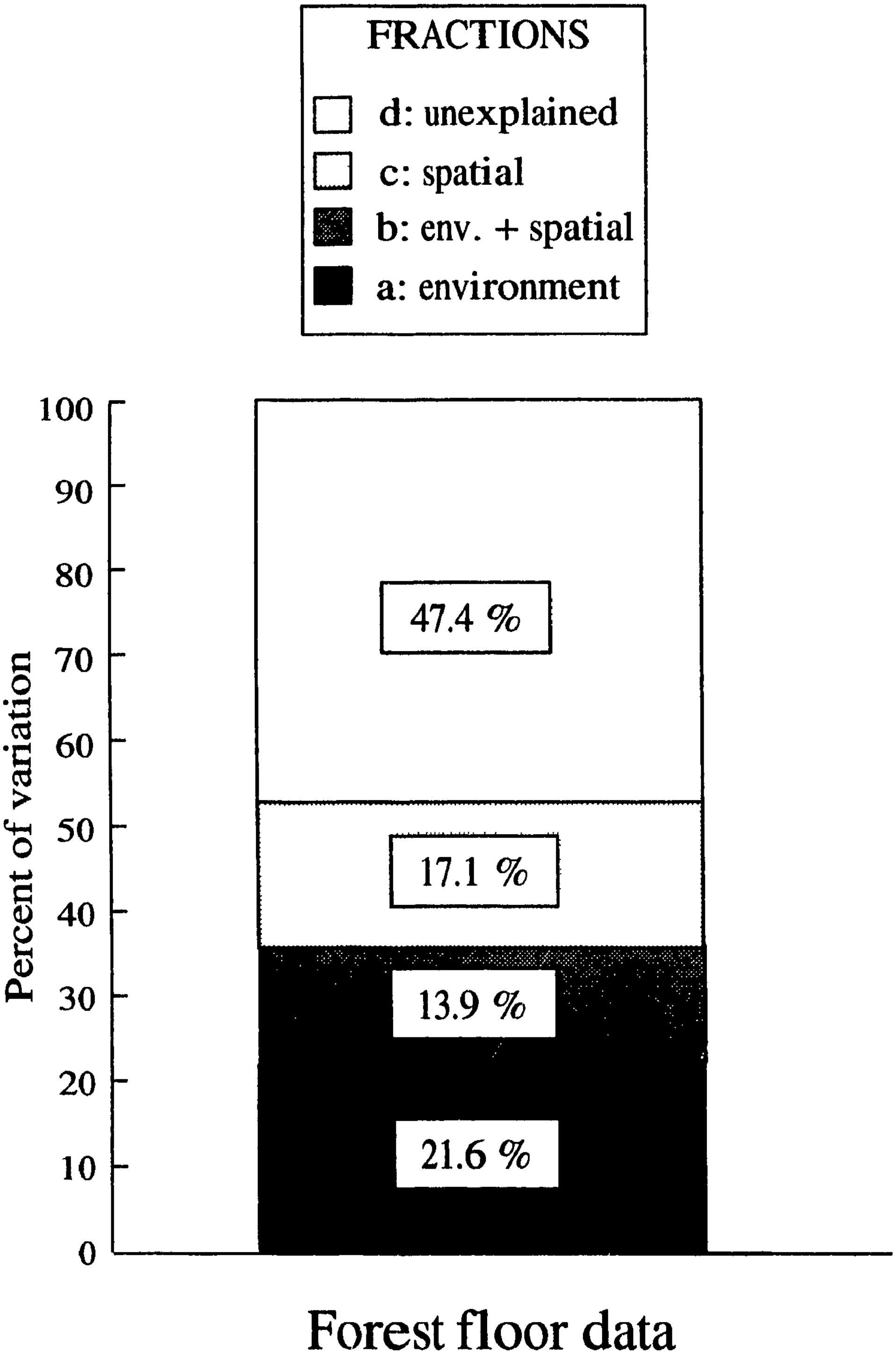


Figure 9. Variation partitioning of the forest floor data in four fractions; environment (a), confounded effect of environment and spatial structure (b), spatial structure (c), and unexplained (d).

CHAPTER TWO

THE ROLE OF TREE SPECIES IN CONTROLLING FOREST FLOOR FERTILITY

INTRODUCTION

Early studies in forest ecology recognized the influence of trees as one of the important factors controlling surface soil properties in forest ecosystems (Alway *et al.* 1933; Lutz and Chandler 1946). The influence of trees on forest soil is part of a combined effect of interacting controlling factors including parent material, topography, climate, disturbance, other biological activities and time (from Jenny 1941).

The nature of the tree influence on forest soil properties is primarily determined by a combination of three different mechanisms. First, the interception, redistribution and alteration of precipitation by contact with the trunk, the branches and the foliage can modify soil characteristics at the base of the tree and under the canopy (Parker 1983). Gersper and Holowaychuk (1971) have demonstrated that the quality and quantity of stemflow differs between tree species. Secondly, there is a relationship between litter decomposition and nutrient release, and characteristics of the upper forest soil (Melillo *et al.* 1989; Boerner 1984a; Tappeiner and Alm 1975; Johnston 1953). Many studies have observed important variation in litter quality, decomposition rate (Rustad and Cronan 1988; White *et al.* 1988; McClaugherty *et al.* 1985; Berg *et al.* 1984; Aber and Melillo 1982; Melillo *et al.* 1982), and acid-base status (Côté and Fyles 1993) of different tree species, that potentially affect forest soil fertility. Thirdly, processes occurring at the rhizosphere level of trees may affect soil properties. Carlyle (1986) indicates that the turnover of fine roots may result in an organic input of 2-5 times that of above ground litterfall. Carlyle (1986) and Côté and Fyles (1993) also stress the importance of considering the input of carbon and nutrients as a factor influencing forest soil fertility. Berendse *et al.* (1989) suggest that root carbon exudates may affect nutrient mineralization rates in the forest floor, and that exudation may differ between species. A recent study has demonstrated the relative importance of root activities in forest soils (Bowden *et al.* 1993). Few studies, however, have studied the mechanisms and processes taking place at the rhizosphere level. In summary, the nature of the tree influence varies among species, indicating that tree species can have different effects on the overall nutrient status of forest stands.

The importance of the effect of a particular species on soil fertility can be inferred from studies comparing the productivity of pure versus mixed stands. Malcolm (1987) observed that Sitka spruce grew better when associated with larch and that this improving effect was linked with higher nitrogen mineralization rates in mixed compared to pure stands (Carlyle and Malcolm 1986). Biondi *et al.* (1992) have demonstrated that ponderosa pine growth was less affected by intra-specific competition with increased presence of gambel oak in pine stands. Although this result can be attributed to an increase in pine spacing caused by the presence of gambel oak, (Biondi *et al* 1992) the positive effect of gambel oak on soil nutrient status (Lefevre and Klemmedson 1980; Klemmedson 1987) is also to be considered. These studies suggest that the presence of certain species may have an ameliorating or deteriorating effect on the nutrient status of forest stands. They demonstrated that understanding the role of tree species in controlling fertility may have practical applications with respect to maintaining or improving soil fertility.

