

Approaches to quantifying forest structures

A. POMMERENING

School of Agricultural and Forest Sciences, University of Wales, Bangor, Gwynedd LL57 2UW, Wales

Summary

For some time, structure indices – quantifying spatial stand structure – have been integrated into forest research and are used to provide a measure of biodiversity. In addition, correlation functions – developed initially for problems outside forestry – enable analysis and characterization of forest stand structures, generating more accessible information. This paper outlines a classification of structural indices measuring alpha diversity and examines typical representatives of the classification groups such as the Shannon index, the aggregation index of Clark and Evans, the contagion index, the coefficient of segregation of Pielou, the mingling index, the diameter differentiation index, the pair correlation and the mark correlation function. These can be used to measure differences between forests in time and space, to generate forest structures, to analyse the differences between observed and expected structures and to characterize modifications of forest structure resulting from selective harvesting. These algorithms are the keys for assessing complex forest structures, which can be the result of continuous cover forestry methods. Continuous cover forests with selective harvesting are being promoted in the new forest policies of Britain. Case studies have shown that from given spatial forest structures one can possibly conclude the suitability for habitats, a hypothesis which has yet to be proved by further appropriate analysis. The equations for the quantification of stand structure presented in this paper have the advantage that they are easier to survey during forest inventory than the more direct measures of ecological variety.

Introduction

Continuous cover forestry has become a common term over the last two decades throughout Europe, although its history is much older (Helliwell, 1997). New forest policies have included several alternatives to clearcutting which are summarized by this term and which are expected to have a major impact on the forests of Great Britain in the future (Forestry Commission, 1998, 2000, 2001; Kerr, 1999). Part of the reason for adopting this new management type is to provide

improved habitats for wildlife dependent on continuity of woodland conditions and stands of diverse structure. Therefore measures are needed, firstly to distinguish between stands of different structure, and additionally to provide surrogate indices of habitat quality.

Spatial stand structure is an important factor in determining habitat and species diversity. Increasing heterogeneity of horizontal and vertical stand structure is linked to a higher number of species and stands with greater ecological stability. Silvicultural options can modify the stand structure

and therefore have an important potential role in securing stand diversity and ecological stability (Pretzsch, 1998; Humphrey *et al.*, 2000).

Ecosystem diversity on a spatial and areal scale is subdivided into alpha, beta, gamma and delta diversity (MacArthur, 1965; Whittaker, 1972). In forest ecosystems, alpha diversity operates within forest stands; beta diversity refers to the variation between forest stands; gamma and delta diversity operate on larger scales (Lähde *et al.*, 1999).

There is an increasing demand for information on alpha diversity, in particular on the spatial distribution of trees and their attributes (Mason and Quine, 1995; Ferris and Humphrey, 1999). Therefore, structural indices have been developed which describe, as mean values or distributions, certain horizontal aspects of forest stand structure (Upton and Fingleton, 1985, 1989).

Since the 1970s, statisticians have been developing functions which not only express forest stand

structures as mean values or as an empirical distribution, but are also able to describe spatial structure on a continuous basis (Ripley, 1977). This paper demonstrates how these functions add to the traditional concepts of structure indices.

The objective of this study is to discuss the methodology of some of the latest developments relating to variables and functions which characterize forest stand structure as a part of alpha diversity. A classification of these measures is presented in order to provide a better understanding of the different concepts (Figure 1). The equations of typical examples of the different concepts are explained and applied to three experimental stands. The results are discussed with the help of simulated references and suggestions made as to how these methods could be applied in British forests. The focus is primarily at the forest and stand scale rather than at a landscape or regional perspective.

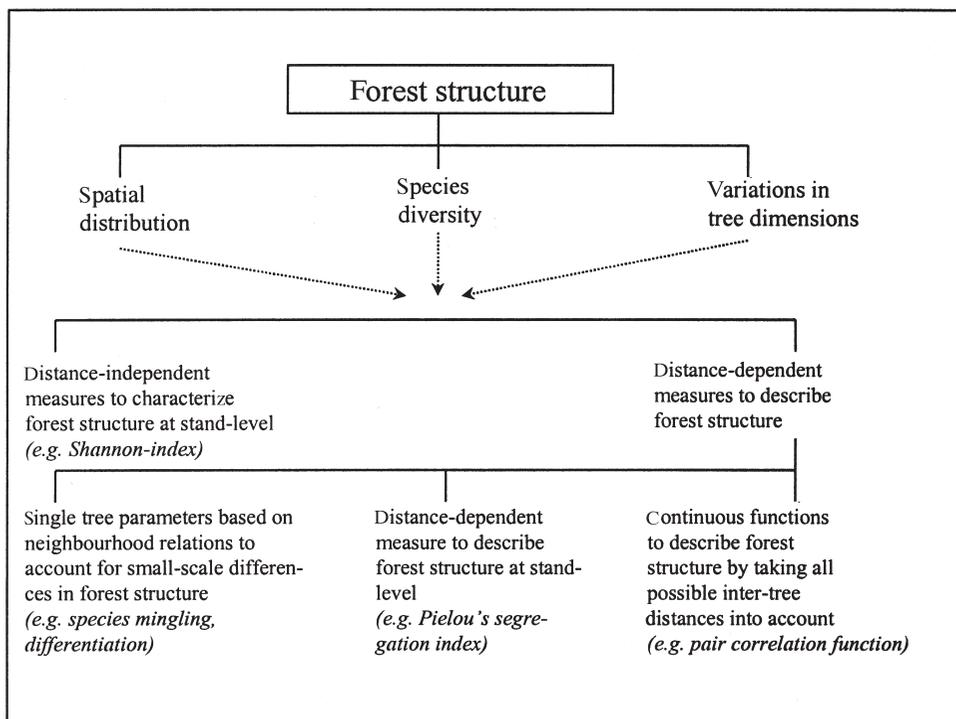


Figure 1. Overview of the three major characteristics of forest structure and the groups of variables by which forest structure is assessed (modified from Albert, 1999).

Brief review of stand structure algorithms

In managed forests, as well as in old-growth ecosystems, biodiversity is a key element for evaluating the stability of the system (Kimmins, 1997, p. 391). Kimmins (1997, p. 352) defines the structure of a plant community in terms of vertical and horizontal spatial organization.

In mathematical terms the majority of indices quantifying forest structure can be divided into two major groups: distance-independent and distance-dependent measures. While the first group evaluates stand structure without any spatial reference, the latter group can be subdivided into: (1) individual or single tree parameters based on neighbourhood relations, accounting for small-scale differences in biodiversity; (2) distance-dependent measures to describe forest stand structure at stand level; and (3) continuous functions. Figure 1 gives an overview of the three major aspects of forest structure and the groups of measures. The following paragraphs present typical examples of these groups.

Distance-dependent variables for characterizing stand structure

Aggregation index of Clark and Evans In the 1950s and 1960s numerical variables were developed to describe aspects of variability of tree locations in forest stands by a single value. One example is the aggregation index of Clark and Evans (1954). It is defined as:

$$R = \frac{\bar{r}_{observed}}{E(r)} \quad \text{where} \quad E(r) = \frac{1}{2 \cdot \sqrt{\frac{N}{A}}}; \quad (1)$$

$$R \in [0, 2.1491]$$

where $\bar{r}_{observed}$ stands for the mean of the distances from the trees to their nearest neighbours in a given forest stand, while $E(r)$ is the mean nearest neighbour distance in a stand with completely random tree locations ('Poisson forest') of intensity $\lambda = N/A$ with A = area of the forest stand and N = number of trees. Usually, the interpretation of R values is as follows: $R > 1$ if the pattern has a tendency to regularity, $R = 1$ if it is completely random (Poisson process), and $R < 1$ if there is clustering in the pattern.

Contagion index As a single-tree-based alternative to the aggregation index, Gadow *et al.* (1998) developed the 'contagion' variable or 'neighbourhood pattern', W_i , to define the degree of regularity of the spatial distribution of tree positions in a forest. Unlike the index of Clark and Evans, this variable is a single-tree parameter. Assuming complete regularity of the positions of the n nearest neighbours around a reference tree i , the expected standard angle α_0 between two neighbours would be equal to $360^\circ/n$. For example, $\alpha_0 = 90^\circ$ in a constellation involving four neighbours. Each pair of neighbours shares two angles, α and β , with $\alpha + \beta = 360$ and $\alpha \leq \beta$. Contagion is defined as the proportion of α angles which are smaller than the standard angle α_0 (see also Figure 2):

$$W_i = \frac{1}{n} \sum_{j=1}^n w_j \quad \text{where} \quad w_j = \begin{cases} 1, & \text{the } \alpha\text{-angle } j \text{ is smaller than } \alpha_0 \\ 0, & \text{otherwise} \end{cases} \quad W_i \in [0, 1] \quad (2)$$

In the 'structural group of four' W_i can be visually assessed in the field by comparing the actual angle α with an angle of 90° . Thus a quick decision can be made in the forest on whether α is smaller than 90° or not. If tree positions are recorded, W_i can be derived from the trees' coordinates. In a constellation involving four neighbours, W_i can assume five possible values (0, 0.25, 0.5, 0.75 and 1.0). The distribution of the W_i allows evaluation of the point pattern of tree positions in a forest. The average contagion (\bar{W}) may be used to classify the point pattern into the categories 'regular', 'random' and 'clumped' (Gadow *et al.*, 1998). In order to carry out a sensitivity analysis for the average contagion (\bar{W}), Albert (1999, p. 67) simulated 10 random, clumped and regular forest stands. The results indicate that stands of trees with a mean contagion value greater than 0.6 can be considered as clumped, those with values between 0 and 0.5 indicate regular tree distributions and between 0.5 and 0.6 are random. However, Albert (1999, p. 67) did point out that these distinctions may not be sharp.

