# Preface

*“Two roads diverged in a wood,*
*and I – I  took the one less travelled by,*
*and that has made all the difference”*

With his poem *The road not taken*, from which these are the final lines, Robert Frost certainly did not intend to write about pathways of forest structural development. Neither was he expressing his concerns about multiple forest functions or sustainable forest management. Nevertheless, these modest lines of poetry in some way are a summary of my view on forestry – and maybe also of life. Aren’t we confronted with a variety of possible ‘roads’, many of which remain to be discovered? Isn’t it difficult to choose between them, especially when we cannot rely on existing ‘travelling experience’? Don’t we agree that some past choices no longer fulfil today’s needs? Shouldn’t we at least try to make a difference?

As this is not meant to be a philosophical treaty – a Ph.D. is no longer what it originally was – I will leave the answering these questions to everyone’s own discretion. Nevertheless, I hope that the scientific issues presented in this work can help in doing so, at least where it concerns forestry.

I owe much gratitude to many colleagues and friends, for helping and supporting me in my work. First of all I thank my promoters Prof. Noël Lust and Prof. Robert De Wulf from Ghent University, and (all good things go by threes) Prof. Frits Mohren from Wageningen University. Many times their expertise helped me in elaborating new ideas, formulating results and in finalising reasoning. Working with three promoters is not the easiest thing to do, but it certainly increases the consciousness that all opinions, including my own, are relative. Further thanks go to the other members of the jury: Prof. Jaques Viane (the chairman), Prof. Eckhart Kuijken, Prof. Raoul Lemeur, Prof. Bart Muys, Olivier Thas and Martine Waterinckx. I experienced their constructive criticism as an appreciation of my work and as a personal encouragement.

Without the concrete help of Irma Jorritsma (for the process-based gap model FORGRA), as well as Ad Van Hees and Sandra Clerkx (for the Dutch forest reserves data) from Alterra (Wageningen, The Netherlands), my research would have been impossible. I very much appreciated their willingness to cooperate and their continuous support. Furthermore, I am very grateful to all those that, in some way or another, acted as a sounding board for my confused thoughts or provided me with concrete help: Etienne De Bruycker, Bert Dejaegher, Inge De Jongh, Andy Delcloo, Elze De Ruiter-Dijkman, Ellen Deschepper, Prof. Josef Fanta, Rudi Hoeben, Patrick Huvenne, Sebastiaan Luyssaert, Ad Olsthoorn, Christel Sabbe, Mart-Jan Schelhaas, Erik Van Boghout, Bert Van Der Werf, Prof. Marc Van Meirvenne, Johan Van Noten, Christophe Verbeke, Pieter Vercammen, Frederik Verdonck, and many others whose name I may have forgotten, but whose help was certainly not less appreciated.

And last but not least, I thank all past and present colleagues at the Laboratory of Forestry and the Laboratory of Forest Management and Spatial Information Techniques, with whom the working together has always been great pleasure. Special thanks go to Guy Geudens, Lieven Nachtergale, An De Schrijver and Robbie Goris, whose expertise and enthusiasm about forest dynamics have stimulated me in starting, elaborating and persisting in this work.

I dedicate this work to all those who supported me without understanding much about what I exactly did: my parents, family and many, many friends.
Thanks to all.

Vincent Kint
Ghent, June 2003

# Table of contents

# Introduction

With an estimated area of three-and-a-half million hectares, homogeneous even-aged Scots pine (*Pinus sylvestris* L.) plantations on acidic and oligotrophic sandy soils constitute one of Western Europe's most important forest types. Until recently, short-rotation silviculture (40-50 years) in these plantations was focused at maximising the production of low diameter pinewood, for use as mine props and construction timber. Today, most Scots pine forests are managed for multiple purposes, and short rotations have been abandoned. Since natural regeneration of broadleaved species establishes easily in many ageing Scots pine stands (50 years and over) there is a growing interest in forest management that makes use of natural vegetation dynamics.

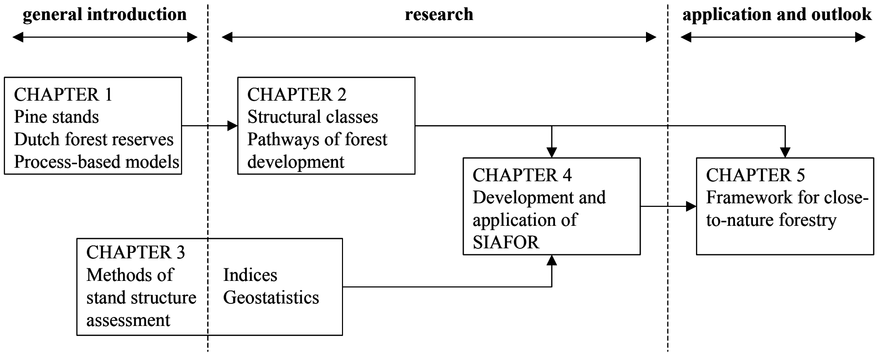
This idea relates to the concept of close-to-nature forestry. Instead of assuming that a forest can be completely controlled, close-to-nature forestry adopts the principle that management should be guided by natural vegetation dynamics to achieve its goals. This approach has undeniable ecological and economic advantages. However, a framework for its implementation in ageing Scots pine forests, based on knowledge on natural vegetation dynamics, has yet to be provided. As a result, most attempts of close-to-nature forest management in these forests are based on limited experience, or lack coherence.

Natural vegetation dynamics and forest management both affect stand structure and structural development. They influence each other through their direct impact on stand structure. Hence, the description of stand structure and structural development within forest ecosystems in relation to biotic factors, disturbances and/or environmental conditions, can help to anticipate natural vegetation dynamics and to incorporate them into management.

The main purpose of this study is to investigate the stand structure and structural development in ageing Scots pine stands resulting from natural vegetation dynamics, as a means to guide close-to-nature forest management in these stands. This is achieved in four steps:

1. the construction of a conceptual model of natural vegetation dynamics in ageing Scots pine forests, describing stand structures and stand structural development (chapter 2);
2. the development of a methodology to quantify spatial characteristics of forest stand structure (chapter 3), and its implementation in a computer programme (chapter 4);
3. the quantification and interpretation of spatial characteristics of stand structure and structural development in ageing Scots pine forests (chapter 4);
4. the providing of a framework for the implementation of close-to-nature forestry in ageing Scots pine forests (chapter 5).

The work is subdivided in five chapters. Each of them addresses a particular aspect of the research, as illustrated in the figure below. The first chapter as well as part of the third chapter introduce the reader to the major topics of interest. The second, third and fourth chapters cover the actual research, and their nature is essentially quantitative. The final chapter instigates possible applications of the results in forestry, and provides an outlook on further research.



The first chapter is a general introduction to forest dynamics research on poor sandy soils. We start with a presentation of forest ecosystems on these sites, considering species composition and natural plant associations, as well as history and management of Scots pine forests on these sites. Subsequently, we review the characteristics of two important forest dynamics research tools (i.e. forest reserves programmes and models of forest development), with special attention to their availability in the Netherlands and Flanders (Northern Belgium). We conclude this chapter with a discussion about the limits and advantages of both tools, and the possibilities for combined approaches.

In the second chapter, we develop a conceptual model of natural vegetation dynamics in ageing Scots pine forests. As stand development is not necessarily directional, but rather multiple development pathways may exist for a single site type, we adopt a pathway approach. Our methodology to describe different pathways consists out of three steps. First, we use agglomerative cluster analysis with data from Dutch forest reserves to define different structural classes, which represent different stand structures in ageing Scots pine forests. Then we predict long-term stand development with the process-based gap model FORGRA. Finally we combine structural classes and model predictions to describe different pathways of stand development. The different pathways are summarised in four main pathway patterns that are interpreted in detail. For each of these, trends of basal area and mean diameter are visualised. In conclusion, we provide an outlook towards limits and possible applications of the pathway model.

In chapter three we present different methods for quantifying spatial characteristics of forest stand structure. These characteristics are tree positioning, distribution patterns of species and size differentiation between trees. We consider two methods in detail. The first calculates a set of four nearest-neighbour indices. The second calculates mark variograms of tree variables. Both methods are applied in a case study of two mixed Scots pine stands with different management history. We compare their ability to accurately quantify stand structure and short-time structural development, and their data requirements. Finally, we formulate recommendations for their use in monitoring programmes of forest stand structure.

The computer programme SIAFOR, designed to calculate the aforementioned set of four nearest-neighbour indices in monitoring plots with stem-mapped data, is presented in chapter four. The programme eliminates edge effects and offers the possibility of virtual sampling. We use SIAFOR for two purposes. The first is to quantify and interpret the stand structure and structural development in ageing Scots pine forests. We use data from Dutch forest reserves at three previously defined information levels: (i) individual monitoring plots, (ii) structural classes and (iii) pathways of stand development. Our second purpose with SIAFOR is to study the minimum sample size and the optimal sample type for the estimation of stand structure with sampling techniques. We simulate two sample types, neighbour sampling and plot sampling, in monitoring plots of varying structural complexity, and determine the minimum sample sizes needed to reach different accuracy levels.

Finally, in chapter five we discuss the implications of our results for close-to-nature forestry in ageing Scots pine forests. We compare our pathway model of natural vegetation dynamics in ageing Scots pine forests with other conceptual models that use a climax approach, and discuss their suitability for guiding close-to-nature forest management. Based on the pathway model we provide a framework for the implementation of close-to-nature forestry in ageing Scots pine stands. In conclusion, we discuss the relationship between our framework and the German concept of forest development types.

The five chapters, although logically connected with each other, are conceived as separate entities and hence can be read independently from each other. To increase the readability of the text as a whole, we tried to avoid repeating parts where possible. Unavoidably, however, some repetitions will still be noticeable to those reading all chapters, especially in the introducing parts.

## Chapter one

# 1 Forest dynamics research in forest ecosystems on poor sandy soils

**Abstract**

Knowledge about forest dynamics has always been recognised as a key aspect of both theoretical and applied forest science. Historically, this knowledge has been based on case studies and field experience. Today, research in this field can benefit from two relatively new research tools: (i) forest reserves programmes, and (ii) process-based models of forest development. We review the characteristics and availability of these two research tools for forest dynamics research in forest ecosystems on poor sandy soils, with special attention to the situation in the Netherlands and Flanders (Northern Belgium). The advantages and limitations of both tools, as well as the possibilities for combined approaches are discussed.

## 1.1 Introduction

Forest dynamics encompass all spontaneous processes of change, occurring without direct anthropogenic influence in forest vegetation, soil or other ecosystem components. Forest dynamics research is of fundamental importance for the management of forest ecosystems where multifunctionality and/or biodiversity are key issues. Insight into structural development within forest ecosystems in relation to forest dynamics, is a precondition for the successful development of new management strategies aimed at maximising functionality with respect to society's needs, while minimising costs (Andersson *et al.* 2000). Forest dynamics is a long-term issue. Research on this has been a relatively recent development in relation to average forest development times. The lack of forests without direct anthropogenic influence, combined with the high quantity of interacting factors makes the study of forest dynamics very complex.

A representative example of this problem can be observed in forest ecosystems located on poor sandy soils. Here we focus on the situation in the Netherlands and Flanders (Northern Belgium), which are geographic neighbours and share the same mesothermal, humid, maritime climate (mean annual temperature of 9.8 °C and mean annual precipitation of 780mm). Furthermore, site types, history and past management in forests on poor sandy soils are similar for both regions, which makes it possible to discuss them together. Many aspects of our discussion are also representative for other temperate regions throughout Western Europe with similar environmental conditions (e.g. Griese 1994, Leuschner 1994, Seidling & Von Lührte 1996, Kenk & Guehne 2001), although local differences will need to be taken into consideration.

Forest dynamics in forest ecosystems on poor sandy soils depend on biotic factors (e.g. Clerkx & Van Hees 1999, Den Ouden 2000, Smit 2002), disturbances (e.g. Goris 2002) and environmental conditions (e.g. Leuschner 1993, Emmer 1995a, Rode 1999a, 1999b). Many of these factors and their interactions are still poorly documented and much of our current understanding about forest dynamics on poor sandy soils is fragmentary. Moreover, it is only partially based on field evidence supplemented with what is felt to be the most logical solution for each problem at hand (Koop 1989). This emphasises the need for long-term empirical data and for synthesis, and has resulted in an increased interest in two major forest dynamics research tools: (i) forest reserves programmes and (ii) models of forest development.