Many studies have examined the specific effects of different tree species on chosen soil characteristics. Generally, these studies have been conducted either at the single-tree level or at the forest stand level. The concept behind single-tree study was developed by Zinke (1962) and refers to the fact that each individual tree has a zone of influence extending from the base of its trunk to outside the canopy. This concept has been used to demonstrate differences in soil properties under the canopy of individual tree of different species (Boerner and Koslowsky 1989; Boettcher and Kalisz 1990; Turner and Franz 1985; Mergen and Malcolm 1955) and to examine variability in soil characteristics on transects going from the base of the trunk to outside the canopy of different species (Pallant and Riha 1990; Lodhi 1977; Zinke 1962).

On the other hand, the studies done at the stand level have compared soil properties beneath plots or stands dominated by a specific tree species (Alban 1982; Alban *et al.* 1978; Lodhi and Ruess 1988; Fyles and McGill 1988; Kuiters and Denneman 1987; Fried *et al.* 1990; Young 1981; Challinor 1968) or beneath stands of different mixtures (Plymale *et al.* 1987; Perry *et al.* 1987; Klemmedson 1987; Lefevre and Klemmedson 1980; Carlyle and Malcolm 1986). In general, most of these studies were able to detect differences in certain forest soil variables attributable to the effect of different tree species.

The different methods used to measure the influence of trees on soil properties have generally worked with ; 1) models explaining the variation for each soil variable taken individually, and 2) forest stands of relatively low diversity. These two aspects must be explored in order to state the objective of this study.

First, instead of examining them separately, soil variables can be considered as integrated elements of a more complex system that is commonly referred to as soil fertility. In fact, soil variables have been shown to be intercorrelated (Norris 1970) and to vary more or less in concert (Webster 1977). Different approaches have been developed in order to consider the soil fertility or nutrient status taken as a whole. For example, a bioassay, in which barley and tree seedlings were grown on soils coming from stands of different tree mixtures, was used by Klemmedson (1991) as a fertility measurement. Another approach is the use of multivariate analysis which examine the variation in a group of variables taken as whole. Multivariate methods assume that the soil variables respond to the same environmental gradients (ter Braak and Prentice 1988). Different multivariate methods have been used with soil data (Odeh *et al.* 1991; Muys and Lust 1992; Fyles *et al.* 1991; Seelig *et al.* 1991; Dinel *et al.* 1991; Ross *et al.* 1975) but rarely in the context of the potential effect of tree species (c.f. Gauch and Stone 1979).

Secondly, in studies of tree effects on soil fertility done on stands of relatively low diversity (pure stands or mixtures of two species) it is easier to detect or infer the effect of a specific tree species. Similar studies working in more diverse stands (Perry *et al.* 1987; Plymale *et al.* 1987) did not aim at isolating specific tree species effects. There is, to my knowledge, no study that has examined the relative effect of different tree species in diverse stands where many species co-exist.

The presence of many co-existing tree species generates more interactions between the different processes involved in structuring the community (see Frelich *et al.* 1993).

In addition, interactions between spatially structured environmental constrains and the differential response of tree species increase the level of complexity in the ecosystem by generating spatial heterogeneity (Milne 1991; Cox and Larson 1992; Collins and Khlar 1991; Whitney 1991). This spatial heterogeneity, in which tree species are distributed neither uniformly nor at random, makes the tree species influence on forest soil fertility difficult to isolate from the confounded effect of other controlling factors. In order to isolate the relative influence of different tree species on forest soil fertility, the statistical model must consider the spatial structure present in the ecosystem (Legendre and Fortin 1989). Recent studies have addressed the problem of heterogeneity and spatial structure in ecological analysis (Dutilleul 1993; Dutilleul and Legendre 1993; Legendre 1993; Legendre and Fortin 1989; Kolasa and Pickett 1991; Borcard *et al.* 1992, Borcard and Legendre 1993) and a method was developed by Borcard *et al.* (1992) to incorporate spatial structure into a model of variation partitioning by using trend surface analysis (c f. ter Braak 1987a).

The goal of the present study was to examine tree species influence on forest floor fertility by using an approach that can: 1) consider the variation in the forest floor variables taken as whole; and 2) work with mixed forest stands composed of many co existing tree species. The model of Borcard *et al.* (1992), using Redundancy Analysis (RDA), was chosen for its potential to address both the intercorrelation of the forest floor variables and the spatial heterogeneity of mixed forest stands (see Chapter 1) In the first Chapter, I have used their model to separate the variation in the forest floor in four fractions : fraction 'a' or variation related to environmental variables (tree species and microtopography) alone; fraction 'b' or variation related to a confounded effect of environmental variables and spatial structure; fraction 'c' or variation related to spatial structure alone; and fraction 'd' or unexplained variation. The model proved efficient in extracting most of the spatial structure that was detected in a preliminary study of the spatial patterns present in the original data set (Chapter one) In this study, the emphasis was put on the fraction of the forest floor variation that is explained by tree species alone The tree species fraction was thus isolated from the spatial and microtopographical components in order to study its relative importance in explaining variation in forest floor properties. A more complete look at the ecological relationships between the specific tree species and the forest floor properties gave useful information about the role of trees in controlling forest floor fertility in mixed stands.

MATERIALS AND METHODS

Please refer to Chapter one for information on ; **Site description, field sampling, forest floor analyses, environmental variables (tree species and microtopography), data transformation, canonical trend surface analysis, and statistical procedures.**

RESULTS AND DISCUSSION

The relative contribution of trees in the variation explained in forest floor data.

The variation in forest floor data was partitioned into eight fractions, using a procedure similar to Borcard *et al.* (1992). The main difference in the method used in this study lies in the fact that the procedure used by Borcard *et al* (1992) only works with a combination of three matrices at a time; two explanatory variable matrices and one response variable matrix. Because my analysis used four matrices (tree species influence, microtopography, terms of the spatial polynomial equation and forest floor variables) the partitioning had to be done by computing a series of combinations of three matrices. Consequently, twelve RDA's of forest floor data were used to compute the different fractions. The sum of the variation explained by all canonical axes (or the sum of axis eigenvalues) of the RDA is equal to the total variation explained by the chosen set of explanatory variables. Table 1 summarizes the procedure and the results obtained. The eight fractions are computed from results of Table 1 as follows:

Fraction '*a1*' (tree species effect alone); RDA 4 = 16.0 %.

Fraction '*a2*' (microtopography alone); RDA 5 = 4.9 %.