Shannon index The Shannon index (Shannon and Weaver, 1949) is an example of a distance-

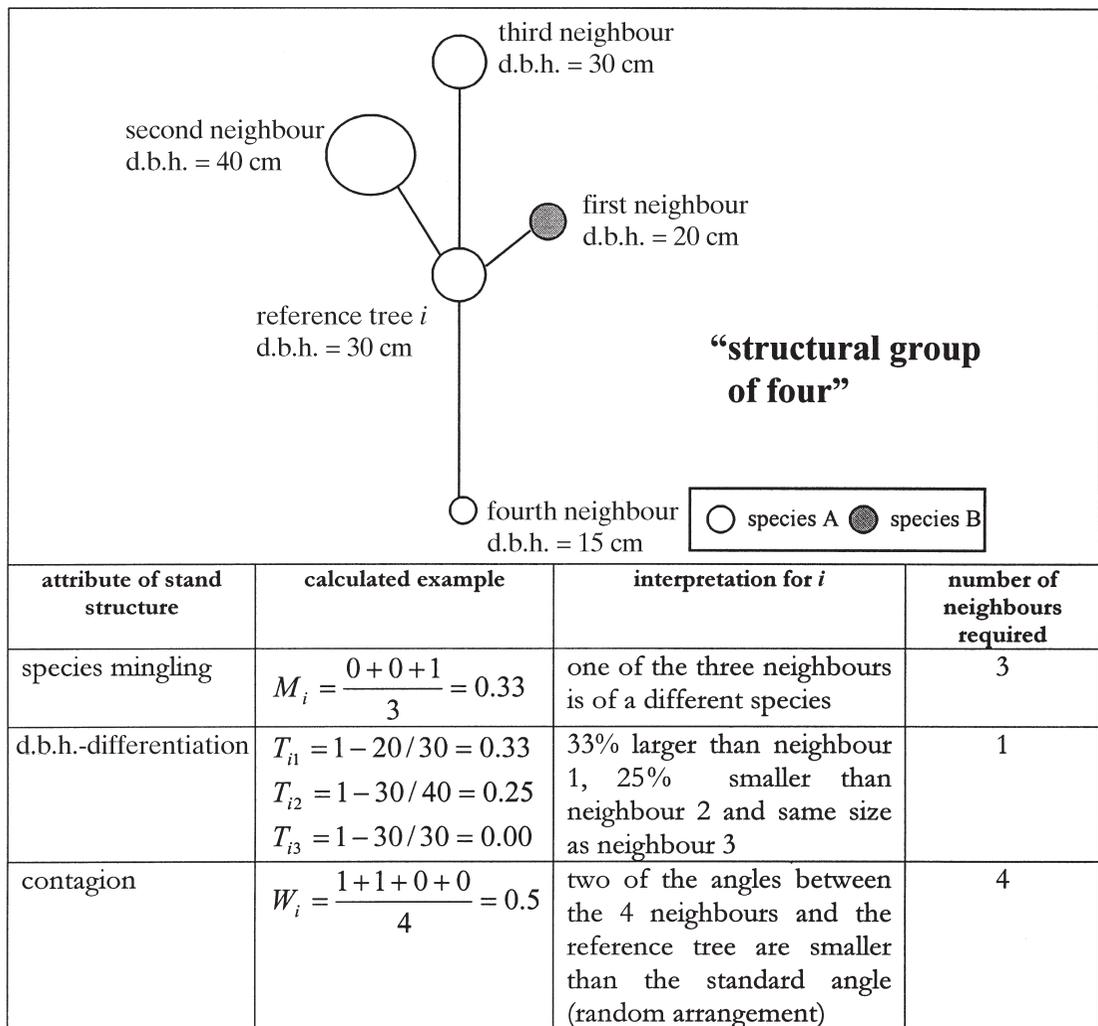


Figure 2. Structural variables (species mingling, d.b.h.-differentiation and contagion) for reference tree i and its nearest neighbours. Note that for calculating the species mingling, three neighbours are required, for the d.b.h.-differentiation one neighbour is needed as a minimum and for the contagion, four neighbours are required (modified after Albert and Gadow, 1998).

independent algorithm (see Figure 1) describing species mingling. It is defined by:

$$H'(p_1, p_2, \dots, p_n) = - \sum_{j=1}^n p_j \cdot \ln(p_j) \quad (3)$$

where p_j = probability of a randomly selected tree belonging to tree species j ; n = number of tree species in the forest.

A similar index, also working with probabilities, was developed by Simpson (1949).

Pielou's coefficient of segregation A further index is the coefficient of segregation, S , of Pielou (1977). It describes the degree of mixing of trees of two species A and B in a forest, and like the aggregation index, R , it is based on the nearest

neighbour tree distances. In Pielou's notation, S is given as follows:

Let N be the number of all pairs of trees (reference tree – nearest neighbour tree), let m and n be the numbers of trees of species A and B, respectively, and let r and s be the number of times trees of species A and B are found as the nearest neighbours of a reference tree. These numbers can be set out in a simple form in a 2×2 table as follows.

		Species of the nearest neighbour		
		A	B	Total
Species of reference tree	A	a	b	m
	B	c	d	n
Total		r	s	N

The coefficient of segregation is defined by

$$S = 1 - \frac{N \cdot (b + c)}{m \cdot s + n \cdot r}; \quad S \in [-1, 1] \quad (4)$$

If the nearest neighbours are always of the same species as the reference trees, then $S = 1$. If all neighbours are of different species $S = -1$. In the case of complete randomness of species distribution, one can expect values around 0.

Mingling index The corresponding single-tree variable to Pielou's coefficient of segregation, known as *mingling* (M_i), gives the proportion of the $n = 3$ nearest neighbours j ($j = 1 \dots n$) of the i th reference tree which do not belong to the same species as the reference tree i (Figure 2):

$$M_i = \frac{1}{n} \sum_{j=1}^n v_{ij}; \quad M_i \in [0, 1] \quad (5)$$

$$\left. \begin{array}{l} \text{where } v_{ij} = \\ \left\{ \begin{array}{l} 1, \text{ reference tree } i \text{ and neighbour } j \text{ are of different tree species} \\ 0, \text{ otherwise} \end{array} \right\} \end{array} \right\}$$

The current state of a forest may be described very effectively using the distribution of the mingling variable (see, for example, Fuldner, 1995; Pommerening, 1997; Albert, 1999). In a constellation involving three neighbours ('structural group of four') M_i can assume four possible values (0.00; 0.33; 0.67; 1.00). For the calculation of the mingling variable for a whole stand,

all M_i values are added up and divided by the number of trees. The bigger the mean mingling M , the more the different tree species are intermingled. Small values indicate large groups of only one tree species and therefore segregation (Pommerening, 1997).

Diameter differentiation index The single tree diameter differentiation variable, T_{ij} , gives the size difference of neighbouring trees on a continuous scale and describes the spatial distribution of tree sizes. For the i th reference tree and its $n = 3$ nearest neighbour j ($j = 1 \dots n$) the diameter differentiation T_{ij} is defined as:

$$T_{ij} = 1 - \frac{\min(DBH_i, DBH_j)}{\max(DBH_i, DBH_j)}; \quad T_i \in [0, 1] \quad (6)$$

where DBH = breast height diameter (d.b.h. in cm).

The value of T_{ij} increases with increasing average size difference between neighbouring trees. $T_{ij} = 0$ means that neighbouring trees have an equal size. This index is based on pairs of reference trees – first, second or third nearest neighbour tree. For the calculation of the diameter differentiation of a whole forest stand, all T_{ij} values are summed and divided by the number of trees, so that three single numbers $T1$, $T2$ and $T3$ describe the size difference of neighbouring trees, taking the first, second and third nearest neighbours, respectively. Diameter differentiation values can be interpreted as follows:

- 1 **small differentiation:** comprises the classes $0.0 \leq T < 0.3$. The tree with the smallest d.b.h. is 70 per cent or more of the neighbouring tree's size
- 2 **average differentiation:** comprises the classes $0.3 \leq T < 0.5$. The tree with the smallest d.b.h. is 50–70 per cent of the neighbouring tree's size
- 3 **big differentiation:** comprises the classes $0.5 \leq T < 0.7$. The tree with the smallest d.b.h. is 30–50 per cent of the neighbouring tree's size
- 4 **very big differentiation:** comprises the classes $0.7 \leq T \leq 1.0$. The tree with the smallest d.b.h. is less than 30 per cent of the neighbouring tree's size.