After a brief presentation of forest ecosystems on poor sandy soils, the purpose of this chapter is to review the characteristics and availability of the two aforementioned research tools for forest dynamics research in such forests.

## 1.2 Forest ecosystems on poor sandy soils in the Netherlands and Flanders

### 1.2.1 Species and natural plant associations

The main natural tree and shrub species occurring on poor sandy soils in the Netherlands and Flanders are pedunculate oak (*Quercus robur* L.), sessile oak (*Quercus petraea* (Mattuschka) Lieblein), silver birch (*Betula pendula* Roth), downy birch (*Betula pubescens* Ehrh.), common beech (*Fagus sylvatica* L.), Scots pine (*Pinus sylvestris* L.), rowan (*Sorbus aucuparia* L.) and alder buckthorn (*Frangula alnus* Mill.). The main characteristics of these species, together with their regeneration strategies and growth potentials are discussed, for example, by Kauppi & Kiviniitty (1988), Perala & Alm (1990), Atkinson (1992), Eisenhauer (1994), Leuschner (1994), Van Hees (1997), Larsen & Johnson (1998), Mosandl & Kleinert (1998), De Waal & Winteraeken (1999), Frost & Rydin (2000), Wijdeven *et al.* (2000), Van Hees & Clerkx (2003).

In addition to the aforementioned species, some exotic tree and shrub species have also been introduced on these sites. The most important of these are American red oak (*Quercus rubra* L.), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), Japanese larch (*Larix leptolepis* (Sieb. et Zucc.) Endl.), Corsican pine (*Pinus nigra* Arnold *ssp. laricio* Maire) and black cherry (*Prunus serotina* Ehrh.). Some of these species may have an important influence on forest dynamics, and hence on forest management, as documented, for example, by Maddelein *et al.* (1990, 1991), Muys *et al.* (1992), Lust *et al.* (2000) and Afdeling Bos en Groen (2001). In this study, however, we only consider natural forest dynamics which involve species native to the site.

Natural plant associations on these sites have been described, for example, by Sougnez (1974), Rogister (1978), Van Der Werf (1991), Vandekerkhove (1998) and most recently by Stortelder *et al.* (1999). We adopted the classification and terminology of Stortelder *et al.* The *Quercetea robori-petraeae* class is composed of mixed broadleaved forests with mainly silver birch, pedunculate oak and common beech. These are found on oligotrophic acidic sandy soils of aeolian or glacial origin, many of which are podzolised. Four associations can be distinguished within the *Quercetea robori-petraeae* class:

(i) *Betulo-Quercetum roboris* on the most acidic and nutrient-poor soils;
(ii) *Fago-Quercetum* on loamy sandy soils;
(iii) *Deschampsio-Fagetum* on sandy soils with a somewhat higher loam content;
(iv) *Luzulo luzuloidis-Fagetum* which is very rare and occurs only in montane and submontane regions on extremely acidic sandy soils.

Stortelder *et al.* (1999) consider the planted Scots pine forests on poor sandy soils to be part of the *Vaccinio-Piceetea* class. In the absence of further anthropogenic influences, however, these forests gradually develop towards forests of the *Quercetea robori-petraeae* class.

Many authors argue that the ecological amplitude of beech is higher than previously thought, and that it can be a dominating species in the terminal stages of undisturbed forest succession on most of the nutrient poor sandy soils of North-Western Europe (Griese 1994, Leuschner 1997, Rode 1999a, Meyer *et al.* 2000). This is due to the increasing water and nutrient supply of the organic layer during succession, which alters the competitive relationships between participating species in favour of oak and beech in particular. For this reason, the *Betulo-Quercetum roboris* plant association is increasingly interpreted as a pioneer stage of beech-dominated plant associations, except for sites where extreme environmental conditions (e.g. pollution, regular high-intensity disturbances) exclude the occurrence of beech.

### 1.2.2 Scots pine forest ecosystems and management

With an estimated area of three-and-a-half-million hectares, homogeneous even-aged Scots pine (*Pinus sylvestris* L.) plantations constitute one of Western Europe's most important forest types (Mason & Alía 2000). From the end of the 18th century until far into the 20th century, Scots pine was systematically planted on poor sandy soils throughout the Netherlands and Flanders. This was originally done to convert drift sands or heathland into production forests, and later to replant forests following clearcutting. Forestry practice in these plantations focused on maximising the production of low diameter pinewood for use in the coalmining industry. This resulted in regular thinnings from below, as well as rotations of 40-50 years (Lust *et al.* 2000).

As a result of the diminishing economic return (partly induced by the closing of the coal mines) and an increased social demand for more nature values and biodiversity in recent decades, the management of these forests has gradually become focused on multifunctionality (Mason & Alía 2000, Ministerie LNV 2000, Afdeling Bos en Groen 2001) and short rotations have been abandoned. Due to former forestry practices, which paid no attention to crown form and branchiness, the production of quality timber is not a feasible option in the majority of cases. Therefore, many Scots pine stands, especially those of private forest owners, are conserved without any human intervention. Since natural regenerating of broadleaved species establishes easily in these ageing Scots pine forests (50 years and over), there is a growing interest in forest management that makes use of natural processes (Kuper 1994, Zerbe 2002). Nowadays, a common management goal of such close-to-nature forestry is the conversion of these ageing Scots pine stands into mixed broadleaved stands, for ecological, economic and social reasons (Maddelein & Neirynck 1995, Mosandl & Küssner 1999, De Schrijver *et al.* 2000, 2002, Kenk & Guehne 2001).

## 1.3 Forest reserves programmes

Forest reserves and other protected forest areas have been established worldwide to investigate forest dynamics in different forest types, with a focus on silvicultural and nature conservation purposes (Norton 1999, Good 2001, www.lternet.edu). The idea of long-term monitoring in natural forests in Europe was initially inspired by silvicultural needs (Leibundgut 1959, 1966, 1990). In this context, Lust (1982), Koop (1989), Zukrigl (1990), Mlinšek (1993) and many others have stressed the necessity of scientific research in forest reserves so that expertise on how to incorporate natural processes in forest management systems can be developed. However, nature conservation purposes have also become increasingly important in justifying and establishing forest reserves (Vandekerkhove 1998, 2001, Parviainen *et al.* 2000, Bücking 1997, 2003). Therefore a distinction can be drawn between 'strict forest reserves', where no silvicultural operations or any other human interventions are allowed, and 'directed forest reserves', where specific interventions are planned to increase specific nature values. Although all reserves serve both purposes to a certain extent, our focus will be on strict forest reserves, since these have been specifically designed as forest dynamics research tools.

### 1.3.1 Strict forest reserves in a European context

Most European countries have established their own forest reserves programmes. An early attempt to exchange experiences at a European level was a workshop on European forest reserves in 1992 (Broekmeyer *et al.* 1993). Since then the COST-action E4 (i.e. a coordinated network of national research projects funded by the EU) has inventoried existing forest reserves programmes in 27 European countries, with the aim of bringing national forest reserves programmes together in a European framework. From this COST-action, it appeared that the interpretation of the term ‘strict reserve’ varied considerably according to regional and local traditions or reserve size limitations: in many cases game and fire control, the removal of invading exotic species, eco-tourism and/or other forms of human impacts are allowed. It is concluded that the concept of complete non-intervention is unrealistic in Europe; human impact and fragmentation result in some degree of intervention in most cases (Parviainen *et al.* 2000).

The COST-action E4 also tried to harmonise the respective monitoring designs and methodologies (Hochbichler *et al.* 2000). The monitoring programme in most European forest reserves consists of two levels of inventory: core areas and a series of permanent sample plots on a systematic grid network. The systematic grid networks provide insights into structures and processes over the whole reserve area, whereas more detailed information on specific topics is retrieved from the core areas. The parameters measured and the monitoring frequency may vary from case to case, but as a result of the aforementioned COST-action some minimum requirements have been proposed. Hence, standardised detailed data sets of long-term stand development under a minimum intervention scenario are being constructed in many different forest types and countries.

Due to their well-considered infrastructure of permanent sample plots and their representativeness for all forest types, the national and European forest reserves networks offer a unique framework for long-term research on all aspects of forest dynamics: regeneration, competition, mortality, vegetation and soil development, disturbance dynamics, impact of diseases and pests, climate change, etc.

### 1.3.2 Forest reserves on poor sandy soils in the Netherlands and Flanders

Forest reserves programmes in the Netherlands and Flanders have been gradually developed since the early 1980s (Broekmeyer & Szabo 1993, Broekmeyer 1995, Vandekerkhove 1998, Vandekerkhove & Van Den Meersschaut 1999). In the Netherlands a network of strict forest reserves is available which comprises some 3000 ha, with a mean area of 35-40 ha per forest reserve. No further management interventions are allowed in any of the reserves. In Flanders the aim is to realise 3000

Table 1.1 Strict forest reserves on poor sandy soils in the Netherlands.

| reserve name | area (ha) | natural plant assoc.[(a)] | reserve since | forest origin and management stop[(b)] | references |
|---|---|---|---|---|---|
| De Heul | 55 | BQm | 1998 | 19-20th century plantations of mainly Pi, La and Pm | Mekkink 2000, Clerkx 2001 |
| Galgenberg | 42 | FQ (*) | 1983 | 19-20th century plantations of Pi, La and Pc; remnants of old Qu forest; unmanaged 1972 storm area | Koop & Boddez 1991a, Knoppersen 1995, Koop & Clerkx 1995a, Mekkink 1995, Clerkx *et al.* 1996 |
| Lheebroeker Zand | 39 | BQ-BQm | 1983 | 19-20th century plantations of Pi and some Pc and Qu | Maas & Van Der Werff 1990, Koop & Boddez 1991b, Koop & Clerkx 1995b, Arntzen 1997, Kemmers & Mekkink 1999, Clerkx *et al.* 2002 |
| Mattemburgh | 106 | FQ (*) | 1997 | 19th century Pi plantations; never managed | Van Ham 1985, Mekkink 1998, Kemmers & Mekkink 1999, Clerkx *et al.* 2001, Goris 2002 |
| Molenven | 42 | BQm (*) | 1995 | 19th century Pi plantations; no management since 1923 | Brock *et al.* 1989, Mekkink 1996a, Bartelds 1997a |
| Noordhout | 38 | FQ | 1980 | 20th century plantation of Pi, Qu and Fa | Brocke & Zonderwijk 1982, Clerkx & Broekmeyer 1997 |
| Stille Eenzaamheid | 85 | BQ | 1997 | 19th century spontaneous Pi forest; 19th century Pi plantations; no management since 1973 | Prach 1989, Kwakkel 2001, Schelhaas & Van Dort 2003 |
| Tongerense Hei | 40 | BQ | 1995 | 19-20th century spontaneous pine forest; never managed | Mekkink 1996b, Rots 1997 |
| Zwarte Bulten | 46 | FQ-(BQ) | 1989 | 19-20th century plantations of Pi, Pm and Fa | Mekkink 1993, Bartelds 1997b, Broekmeyer & Clerkx 1997 |

(a) BQ *Betulo-Quercetum roboris*, FQ *Fago-Quercetum*, m subassociation *molinietosum* (according to Stortelder *et al.* 1999). (*) The actual vegetation in parts of the reserve is considered to be a good approximation of the natural plant association.

(b) Pi *Pinus sylvestris*, Be *Betula spp.*, Qu native *Quercus spp.*, Fa *Fagus sylvatica*, La *Larix spp.*, Pm *Pseudotsuga menziesii*, Pc *Picea spp*. The year of management stop is only mentioned when it differs from that of the reserve establishment.

ha of both strict and directed forest reserves. To date about 1780 ha have been assigned (Vandekerkhove 2003).

Koop (1987, 1989) developed a detailed core-area monitoring system, including a computer package for the analysis of long-term observations of forest dynamics, SILVI-STAR. His work inspired forest reserves monitoring in the Netherlands and Flanders. In each reserve a core area (140m x 70m) and a series of circle plots (each 500m²) on a regular grid network are permanently marked and regularly monitored. Measured individual tree data for all living trees with a diameter at breast height (DBH) of at least 5cm include the species, DBH, height, spatial position, crown length and tree vigour (Stuurman & Clement 1993, Vandekerkhove 2001).

No long-term development series are available yet. The only readily available data are measurements of stand structure in forests of different types and development histories. In some cases the data is drawn from two surveys. To date all of this data has been obtained from the Dutch forest reserves network. Table 1.1 gives an overview of strict forest reserves on poor sandy soils in the Netherlands. The most recent overview of strict forest reserves on poor sandy soils in Flanders has been documented by Vandekerkhove (2003).