Fraction '*a3*' (confounded effect of tree species and microtopography);[RDA 7 - RDA 4] or [RDA 10 - RDA 5] = 0.7 %

Fraction '*b1*' (confounded effect of tree species and spatial structure); [RDA 8 - RDA 4] or [RDA 12 - RDA 6] = 12.9 %.

Fraction '*b2*' (confounded effect of microtopography and spatial structure); [RDA 9 - RDA 5] or [RDA 11 - RDA 6] = 1.4 %.

Fraction '*b3*' (confounded effect of tree species, microtopography and spatial structure); [RDA 1 -(RDA 7 + RDA 28 - RDA 4)] or [RDA 2 - (RDA 9 + RDA 10 - RDA 5)] or [RDA 3 - (RDA 11 + RDA 12 - RDA 6)] = -0.4 %.

Fraction '*c*' (spatial alone); RDA 6 = 17.1 %.

Fraction '*d*' (unexplained); 100 % - total variation explained by the summation of the seven fractions of the model (52.6 %) = 47.4 %.

Figure 1 shows the variation in forest floor data explained by the different fractions.

Fraction '*a1*' (16.0 %) is the forest floor variation explained by tree species influence alone after removing the effect of microtopography and spatial structure as covariables. Variability in the nature of tree species influence on forest floor fertility is potentially caused by the differential species effect in terms of stemflow and throughfall, litterfall, and fine root turnover and exudation. For example, because of its smooth bark the volume of stemflow under beech is usually higher than under other species (Crozier and Boerner 1984; Gersper and Holowaychuk 1971). These studies also observed slight differences between soil characteristics under beech compared to red oak (Gersper and Holowaychuk 1971) and red maple (Crozier and Boerner 1984) Boerner and Koslowski (1989) suggest that the variation in soil properties at microsites located under beech, white ash and sugar maple was mainly caused by differences in stemflow. Differences in the quality, the decomposition rate and the nutrient release of litter among the tree species present on our site are suggested by other research. For example, Côté and Fyles (1993) have grouped some hardwood species in terms of their litter acid-base status and their potential effect on soil acidification, and have suggested that paper birch and yellow birch could have a beneficial effect on soil fertility compared to red oak, American beech and red maple. Nutrient concentration in foliage litter of red maple, paper birch, yellow birch, red oak and American beech (Côté and Fyles 1993) and American beech, striped maple (Goel and Fyles unpubl.) and hemlock (unpubl.) from the Morgan Arboretum showed important differences, mainly elevated levels of base-cations in paper birch, yellow birch and striped maple compared to the other species. In other studies, beech litter has been shown to have a higher concentration of lignin and a slower decomposition rate than red maple and paper birch (Melillo *et al.* 1982). Gosz *et al.* (1973) have also demonstrated a slower decomposition rate in beech litter than in yellow birch litter. Red oak and hemlock litter are also known to have a relatively high levels of lignin (Berg *et al.* 1984). These studies, therefore, suggest that variation in litterfall among species could potentially be related to the variation in the forest floor properties extracted in fraction '*a1*'. Information is lacking, however, about the influence of fine root turnover and exudation on soil fertility and we can only hypothesize that the different tree species present on the study site may have a differential effect. A more detailed examination of the ecological relationships involved in fraction '*a1*' is presented below.

Fraction '*a2*' (4.9 %) is the variation in forest floor due to the effect of the three microtopographical variables; slope, mound and depression. In general, the effect of microtopography on soil properties is a consequence of variability in litter decomposition between mound and pits caused by different litter distribution and accumulation (Dwyer and Merriam 1981), and soil moisture. Since microtopography is usually created by windthrow and tree decay (Beatty and Stone 1986) it can also be related to the disturbance regime. Beatty (1984), Beatty and Stone (1986), and Sauvesty *et al* (1993) have observed differences in the properties of forest soil sampled from mounds and depression. In my study, the importance of the microtopography in explaining the variation in forest floor is relatively small. This is consistent with observations reported by Messier and Kimmins (1992) who found no differences between soil characteristics on mound, depression and flat microsites. In the present study, however, the fact that extreme cases in microtopography were avoided when locating the sampling point at each microsite, may have reduced the importance of microtopography.

Fraction '*a3*' (0.7 %) is the variation related to a confounded effect of tree species influence and microtopography. It may be caused by a relationship between the occurrence of mounds and depression, and tree species, either because different species may react differently to disturbances creating a more disturbed topography or because some tree species will establish themselves more easily in disturbed areas (Ruel *et al* 1988; McClure and Lee 1993) and by interacting processes in which litter accumulation and decomposition of different tree species would be affected differently by the microtopographical status (Beatty 1984). This fraction does, however contribute very little to the overall variation in forest floor.

Fraction '*b1*' (12.9 %) is the variation in forest floor related to a confounded effect of tree species influence and spatial structure. Two hypotheses can be generated. First, tree species are themselves spatially structured over the site as patches of different tree association are observed. This structure may be either related to spatial structure of some biological processes involved in patch formation or to the establishment of the different tree species following spatial patterns of some abiotic controlling factors (parent material, drainage) (c.f Frelich *et al.* 1993). Alternatively, these same spatially structured abiotic factors may have a independent effect on forest floor properties in which case the causal relationship between tree species influence and forest floor fertility is impossible to verify. The importance of this fraction, which represents a quarter of all the explained variation in forest floor, confirms that spatial heterogeneity was important over the study site (see Chapter one). In fact, without considering this confounded effect, the interpretation of the tree species effect on forest floor would have been biased.

Fraction '*b2*' (1.4 %) is the variation in the forest floor related to a confounded effect of spatial structure and microtopography. This suggests that the presence of mounds, depressions and slope is spatially structured over the site. This could be linked to differences in disturbances over the site as some areas may be more susceptible to windthrow and tree fall because of some characteristics of the forest stand (eg. protection from the wind, type of humus). Alternatively the confounded effect of microtopography and spatial structure could be linked to human disturbances because the forest of the study area has been managed as a farm woodlot in the past. The forest floor data, however, is not greatly affected by this fraction.

Fraction '*b3*' (-0.4 %) is the variation in the forest floor related to a confounded effect of tree species influence, microtopography, and spatial structure. Based on the hypotheses mentioned above in the explanation of the other confounded effects, this fraction could be linked to a relationship between microtopography and spatially structured tree species or to spatial structure in disturbance regime affecting both tree species and microtopography. For my data set this fraction is negative, suggesting multicollinearity between some variables that have an opposite effect on forest floor but that belong to different explanatory groups. As a consequence, the response variable is best explained when the masking effect of the other group is removed as a covariable, meaning that the confounded effect will be, in fact, negative.

Fraction '*c*' (17.1 %) is the variation related to spatial structure alone. This variation could be linked to unmeasured spatially structured factors and is discussed in detail in Chapter one.