Diameter differentiation, mingling and contagion indices may be established for the stand as a whole or for a given sub-population.

Figure 2 shows a hypothetical sampling group of four and the corresponding values of the structural attributes of species mingling, d.b.h.-differentiation and contagion for the reference tree i . All single-tree parameters can also be calculated as frequency distributions which will be demonstrated later in this paper. Fuldner (1995) used species-specific indices as well as variables relating to the dominant height.

The single-tree structure variables have the additional advantage that it is possible to assess them easily from common forest inventories. Pommerening (1997), Pommerening and Schmidt (1998) and Pommerening and Gadow (2000) evaluated the performance of the sampling method 'structural group of four' and the standard fixed-area plot commonly used in forest inventories concerning these variables and found that both methods are useful and imply only a small sampling error. This offers the possibility of incorporating structural indicators in forest inventories and monitoring.

There are a considerable number of other indices for describing spatial structure, which are based on similar concepts. They cannot be discussed in detail here, as this would be beyond the scope of this paper. For further information, see Gadow and Hui (1999), Gadow *et al.* (1998), Gleichmar and Gerold (1998), Smaltschinski (1998), Upton and Fingleton (1985, 1989), Lähde *et al.* (1999), Latham *et al.* (1998), Neumann and Starlinger (2001), O'Hara *et al.* (1996), Spies (1998), and Zenner and Hibbs (2000).

Pair correlation function Modern point process statistics use functions instead of indices or empirical distributions. These functions depend on the inter-tree distance r .

Unlike the aggregation index, R , the pair correlation function $g(r)$ does not result in one number, but in a function, which can be plotted as a graph. It characterizes the variability of the pattern of tree locations. This function is based on the mathematical theory of marked point processes. In the marked point process model, the points are tree positions given with respect to a Cartesian coordinate system. The marks are qualitative or quantitative tree characteristics; for example, tree species, diameter at breast height or total tree height (Penttinen *et al.*, 1992). Assuming that the observed forest stand can be described by a

homogeneous point process (i.e. there are no systematic fluctuations of point density and no preferred directions in the point pattern), the tree density or intensity λ is defined as the mean number of trees per area. The familiar forest variable 'stems per hectare' can be used as intensity. Intensity λ has the following interpretation. Consider an infinitesimally small circle of area dF , then the probability of finding one tree in it is λdF , because the area is too small to find two or more trees. When describing variability and correlations in tree stands we have to consider pairs of trees. Let us consider two infinitesimally small circles of areas dF_1 and dF_2 of inter-centre distance r . Let $P(r)$ denote the probability that both circles each contain a point of the point process, therefore:

$$P(r) = \lambda^2 \cdot g(r) \cdot dF_1 \cdot dF_2 \quad (7)$$

The function $g(r)$ is called the pair correlation function and is a function of the inter-point distance r . It answers similar questions to the aggregation index of Clark and Evans (for interpretation examples, see Tomppo, 1986; Penttinen *et al.*, 1992; Pommerening *et al.*, 2000; Shimatani, 2001). Figure 3 shows the pair correlation functions for two fundamental types of point processes, namely for a cluster process (positive correlation of tree locations, mutual attraction) and for a process with mutual inhibition between the trees (negative correlation of tree locations). For a forest with trees distributed at random, $g(r) = 1$, which means that the tree locations are spatially uncorrelated. The dotted graph in Figure 3, which runs parallel to the abscissa at a value of 1, illustrates this. In this case, according to the product formula of the theory of probabilities, $P(r) = \lambda \cdot dF_1 \cdot \lambda \cdot dF_2$.

If the tree locations show a tendency towards regularity, e.g. in very young stands planted in rows or in very old stands (where there are large distances between the trees, contradicting the assumption of random tree locations), then for small values of r , $g(r)$ takes the form $g(r) = 0$, because pairs of trees at these distances do not exist (Figure 3). This is the case at the so-called hardcore distance r_0 , which is the smallest observed inter-tree distance. For bigger values of r , $g(r) > 0$ and $g(r)$ approaches the value of 1. Young forest stands of natural origin very often have trees arranged in clusters where the values of

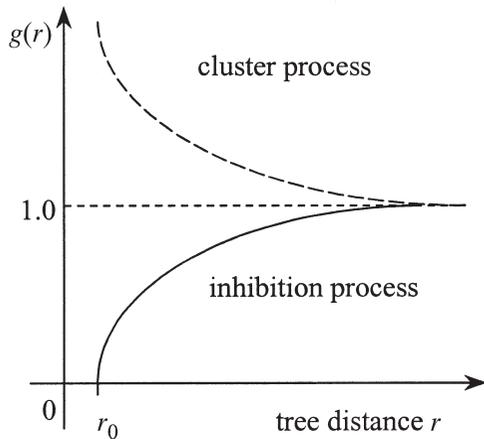


Figure 3. Schematic diagram of the pair correlation function $g(r)$ for analysing forest structures. The hardcore distance r_0 is the smallest possible inter-tree distance of a forest stand. Values of $g(r) > 1$ indicate that interpoint distances around r are relatively more frequent than those in a forest with random tree locations. Small values of r typically mean clustering. Conversely, values of $g(r) < 1$ indicate that the corresponding inter-tree distances are rare in the forest stand under study, which may indicate inhibition of trees caused by competition.

the pair correlation function tend to be larger than 1 at small inter-tree distances r (indicated by the dotted graph called ‘cluster process’ in Figure 3). Values of the pair correlation function $g(r)$ larger than 1 indicate that the inter-tree distances around r are relatively more frequent compared to those in a completely random point process. If this is the case for small values of r , typically there is clustering. Conversely, values of $g(r)$ smaller than 1 indicate that the corresponding distances are rare, which may indicate inhibition (Penttinen *et al.*, 1992). Estimated pair correlation functions reflect the behaviour often reported in forestry literature, that natural forests often begin with cluster-process-like patterns. Competition between trees causes (self) thinning, and at the final stage the forest is similar to a Poisson process with random tree locations or even more regular (Stoyan and Penttinen, 1998). Unlike the aggregation index, the pair correlation function depends on the inter-tree distance and allows spatially explicit investigations of the interaction between trees (e.g. type

of interaction, determination of the range of interaction and estimation of its strength). Shimatani (2001) suggested an interesting combination of the Simpson index (Simpson, 1949) and the pair correlation function.

Mark correlation function Clearly, not only the number of trees in a stand is of interest but also their diameters, heights, damage class, tree species and other so-called ‘marks’. In the theory of point processes a ‘mark’ is a value, which is assigned to a point. If the ‘point’ is a tree location, the ‘mark’ is a tree attribute (see Penttinen *et al.*, 1992). As in the pair correlation function, a pair of trees is regarded as having the inter-tree distance r . From the marks m_1 (e.g. the d.b.h. of the first tree) and m_2 (e.g. the d.b.h. of the second tree) a value is calculated, which assesses the dissimilarity or similarity of the trees’ marks. This relationship is quantified by $f(m_1, m_2)$, where f is a suitable ‘test’ function. Here, f is defined as $f(m_1, m_2) = m_1 \cdot m_2$. From these single values a mean value is calculated while the inter-tree distance r remains constant. Thus we conceive a function $\kappa_m(r)$, which is dependent on r . It is advisable to divide the function $\kappa_m(r)$ by the square of the mean value m of the observed tree parameters in order to make interpretation easier (Penttinen *et al.*, 1992; Stoyan and Penttinen, 1998). The mark correlation function, $k_m(r) = \kappa_m(r)/m^2$ is very suitable for analysing the mutual influence of trees as far as it affects the observed tree parameter. If d.b.h. is used, then it is often the case that for small inter-tree distance r values, $k_m(r)$ is < 1 . This indicates a tendency that at small inter-tree distances both trees of a pair have smaller diameters than the average of the stand. This behaviour may indicate that the price which trees have to pay for being close together is that their diameters tend to be smaller than the mean in the whole forest. However, small values of $k_m(r)$ can also be the consequence of clusters with young and thin trees (Stoyan and Penttinen, 1998). Penttinen *et al.* (1992), Gavrikov and Stoyan (1995) and Pommerening *et al.* (2000) give some examples.

Reference values and edge effects

Before applying the presented parameters and functions to trial stands in order to find out how

they work, there are two important issues which need to be addressed.