## 1.4 Models of forest development

There is a considerable diversity of models and model approaches in forestry and forest ecology. Forests are complex biological systems that can be viewed, from a modeller's perspective, on different scales in time and space, with varying degrees of detail and for different purposes. Different model classifications and/or comparisons of models, including those beyond the scope of predicting forest development, can be found in the reviews of Vanclay (1994, 1995), Liu & Ashton (1995), Battaglia & Sands (1998), Chertov *et al.* (1999), Von Gadow & Hui (1999), Franc *et al.* (2000), Hasenauer *et al.* (2000), Peng (2000), Bugmann (2001), Pretzsch (2001) and Porté & Bartelink (2002).

Here we focus on dynamic models for the long-term prediction of forest development (i.e. regeneration, growth and mortality) in mixed uneven-aged stands. We discuss the model characteristics required for this purpose, the corresponding model approaches that can be distinguished and the currently available models that can be applied to forest ecosystems on poor sandy soils.

### 1.4.1 Model characteristics

#### 1.4.1.1 Process-based models versus empirical models

Process-based models are mathematical representations of biological systems that incorporate our understanding of physiological and ecological mechanisms into predictive algorithms (Mäkelä *et al.* 2000, Johnsen *et al.* 2001). These are in contrast to empirical models that use statistical techniques to describe the essential characteristics of a field data set. Empirical models have primarily been directed towards problems concerning the prediction of outcomes, whereas process-based models have primarily been directed towards understanding relationships (Korzukhin *et al.* 1996). In reality most process-based models have considerable empirical elements, and empirical models may include process elements, e.g. by choosing appropriate mathematical functions. The advantages, limitations and merits of both model approaches in forest modelling have been discussed by many authors, for example, Sharpe (1990), Mohren & Burkhart (1994), Korzukhin *et al.* (1996) and Peng (2000).

#### 1.4.1.2 Tree models versus stand models

We use the classification of Porté & Bartelink (2002) to distinguish between tree models and stand models since they clarify how their classification relates to that from other authors, and this makes their terminology more transparent. Tree models simulate the recruitment, growth and mortality of individual trees. The impact of competitive tree interaction on these processes can be simulated using competition indices (empirical models, e.g. Pretzsch *et al.* 2002), or by implementing species-specific reactions to environmental conditions (most process-based models). Tree models are generally classified as distance-dependent models and distance-independent models, depending on whether or not tree location is considered. Stand models, on the other hand, do not simulate each individual tree but rather average trees within a stand or tree distributions, depending on the approach used.

#### 1.4.1.3 Model characteristics for the long-term prediction of forest development in mixed uneven-aged stands

In contrast to empirical models, process-based models are general, i.e. applicable to a whole range of cases (Sharpe 1990). This means that process-based models maintain some degree of relevance for new objects or conditions, whereas empirical models are limited in their application by the range of the data set used (Kimmins 1990, Korzukhin *et al.* 1996, Porté & Bartelink 2002). An important consequence is that process-based models should be used for long-term predictions with extrapolations outside the range of the currently available data.

The spatial structure of a forest stand plays a key role in the dynamics of forest ecosystems, especially for mixed stands (Goreaud *et al.* 2002). In mixed uneven-aged forests, individual trees differ with respect to size, species, age and location, and this influences competitive tree interactions and succession patterns (Liu & Ashton 1995, Pacala & Deutschman 1995, Kint *et al.* 2003). The description of tree-to-tree interactions is necessary for the provision of reliable estimates of stand development. Models of forest development should therefore consider individual trees as the smallest unit of modelling, rather than less detailed entities such as tree distributions or stands (Judson 1994, Goreaud *et al.* 2002, Porté & Bartelink 2002).

Therefore, the long-term prediction of development in mixed uneven-aged stands requires a model approach with two main characteristics: (i) it should be process-based and (ii) it should consider individual trees. Other approaches for modelling forest development have been omitted, as they serve other purposes, e.g. Markov chains or matrix models (which are stand models) to simulate species dynamics on a landscape scale without information about stand structural development (Porté & Bartelink 2002).

### 1.4.2 Approaches in process-based tree modelling

Many process-based tree models of forest development have been developed, with varying degrees of detail in the process implementation and/or spatial resolution, and for different purposes. Among these, many authors distinguish two major model categories: (i) models where vegetation dynamics are determined mostly by plant population dynamics and (ii) models where vegetation dynamics are determined mostly by plant physiology (Bossel 1991, Hasenauer *et al.* 2000, Reynolds *et al.* 2001). The most important representatives of these categories are 'gap models' and 'biogeochemical models' respectively. In the following sections we briefly discuss these two model approaches. It should be noted that this distinction is somewhat artificial, and that models combining elements from both approaches exist (e.g. Friend *et al.* 1993, Keane *et al.* 1996).

#### 1.4.2.1 Gap models

The gap model is the most common model approach for ecological research concerning long-term forest development. The primary purpose of gap models is to examine the dynamics of *forest vegetation structure and species composition* based on plant population dynamics (Reynolds *et al.* 2001). The dying and falling of trees (due to ageing or minor disturbances) and the subsequent recruitment in the gaps is considered to be the basis of forest dynamics. A gap model simulates regeneration, growth and mortality of individual trees in a series of independent simulation plots (representing different gaps), typically of 0.01-0.1 ha. The plots are horizontally homogeneous, i.e. tree position within a patch is not considered. Together these plots form the mosaic of development stages within a forest (Bugmann 2001).

All gap models are in some way or other related to the parent model JABOWA (Botkin 1993) and its immediate successor FORET (Shugart 1984). A brief historical overview of gap models is given by Liu & Ashton (1995) and Hasenauer *et al.* (2000). However, many advances have been made since the introduction of gap models, particularly with respect to: (i) incorporating more physiology in the implementation of regeneration, growth and mortality (Reynolds *et al.* 2001), and (ii) the basic assumptions underlying the models. In this context, Bugmann (2001) compares the first, rather descriptive, JABOWA model with recent, more process-based gap models. Detailed reviews of process implementations and model construction can be found in Liu & Ashton (1995), Bugmann *et al.* (1996), Keane *et al.* (2001), Norby *et al.* (2001), Price *et al.* (2001), Wullschleger *et al.* (2001) and Porté & Bartelink (2002). Here we just summarise the major trends:

(i) In process implementation, recruitment and mortality are mostly modelled as stochastic processes over an annual time step. More variation exists for the simulation of tree growth, ranging from models that use deterministic empirical functions to models that base tree growth on photosynthesis (e.g. Prentice & Leemans 1990) or use a carbon balance (e.g. Jorritsma *et al.* 1999). In all gap models light availability plays a key role in the regeneration and tree growth processes (Porté & Bartelink 2002). However, many also consider water, nutrients, biotic factors and/or disturbances.

(ii) With respect to basic assumptions, some models also consider neighbourhood relations between simulated plots (e.g. Urban *et al.* 1991, Lexer & Hönninger 2001). Furthermore, the horizontal homogeneity within patches is sometimes challenged by making the model spatially explicit (e.g. Busing 1991, Pacala *et al.* 1993), or by refining the patches to the level of interacting small-volume cells (e.g. Williams 1996, Chave 1999), thus simulating the detailed three-dimensional development of forest stands. As these latter models strongly alter the assumption of traditional gap models, their status as gap models may be questioned.

Gap models have been used to study forest dynamics in relation to biotic factors (e.g. Jorritsma *et al.* 1999, Seagle & Liang 2001), disturbances (e.g. Mailly *et al.* 2000, Ménard *et al.* 2002), environmental factors (e.g. Weishampel & Urban 1996, Van Der Meer *et al.* 2002), and forest management (e.g. Lindner 2000).

#### 1.4.2.2 Biogeochemical models

The primary purpose of biogeochemical models is to examine the dynamics of *forest functioning* (Reynolds *et al.* 2001). They describe the circulation, transformation and accumulation of energy and biomass through ecosystems. These models are aimed at tackling physiology-based problems, and as such they go beyond the scope of modelling vegetation dynamics. Some of these models, however, have been specifically developed to study the interaction between environmental factors and succession. With these models, for example, the effects of climatic change (Kellomäki & Väisänen 1997) and historic $CO_2$ levels and nitrogen inputs (Van Oene *et al.* 1999) on forest dynamics have been studied. Keane *et al.* (1996) coupled a biogeochemical model to a gap model to study the effect of fire on nitrogen and water cycles, and the related successional changes.

### 1.4.3 Models of forest development on poor sandy soils

In theory, process-based models are general, and can be used for forest dynamics research in any forest ecosystem. However, all process-based models are abstractions of highly complex biological systems. Their characteristics, from general structure to more specific parameterisations, should be carefully compared and tested to determine the limitations and suitability of the models for attaining certain objectives (Porté & Bartelink 2002). Comparisons of different gap models, for example, have indicated that in most cases these perform better when applied in the subspace of the environmental conditions for which they were originally developed. Their application in other forest types is only recommended after a thorough revision of the models (Lasch & Lindner 1995, Badeck *et al.* 2001). In this section we try to summarise the models currently available that are validated for use in forest ecosystems on poor sandy soils, and could therefore be used for research in the Netherlands and Flanders.

Verification and validation of ecological models can be performed at different levels, depending on data availability and system understanding (Rykiel 1996). For models of long-term forest development, availability of validation data – such as tree ring series, pollen analyses and/or long-term forest trials – is generally low. In these cases only single-point validation approaches are possible (sensu Bugmann 2001), using either sample data from specific points in time and space, or prior information about the forest system itself (e.g. expert assessment on what constitutes the potential natural vegetation). Table 1.2 lists process-based tree models currently available for the prediction of long-term forest development in mixed uneven-aged stands on poor sandy soils, which have been validated using single-point approaches.

Table 1.2 Examples of models of forest dynamics that are currently available and validated for use in forest ecosystems on poor sandy soils.

| model name and author | model specifications | applications on poor sandy soils |
|---|---|---|
| **FORGRA** (Jorritsma *et al.* 1997a, 1999) | gap model; uses a carbon balance to simulate growth; detailed description of the regeneration process and of herbivore grazing (cf. Price *et al.* 2001) | - forest dynamics in relation to herbivore grazing (Jorritsma *et al.* 1997b, 1999)<br>- forest dynamics in relation to climatic change (Van Der Meer *et al.* 2002)<br>- long-term prediction of vegetation development (Kint *et al.* 2002) |
| **FORSKA** (Prentice & Leemans 1990) | gap model; based on photosynthesis to simulate growth | - forest dynamics in relation to climatic change (Lasch & Lindner 1995, Lindner 1998)<br>- forest dynamics in relation to forest management (Lindner 2000) |
| **ZELIG** (Urban *et al.* 1991) | gap model; considers neighbourhood relations between simulated plots | - long-term prediction of vegetation development and consequences for forest management (Mohren *et al.* 1991) |
| **unnamed** (Van Oene *et al.* 1999) | biogeochemical model; combines plant competition processes and flows of nutrients, carbon and water | - forest dynamics in relation to historic $CO_2$ levels and nitrogen inputs (Van Oene *et al.* 1999) |

## 1.5 The combination of forest reserves and models

Knowledge about forest dynamics has always been recognised as a key aspect of both theoretical and applied forest science. Historically, this knowledge has been based on case studies and field experience. Today, research in this field can benefit from the worldwide realisation of forest reserves programmes, and the development of numerous models of forest development.

Some conceptual models of forest dynamics that describe long-term structural development have been constructed for forest ecosystems on poor sandy soils, based on thorough insights into species autecology and competitive tree interactions, but using relatively little empirical evidence (e.g. Fanta 1982, 1986, Leuschner 1991, 1994). Forest reserves programmes on these sites are indeed recent, so long-term development series are not yet available. Consequently, these conceptual models describe only general development patterns, with few details or quantitative aspects.

Since the availability of computers, forest dynamics on poor sandy soils have also been studied using process-based models, which in most cases have been gap models (e.g. Mohren *et al.* 1991, Lasch & Lindner 1995, Jorritsma *et al.* 1999). These models summarise current insights into forest dynamics, and have the ability to make long-term quantitative predictions under different scenarios. The credibility of these predictions, however, is based solely on their correspondence with theoretical insights due to a lack of long-term empirical data.