Fraction '*d*' (47.4 %) or the unexplained fraction is the variation not explained by the model. Again, we refer to chapter one for further discussion on this fraction.

In summary, the first step of this study has allowed me to isolate the effect of tree species alone from the confounded effect of spatially structured factors. Essentially, this process consisted in separating the tree species and microtopographical fractions that were combined in the '*a*' fraction of chapter one.

The relative importance of the tree species effect on single forest floor variables.

The total variation explained in the forest floor data as a whole that is computed by RDA can also be thought of as the average of the variation explained for each individual forest floor variable. It was thus possible to look at the forest floor variables that contribute the most to the explained variation extracted in the different fractions of Figure 1 and, at the same time, examine the relative influence of tree species, microtopography or spatial structure for each of the different forest floor variables The procedure described in Table 1 was therefore used for each variable, although each RDA was thus simply a multiple regression analysis.

Table 2 illustrates the variation of each forest floor variable explained by the different fractions and the relative importance of each fraction expressed as a percentage of the total variation explained for each variable. The total variation explained varied from 75.9 % for total N to 36.1 % for NH_4^+. The relative importance of the tree species fraction '*a1*' is, however, more important for NH_4^+ as it represents 54.7 % of its variation explained, compared with 13.5 % for total N. In fact the variation explained in total N is mostly found in the spatially structured fractions '*b1*' and '*c*'. Magnesium (Mg), CO_2 and pH are in a situation similar to total N where over 70 % of their variation explained is spatially structured. Phosphorus is the variable the most affected by microtopography The total and extractable calcium are clearly the forest floor variables that are the most influenced by tree species alone. Over 85 % of the variation in calcium is related to tree species effect which is consequent with other studies that demonstrated that calcium was one the variables that varies the most under different tree species (eg. Young 1981, Xiao *et al.* 1991). Tree species influence was also important for extractable Mg and extractable K.

In summary, the results shown in Table 2 illustrate that the different forest floor variables are not equally influenced by tree species, microtopography or spatially structured factors, indicating that the mechanisms and processes involved in the control of these variables differ substantially. Although the objective of this study was to examine the variation in the forest floor data taken as a whole, the results obtained in this section can generate useful information about the contribution of the different forest floor properties to the characterization of forest soil fertility.

Ecological relationships between forest floor variables and tree species influence.

The final step of this analysis was to study the ecological relationships between forest floor variables and the influence of the different tree species by focusing on fraction '*a1*', the variation in forest floor data explained by the principal canonical axes of the RDA 4 of Table 1.

In this RDA , the first axis , which is chosen to minimize the total sum of squares in forest floor data, is constrained to be a linear combination of the tree species variables. In other words, the first axis represents the linear combination of tree species variables that best explain the variation in the forest floor data. The second axis is derived from the variation remaining after fitting the values of the estimates of microsite scores obtained with the least square regression used to find axis one. The second axis is made orthogonal with the first axis. Subsequent axes are derived following the same procedure. All axes are centred and standardized so the microsite scores have a mean of zero and variation of one. RDA is also interpreted as a Principal Component Analysis on the estimates of the multiple regression of the tree species variables on each forest floor variable (Legendre 1993). Each canonical axis explains a certain fraction of the 16 % explained by tree species alone and can be represented in an ordination graph. The forest floor and tree species variables can be displayed on the ordination by plotting arrows. The coordinates of the arrow heads of each variables are the weighted sum of the microsite scores. Angles between arrows (and axes) represent correlation between variables and can be interpreted as follows; acute angle = positive correlation, obtuse angle = negative correlation, and right angle = no correlation. The projection of an arrow on a canonical axis indicates the extent of its relationship with the axis. The longer the arrow the more confident one can be about the inferred relationship. For additional information on RDA see ter Braak (1987c).

The first and second axes of Figure 2 represent 48 % and 25 % of the variation in forest floor that is explained by tree species alone. The first axis represents the main source of variation in the forest floor data and is associated with a gradient in the level of total and extractable calcium. Figure 2 also suggests that this variation is related to an opposite effect of beech and hemlock, which are the most dominant tree species on the site. Beech also has the strongest relationship with axis one, and its opposite angle with calcium suggests that the negative effect of beech on calcium may be the principal source of variation in the forest floor fertility of the study site. The Figure 2 also illustrates that forest floor is generally more acidic and less fertile under beech. A combination of different mechanisms may be responsible for the negative effect of beech. Of the fourteen hardwood species analyzed by Côté and Fyles (1993) beech litter had the lowest calcium concentration. Gosz *et al.* (1973) found that the percentage of calcium was lower in beech litter than in yellow birch litter. Consequently the effect could be related to a lower concentration of calcium in the litter. High levels of lignin and polyphenols found in American beech (Melillo *et al.* 1982 ; Aber *et al.* 1990) and European beech (Kuiters and Denneman 1987) may complex with calcium and magnesium and increase leaching of these elements from the organic horizon (Davis 1971). This effect is supported by the fact that beech growing on Mor humus that is low in fertility may produce more tannins (Davis 1971). The acid-base status of beech litter suggests that beech has potential for acidifying forest soil (Côté and Fyles 1993). Lower pH caused by stemflow was also observed under beech (Crozier and Boerner 1984; Boerner and Koslowsky 1989). The fact that the study site has relatively low concentrations of exchangeable cations (Table 3) indicates that soils may have a low buffering capacity (Johnson *et al.* 1982) against the acidifying effect of beech litter causing further depletion of calcium (Federer *et al* 1989).

Although the correlation between hemlock and calcium is not as strong as for beech and calcium, Figure 2 suggests that hemlock may have a positive effect on calcium. Except for Mergen and Malcolm (1955) who found one case where calcium was higher under hemlock than under red pine, most studies have observed that hemlock was associated with forest soils of low pH (Lodhi and Ruess 1988) or low pH and calcium level (Beatty 1984; Boettcher and Kalisz 1990; Gauch and Stone 1979). Lower pH and exchangeable cations in forest floor were also found under western hemlock compare to western redcedar (Turner and Franz 1985). For some of these studies , however, the level of pH and base cations measured under hemlock was higher than the highest values obtained in my study (Table 3), indicating that these studies were conducted on more fertile sites. For example, in one of their study site, Boettcher and Kalisz (1990) observed a mean value of 6.3 mg/g for calcium under hemlock relative to 10.4 mg/g under tulip poplar, which is more than twice the amount measured on my study site (Table 3). The positive effect of hemlock on calcium observed in this study has thus to be examined in the context of a site of very low fertility co-dominated by beech. In other words, the data suggest that on low fertility sites, hemlock is able to maintain a certain level of calcium in forest floor relative to beech. These results also suggest that the ameliorating or deteriorating quality of a particular tree species may be related to the site fertility. Fyles and Côté (1993), Perry *et al.* (1987) and Boerner (1984b) have suggested that the nutrient cycling of certain species may vary as a function of the site conditions. In addition, the fact that the forest floor thickness and bulk density were also related to the first axis suggest that the differential effect of hemlock and beech have generated two relatively different types of forest floor over the study site. The thicker forest floor under hemlock was also observed by Beatty (1984). The mechanisms involved in that differential effect between hemlock and beech growing on low fertility sites requires to be investigated in more detail.