One question often asked is what an observed number means exactly. For example should an observed mingling be regarded as desirable or not and, if so, to what extent? This question is about a *reference* which can be used to compare with observed values. Fuldner (1995) calculated structural variables for different forest compartments and for the main tree species in a stand within each compartment before and after thinning. He made comparisons between compartments, between the two main tree species within each compartment and assessed changes in structure caused by thinning. This approach could be used to select particular forest compartments as references in that they reflect a typical or desired spatial structure. Research within nature reserves also uses the concept of reference plots to monitor natural forest development. The spatial structure of such 'untouched' forest compartments could be compared with that of managed stands.

The disadvantage of this method is that it assumes uniformity in natural stand structures: no forest compartment is like another, and it may not be justified to use a limited number of research plots as references. Until now no study has made an attempt to derive generally applicable values of structure indices for particular tree species mixtures and management types. Moreover, Sprugel (1991) concluded that naturalness is difficult, if not impossible, to define. A great variety of forest communities might only be described as natural for a given site and a given time. Shape, dimension, altitude, relief, slight differences in species compositions and site conditions, to name only a few factors, can make the suitability of comparison questionable.

To overcome this disadvantage Pommerening (1997) suggests using computer simulation to make comparisons between observed structural variables and those expected in a random forest. Using random permutations, it is possible to calculate a test criterion which can be used to evaluate differences between observed and expected forest structures. The advantage of this method is that the tree species composition and other tree attributes from the stand under study are used to derive the reference rather than those from a different forest compartment. One can criticize

this approach by arguing that the random arrangement of tree attributes which is used as a reference may not correspond to a particular biological meaning. However, Stoyan and Penttinen (1998) investigated a number of different stand development phases and came to the conclusion that old-growth stands do often tend to have random tree locations. Randomness as a reference is very often used in statistics, and is easy to establish. This approach has been adopted in a number of studies of stand structure (e.g. Clark and Evans, 1954; Zenner and Hibbs, 2000). By using randomness as a substitute for naturalness it is possible to quantify how much the value of a structural variable in a given forest compartment differs from this theoretical reference and to suggest the reason for this.

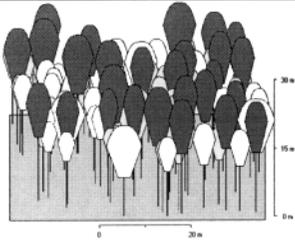
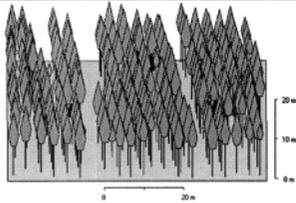
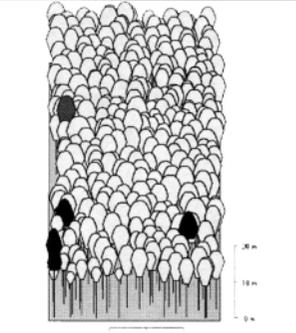
In this paper, randomness is used as a reference and the results of the random simulations are mean values of 5000 independent single simulations per forest compartment.

Another important issue is that of edge effects, which need to be addressed if distance-dependent structural parameters are applied. The problem is that neighbourhood relationships are not truly represented at the stand or plot boundary when potential neighbours lie outside the research plot. This edge bias becomes bigger the smaller the research plot is and the fewer trees are involved. This problem is shared with distance-dependent competition indices (Biging and Dobbertin, 1992). To overcome this effect, several methods have been developed (Monserud and Ek, 1974; Martin *et al.*, 1976; Radtke and Burkhardt, 1998). All of these methods, however, have considerable disadvantages and there is no one method which can be applied to all distance-dependent structure variables and plot shapes. There is still considerable need for research in this area. Due to the fact that most of the boundaries of the three trial stands used in this paper are real forest boundaries (forest and public roads), no edge correction has been applied to the structure variables. The correlation functions, however, have internal edge corrections integrated in their algorithms.

Study sites

Data from three forest stands are used to demonstrate the reviewed indices (see Table 1). The three

Table 1: Forest yield data of the stands Manderscheid 198, Manderscheid 187 and Ammeloe 14e. In the schematic pictures beech trees appear white, oaks dark grey, Douglas firs light grey and Scots pine black. G = basal area per hectare ($m^2 ha^{-1}$), N = number of trees per hectare, V = volume per hectare ($m^3 ha^{-1}$)

compartment	Manderscheid 198				Manderscheid 187				Ammeloe 14e			
schematic picture												
survey	1996				1996				1996			
natural production		G	N	V		G	N	V		G	N	V
	Oak	16.31	112	293.86	Doug. Fir	27.30	660	246.86	Beech	18.76	546	211.14
	Beech	10.95	253	140.64	Scots pine	0.53	53	2.86	Oak	0.21	3	3.03
	-	-	-	-	Other	0.20	23	0.69	Scots Pine	1.07	6	13.72
	Total	27.26	365	434.5	Total	28.03	736	250.41	Total	20.04	555	227.89
age	118 years				24 years				53 years			
area	0.24 ha				0.36 ha				0.65 ha			

stands were especially selected to reflect rather different spatial structure. Comparable data from Britain were not available when this study started. However, current research projects at the University of Wales, Bangor and the Forestry Commission's Northern Research Station aim at filling this gap.

The stands Manderscheid 198 and 187 are situated in the forest district of Manderscheid in the German federal state Rhineland-Palatinate. The compartment Ammeloe 14e is situated west of Münster in the federal state Northrhine-Westphalia.

Compartment Manderscheid 198 covers an area of 0.24 ha and is a part of a 11.9 ha forest stand. It is stocked with 120-year-old oak (*Quercus petraea* Lieth), intermingled with beech (*Fagus sylvatica* L.) occurring mostly in small groups. This compartment was included in this study because it reflects a mature stand with an intimate species mixture.

Compartment Manderscheid 187 covers an

area of 0.36 ha and is stocked with 24-year-old planted Douglas fir trees (*Pseudotsuga menziesii* (Mirb.) Franco). The compartment was originally established as a pure stand and the planting rows are still distinctly visible, but the area now includes a few isolated, naturally regenerated beech (*Fagus sylvatica* L.), pine (*Pinus sylvestris* L.), spruce (*Picea abies* (L.) Karst.), birch (*Betula pendula* Roth.) and larch (*Larix decidua* Mill.) trees. This compartment was selected because it is a young plantation with regular tree positions and a rather low degree of species mingling.

Compartment Ammeloe 14e covers an area of 0.65 ha and is stocked mainly with beech (*Fagus sylvatica* L.), apart from some pines (*Pinus sylvestris* L.) and oaks (*Quercus robur* L.). The trees are 53 years old. Ammeloe 14e reflects typical more or less mono-species beech forests of Central Europe. In terms of overall stand age it is between Manderscheid 187 and Manderscheid 198.

The following parameters were recorded

within each compartment: diameter at breast height (d.b.h.), tree species and the Cartesian coordinates of the tree locations. The data collection was conducted by the Institute of Forest Management and Forest Yield Sciences (University of Göttingen, Germany) in 1996 as part of a pilot project with the state forest services of Rhineland-Palatinate and Northrhine-Westphalia. The three plots selected for this study were part of a larger network of reference plots where new methods of forest management were tested. These new methods aimed at combining conventional surveying of yield and stocking information with a detailed quantitative description of stand structure.

Results and discussion

Spatial distribution

The aggregation index R (Clark and Evans, 1954) and the 'contagion' or 'neighbourhood pattern' index W both describe the horizontal spatial arrangement of tree positions. According to the aggregation index, compartment Manderscheid 187 shows the most regular tree patterns (Table 2), as might be expected from a young Douglas fir plantation. The Ammeloe 14e beech stand also appears to be quite regular while the mixed oak-beech compartment of Manderscheid 198 reflects random tree positions. The observed contagion distribution (which also describes the horizontal arrangement of tree locations) can be compared to the simulated contagion distribution (assuming that the given trees of each of the three forest compartments are arranged randomly). The comparison in Figure 4 shows that each of the three stands tend to have only small deviations from the corresponding random distribution of tree locations. The deviation between observed and simulated distributions can be quantified by the absolute discrepancy algorithm AD (Gregorius, 1974; Pommerening, 1997, p. 77):

$$AD = \frac{1}{2} \cdot \sum_{i=1}^k |\hat{\theta}_i - \theta_i|; \quad AD \in [0, 1] \quad (8)$$

with $\hat{\theta}_i$ simulated relative frequency in the distribution classes i to k , and θ_i observed relative frequency in the distribution classes i to k .

Using this algorithm we find that $AD = 0.068$ for compartment Manderscheid 198, $AD = 0.106$ for compartment Manderscheid 187 and $AD = 0.067$ for compartment Ammeloe 14e. This simply means that approximately 7 per cent of some of the five classes of the observed contagion distributions in Manderscheid 198 and in Ammeloe 14e would need to be swapped over to other classes to obtain a contagion distribution under random conditions. The analysis of Manderscheid 187 shows that 10 per cent need to be swapped. Therefore the observed arrangement of tree locations in Manderscheid 187 is slightly less random than the other two compartments. The reason for this can be found in the regular arrangement of tree locations in the Douglas fir plantation. The comparison of the observed relative frequencies to the simulated frequencies is what the Clark and Evans index does internally. Comparing the observed value to the random value, when the aggregation index $R = 1$, yields similar information. Due to different algorithms (as explained in the review) the results calculated by the index of Clark and Evans and contagion are slightly different: Manderscheid 198 and Ammeloe 14e show a similar deviation from randomness in terms of contagion. Ammeloe 14e, however, seems to be slightly closer to randomness, although the index of Clark and Evans hints that Manderscheid 198 is closer to random conditions.