There is no doubt that the forest reserves programme will increase our insights into forest dynamics as more data becomes available. Theoretically, the monitoring of forest development at many places and for long time periods could lead to detailed descriptive models of all possible development pathways on poor sandy soils, making any conceptual or process-based model redundant. This might, however, only be possible after many decades or centuries of continuous monitoring. From a purely statistical point of view this is probably impossible, due to the elevated number of interacting factors that requires too many degrees of freedom to produce accurate descriptive models for all circumstances.

Since both forest reserves and models have specific advantages and limitations, it seems plausible that science might benefit from a combined approach. Together the predictive ability of models and the empirical strength of forest reserves data might result in new conceptual models to describe development patterns in a detailed and quantitative manner. As long as the forest reserves data were not used for model construction then in our view this principle has two main applications:

(i) In the short term, forest reserves data can be used to mimic model predictions. This means that for each model prediction, the most similar field example within the forest reserves is indicated. In this way the sequence of a model prediction is replaced with a sequence of field observations. The latter can then be analysed on aspects that are absent in the model predictions, such as the development of detailed structural patterns. This application can be interpreted as an attempt to construct long-term empirical data series from the readily available short-term data, by using a predictive model as the upscaling criterion, as done in this study.

(ii) In the long-term, forest reserves data could be used to validate (parts of) models with time-series approaches (Bugmann 2001). In contrast to data from tree ring analysis or long-term forest trials, the forest reserves data do not merely document growth; tree regeneration and mortality are also monitored and can be used in the validation process.

In this study we combine forest reserves data and model predictions to produce a new conceptual model of forest dynamics, which describes structural development in forest ecosystems on poor sandy soils. Based on this model we formulate implications for close-to-nature forestry. We are not aware of other research in these forests that uses the same approach. We believe that the effort presented here should be further repeated by taking into account aspects of forest dynamics other than structural development and that the approach should be extended to other forest ecosystems. A sustained and multidisciplinary effort will significantly increase our knowledge of forest dynamics in the long run.

# 2 Pathways of stand development in ageing Scots pine forests

Kint, V., Mohren, G.M.J., Geudens, G., De Wulf, R. & Lust, N.
Submitted for publication in an international forestry journal.

### Abstract

Long-term stand development in forest ecosystems on oligotrophic and acidic sandy soils is generally described as a fixed sequence of development stages towards a climax. However, stand development is not necessarily directional, but rather multiple development pathways may exist for a single site type. The aim of this study is to quantitatively describe the main development pathways in ageing Scots pine (*Pinus sylvestris* L.) forests that are no longer managed and where massive regeneration of broadleaved species is often reported. We used agglomerative cluster analysis on data from Dutch forest reserves to define 19 empirical structural classes, which represent different stand structures in ageing Scots pine forests. Sequences of these structural classes were constructed with the aid of long-term predictions from a process-based gap model that has been shown to accurately predict forest dynamics on these sites. Sequences of structural classes, representing different actual pathways of stand development, showed similar patterns. We distinguished four main pathway patterns: three presumably linked to gap dynamics and one to major disturbance dynamics. The three pathways linked to gap dynamics lead towards dominance of birch, oak or beech. They differ in light availability for regeneration (depending on gap origin and gap size) and/or seed tree availability. The pathway linked to major disturbance dynamics shows many different development patterns after major disturbances. For each of the main pathway patterns, trends of basal area and mean diameter are visualised. The results are compared with previous studies on vegetation dynamics, and the limits of the pathway concept and its possible applications in forestry are discussed.

## 2.1 Introduction

With an estimated area of three-and-a-half million hectares, homogeneous even-aged Scots pine (*Pinus sylvestris* L.) plantations constitute one of Western Europe's most important forest types (Mason & Alía 2000). Just as for other anthropogenic conifer plantations, many attempts are being made to increase nature values. These range from the implementation of multipurpose management to ecosystem restoration and conservation (Kenk & Guehne 2001, Peterken 1996). Knowledge about stand dynamics is an important prerequisite in all of these cases.

Our discussion is focused on the situation in the Netherlands and Flanders (Northern Belgium). In these two countries Scots pine forests are mostly first generation forests on oligotrophic and acidic sandy soils, of aeolian or glacial origin. Natural plant associations on these sites are *Betulo-Quercetum roboris*, *Fago-Quercetum* and *Deschampsio-Fagetum* (Stortelder *et al.* 1999).

Most Scots pine stands are no longer managed solely for timber production, and some have been conserved without any human intervention to far beyond their initial rotation period of 40-50 years. Massive natural regeneration of broadleaves under various circumstances and cover has been reported in many of these ageing stands (Leuschner 1994, Lust *et al.* 1998, Zerbe 2002). The species concerned are mainly silver birch (*Betula pendula* Roth), downy birch (*Betula pubescens* Ehrh.), pedunculate oak (*Quercus robur* L.), sessile oak (*Quercus petraea* (Mattuschka) Lieblein), common beech (*Fagus sylvatica* L.), rowan (*Sorbus aucuparia* L.) and alder buckthorn (*Frangula alnus* Mill.).

Few attempts have been made to summarise the vegetation dynamics in these forests. Fanta (1986), Prach (1989) and Leuschner (1994) developed conceptual models of primary and secondary succession towards a climax forest, in forest ecosystems on oligotrophic and acidic sandy soils. Their models describe similar development patterns, although with different nuances and degrees of detail, from homogeneous Scots pine forests towards oak-birch forests and further towards oak-beech forests. Zerbe (2002) and Clerkx *et al.* (2002) distinguish general development scenarios of ageing Scots pine stands towards oak or oak-beech forests, based on the current vegetation community. Their findings, although much less detailed, are consistent with the aforementioned models.

These models represent vegetation dynamics as a fixed sequence of development stages after disturbance, in accordance with the climax concept (sensu Clements 1916). However, stand development is not necessarily directional, but rather multiple development pathways may exist for a single site type, each depending on biotic factors, disturbances and environmental conditions (Cattelino *et al.* 1979, Pickett *et al.* 1987). Different pathways can occur simultaneously within a forest, can operate at different spatial and temporal scales, and may or may not lead to similar structures (Cook 1996, Spies & Turner 1999, Frelich 2002).

Pathways of stand development in forest ecosystems on poor sandy soils have not yet been described. The purpose of this chapter is to describe the main development pathways in ageing Scots pine (*Pinus sylvestris* L.) forests that are no longer managed. Our analysis is limited to 'natural' vegetation dynamics, i.e. where anthropogenic factors that strongly hamper natural processes, such as artificially high herbivore impacts or the presence of exotic species, have only a marginal importance. Our analysis consists of three parts:

(i) Development of a methodology to describe pathways of forest stand development in ageing Scots pine stands, based on data from forest reserves and model predictions of long-term forest development;

(ii) Assessment of similar development trends within the described pathways, resulting in a limited number of main pathway patterns that are interpreted in detail;

(iii) Comparison of the results with previous studies on vegetation dynamics, and a discussion of the limits to and possible applications of the pathway concept.

## 2.2 Materials and methods

There are two major ways of describing pathways of stand development: (i) with discrete development stages, each being a summary of processes taking place within the stand and (ii) with various occurring stand structures ('structural classes'), independent of the processes leading to them (Oliver & Larson 1996 p.165). Similar names are given to development stages and structural classes (e.g. stand initiation, stem exclusion, understorey reinitiation, old growth). However, the two approaches are not necessarily interchangable, as specific stand structures can often be achieved in different development stages.

We use the concept of structural classes, because these can easily be derived with a high degree of detail from field data but without the need for assumptions about ongoing processes and interactions. In this perspective, the description of pathways first of all requires the description of empirical structural classes and then the development of a criterion for ordering these structural classes into logical sequences. Our methodology can be summarised in three main steps (Fig. 2.1) which are further elaborated on in the next sections.

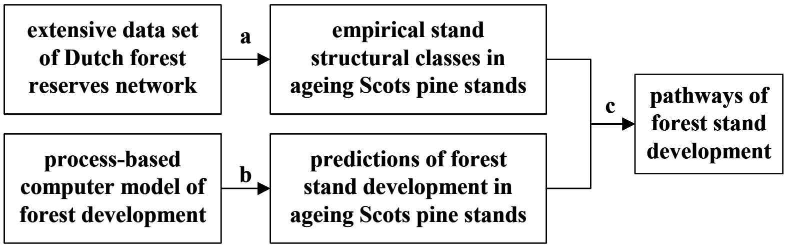


Figure 2.1 Three main steps of the methodology used: (a) cluster analysis, (b) model simulation and (c) pathway construction.

### 2.2.1 Structural classes in ageing Scots pine stands

The first step in our methodological approach was to describe the different stand structural classes (SCs) that might exist in ageing Scots pine stands (step ‘a’ in Fig. 2.1). Detailed data on stand structure and species composition in these stands were available from forest reserves. Different SCs in this data were distinguished using statistical cluster analysis.

#### 2.2.1.1 Forest reserves data

Forest reserves programmes in the Netherlands and Flanders have been gradually developed since the early 1980s. Therefore no long-term development series are available at present. To date, all of available data have come from the Dutch forest reserves programme. Flanders is a geographic neighbour and shares the same climate. Also the site types, forest history and past management in Scots pine stands are similar. Therefore, data from the Dutch reserves in these forests are considered to be representative for the Flemish conditions.

From the 60 existing forest reserves in the Netherlands, we selected three in their entirety and six in part. Criteria for retaining (parts of) forest reserves were that they should be (i) forests on poor sandy soil; (ii) old homogeneous Scots pine stands with varying stand development since management stop and (iii) stands without significant impact of anthropogenic factors that strongly hamper natural processes. The third criterion mainly concerned the presence of exotic species (i.e. no more than 10% of total basal area and no dominating trees). Herbivore impact (roe deer and red deer) in the selected forest reserves did not seem to strongly hamper natural regeneration processes.

In each of the selected reserves we had detailed measurements in a core area (70m x 140m; 0.98 ha) and/or in a network of permanent circle plots (each 500 m²) at our disposal. Measured individual tree data for all living trees with a diameter at breast height (DBH) of at least 5cm, included the DBH, height, species, spatial position, crown length and tree vigour. All of the selected reserves had been completely surveyed once; in three reserves a second limited survey had been carried out after 9 to 12 years. General information about the reserves and the number of available core areas and circle plots is given in Table 2.1.

#### 2.2.1.2 Cluster analysis

In defining SCs Oliver & Larson (1996), Franklin *et al.* (2002), Sallabanks *et al.* (2002) and others use canopy closure, basal area stocking or tree size classification rules. The resulting number of SCs is always limited and subject to a more or less arbitrary rule definition. Cluster analysis allows for a more detailed and quantitative classification based on extensive data. Divisive cluster analysis based on species composition can be used to describe successional forest types (e.g. Nansen *et al.* 2001). However, neither stand structure nor SCs can be described purely on the basis of species composition (Kint *et al.* 2003). We opted for an agglomerative clustering method, based on different stand structure variables.

Table 2.1 General information about the forest reserves selected.

| reserve name | area (ha) | selected measurement plots[a] | | | survey year(s) | | natural plant assoc.[d] | description of selected part(s)[e] |
|---|---|---|---|---|---|---|---|---|
| | | No. core areas | No. circle plots[b] | area (ha) | first[c] | second | | |
| De Heul | 55 | - | 24 | 1.2 | 1999 | | BQm | 19-20th century Pi plantations; no management since 1998 |
| Galgenberg | 42 | 1 | 48 (46) | 3.38 | 1986-88 | 1995 | FQ (*) | 19th century Pi plantations; remnants of old forest; unmanaged 1972 storm area; no management since 1983 |
| Lheebroeker Zand | 39 | 1 | 61 (28) | 4.03 | 1987-88 | 1999 | BQ-BQm | 19-20th century Pi plantations; no management since 1983 |
| Mattemburgh | 106 | 1 | 43 | 3.13 | 1997-98 | | FQ (*) | 19th century Pi plantations; never managed |
| Molenven | 42 | - | 11 | 0.55 | 1995 | | BQm (*) | 19th century Pi plantations; no management since 1923 |
| Noordhout | 38 | 1 | - | 0.98 | 1982 | 1992 | FQ | 20th century Pi plantation with underplanting of Qu and Fa; no management since 1980 |
| Stille Eenzaamheid | 85 | 1 | 42 | 3.08 | 2000 | | BQ | 19th century spontaneous Pi forest; 19th century Pi plantations; no management since 1973 |
| Tongerense Hei | 40 | 1 | 56 | 3.78 | 1996-94 | | BQ | 19-20th century spontaneous Pi forest; never managed |
| Zwarte Bulten | 46 | 1 | 63 | 4.13 | 1991 | | FQ-(BQ) | 19-20th century Pi plantations; no management since 1989 |
| **total values** | **493** | **7** | **348** | **24.26** | | | | |

(a) Criteria for selection of (parts of) reserves: see text.