The other ecological relationship associated with the first axis of Figure 2 is the positive correlation between yellow birch and calcium. Based on the acid-base status of its litter, yellow birch was considered as potentially beneficial for soil fertility (Côté and Fyles 1993). Gosz *et al.* (1973) and Côté and Fyles (1993) have measured relatively high levels of calcium in yellow birch foliage litter.

The variation in forest floor expressed by the second axis of Figure 2 is associated with a general fertility gradient, with all of the forest floor chemical and biological variables related to the presence of red maple, paper birch, red oak, yellow birch and the 'other' tree species (sugar maple, amelanchier sp.). The presence of these tree species on this low fertility beech-hemlock dominated site seems to have a general beneficial effect on the overall fertility of the site.

A trend in the upper left quadrant of Fig.2 suggests that paper birch, red maple and the 'other' tree species have a beneficial effect on pH, total and extractable magnesium, and phosphorus. Côté and Fyles (1993) have identified paper birch as a species that could potentially improve soil fertility on the basis of its acid base status. Miller (1984) reviewed the beneficial effects of birch on soil fertility. On the other hand, the positive effect of red maple on pH and magnesium seems in contradiction with the results from Côté and Fyles (1993) who have identified red maple as a potentially acidifying species. This beneficial influence needs to be examined in the context of a site that is dominated by hemlock and beech, both known for their acidifying potential (Côté and Fyles 1993) The red maple influence can thus be interpreted either as a relative positive or 'less negative' effect on soil fertility compared to hemlock and beech, or as a beneficial effect caused by a modification of its nutrient cycling in order to adapt to sites of very low fertility. Boerner (1984b) has demonstrated that red maple can adjust its nutrient use efficiency in order to adapt to sites of lower fertility. In addition, red maple is recognized for its ability to establish itself under a wide range of environmental conditions (Walters and Yawney 1990), suggesting that red maple has the capacity to adapt to different site fertility conditions.

Another trend associated with the second axis in the upper right quadrant of Figure 2, is one involving a positive relationship between potassium and red oak. The positive correlation between red oak and potassium was not reflected in results obtained in other research (Challinor 1968; Lodhi 1977; Gersper and Holowaychuk 1971) or to potassium concentrations found in oak litter from the Morgan Arboretum (Côté and Fyles 1993) The relation between red oak and potassium may be linked to a slower decomposition of red oak litter caused by high lignin concentration (Aber *et al.* 1990) Young (1981) observed that, although the soil potassium levels were not different, the standing biomass of red oak contained 2.5 times more potassium than tulip poplar, suggesting the ability of red oak to extract potassium from the soil. Challinor (1968) has suggested that the high level of potassium under Norway spruce was linked with the fact that fine roots distributed near the surface were able to cycle and maintain potassium before it is leached. The present data set cannot verify, however, the relevancy of this hypothesis for red oak and further study is necessary. A negative correlation between potassium and both striped maple and hemlock is also illustrated by their opposite angles (Fig. 2). The negative correlation between striped maple and potassium may be linked to the fact that striped maple has a fast decomposition litter that could promote rapid leaching of potassium. Goel and Fyles (unpubl.) have found similar results in which forest floor potassium concentration was significantly lower under than outside the canopy of striped maple. Finally, potassium is negatively correlated with hemlock. Boettcher and Kalisz (1990) observed that the potassium concentration in forest floor was significantly lower under hemlock then tulip poplar but only when herbs and ferns were present in the understorey of the trees. This suggests a possible interaction of the tree and the herb layer effect on potassium cycling. In other studies, hemlock dominated stands have been shown to support less understorey and herbs than deciduous stands because of soil characteristics (Beatty 1984) or light and allelopathic effects (Daubenmire 1930 cited by Beatty 1984). Since herbaceous litterfall is known to have high concentration of potassium (Scott 1955 cited by Tappeiner and Alm 1975), it is possible that the effect of hemlock on the quantity and species composition of the herb layer may have had an indirect effect on the potassium cycling. Data relative to the understorey and the herb layer of the study site was not collected and further analyses would be necessary to verify the potential role of these layers in the overall fertility of the site.

Mineralizable nitrogen (NH_4^+) is also positively correlated with red oak and negatively correlated with hemlock and striped maple (Fig. 2). The laboratory mineralizable N method used in this study is an expression of the inherent quality of the organic matter of the sampled forest floor and hence the effect of red oak, striped maple and hemlock on mineralizable N may be related to the quality of the input of organic matter as leaves and roots and also to the degree of decomposition of the fermentation and the humus layers. The relationship between litter quality, decomposition and nutrient dynamics has been widely demonstrated (Aber and Melillo 1982; Aber *et al.* 1990: McClaugherty *et al.* 1985). Lodhi (1977) measured large amounts of ammonium in the upper mineral soil under red oak relative to elm, sycamore, hackberry and white oak. On the other hand, Lodhi and Ruess (1988) observed low ammonium in mineral soil under red oak compared to hemlock, which is contradictory to our results. The results of Lodhi (1977) and Lodhi and Ruess (1988), however, were obtained from measurements of mineral soils and comparison with the results from the present study should be made with caution. The finding that mineralizable N in forest floor under a mixed beech-red oak stand in the Morgan Arboretum was twice that under hemlock (Fyles unpubl.), is consistent with my results.

In summary, the dominating tree species, beech and hemlock, have the greatest influence on the overall forest floor fertility of the site. The differential influence of beech and hemlock on calcium is the principal source of variation in the forest floor characteristics. The presence of the other tree species has generally improved the fertility of the forest floor. Different hypothesis have been generated to explain the ecological relationships suggested by Figure 2.