Figure 5 shows how the contagion distribution of the two main tree species of one forest compartment can be compared with each other. Oaks in Manderscheid 198 are more randomly distributed, while beech shows a tendency towards a clumped arrangement. This is referred to later when the species mingling of this stand is discussed.

Even more information on the spatial arrangement of tree locations is available by applying the pair correlation function $g(r)$. The pair correlation function (see Table 2) is also associated with an internal reference. A parallel to the abscissa through the value 1 defines a complete random arrangement of tree locations. Up to an inter-tree distance of 6 m, the pair correlation function in the compartment Manderscheid 198 is located below the value 1.0 which means that at these distances there are fewer trees observed than would be expected under random

Table 2: A quantitative description of the structure of the three sample stands by means of variables and correlation functions. The label of the ordinates of contagion, mingling and T1 distributions is relative frequency. The label of the ordinates of the correlation functions is correlation. In the square plots, beech trees appear white, oaks dark grey, Douglas firs light grey and Scots pine black.

compartment	Manderscheid 198	Manderscheid 187	Ammeloe 14e
square plots			
Clark & Evans	1.0073	1.3508	1.2481
contagion	0.5710	0.5646	0.5342
Shannon	0.6165	0.4249	0.0997
mingling	0.4886	0.1888	0.0307
Pielou	-0.2818	0.1141	-0.0138
T1	0.4173	0.2495	0.2145
contagion distribution			
mingling distribution			
T1 distribution			
correlation functions			

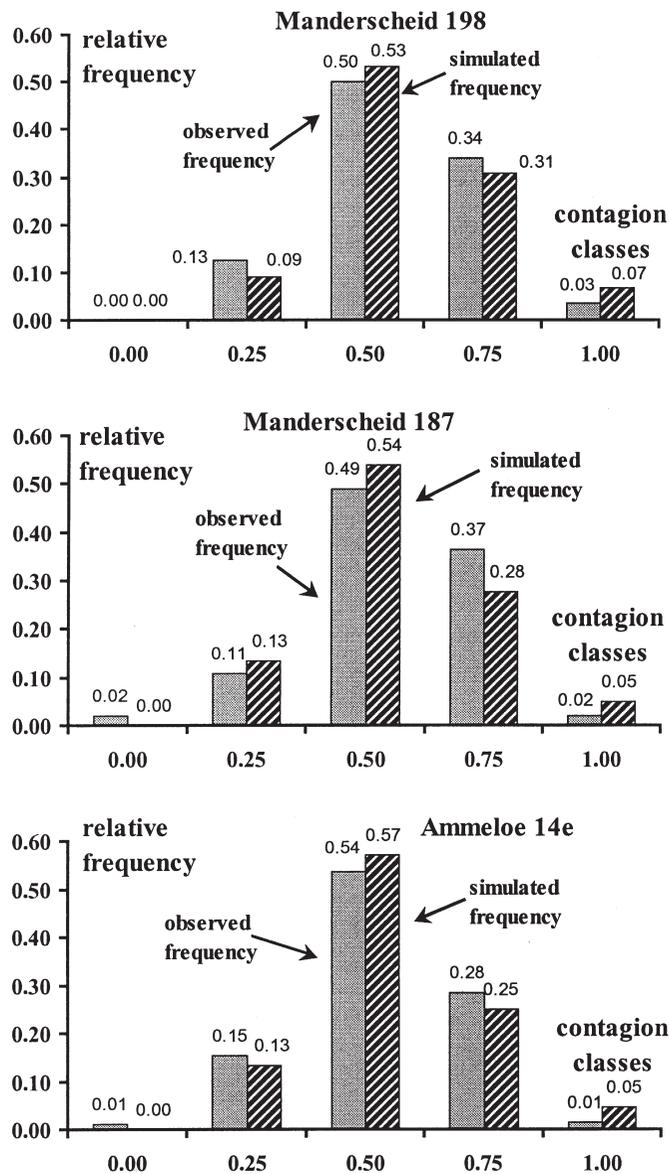


Figure 4. Observed and simulated values of the contagion distribution for the three forest compartments.

conditions. At an inter-tree distance of 6.5 m the pair correlation function has a value of 1.26, which means that there are more trees having between them a distance of about 6.5 m than would be expected. The pair correlation function behaves similarly in the compartments

Manderscheid 198 and Ammeloe 14e. Since the curve for $g(r)$ reaches 1 at $r \approx 8$ m in Manderscheid 198 (if random fluctuations around 1 are ignored) one can conclude that the inter-tree interaction does not go further than 8 m. Trees with an inter-tree distance less than 8 m seem to

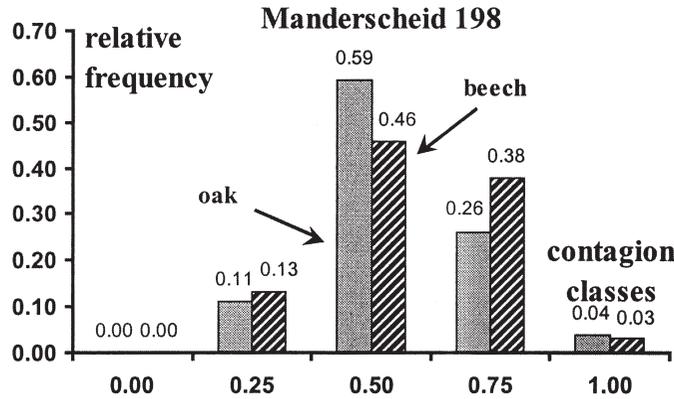


Figure 5. Differences in the contagion index distribution between the two main tree species recorded within the Manderscheid 198 compartment.

be rare, so that there must be an inhibition caused by competition and/or thinning. The corresponding critical distance in Ammeloe 14e is 5 m. These results are very plausible because both stands are older than Manderscheid 187 and their trees have greater diameters; large trees require big inter-tree distances. The pair correlation thus offers information about the interaction radius, which is the maximum radius of direct tree interaction. Penttinen *et al.* (1992) observed similar patterns in an 80-year-old Norway spruce forest in Saxony (Germany) and a 50-year-old mixed stand in Northern Finland consisting of Scots pine and silver birch. A very different picture is drawn by the pair correlation function in the compartment Manderscheid 187. The regular pattern of fluctuations very much reflects a current spacing of 3×3 m. The maxima of the function indicate that trees were preferably located at the corresponding distances, while values below 1 leading to a minimum show that trees can be found at these distances with increasing difficulty. In this case the interaction radius of 3 m can be more easily identified in the curve of the mark correlation function. Pommerening *et al.* (2000) investigated a selection forest in the Bavarian forest and, in contrast to the results of this study, found that the pair correlation function always had values above 1.0 up to a distance of 4 m. This was caused by clumps of regeneration trees which can be typically found in selection forests. The authors also derived species specific inter-tree interaction radii for that stand between 6.5 and 9 m.

Species diversity

The distance-independent Shannon index suggests that species mingling is highest in compartment Manderscheid 198, lower in Manderscheid 187 and that there is almost no species diversity in Ammeloe 14e (Table 2). The Shannon index gives a higher value the more species there are in a forest compartment and the more equally they are represented in terms of relative abundances. Shannon index values are higher in compartment Manderscheid 198, because oak and beech are quite equally represented, rather than in compartment Manderscheid 187, where there are more tree species but Douglas fir is dominant.

The distance-dependent measure of segregation *S* of Pielou (Table 2) indicates aggregation of different tree species in Manderscheid 198, species segregation in Manderscheid 187 and more or less random species distribution in Ammeloe 14e.