(b) The number of remeasured plots in the second survey, when different from the first, is given between brackets.

(c) When two years are mentioned, the first refers to the survey year of the core area and the second to that of the circle plots.

(d) BQ *Betulo-Quercetum roboris*, FQ *Fago-Quercetum*, m subassociation *molinietosum* (according to Stortelder *et al.* 1999). (*) The actual vegetation in parts of the reserve is considered to be a good approximation of the natural plant association.

(e) Pi *Pinus sylvestris*, Qu *Quercus spp.*, Fa *Fagus sylvatica*.

The statistical technique of *hierarchical agglomerative cluster analysis* groups similar objects (here measurement plots), where similarity is based on a multivariate distance measure (Legendre & Legendre 1998). The grouping algorithm, the distance measure and the standardisation of variables can all be chosen. We chose furthest neighbour sorting (complete linkage) as the grouping algorithm. In this method, the fusion of two clusters depends on the most distant pair of objects. This increases the contrast between clusters. Furthermore, we used Euclidian distance as the multivariate distance measure and variables were standardised using Z scores. Discriminant analysis was used to determine the degree of refinement that needed to be considered in interpreting our results (Huberty 1994). All analyses were carried out using the SPSS 10.0 statistical software package. The cluster analysis in SPSS provides additional information about the proximities between clusters, which gives an indication of their similarity.

The cluster analyses were performed using a two-stage approach. A first series of cluster analyses, one per reserve, was aimed at describing each reserve's internal structural patterns, based on its network of circle plots. Based on the data of the first survey we calculated values for basal area, tree density, mean DBH and mean height in each circle plot. These four variables were calculated separately for pine, birch, oak and beech, as well as for all species together. The resulting multivariate set of structure characteristics (20 variables in 348 plots) served as an input to the cluster analyses. The resulting clusters were named 'first-stage clusters'. This method has some major ecological and practical advantages compared to clustering all circle plots for all reserves into one single analysis:

(i) Reserves are separate geographic areas, with different histories and environmental conditions. First-stage clusters can be interpreted within a reserve's characteristic context;

(ii) We observed that many of the first-stage clusters consist of neighbouring circle plots, suggesting continuous areas with similar stand structure. Consequently, the assumption that the first-stage clusters are preserved over time (i.e. all plots within a cluster develop in a similar way, so a cluster remains a structural entity over time) is acceptable, at least for short time periods. In reserves with two surveys, we assumed identical cluster composition during both surveys;

(iii) The resulting clusters proved to be much less sensitive to the cluster analysis methods used than would be the case for a single cluster analysis.

In a second stage, the core areas and the first-stage clusters, from all reserves and both surveys, were grouped in a limited number of second-stage clusters. It was assumed that core areas were structurally homogeneous. The inputs for this cluster analysis were stand level values (per ha) for the same variables as used in the first-stage cluster analyses. However, to avoid extreme values we required at least 40 trees in each first-stage cluster for these stand-level variables to be calculated (value derived from the definition of representative sample plots by Hochbichler *et al.* 2000). In this way five first-stage clusters (together grouping six circle plots) were excluded.

Whereas the first-stage clusters and the core areas represented concrete field examples of structural entities within the reserves, the second stage clusters grouped similar examples between reserves and thus described average stand structures. To emphasise their specific characteristics, we distinguish between 'structural classes' (SCs) on the one hand, referring to the stand structures as defined by the second-stage clusters, and 'structural class objects' (SCOs) on the other hand, referring to the first-stage clusters and core areas.

### 2.2.2 Predictions of development in ageing Scots pine stands

Ultimately, we wish to describe the pathways of forest development and not just discrete SCs. We used model predictions of stand development as criteria for sequencing our SCs and adopted a process-based gap model for our purpose of predicting stand development in forests with a varying mixture and/or age distribution (step 'b' in Fig. 2.1).

#### 2.2.2.1 The process-based gap model FORGRA

The gap model (Shugart 1984, Bugmann 2001) is the most commonly used type of model for ecological research on long-term forest development. In this family of models, the basis of forest dynamics is the death and toppling of trees (due to ageing or minor disturbances) and the subsequent recruitment in the gaps. A gap model simulates regeneration, growth and mortality of individual trees in a series of independent simulation plots (representing different gaps), typically of 0.01-0.1 ha. The plots are horizontally homogeneous, i.e. tree position within a patch is not considered. Together these plots form the mosaic of development stages within a forest (Bugmann 2001).

FORGRA (Jorritsma *et al.* 1999) is a process-based gap model for forest ecosystems on poor sandy soils (cf. Addendum A). It was originally developed to investigate the impact of elevated grazing densities on forest development, and therefore includes a detailed mechanistic recruitment module (Price *et al.* 2001). This renders it particularly suitable for the prediction of stand development in ageing Scots pine stands, as massive regeneration is often observed in these stands. Other gap models that have been used in forest ecosystems on poor sandy soils (e.g. Mohren *et al.* 1991, Lindner 1998) do not consider as much mechanistic detail in process implementation and thus seemed less suitable for our purposes. The grazing module of FORGRA was not used, since our analysis is limited to vegetation dynamics without elevated herbivore impact, and the forest reserves selected (whose data will be compared to model predictions) scarcely seemed to be affected by herbivore grazing.

FORGRA has been shown to accurately predict dynamics in forests on poor sandy soils in the Netherlands (Jorritsma *et al.* 1999) and Flanders (Kint *et al.* 2002). It simulates monthly development in 400 m² plots. The vertical exponential extinction of incoming PAR is proportional to leaf density. The radiation-use efficiency concept (RUE) is used to calculate the biomass increase of individual trees based on the absorbed light (Bartelink *et al.* 1997). Allocation of biomass to plant organs is based on observed biomass distributions. DBH growth is derived from stem biomass and tree height, assuming a specific cone-shaped stem form. Incoming seeds in a simulation plot mainly come from trees in the plot, although seeds can immigrate from neighbouring plots. The number of germinating seeds depends on the light availability at the forest floor. Seedlings grow up in cohorts and eventually become adult trees. Their growth depends on a light-dependent relative growth rate. Mortality of trees can be caused by age, instability or competition. Some processes include stochastic elements.

Competition for light is the main driving force behind the growth and recruitment of individual trees, although the RUE concept implicitly accounts for water and nutrient deficiencies. Other factors that may have an influence on forest development, such as soil development, climate, diseases, etc, are considered to be of secondary importance, and are not implemented in the model. The assumption that light is the main driving force behind forest development holds in the case of forests with high densities of light-demanding species, on sites without important soil gradients. This is the case for the majority of the ageing Scots pine forests we investigated. However, as errors tend to increase with simulation time, we limited our predictions to 120 years, the time needed for all simulation plots to reach a next forest generation.

FORGRA has been parameterised for six main tree species (silver birch, downy birch, pedunculate oak, sessile oak, Scots pine and common beech) and two shrubs (rowan and alder buckthorn). Also three exotic species are included: American red oak (*Quercus rubra* L.), black cherry (*Prunus serotina* Ehrh.) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). Since our aim was to predict stand dynamics for native species only, the regeneration of exotic species in the model was disabled.

#### 2.2.2.2 Model predictions with FORGRA

The model input consists of individual tree data (species, DBH, height, crown length and approximate age) for all trees with a DBH of at least 5cm in 400 m² simulation plots. We used data from reduced circle plots in two forest reserves to obtain different model inputs. The reserve ‘De Heul’ was selected because it is a good example of an ageing Scots pine stand shortly after management stop. The reserve ‘Galgenberg’, where management has been stopped for two decades, was selected because of its high structural diversity (Table 2.1). A total number of 69 simulation plots, scattered over four geographic areas within these reserves, gathered representatives of nearly all SCs including homogeneous Scots pine plots, plots with different proportions of oak and birch, as well as regeneration areas following a storm. Different geographic areas were kept separate in the model to avoid seed exchange, which resulted in four different model input groups with 26, 21, 11 and 11 plots respectively.

Model outputs included basal area, tree density and mean tree dimensions per species in each simulation plot and at yearly time steps. To ascertain maximum comparability with SCs, output values were based only on trees with a DBH of at least 5cm. With respect to model stochasticity, stable model predictions were obtained by averaging 50 model runs. It should be noted that FORGRA output variables apply to 400 m² plots. For the comparison with SCs it is necessary to upgrade output variables to a scale of 1 ha. This may cause extreme values as well as unusual time patterns that would not normally be observed at the stand level. Upgraded model predictions should therefore not be interpreted with absolute values or timescales, but rather in relative terms of relationships between species.

### 2.2.3 Pathways of stand development: the combination of structural classes and model predictions

A final methodological step in the construction of pathways is the ordering of the empirical SCs in logical sequences using the model predictions as the ordering criteria (step 'c' in Fig. 2.1). This is a two-stage process: (i) the construction of a sequence of SCs with each model prediction and (ii) uncertainty analysis with these sequences.

#### 2.2.3.1 Sequence construction

The model prediction for a simulation plot p ($MP_p$) can be thought of as a series of 120 output vectors ($OV_{p,t}$), one for each time step t, each consisting of a number of output variables. SCOs can also be written as vectors of similar variables. For each $OV_{p,t}$ we searched for the most similar SCO, i.e. the best approaching field reference. With some additional transformations this results in a sequence of SCs for each $MP_p$.

To evaluate the degree of similarity between an $OV_{p,t}$ and an SCO, both vectors should contain the same variables. We selected eight variables that were best predicted by the model: the basal area and the mean DBH for Scots pine, birch, oak and beech. Together these variables describe some of the most important structural features of ageing Scots pine stands, such as the mean dimensions of trees and relative abundances of species. Using discriminant analysis (Huberty 1994), 98% of the SCOs were correctly assigned on the basis of these eight variables. This confirms the adequacy of this set of variables to discriminate the different observed stand structures.

As mentioned before, stand level values of model output variables may include extreme values and so comparing the absolute values between OVs and SCOs is not an appropriate way of evaluating their degree of similarity. Therefore, we recoded the values of all of the variables into six categories, ranging from 'very low' (code 1) to 'extremely high' (code 6). Each category is univocally defined by dividing the range between zero and a specified maximum value into six equal parts (Table 2.2).

Table 2.2 Definition of upper category limits for the recoding of the model output vector (OV) and structural class object (SCO) variables into six categories.

| | | upper category limits | | | | | |
|---|---|---|---|---|---|---|---|
| | | very low | low | medium | high | very high | extremely high[(b)] |
| **OV variables**[(a)] | | | | | | | |
| basal area (m²/ha) | Pi | 7.1 | 14.3 | 21.4 | 28.6 | 35.7 | 42.9 |
| | Be | 6.6 | 13.1 | 19.7 | 26.2 | 32.8 | 39.3 |
| | Qu | 7.8 | 15.6 | 23.4 | 31.2 | 39.0 | 46.8 |
| | Fa | 6.2 | 12.4 | 18.6 | 24.7 | 30.9 | 37.1 |
| mean DBH (cm) | Pi | 11.2 | 22.4 | 33.6 | 44.8 | 56.0 | 67.2 |
| | Be | 7.3 | 14.6 | 21.9 | 29.2 | 36.5 | 43.8 |
| | Qu | 15.0 | 29.9 | 44.9 | 59.8 | 74.8 | 89.8 |
| | Fa | 13.2 | 26.3 | 39.5 | 52.7 | 65.8 | 79.0 |
| **SCO variables**[(a)] | | | | | | | |
| basal area (m²/ha) | Pi | 5.7 | 11.4 | 17.2 | 22.9 | 28.6 | 34.3 |
| | Be | 4.7 | 9.4 | 14.0 | 18.7 | 23.4 | 28.1 |
| | Qu | 3.6 | 7.3 | 10.9 | 14.6 | 18.2 | 21.9 |
| | Fa | 4.3 | 8.6 | 12.9 | 17.2 | 21.5 | 25.8 |
| mean DBH (cm) | Pi | 9.0 | 18.0 | 27.0 | 36.0 | 45.0 | 54.0 |
| | Be | 6.2 | 12.4 | 18.7 | 24.9 | 31.1 | 37.3 |
| | Qu | 6.4 | 12.7 | 19.1 | 25.5 | 31.8 | 38.2 |
| | Fa | 7.0 | 13.9 | 20.9 | 27.8 | 34.8 | 41.7 |

(a) Pi *Pinus sylvestris*, Be *Betula spp.*, Qu *Quercus spp.*, Fa *Fagus sylvatica*.