The axes plotted in Figure 2 represented 73 % of the variation explained in forest floor data by tree species influence. The remaining 27% is expressed by the subsequent axes. The amount of variation extracted by the first four canonical axes for each forest floor variable is given in Table 4. The cumulative sum of all the axes is equal to the variation explained in the fraction '*a1*' of Table 2. Table 4 shows that the first and second axes are influenced by the variables that are the most explained by the tree species. Because the later axes are held in the context of the first axis extracted, it is possible that some ecological processes of interest may be either expressed in late axes or more or less divided over the different axes. For example, Table 4 illustrates that the relationship involving total N, CO_2 or bulk density would be better represented by an ordination of the third and fourth axes. If one is particularly interested in relationships not well explained by the first axes, Allen and Hoekstra (1991) have proposed an approach using transformation of data matrix in order to move to the front some of the patterns formerly relegated to late axes so as to express their ecological relationship with more clarity

Table 5 illustrates the intraset correlations of the tree species variables with the fourth first axes. The intraset correlations are the correlations between the tree species variables and the microsites scores that are linear combination of tree species variables (ter Braak 1986). Table 5 shows to what level different tree species are associated with the different axes. The relationship between the different tree species and the first two axes supports the results described in Figure 2. The variation in the forest floor data explained by the third axis is mostly related to variation in total N and K, CO_2 and NH_4^+

(Table 4) and is associated with the opposite effect of two groups of tree species; red oak, hemlock, yellow birch and paper birch on one side and red maple, the 'other' tree species, beech and striped maple on the other. Red oak contributes the most to the effect of the third axis with a correlation of 0.56 The two opposing groups of tree species correspond relatively well to the association of tree species observed in the field, suggesting that the variation in forest floor data extracted by the first axis may be related to an effect of tree species association rather than the cumulative effect of the individual species. The fourth axis is associated with the presence of yellow birch and the 'other' tree species (Table 5) and with the variation of extractable K, CO_2, and the physical properties (thickness, bulk density) of forest floor (Table 4).

CONCLUSION

The results obtained in this study have demonstrated the ability of the RDA-partitioning method to extract information about the role of different tree species on the fertility of a mixed forest stand. The method was used as an exploratory tool to generate hypotheses about the potential ecological relationships between the different tree species and forest floor properties. Many hypotheses generated by this study may have been difficult to formulate with other methods and most require testing in further experiments because, as this study emphasized, many of the ecological and physiological processes involved in the relationship between the different tree species and their nutrient dynamics are unknown. Experiments that would examine the influence of a particular tree species by integrating the role of the stemflow, throughfall, litterfall, rhizosphere dynamics and other physiological processes are necessary in order to understand the role of the species on the soil fertility of mixed stands. The influence of the initial site conditions on the behaviour of certain tree species also needs to be considered as potentially deteriorating species on one site may prove beneficial on another site.

This research has identified several other experiments that could be developed from the approach used in this study. First, the method could be adapted to study the stand level instead of the microsite level in order to verify whether, by removing some of the noise in the data caused by the scale of the study, the effect of trees would be more distinct. Studies working at the stand level may use the 'usual' basal area measurement (Grosenbaugh 1952) to determine the influence of tree species on the overall fertility of different stands. Secondly, a method examining the influence of different tree associations instead of individual tree species may take in account potential interactions or confounded effects between the influence of different tree species. Such a study might use cluster analysis to identify different associations of species and a discriminant analysis of the forest floor data with respect to these associations. Thirdly, a study examining the spatially structured factors influencing the '*bI*' fraction (Fig. 1) could be useful in understanding the effect of initial site conditions on tree species behaviour. Finally, the potential to develop a tree species influence index that is more precise could be examined. A parallel study (Nguyen Xuan unpubl.) conducted with half the microsites demonstrated that the weight of litterfall for each microsite could be used as an integrated measurement of tree species influence instead of the tree index used in this study. RDA's using the two indexes were compared and yielded similar results and conclusions. The advantage of the litterfall index is that it would take less time then measuring tree diameter and distance from microsites.

The method has shown potential as a tool to study the role of trees in mixed forest stands but it should be tested on other forests in order to evaluate its validity. In effect, this method should be used to examine the ecological relationships in forest stands with relatively similar conditions (species composition, parent material, topography, climate) in order to compare the results with those obtained in my study. The application of this approach to other forest types may also generate useful hypotheses about the potential role of the tree species present on these stands. A better understanding of tree effect on forest floor and soil properties may be helpful in establishing better management practices that would maintain or improve fertility of mixed forest stands.

Table 1. Variation explained in forest floor data with RDA's and partial RDA's using different combinations of explanatory variable matrices: tree species, microtopography, and spatial structure captured by the polynomial equation. All RDA's are significant at the 0.05 level using the Monte Carlo permutation test.

RDA	Explanatory variables	covariables	R^2
1	tree species	none	29.2 %
2	microtopography	none	6.5 %
3	spatial	none	31.0 %
4	tree species	mic + spa	16.0 %
5	microtopography	tree + spa	4.9 %
6	spatial	tree + mic	17.1 %
7	tree species	spatial	16.7 %
8	tree species	microtopography	28.9 %
9	microtopography	tree species	6.2 %
10	microtopography	spatial	5.5 %
11	spatial	tree species	18.5 %
12	spatial	microtopography	30.1 %

Table 2. Variation of the forest floor variables explained by the different fractions and the relative contribution (%) of each fraction to the total variation explained (*in italics*).

	a1	a2	a3	b1	b2	b3	c	TOT.
N	10.2	2.3	-0.4	33.8	1.4	-1.1	29.6	75.9
	13.5	*3.0*	*-0.5*	*44.5*	*1.9*	*-1.5*	*39.0*	*100*
P	8.3	15.8	-0.1	4.0	0.9	-0.4	15.1	43.5
	18.9	*36.2*	*-0.2*	*9.1*	*2.1*	*-0.9*	*34.7*	*100*
K	17.2	3.9	-0.5	2.7	4.9	-0.8	14.7	42.2
	40.8	*9.4*	*-1.2*	*6.5*	*11.6*	*-1.8*	*34.8*	*100*
Ca	31.5	2.0	3.2	19.1	-1.1	-2.2	6.8	59.2
	53.2	*3.3*	*5.4*	*32.2*	*-1.9*	*3.7*	*11.4*	*100*
Mg	10.2	2.7	0.8	33.6	-1.3	-1.8	20.3	64.5
	15.8	*4.1*	*1.3*	*52.1*	*-2.0*	*-2.7*	*31.5*	*100*
ex. K	16.5	4.0	-2.1	6.9	2.5	0.4	31.2	59.5
	27.8	*6.8*	*-3.6*	*11.6*	*4.3*	*0.6*	*52.5*	*100*
ex. Ca	37.0	1.1	2.7	14.3	-0.9	-1.7	6.0	58.5
	63.2	*1.9*	*4.5*	*24.5*	*-1.5*	*-2.9*	*10.3*	*100*
ex. Mg	16.7	5.0	2.1	10.0	-2.2	-1.6	11.5	41.4
	40.4	*12.0*	*5.0*	*24.0*	*-5.2*	*-3.9*	*27.7*	*100*
pH	8.1	0.9	0.7	20.4	0.8	-0.0	19.1	49.9
	16.2	*1.7*	*1.3*	*40.9*	*1.6*	*-0.1*	*38.3*	*100*
CO_2	7.3	5.4	-0.4	12.7	0.4	-1.1	16.5	40.7
	17.8	*13.3*	*-0.9*	*31.1*	*0.9*	*-2.7*	*40.5*	*100*
NH_4^+	19.7	7.5	1.1	0.5	1.7	-1.7	7.4	36.1
	54.7	*20.7*	*3.0*	*1.4*	*4.7*	*-4.8*	*20.4*	*100*
thic.	13.3	6.6	3.3	1.8	4.8	6.8	19.6	56.2
	23.7	*11.7*	*5.9*	*3.2*	*8.6*	*12.1*	*34.9*	*100*
B.Dens	12.0	6.5	-1.9	8.0	5.4	0.3	25.1	55.5
	21.7	*11.7*	*-3.3*	*14.5*	*9.8*	*0.5*	*45.2*	*100*
RDA	16.0	4.9	0.7	12.9	1.3	-0.4	17.1	52.5
	30.5	*9.3*	*1.2*	*24.6*	*2.6*	*-0.7*	*32.6*	*100*

Table 3. Mean and standard deviation of untransformed forest floor variables before the regression on ash content.