This picture can be completed by examining the mingling variable *M* (see Figure 6). Using equation (8) we find that $AD = 0.072$ for compartment Manderscheid 198, $AD = 0.052$ for compartment Manderscheid 187, and $AD = 0.007$ for compartment Ammeloe 14e. This means that in the two Manderscheid compartments between 5 and 7 per cent of some of the four classes of the observed species, mingling distributions need to be swapped over to other classes to obtain random conditions. In Ammeloe 14e this is only 0.7 per cent. In contrast to the

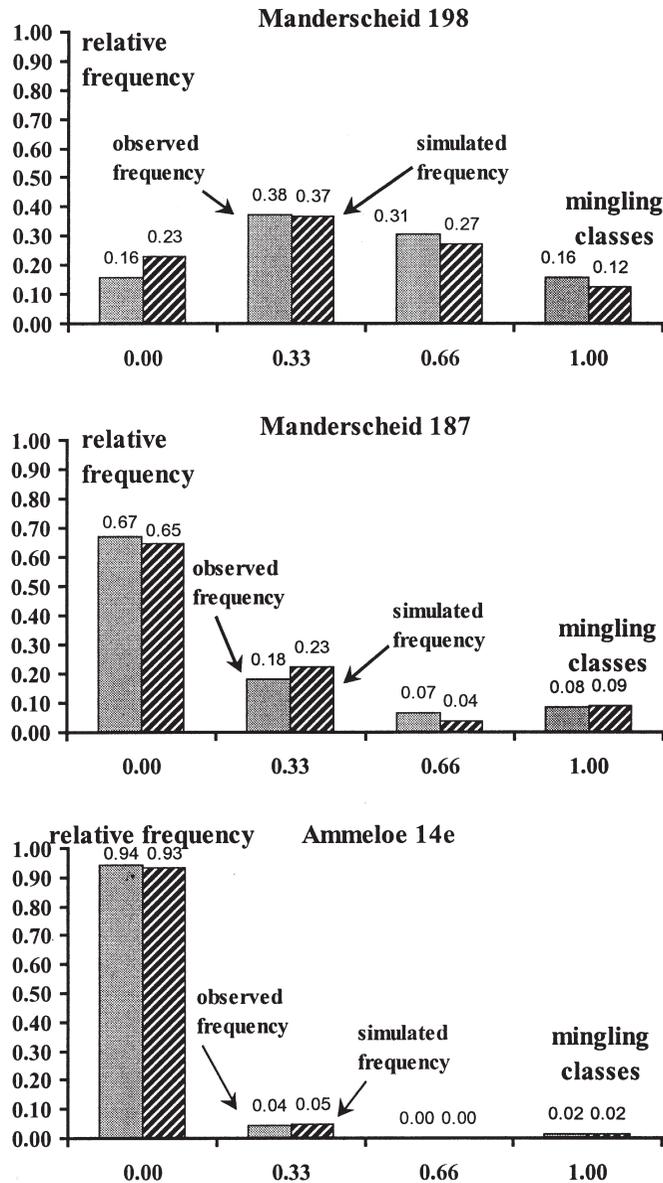


Figure 6. Observed and simulated values of the species mingling distribution for the three forest compartments.

contagion simulations, the tree positions were regarded as constant while the attribute 'tree species' was assigned at random to these positions. In the three sample forest stands we can detect only very small deviations from a random distribution.

The general tendencies of the values of the three measures of species diversity are therefore similar. Figure 7 shows how the species mingling distribution of the two main tree species of compartment Manderscheid 198 can be compared to each other without using a theoretical reference.

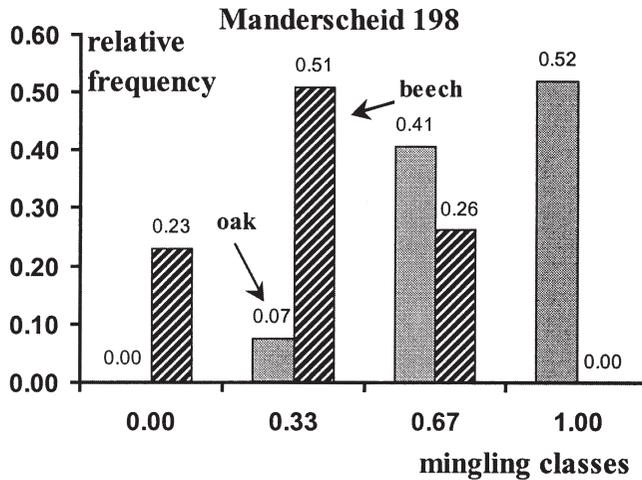


Figure 7. Differences in mingling of the two main tree species within the Manderscheid 198 compartment.

The compartment seems to have been managed in such a way that oaks are closely intermingled with beeches, while the latter are arranged in clumps. We come to this conclusion because of the fact that most of the oaks belong to the higher mingling classes, while most of the beeches are located in the smaller mingling classes. When the species-specific contagion distribution of Manderscheid 198 was discussed (see above), it was clear that oak was more randomly distributed than beech, with the latter appearing more clumped. Obviously the mingling and contagion variables are in many ways related to each other. Figure 7 underpins the visual impression gained from the schematic picture in Table 1 or from a field visit to the forest with a quantitative description. The spatial pattern of the stand is set by a special management of this woodland type which promotes oak and keeps beech as an admixture serving the oak. Fuldner (1995, p. 77) investigated mixed beech–ash stands with admixtures of sycamore and maple in the Bovenden forest district near Göttingen, and came to a very similar result with regard to the mingling of the main species beech and ash.

Variations in tree dimensions

The diameter differentiation $T1$ (Table 2) is the spatially explicit counterpart to the distance-independent diameter distribution in that it

allows the difference between immediate tree neighbours to be measured.

The mean $T1$ values indicate a quite high diameter differentiation in Manderscheid 198 but a very low one in both the other compartments. The distribution (Table 2 and Figure 8) shows that most of the trees within compartments Manderscheid 187 and Ammeloe 14e belong to the first two differentiation classes, which means that their immediate neighbours have a diameter from 50 per cent and predominantly more than 70 per cent of their own diameter. By contrast, in Manderscheid 198, the trees seem to be almost equally distributed over all the four classes. These differences are not only a function of age and stand development stage but are very much due to the special character of the management of mixed oak–beech stands, where oak is systematically promoted while beech is managed to serve the oaks and improve their timber quality. This results in bigger diameters of oak and smaller diameters of beech.

Using equation (8), we find that $AD = 0.205$ for compartment Manderscheid 198, $AD = 0.108$ for compartment Manderscheid 187 and $AD = 0.151$ for compartment Ammeloe 14e (Figure 8). These results show marked deviations from a random distribution of tree diameters. As with the mingling simulations, the tree positions were regarded as constant while the tree attribute ‘diameter’ was assigned randomly. The small

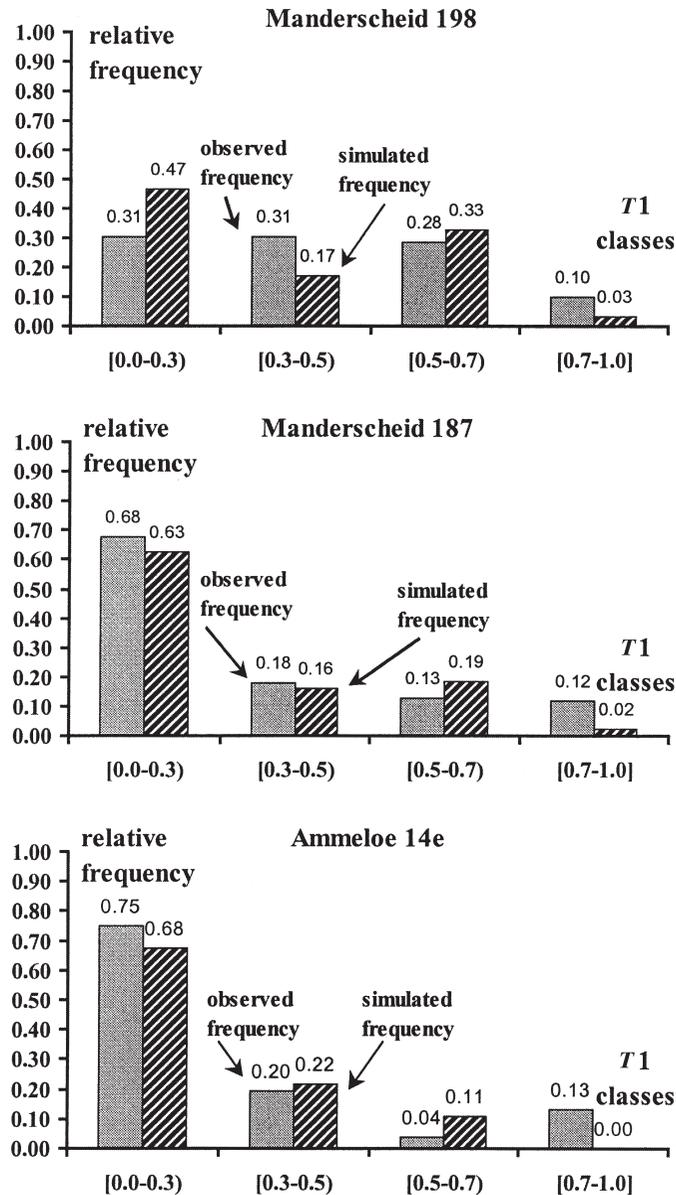


Figure 8. Observed and simulated values of the diameter differentiation T_1 distribution for the three forest compartments.

deviation in Manderscheid 187 might be due to the fact that the dimensions of young plantation trees are very similar to each other anyway so that a random assignment presents no great difference in terms of diameter differentiation. In Mander-

scheid 198 the differences are especially large in the first two classes, indicating small and average differentiation. This might indicate that special management has taken place to protect the light-demanding oaks from the climax tree species

beech, perhaps by removal of some of the latter. Although randomness as a reference is no substitute for naturalness, deviation from randomness is a suitable indicator that in a particular forest compartment something special has been detected.