(b) Maximum values for OV and SCO variables within 120 years of development. Derived from all available simulations (for OVs); derived from Jansen *et al.* 1996 (for SCOs). See text for more details.

The maximum values for OV variables (upper right column in Table 2.2) are defined by the maximum observed values over all available simulations. They should be interpreted as the maximum predicted values over a time-span of 120 years of simulated development, not as the absolute maximum after an unlimited number of years. This distinction is particularly important for beech. The maximum values for

SCO variables (lower right column in Table 2.2) are defined on the basis of yield tables (Jansen *et al.* 1996), using the following procedure:

(i) Define a yield class based on the height and age of individuals in the forest reserves. This results in yield classes 5 (birch and oak), 6 (beech) and 10 (Scots pine);

(ii) Search the yield tables for the basal area in homogeneous regularly thinned plantations at the age of 90 (birch) or 120 (other species);

(iii) Search the yield tables for the corresponding mean DBH.

The values obtained are the best approximation we can make about maximum basal area and mean DBH per species on the selected forest reserve sites within a 120-year development period. However, it is unlikely that these values defined for homogeneous forests will be observed in many non-managed forests and so a classification as 'extreme values' is appropriate.

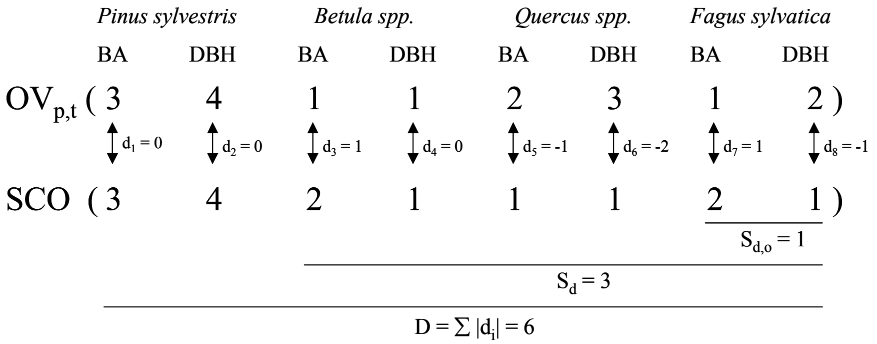


Figure 2.2 Definition of $d_i$, D, $S_d$ and $S_{d,o}$ to describe the dissimilarity between two vectors $OV_{p,t}$ and SCO, based on the comparison of corresponding category values for eight variables.

After the variables had been recoded, new vectors of eight category values were obtained. These indicated to which category each of the eight original variables belonged. The comparison of corresponding category values between an $OV_{p,t}$ and an SCO indicates to what extent the basal area and mean DBH for the four main species are similar (identical categories) or not (divergent categories). This results in a number of criteria that help describe the dissimilarity between both vectors (Fig. 2.2), i.e. the level $d_i$ of each divergence, the sum D of all divergences, the number of species $S_d$ with divergent variables and the number of species $S_{d,o}$ with divergent variables in opposite directions.

Our intention was to find the SCO most similar to each $OV_{p,t}$. Based on the aforementioned dissimilarity criteria, we developed a set of rules to eliminate all SCOs that could not be considered as similar to a certain $OV_{p,t}$ and to decide which one of the remaining SCOs (if any) was more similar to $OV_{p,t}$ than the rest (Fig. 2.3).

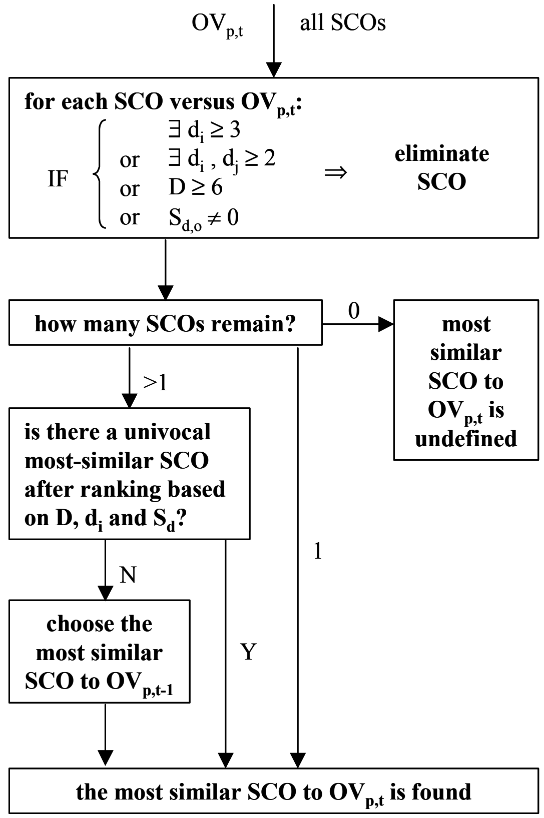


Figure 2.3 Set of rules to find the most similar SCO to a certain model output vector $OV_{p,t}$. See Fig. 2.2 for the definition of $d_i$, D, $S_d$ and $S_{d,o}$.

The elimination rules were based on the rationale that an SCO does not have any structural similarity to an $OV_{p,t}$ when the comparison of both indicates (i) divergences which are too many and too high, and/or (ii) for a given species a basal area and mean DBH which diverge in opposite directions. If after elimination a ranking of the remaining SCOs, based on the dissimilarity criteria, did not unequivocally indicate the one most similar to $OV_{p,t}$, the most similar to $OV_{p,t-1}$ was selected. It was possible for all of the SCOs to be eliminated following the application of these elimination rules. Such cases where the field example most similar to the $OV_{p,t}$ remained undefined, were labelled ‘undefined structures’.

For each $MP_p$ the result was a series of 120 SCOs that can be interrupted with undefined structures. We applied three additional transformations to these series that upgraded these from concrete field cases towards more general sequences of stand structure development:

(i) the elimination of undefined structures if these did not occur over more than 10 succeeding time steps, since in these cases we could assume that they are negligible transitions between two SCOs;

(ii) summarising the series into a sequence of SCOs and undefined structures by eliminating all redundancies;

(iii) the replacement of all SCOs with the SC they belonged to.

### 2.2.3.2 Uncertainty analysis

The application of the aforementioned procedure to all of the MPs resulted in 69 sequences of SCs and/or undefined structures. However, it is clear that these sequences depend on the category limits as defined in Table 2.2, and that the use of slightly shifted categories can have an impact on the results. To assess this impact we recalculated all of the sequences with two additional sets of category limits: one with broader categories for OVs and narrower categories for SCOs (defined by a 5% increase and decrease of the values in Table 2.2 respectively), and in a second recalculation the other way round. At the end of this procedure we have three sequences for each $MP_p$: one based on the original values in Table 2.2 and two others based on slightly different values. The comparison of these three sequences gives an indication as to the uncertainty of our results: the more dissimilar these sequences are (i.e. the more the results depend on the redefinition of categories in Table 2.2 within reasonable limits), the less certain we are that the original sequence is a good approximation of $MP_p$.

It is likely that most original sequences will to some degree differ from the two additional sequences, meaning that there is uncertainty about the correct sequence.

We masked this uncertainty by comparing the three calculated sequences and summarising them in one final sequence, in which all dissimilar parts are replaced by undefined structures and all similar parts are conserved. We used the following rules to construct this final sequence for each $MP_p$ based on the three calculated sequences:

(i) If between the calculated sequences the succession of two SCs is not identical, these are grouped in the final sequence (e.g. A-B-C and B-A-C become AB-C);

(ii) If between the calculated sequences the succession of more than two SCs is not identical, these are indicated as undefined structures in the final sequence (e.g. A-B-C-D and C-E-A-D become ?-D);

(iii) SCs that only appear in one of the three calculated sequences or for a very short time, are marked between brackets in the final sequence (e.g. B-E and B-C-E become B-(C)-E);

(iv) All other dissimilarities between the calculated sequences become undefined structures in the final sequence.

In most cases, the resulting final sequence is less detailed than any of the calculated sequences (i.e. it contains more undefined structures and/or grouped SCs). However, it only provides information that has not been affected by the accidental choice of parameter values during sequence calculation.

## 2.3 Results

### 2.3.1 Structural classes in ageing Scots pine stands

The cluster analyses of circle plots within the reserves resulted in 31 different first-stage clusters that met the condition of grouping at least 40 trees each. Eight of these were also defined for a second survey. In seven reserves a core area was available, three of which were also defined for a second survey. Together these first-stage clusters and core areas from both surveys defined 49 SCOs. The cluster analysis of these resulted in 19 second-stage clusters or SCs (summarised in Table 2.3). For all SCOs defined in two surveys, both surveys were classified within the same SC.

Table 2.3 Summary of characteristics of the structural classes (SCs) and description of stand composition.

| SC | SCOs (a) | basal area ($m^2$/ha)(b) | | | | | mean DBH (cm) (b) | | | | | description of stand composition(b) (c) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Pi | Be | Qu | Fa | total | Pi | Be | Qu | Fa | total | (+) | (...) | (\|) | (°) |
| A | 5 | 19.9 | 1.4 | 0.0 | 0.0 | 21.4 | 16.1 | 9.0 | 6.9 | 7.3 | 14.7 | | Pi | | Pi - Be |
| B | 3 | 27.9 | 0.0 | 0.0 | 0.0 | 28.0 | 22.1 | 0.0 | 0.0 | 17.0 | 22.1 | | Pi (!) | | Pi |
| C | 1 | 18.4 | 0.0 | 0.0 | 0.0 | 18.5 | 24.5 | 28.0 | 5.0 | 0.0 | 24.5 | | Pi | | (Pi) |
| D | 3 | 16.6 | 0.7 | 4.5 | 6.3 | 28.4 | 37.1 | 12.3 | 12.4 | 30.6 | 20.1 | Pi | | Fa | Qu - (Be) |
| E | 1 | 14.4 | 3.7 | 0.2 | 6.7 | 24.9 | 19.5 | 12.6 | 11.0 | 64.3 | 18.6 | Pi | (Fa) | | Be - (Qu) - (Pi) |
| F | 4 | 1.7 | 4.3 | 1.5 | 0.4 | 7.9 | 10.0 | 9.6 | 11.4 | 27.3 | 10.1 | | | | Be - Pi - Qu |
| G | 2 | 0.3 | 10.9 | 6.8 | 0.6 | 18.5 | 9.1 | 22.7 | 10.5 | 15.1 | 13.6 | (Pi) | | Be | Qu - (Fa) - (Pi) |
| H | 2 | 4.9 | 9.5 | 7.2 | 1.2 | 22.7 | 33.3 | 15.0 | 10.3 | 13.8 | 13.2 | Pi | | Be | Qu - (Fa) |
| I | 2 | 4.1 | 10.9 | 5.9 | 0.2 | 21.1 | 26.3 | 8.6 | 11.4 | 8.0 | 9.8 | Pi | | | Be (!) - Qu - (Fa) |
| J | 1 | 0.5 | 19.9 | 0.4 | 0.0 | 22.2 | 32.0 | 16.2 | 10.7 | 0.0 | 13.8 | (Pi) | | Be | (Qu) |
| K | 2 | 20.1 | 0.5 | 5.7 | 0.5 | 27.4 | 39.0 | 8.7 | 15.2 | 31.4 | 22.4 | | Pi | (Fa) | Qu - (Be) |
| L | 2 | 9.2 | 0.3 | 7.5 | 0.1 | 17.3 | 20.2 | 9.6 | 23.4 | 17.5 | 18.9 | Pi | | Qu - (Fa) | (Be) - (Pi) |
| M | 7 | 20.7 | 0.5 | 1.4 | 0.0 | 22.7 | 26.7 | 9.0 | 14.2 | 6.3 | 22.0 | | Pi | | (Qu) - (Be) |
| N | 5 | 19.1 | 1.5 | 1.9 | 0.5 | 23.3 | 28.9 | 11.1 | 10.2 | 13.9 | 18.8 | | Pi | | Qu - Be - (Fa) |
| O | 4 | 12.2 | 5.2 | 2.7 | 0.0 | 20.4 | 29.6 | 11.2 | 18.1 | 0.0 | 16.0 | Pi | | | Be - (Qu) |
| P | 1 | 23.9 | 8.6 | 1.8 | 0.0 | 34.6 | 21.8 | 10.4 | 23.5 | 0.0 | 16.1 | | Pi | | Be - (Qu) - (Pi) |
| Q | 1 | 7.5 | 11.8 | 13.3 | 0.0 | 32.6 | 36.3 | 27.1 | 22.3 | 0.0 | 25.9 | Pi | | Be - Qu | |
| R | 2 | 23.5 | 0.7 | 0.0 | 0.0 | 24.2 | 9.3 | 6.9 | 0.0 | 0.0 | 9.2 | | | | Pi (!) - Be |
| S | 1 | 15.5 | 2.0 | 0.0 | 0.0 | 17.5 | 6.6 | 18.0 | 0.0 | 0.0 | 6.8 | | | (Be) | Pi (!) |

(a) Number of ‘structural class objects’ (first-stage clusters and core areas from both surveys) that are grouped in the SC.