Variables	Units	Mean	Std.Dev
N	mg/g	15.23	2.06
P	mg/g	0.67	0.08
K	mg/g	0.97	0.12
Ca	mg/g	2.81	1.05
Mg	mg/g	0.70	0.15
extr. K	mg/g	0.41	0.10
extr. Ca	mg/g	2.30	0.99
extr. Mg	mg/g	0.34	0.09
pH	-	3.91	0.19
CO_2	µg/g/h	38.57	7.96
NH_4^+	µg/g	538.55	121.35
Thickness	cm	5.67	2.07
Bulk density	mg/cm^3	112.81	30.82

Table 4. Fraction of the variation of forest floor variables explained by tree species and extracted by the first four axes.

	AXIS				
	1	2	3	4	All axes
Eigenvalues	7.7	4.1	2.1	1.1	16.0
N	0.1	0.4	7.2	0.2	10.2
P	0.5	5.3	0.5	0.1	8.2
K	0.8	9.8	5.7	0 1	17.2
Ca	30.6	0.7	0.1	0.0	31.5
Mg	0.2	7.3	2.0	0.2	10.2
extr. K	8.1	6.0	0.1	1.5	16.5
extr. Ca	36.2	0.5	0.1	0.0	37.0
extr. Mg	7.6	7.1	0.1	0.1	16.7
pH	1.7	3.9	1.4	0.2	8.1
CO_2	0.7	0.1	3.6	2.0	7.3
NH_4^+	4.5	8.7	5.6	0.1	19.7
THICKNESS	6.6	2.3	0.4	3.7	13.3
BULK DENSITY	2.6	0.8	0.1	5.6	12.0

Table 5. Intraset correlations between the tree species variables and the first four canonical axes.

	Axis			
	1	2	3	4
Hemlock	-0.74	-0.21	0.35	0.11
Beech	0.87	-0.20	-0.25	0.08
Red maple	-0.09	0.52	-0.39	0.19
Striped maple	-0.24	-0.34	-0.23	0.12
Red oak	0.19	0.62	0.56	0.12
Paper birch	-0.31	0.54	0.11	-0.13
Yellow birch	-0.37	0.07	0.17	0.55
Others	-0.31	0.26	-0.35	0.36

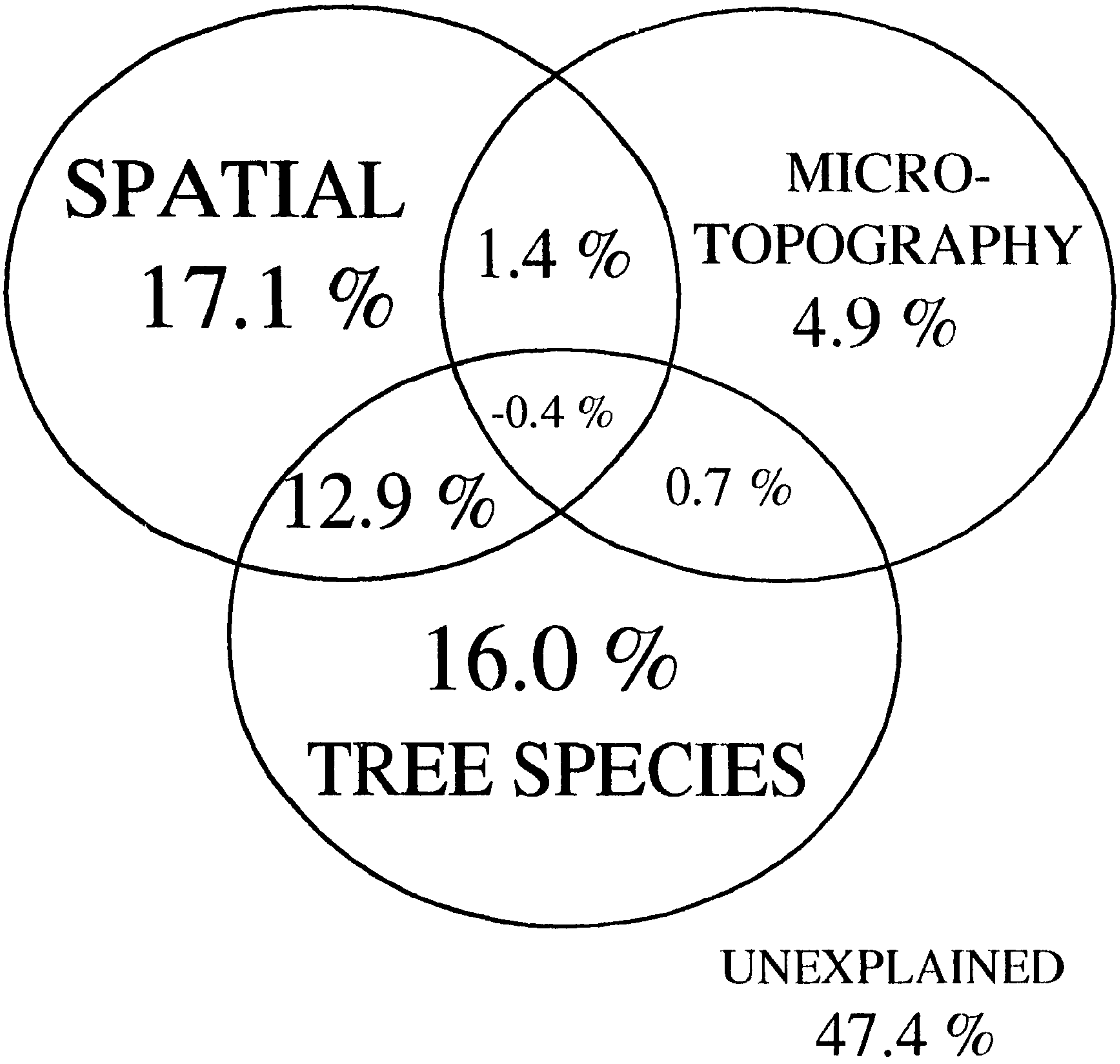


Figure 1. Fractions of the variation in forest floor data explained by tree species, microtopography, spatial structure and their confounded effects.