Applying the mark correlation function $k(r)$ as another measure to characterize the spatial arrangement of tree dimensions, we find that there are correlations between the diameters of trees only at small distances between trees. In Manderscheid 187 the diameters of trees located more closely to each other tend to be negatively correlated, because at distances of up to 3 m between trees the values of $k(r)$ are below 1. This indicates a trend that at small inter-tree distances both trees of a pair have smaller diameters, which is the price that they have to pay for being close together. At distances greater than 3 m, there are only random fluctuations around 1, indicating that there is no longer any correlation between diameters. In Ammeloe 14e we see a similar tendency; however, the value of 1 is reached later, at an inter-tree distance of 5.5 m. The speed with which the function approaches the value 1 depends on the extent of interaction between trees based on their dimensions. Obviously the older compartment Ammeloe 14e has larger tree interaction radii than the comparatively young plantation Manderscheid 187. Similar results were found by Pommerening *et al.* (2000) in a selection stand of the Bavarian forest. The value of $k(r)$ has an interesting peak at an inter-tree distance of 1 m in compartment Manderscheid 198. Occasionally, where two or more dominant trees are located closely to each other, they still appear to be growing satisfactorily, perhaps as a result of local management and/or good site conditions. After this peak, $k(r)$ shows quite 'normal behaviour' and approaches the value of 1 again at an inter-tree distance of 6 m.

Conclusions

Forestry in Britain as well as in Europe has to demonstrate that its management is sustainable in terms of providing wildlife habitat. Landscape and forest compartment structures determine to a large extent the occurrence and population dynamics of a range of species. From given spatial

forest structures one can identify the suitability of habitats or the population development of important wildlife and plant species (McKelvey *et al.*, 1993; Pitkanen, 1997; Letcher *et al.*, 1998; Wiegand, 1998). The equations for the quantification of stand structure presented in this paper have the advantage that they are easier to survey by means of common forest inventories than more direct measures of diversity. The latter can be surveyed only selectively at certain points and after considerable effort. At least with some of the variables discussed in this paper the more direct measures of diversity seem to correlate reasonably well (Spanuth, 1998; Neumann and Starlinger, 2001), but the correlation still needs to be verified by further appropriate analysis. While there are many studies comparing structural indices which focus on methodology, only a few studies exist on the relationship between stand structure and direct measures of diversity (Neumann and Starlinger, 2001).

Apart from using these algorithms and concepts to relate forest stand structure to habitat functions, they can also be used to inform managers about the consequences of silvicultural activities. As continuous cover forestry in Britain will certainly give rise to more diverse forests, it might be sensible to define 'ecological' management objectives. The indices and functions discussed can be used to determine quantitative critical values which need to be exceeded to ensure a minimal amount of biodiversity. As these methods are relatively new, and researchers are currently only at the early stages of understanding spatial stand structure, further follow-up studies are needed in order to be able to relate quantities like the ones presented in this paper to habitat functions or to derive critical values for forest management. There are only a few studies comparing different indices over a wide range of ecological conditions (Neumann and Starlinger, 2001). As a consequence of new forest policies in Britain (e.g. Forestry Commission, 2001), increased research in irregular forest management now includes investigations on the dependence of tree growth on tree location. This will provide a number of forest stands with accurately mapped tree positions and their development over time, which can be used for studying this in greater detail.

The process of analysing and quantifying forest

structures can also be seen in reverse. Starting with a quantitative statement and quantifying suitable variables describing a desired forest structure, the spatial arrangement of trees can be reproduced on the computer to meet these objectives (Lewandowski and Gadow, 1997; Pretzsch, 1997). Using these approaches it is possible to develop a forest structure or habitat generator, which is able to simulate the habitats preferred by certain animal species (Wiegand, 1998). These computer simulations can then be translated into management guidelines or recommendations to be used by woodland managers and conservationists. The quoted papers present first steps in this direction and still need to be followed up in greater detail. However, this work undoubtedly offers great potential for conservation and ecological woodland management.

Over the last 20 years, new methods have been developed for describing complex forest structures and their possible changes resulting from growth, natural mortality and selective harvests. With these tools, scientific forest management will be in a much better position to establish, manage and maintain a great variety of complex structures without jeopardizing the traditional emphasis on sustainable harvests. One of the keys to achieving sustainable management in any type of forest is having spatial variables which can be assessed in the field at low cost and which can be used to describe, compare and evaluate forest structures and their modification by harvesting activities (Gadow and Pogoda, 2000). The sampling method 'structural group of four' (Figure 2), especially designed to assess structural information in forest stands, does not require time-consuming distance measurements and takes into account neighbourhood relationships. The Shannon index (Shannon and Weaver, 1949), the contagion index (Gadow *et al.*, 1998), the coefficient of segregation of Pielou (1977), the mingling index (Füldner, 1995) and the diameter differentiation index (Füldner, 1995) can be easily combined with the 'structural group of four' or traditional circular sample plots. When presented as a frequency distribution, the individual values of these neighbourhood-based parameters also indicate small-scale differences in the structure of forests. Algorithms such as the correlation functions and other indices, which require the surveying of coordinates, can be measured in research

plots where normally more detailed research work is carried out. However, Tomppo (1986) presented a method which allows the estimation of correlation functions from traditional circular sample plots used in forest inventories.

A disadvantage of the indices and variables is that they are based on small-scale data and thus can only give information on the variability within this range. The nearest neighbour of a reference tree, however, may be located some distance from the reference tree and thus this inter-tree distance can often encompass various ecological scales. If distances between trees are large, it is possible that there is only little or sometimes no interaction between them, while small distances between reference trees and nearest neighbours imply strong interactions. Measures based on the nearest-neighbour concept make no distinction between these two cases. They mix together the influence of ecological patterns on various scales. However, these indices are of particular value in terms of practicability when applied *in situ* in a forest, when only the nearest neighbour distances are measured or estimated and not tree locations. Usually short distances or counting in sampling units of small area are practical. If the tree locations are recorded, correlation functions, which avoid the mixing of different ecological scales, can provide more information on forest structure and tree interaction. In particular, the additional information on tree interaction radii can lead to a better understanding of competition effects in mixed stands.

Acknowledgements

This paper is dedicated to my mentor, Klaus von Gadow, Professor in Forest Management and Forest Yield Sciences at the University of Göttingen (Germany) and Head of IUFRO's Division IV, on the occasion of his 60th birthday. I would like to thank my colleagues, Roger Cooper, Douglas Godbold, Jonathan Humphrey, Tom Jenkins, Steve Murphy, Owen Davies and an anonymous referee for helpful comments on earlier drafts of the text. The Institute of Forest Management and Forest Yield Sciences (University of Göttingen) helped me out with the spatial tree data which were used in this study, for which I am very grateful.

References

Albert, M. 1999 *Analyse der eingriffsbedingten Strukturveränderung und Durchforstungsmodellierung in*