(b) Pi *Pinus sylvestris*; Be *Betula spp.*; Qu *Quercus spp.*; Fa *Fagus sylvatica*; total also includes *Frangula alnus* and *Sorbus aucuparia*.

(c) Based on the values is this table and on values for tree density and mean height per species. Sporadic species are omitted. Legend: (+) declining species; (...) ageing species; (|) emerging species; (°) regeneration; (!) high basal area density; (species) low tree density.

Each SC in Table 2.3 represents a specific stand structure, described by density and mean dimensions of the main species. Some of these are similar with respect to species composition, which makes it possible to distinguish general categories:

(i) Ageing pine stands without much broadleaved regeneration (A, B, C);
(ii) Declining pine stands with relatively high beech density (D, E);
(iii) Mixed regenerations of birch, pine and oak on open areas (F);
(iv) Birch stands with oak regeneration and few old pine trees (G, H, I, J);
(v) Declining pine stands with relatively high oak densities (K, L);
(vi) Ageing pine stands with regeneration of birch and oak (M, N, O, P);
(vii) Mixed oak-birch stands with few old pine trees (Q);
(viii) Very dense pine regeneration on open areas, with some birch (R, S).

### 2.3.2 Predictions of development in ageing Scots pine stands

Figure 2.4 illustrates FORGRA model predictions of basal area and mean DBH for two representative simulation plots with different initial conditions. Remember that the upgraded model predictions (from 400 $m^2$ to 1 ha) should be interpreted in terms of relative relationships between species.

The first model prediction (Fig. 2.4A) starts from an ageing Scots pine stand (pine age approximately 80 years) with seed trees of birch. The tree density of pine gradually decreases from the start (not shown in the figure). As the growth rate of the pine trees is still relatively high, basal area and mean DBH initially increase. After approximately 40 years pine mortality exceeds increment, and the basal area starts to decrease. Near the end of the simulation, when most old pine trees have disappeared, the mean DBH also decreases. Birch capitalises on the decline of the pine, and rapidly reaches a high tree density and basal area in the second half of the simulation.

The second model prediction (Fig. 2.4B) starts from a declining pine stand with some oak and birch regeneration already present and with seed trees of beech. After a short and moderate increase of pine basal area, the species disappears completely from the stand. The birch density also gradually decreases until no trees are left. Stand development is clearly dominated by the oak regeneration, that gradually emerges as pine declines, and leaves no space for birch. At the end of the simulation, oak basal area and mean DBH have reached high values. Next to these, some sporadic seed trees of beech have also grown to relatively large dimensions.

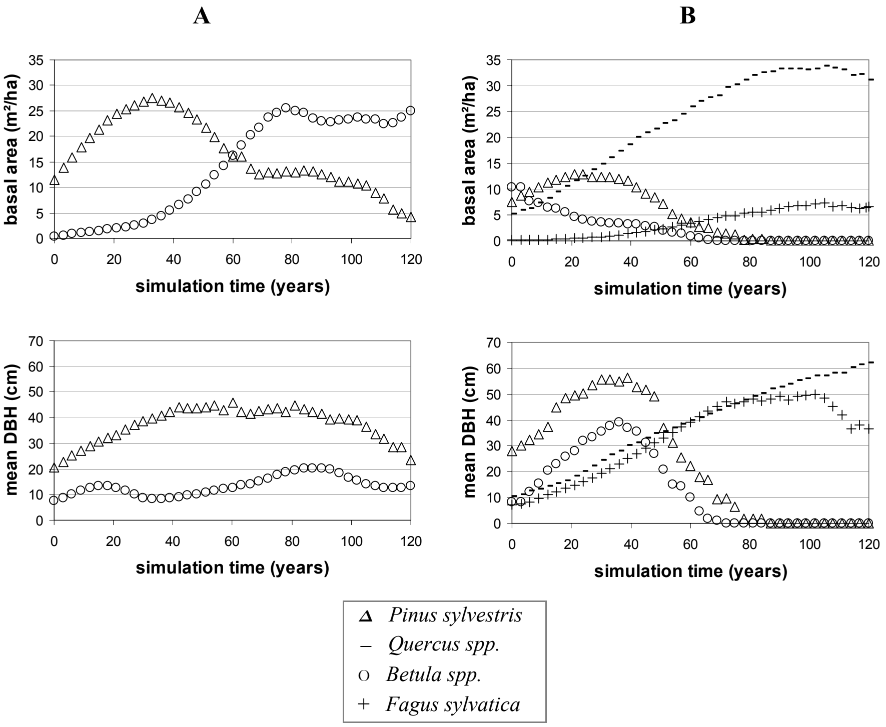


Figure 2.4 Model predictions of basal area and mean DBH for two representative 400 m² simulation plots with different initial conditions: (A) ageing Scots pine with seed trees of birch and (B) declining Scots pine with oak and birch regeneration and seed trees of beech.

### 2.3.3 Pathways of stand development

Table 2.4 summarises the 69 final sequences of SCs (one for each simulation plot). Each of these describes a pathway of stand development in a given simulation plot. Undefined structures (marked as question marks) are recorded 85 times within the final sequences, indicating that the defined SCs do not cover the entire range of possible structures in ageing Scots pine stands. Some of the most striking examples are plots that immediately switch to an undefined structure after one SC. As was to be expected, most of the undefined structures appear at the end of the sequences (59 out of 85), when stands develop towards structures that are not yet observed in the forest reserves simply because the development time was not long enough.

Table 2.4 Final sequences of SCs for all 69 simulation plots.

| plot | sequence(a) | plot | sequence(a) |
|---|---|---|---|
| 1 | (N) – OK – ? – L – ? | 36 | F – G – ? |
| 2 | ? – J – ? | 37 | F – E – DK – ? |
| 3 | A(C) – (MO) – ? – J – (F) | 38 | F – O? – (C) – MN – O – IJ |
| 4 | AB – MN – O – I – J? – F | 39 | F – J – GH – Q – (L) – ? |
| 5 | F – R – A – MN – O – I(J) | 40 | F – G – ? |
| 6 | AB – (M) – NO – IJ – F – ? | 41 | F – G – ? |
| 7 | A – MN – OK – I – F – ? – L | 42 | F – G – ? |
| 8 | R – A – O – ? – J(I) | 43 | F – G(H) – ? |
| 9 | A – O – ? – J – ? | 44 | H – ? – F – ? |
| 10 | MN – A – ? – J – ? | 45 | GH – J – Q – L – ? |
| 11 | MO – ? | 46 | H – O – K? – L – ? |
| 12 | A – MN – ? – J – ? | 47 | H – ? |
| 13 | B – MN – OI – F – J – ? | 48 | G – ? |
| 14 | RS – A – B – M – N – O – I | 49 | G – ? |
| 15 | A – MN – O – ? – J | 50 | N – O – H – ? |
| 16 | F – ? – J – ? | 51 | G – ? |
| 17 | A – MN – O – I(J) – F – ? – L | 52 | G – ? |
| 18 | AB – MN – ? – OI | 53 | G – ? |
| 19 | (R) – AB – MN – F – ? | 54 | G – ? |
| 20 | (R) – B – AM – O – I – F – ? | 55 | G – ? |
| 21 | B – MN – O – F – IJ – ? | 56 | G – ? |
| 22 | (A) – MN – K – I – (F) – R – ? | 57 | G – ? |
| 23 | M – N – O – K – I – H – F – ? | 58 | H – ? |
| 24 | N – ? | 59 | GH – Q – ? – L – ? |
| 25 | A – N(M) – O – H – F – G – ? | 60 | G? – Q? – K – LO – ? |
| 26 | MN – AB – MN – F – ? | 61 | G? – IQ – L – ? |
| 27 | M – N – ? – F – G – ? | 62 | G – ? |
| 28 | (A) – M – NO – IH – FG – ? | 63 | Q? – H – F – ? |
| 29 | NK – (D) – H – F – ? | 64 | GH – Q – L – ? |
| 30 | N – D – ? | 65 | G – (Q) – L – ? |
| 31 | (A) – MN – (O) – IH – F – ? | 66 | G – ? |
| 32 | N – D – ? | 67 | HI – ? – K – D – ? |
| 33 | F – AN – B – MN – K – ? | 68 | F – G – H – ? – Q – (L) – ? |
| 34 | F – N(M) – (A)C – M – K – L | 69 | IO – ? – H – ? – KD – ? |
| 35 | F – A – M(N) – B – NK – ? | | |

(a) for meaning of letters: see Table 2.3.

It appears that none of the sequences contains the structural class P. This SC has thus never been indicated as being the most similar to a model prediction. This can probably be explained by the fact that P is relatively similar to M, N and O (as we know from their statistical proximities), the latter having more chance of being selected since they are represented by 16 SCOs as opposed to only one for P.

Many of the sequences in Table 2.4 are similar and patterns can be observed. The block diagram in Fig. 2.5 is a simplified graphical summary of Table 2.4. Blocks represent SCs, whereas arrows indicate their sequence during stand development. Some SCs are grouped (i.e. ABC, DE, GHIJ, RS). Within such groups, SCs did not manifest a fixed sequence pattern based on the data in Table 2.4. The information in Fig. 2.5 has been checked for consistency by using statistical proximities of SCs.