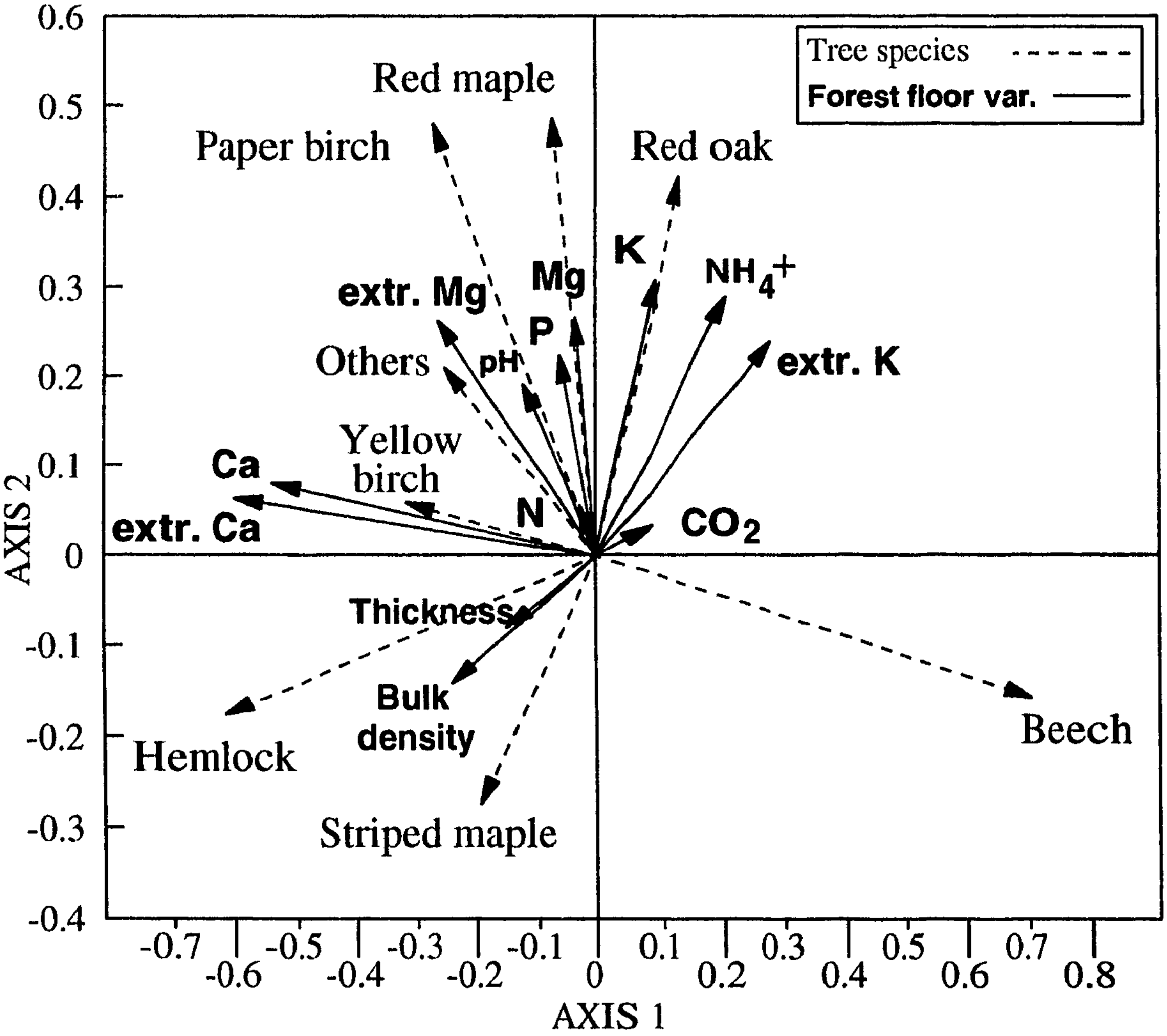


Figure 2. Biplot based on partial redundancy analysis of forest floor variables with respect to tree species effect after removing spatial structure and microtopography as covariables. The first two axes represent respectively 48 % and 25 % of the variation in forest floor explained by tree species. The RDA was significant at the 0.01 level (Monte-Carlo permutation test).

CONCLUSION

The objective of this study was to extract information about the role of different tree species in a mixed-forest stand. The RDA-variation partitioning method was able to isolate the effect of tree species on forest floor fertility by taking in account the spatial heterogeneity that was detected with spatial correlograms. The method adopted in this study was used as an exploratory tool to generate hypotheses about ecological relationships between tree species and forest floor variables.

This study highlighted the fact that a lot of information is missing about the influence of specific tree species on soil fertility and the mechanisms by which they affect soil properties. Studies examining the effect of a particular species by integrating processes such as the stemflow and throughfall, aboveground litter decomposition and activities of the rhizosphere may be necessary in order to get a better understanding of the tree-soil relationship. More information concerning processes and mechanisms taking place in the rhizosphere is very important since a major part of the trees effect on soil fertility may occur at that level. The results of this study also suggest that tree species may behave differently on sites that differ in fertility.

In order to evaluate the method proposed in this study, three independent aspects need to be considered; the multivariate approach (RDA), the incorporation of spatial structure in a variation partitioning model, and the scale of the study (microsites).

First, the advantage of the multivariate approach is that, by considering forest floor fertility as a complex ensemble of interacting variables, it is possible to get a better insight into the main patterns occurring over the entire study site. Multivariate analysis can also be used to put information obtained from univariate analysis in a more global context. There are very few studies, however, that have used direct gradient anlaysis with soil data and further studies are required to assess the ability of these techniques to extract useful information about the relationship between soil fertility and environmental factors.

Secondly, this study demonstrated the importance of considering spatial structure when studying ecological data. The incorporation of spatial structure in a variation partitioning model has recently been developed for studies dealing with ecological communities and although results obtained from this study suggest that this approach may be applicable to soil data, further studies are required in order to asses the ability of trend surface analysis to detect ecologically meaningful spatial patterns in soils.

Finally, this study was similar to single-tree studies working at the microsite level with the difference that microsites were under the influence of more than one tree at a time. By locating many microsites over the site it was also possible to have an insight in processes occurring at the site level. The inconvenience, however, is that microsite studies are susceptible to local variation that can give noisy data.

In summary, the method used in this study proposed an approach that aims at integrating processes taking place in relatively complex and heterogeneous ecosystems. Its purpose is primarily to explore complex data sets and to generate hypotheses that would otherwise be very difficult to obtain. The results obtained in this study demonstrated that the RDA-variation partitioning model has the potential to become a useful tool in the study trees influence on soil fertility.

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