- Mischbeständen*. (Analysis of thinning-induced changes in stand structure and modelling of thinnings in mixed-species stands.) Ph.D. dissertation, Faculty of Forestry and Forest Ecology, University of Göttingen, Hainholz Verlag Göttingen, 195 pp.
- Albert, M. and Gadow, K. v. 1998 Assessing biodiversity with new neighbourhood-based parameters. In *Data Management and Modelling Using Remote Sensing and GIS for Tropical Forest Land Inventory*. Y. Jaumonier, B. King, C. Legg and K. Rennolls (eds). Proceedings of the FIMP-INTAG International Conference, October 26–29, 1998, Jakarta, Indonesia, pp. 433–445.
- Biging, G.S. and Dobbertin, M. 1992 A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. *For. Sci.* **38**, 695–720.
- Clark, P.J. and Evans, F.C. 1954 Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology* **35**, 445–453.
- Ferris, R. and Humphrey, J. W. 1999 A review of potential biodiversity indicators for application in British forests. *Forestry* **72**, 313–328.
- Forestry Commission 1998 *The UK Forestry Standard*. Forestry Commission, Edinburgh, 74 pp.
- Forestry Commission 2000 *Forests for Scotland: the Scottish Forestry Strategy*. Edinburgh, 92 pp.
- Forestry Commission 2001 *Coetiroedd i Gymru. Y Cynulliad Cenedlaethol i Gymru Strategaeth am Coed a Choetir*. Woodlands for Wales. The National Assembly for Wales Strategy for Trees and Woodlands. Aberystwyth, 49 pp.
- Füldner, K. 1995 *Strukturbeschreibung von Buchen-Edellaubholz-Mischwäldern*. (Describing forest structures in mixed beech–ash–maple–sycamore stands.) Ph.D. dissertation, Faculty of Forestry, University of Göttingen, Cuvillier Verlag Göttingen, 163 pp.
- Gadow, K. v. and Hui, G. 1999 *Modelling Forest Development*. Kluwer Academic, Dordrecht, The Netherlands, 213 pp.
- Gadow, K. v. and Pogoda, P. 2000 Assessing forest structure and diversity. *Man. For.* **1**, 1–8.
- Gadow, K. v., Hui, G.Y. and Albert, M. 1998 Das Winkelmaß – ein Strukturparameter zur Beschreibung der Individualverteilung in Waldbeständen. (The neighbourhood pattern – a new parameter for describing forest structures.) *Centralbl. Gesamte Forstwes.* **115**, 1–10.
- Gavrikov, V. and Stoyan, D. 1995 The use of marked point processes in ecological and environmental forest studies. *Environ. Ecol. Stat.* **2**, 331–344.
- Gleichmar, W. and Gerold, D. 1998 Indizes zur Charakterisierung der horizontalen Baumverteilung. (Indices for the description of horizontal tree distribution.) *Ger. J. For. Sci.* **117**, 69–80.
- Gregorius, H.-R. 1974 Genetischer Abstand zwischen Populationen. I. Zur Konzeption der genetischen Abstandsmessung. (Genetic distance among populations.) *Silvae Genet.* **23**, 22–27.
- Helliwell, D.R. 1997 Dauerwald. *Forestry* **70**, 375–380.
- Humphrey, J.W., Newton, A.C., Peace, A.J. and Holden, E. 2000 The importance of conifer plantations in northern Britain as a habitat for native fungi. *Biol. Conserv.* **96**, 241–252.
- Kerr, G. 1999 The use of silvicultural systems to enhance the biological diversity of plantation forests in Britain. *Forestry* **72**, 191–205.
- Kimmins, J.P. 1997 *Forest Ecology: A Foundation for Sustainable Management*. Macmillan, New Jersey, 596 pp.
- Lähde, E., Laiho, O., Norokorpi, Y. and Saksa, T. 1999 Stand structure as the basis of diversity index. *For. Ecol. Manage.* **115**, 213–220.
- Latham, P.A., Zuuring, H.R. and Coble, D.W. 1998 A method for quantifying vertical forest structure. *For. Ecol. Manage.* **104**, 157–170.
- Letcher, B.H., Priddy, J.A., Walters, J.R. and Crowder, L.B. 1998 An individual-based, spatially-explicit simulation model of the population dynamics of the endangered red-cockaded woodpecker, *Picoides borealis*. *Biol. Conserv.* **86**, 1–14.
- Lewandowski, A. and Gadow, K. v. 1997 Ein heuristischer Ansatz zur Reproduktion von Waldbeständen. (A method for reproducing uneven-aged forest stands.) *Allg. Forst- Jagdztg.* **168**(9), 170–174.
- MacArthur, R.H., 1965 Pattern in species diversity. *Biol. Rev.* **40**, 510–533.
- Martin, G.L., Ek, A.R. and Monserud, R.A. 1976 Control of plot edge bias in forest stand growth models. *Can. J. For. Res.* **7**, 100–105.
- Mason, W.L. and Quine, C.P. 1995 Silvicultural possibilities for increasing structural diversity in British spruce forests: the case of Kielder Forest. *For. Ecol. Manage.* **79**, 13–28.
- McKelvey, K., Noon, B.R. and Lamberson, R.H. 1993 Conservation planning for species occupying fragmented landscapes: the case of the northern spotted owl. In *Biotic Interactions and Global Change*. P.M. Kareiva, J.G. Kingsolver and R.B. Huey (eds). Sinauer Associates, Sunderland, MA, USA, pp. 424–450.
- Monserud, R.A. and Ek, A.R. 1974 Plot edge bias in forest stand growth simulation models. *Can. J. For. Res.* **4**, 419–423.
- Neumann, M. and Starlinger, F. 2001 The significance of different indices for stand structure and diversity in forests. *For. Ecol. Manage.* **145**, 91–106.
- O'Hara, K.L., Latham, P.A., Hessburg, P. and Smith, B.G. 1996 A structural classification for inland northwest forest vegetation. *West. J. Appl. For.* **11**, 97–102.

- Penttinen, A., Stoyan, D. and Henttonen, H.M. 1992 Marked point process in forest statistics. *For. Sci.* **38**, 806–824.
- Pielou, E.C. 1977 *Mathematical Ecology*. Wiley, New York, 385 pp.
- Pitkanen, S. 1997 Correlation between stand structure and ground vegetation: an analytical approach. *Plant Ecol.* **131**, 109–126.
- Pommerening, A. 1997 *Eine Analyse neuer Ansätze zur Bestandesinventur in strukturreichen Wäldern*. (An analysis of new approaches towards stand inventory in structure-rich forests.) Ph.D. dissertation, Faculty of Forestry and Forest Ecology, University of Göttingen, Cuvillier Verlag Göttingen, 187 pp.
- Pommerening, A. and Gadow, K. v. 2000 Zu den Möglichkeiten und Grenzen der Strukturerfassung mit Waldinventuren. (On the possibilities and limitations of quantifying forest structures by forest inventories.) *Forst Holz* **55**, 622–631.
- Pommerening, A. and Schmidt, M. 1998 Modifizierung des Stammabstandsverfahrens zur Verbesserung der Stammzahl- und Grundflächenschätzung. (Modifications of the distance method for improved estimates of number of stem and basal area.) *Forstarchiv* **69**, 47–53.
- Pommerening, A., Biber, P., Stoyan, D. and Pretzsch, H. 2000 Neue Methoden zur Analyse und Charakterisierung von Bestandesstrukturen. (New methods for the analysis and characterization of forest stand structures.) *Ger. J. For. Sci.* **119**, 62–78.
- Pretzsch, H. 1997 Analysis and modeling of spatial stand structures: methodological considerations based on mixed beech-larch stands in Lower Saxony. *For. Ecol. Manage.* **97**, 237–253.
- Pretzsch, H. 1998 Structural diversity as a result of silvicultural operations. *Lesnictví-Forestry* **44**, 429–439.
- Radtke, P.J. and Burkhart, H.E. 1998 A comparison of methods for edge bias compensation. *Can. J. For. Res.* **28**, 942–945.
- Ripley, B.D. 1977 Modelling spatial patterns. *J. R. Stat. Soc. Ser. B* **39**, 172–192 and discussion, 192–212.
- Shannon, C.E. and Weaver, W. 1949 *The Mathematical Theory of Communication*. University of Illinois Press, Urbana.
- Shimatani, K. 2001 Multivariate point processes and spatial variation of species diversity. *For. Ecol. Manage.* **142**, 215–229.
- Simpson, E.H. 1949 Measurement of diversity. *Nature* **688**, 163.
- Smaltschinski, T. 1998 Charakterisierung von Baumverteilungen. (Characteristics of spatial stem distributions.) *Ger. J. For. Sci.* **117**, 355–361.
- Spanuth, M. 1998 *Untersuchungen zu den Hauptschlafbaumarten Eiche, Fichte und Buche des Waschbären (Procyon lotor) im südlichen Solling*. (Investigation of the main tree species oak, spruce and beech preferred by racoons (*Procyon lotor*) as resting places in the southern Solling.) Diploma thesis, Faculty of Forestry and Forest Ecology, University of Göttingen, 64 pp.
- Spies, T.A. 1998 Forest structure: a key to the ecosystem. *Northwest Sci.* **72**, 34–39.
- Sprugel, D.G. 1991 Disturbance, equilibrium and environmental variability: what is natural vegetation in a changing environment? *Biol. Conserv.* **58**, 1–18.
- Stoyan, D. and Penttinen, A. 1998 *Spatial Point Process Methods in Forestry Statistics*. Technical University Freiberg, Faculty of Mathematics and Informatics, Preprint 98-7, 66 pp.
- Tomppo, E. 1986 *Models and Methods for Analysing Spatial Patterns of Trees*. Communicationes Instituti Forestalis Fennica 138, Helsinki, 65 pp.
- Upton, G. and Fingleton, B. 1985 *Spatial Data Analysis by Example: Categorical and Directional Data*. Wiley, Chichester, 416 pp.
- Upton, G. and Fingleton, B. 1989 *Spatial Data Analysis by Example: Point Pattern and Quantitative Data*. Wiley, Chichester, 410 pp.
- Whittaker, R.H. 1972 Evolution and measurement of species diversity. *Taxon* **21**, 213–251.
- Wiegand, T. 1998 *Die zeitlich-räumliche Populationsdynamik von Braunbären*. (The temporal and spatial population dynamics of brown bears.) Forstwissenschaftliche Fakultät der Ludwig-Maximilians-Universität München, 202 pp.
- Zenner, E.K. and Hibbs, D.E. 2000 A new method for modelling the heterogeneity of forest structure. *For. Ecol. Manage.* **129**, 75–87.

Received 14 February 2001