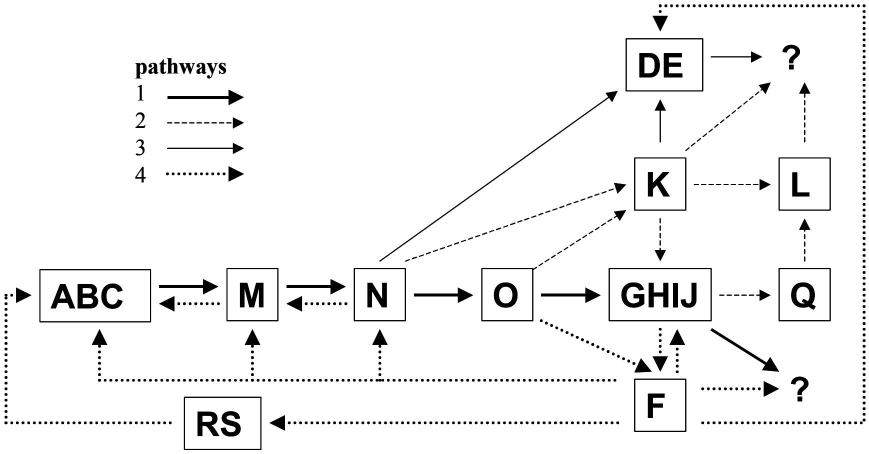
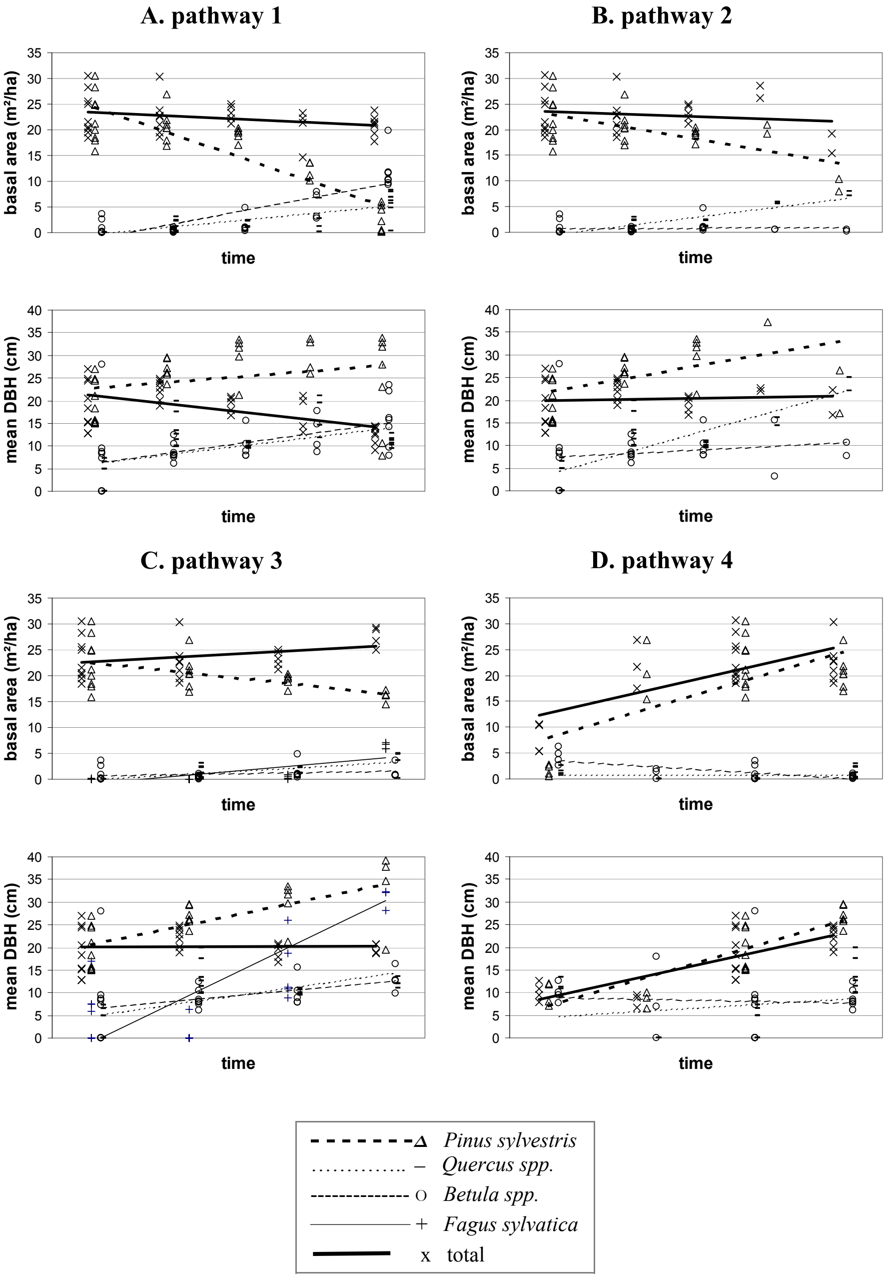


Figure 2.5 Block diagram of the four main pathway patterns. (1) pine to birch; (2) pine to oak; (3) pine to beech; (4) major disturbances. Meaning of letters (SCs) is explained in Table 2.3.

In Fig. 2.5 we distinguish four main pathway patterns that will be described in detail: three presumably linked to gap dynamics and one to major disturbance dynamics. It should be stressed, however, that these are no pathways in themselves, but rather descriptions of the main development patterns within the sequences in Table 2.4. Since these sequences (each describing a 120 years pathway) often combine different development patterns, it is not possible to put a timescale on the four main pathway patterns. We further use the term ‘pathway’ to indicate the main pathway patterns. We only distinguish between 'main pathway (pattern)' and 'actual pathway' where confusion with specific development trajectories is possible.


A. pathway 1

B. pathway 2

C. pathway 3

D. pathway 4

Figure 2.6 Basal area and mean DBH trends in the four main pathways.

For each of the pathways, trends of basal area and mean DBH are visualised (Fig. 2.6). Each of the SCs in the pathways is positioned at a discrete time stage (one point on the abscissa) and is represented on the ordinate by its SCOs to obtain an idea about variability of concrete field situations. A linear trend line is included for each variable.

#### 2.3.3.1 Pathway 1: Scots pine to birch

The first main pathway pattern is indicated with thick arrows in Fig. 2.5. It starts from dense homogeneous Scots pine stands (ABC). During development we first of all observe a spontaneous regeneration of broadleaved species (M and N), mainly birch and oak. A rather abrupt decline of pine density gives an advantage to birch regeneration that finally results in forest structures with hardly any remaining pine trees, increased densities of emerging birch and varying densities of oak and birch regeneration (O to GHIJ). After this stage, development can continue towards pathway 2(b) or 4, or towards undefined structures. Basal area and mean DBH trends for this pathway are shown in Fig. 2.6A.

This is the most common pathway in our sequences (see Table 2.4). Gap origin is probably linked to minor disturbance events (such as storms), which cause the death and toppling of groups of trees throughout the forest. It seems logical that homogeneous even-aged pine stands, when left unmanaged, can easily degrade within a relatively narrow time-frame. This is likely to be the case under circumstances of stress or minor disturbances, especially if these are combined with the low genetic variability of pine trees. This can lead to locally large gaps where a pioneer species such as birch can develop and reach high densities (Perala & Alm 1990).

#### 2.3.3.2 Pathway 2: Scots pine to oak

Like the first main pathway, the second main pathway pattern (dashed arrows in Fig. 2.5) starts from homogeneous Scots pine stands where spontaneous regeneration of birch and oak establish (ABC to M to N). However, pine density decreases more gradually than in the first pathway (N to K). Oak density does not seem to be particularly affected by the rate of decline of pine (Fig. 2.6B); birch density, however, is much lower in the second pathway than in the first due to the less favourable light conditions. The forest develops towards a relatively open canopy of old pine with an understorey of emerging oak and some birch regeneration (K and L). After this stage, development can continue towards pathway 3, or towards undefined structures.

Next to this pathway, we distinguish a subpathway 2(b) with slightly different development trends. The decline of pine density stands midway between pathways 1 and 2 (N to O to K), allowing some more birch regeneration. This implies that stand structure does not necessarily develop directly towards a pine-oak forest (L), but may pass through a stage where birch and oak compete (GHIJ to Q). Eventually, stand development may pass from this subpathway to pathway 1. Note there are some density jumps of species along this subpathway as a result of the methodology used, namely searching for the most similar SC which in this case repeatedly switched between two or more possibilities (probably because the real development was situated somewhere in the middle). For this reason we consider this trajectory to be a subpathway rather than a full pathway.

The pathways 2 and 2(b) occur regularly in our sequences, but not as much as pathway 1. In these forests, the main driving force behind stand development is presumably the mortality of individual trees. Goris (2002) showed that gap origin in the second pathway is also linked to minor disturbances, rather than biotic factors. Differences with the first pathway are therefore mainly due to disturbance intensity and/or frequency, causing different gap sizes. Within these single-tree gaps, light conditions are optimal for the advance regeneration of oak (seedlings established prior to gap formation) that grows up rapidly without the risk of massive birch regeneration (Larsen & Johnson 1998).

#### 2.3.3.3 Pathway 3: Scots pine to beech

The third main pathway pattern is indicated with thin arrows in Fig. 2.5. After the initial development to Scots pine forests with regeneration of broadleaves (ABC to N), this pathway develops towards an understorey of beech under a canopy of pine (N to DE). Basal area and mean DBH trends are illustrated in Fig. 2.6C. Note that this is the only pathway linked to gap dynamics in which the total basal area trend increases, clearly as a result of the presence of beech. The emerging of beech may be preceded by a stage with the regeneration of oak (K). Development always continues towards undefined structures.

This third pathway was only observed occasionally in our sequences, probably because few SCs with beech are available in the data set. There is in fact a widespread scepticism concerning the potentialities of beech in forests on poor sandy soils, which explains the species' marginal importance in past management regimes (Griese 1994). Today there is a growing consensus that the ecological amplitude of beech is higher than was previously thought, and that it can be a dominating species in the terminal stages of undisturbed forest succession on most of the nutrient poor sandy soils of North-Western Europe (Leuschner 1997, Rode 1999a). This was confirmed by the model predictions, where in 19 of the 69 simulation plots beech appeared in low to moderate densities. In our data set however, we only distinguished two SCs with adequate beech densities (D and E) that certainly do not cover the entire range of possible forest structures with beech. As a result, a most similar SC was not found for many of the simulation plots with beech.

#### 2.3.3.4 Pathway 4: major disturbances

The fourth main pathway pattern, indicated in Fig. 2.5 with dotted arrows, is actually a group of pathways that involve major disturbances. The structural class F is in fact a field example of stand structure on a cleared area after a storm. Whereas in many forest ecosystems major disturbances are the main source of variation between pathways, these are only considered to be of secondary importance in ageing Scots pine stands where fire or large-scale uprooting by storm are rare and where management has stopped only recently. Nevertheless, many of the sequences in Table 2.4 develop towards one of these SCs. However, these cases should be interpreted with caution, since all sequences are constructed using the model predictions and major disturbances as such are not included in the model. The only way a major disturbance is reproduced indirectly is when, in a 400 m² simulation plot, all canopy trees die at the same point in time. On the scale of our simulation plots this can easily occur when all canopy trees are of the same species and age, but of course this tells us nothing about the actual frequency of real-scale major disturbances under natural circumstances. Therefore we should not interpret these cases in terms of when and where major disturbances occur; they only tell us that they occur and how they will develop after disturbance.

Based on the sequences in Table 2.4, we can distinguish three cases of stand development after major disturbance: (i) towards one of the three pathways described earlier; (ii) towards undefined structures or (iii) towards a new generation of Scots pine. This last possibility is achieved when a massive regeneration of pine on a cleared area becomes established (F to RS) and the regeneration of broadleaved species is suppressed. Basal area and mean DBH trends for this case are illustrated in Fig. 2.6D. However, less radical circumstances can also cause a more gradual decline of broadleaves in favour of pine, as illustrated in Fig. 2.5 by the arrows from F towards the structural class ABC, possibly passing through N and/or M.

## 2.4 Discussion

Up until now, long-term development series in ageing Scots pine stands on poor sandy soils have not been available. But we make use of field data in forest reserves on the one hand, and model predictions on the other. Forest reserves data are very detailed, but are snapshots in time. Model predictions are consistent with known successional trends in these forests (Jorritsma *et al.* 1999, Kint *et al.* 2002) and with other succession models (Mohren *et al.* 1991), but due to the process-based concept of the model they lack precision (Sharpe 1990). Our research combined both, by defining empirical structural classes with the forest reserves data and using the model predictions to order these in logical sequences. These sequences can then be analysed on aspects that are absent in the model predictions, such as the development of detailed structural patterns. This application can be interpreted as an attempt to construct long-term empirical data series from the readily available short-term data, by using a predictive model as the upscaling criterion.

Our results indicate four main pathway patterns of forest stand development in ageing Scots pine stands: three presumably linked to gap dynamics and one to major disturbance dynamics. The three former pathways differ in light availability for regeneration (depending on gap origin and gap size) and/or seed tree availability (mainly for beech), which results in different types of gap dynamics (Coates & Burton 1997). It is not possible to put a timescale on these four main pathway patterns.

### 2.4.1 Comparison with previous studies on vegetation dynamics

Given a starting point of old Scots pine forests on acidic sandy soils in Western Europe, most forest ecologists would agree that the balance between birch, oak and beech in the subsequent succession will depend on how fast the canopy opens and what seed sources are available. They will also recognise that stand development may be short-circuited or deflected by disturbances, and that these are unpredictable. In this sense, our findings are consistent with results from previous research (e.g. Fanta 1986, Prach 1989, Leuschner 1994, Clerkx *et al.* 2002, Zerbe 2002) and with the vegetation dynamics in forests on poor sandy soils as described in many case studies (Griese 1994, Seidling & Von Lührte 1996, Clerxk & Van Hees 1999, Meyer *et al.* 2000). Although the explicit validation of our results and the description of appropriate timescales for each pathway will only be possible in the long run, when long-term development series become available, we interpret the concordance with previous independent studies as an indirect confirmation of the plausibility of our findings.

However, our study is characterised by some important features that distinguish it from previous studies. As far as we know it is the only attempt to describe vegetation dynamics in ageing Scots pine forests using the pathway concept. Moreover, we are not aware of other research in these forests where the empirical strength of forest reserves data and the predictive ability of process-based models are combined. These elements made it possible to detail and quantify insights into the structure and dynamics of forests on poor sandy soils. This is illustrated by the following aspects of our study:

(i) The SCs are the result of a statistical clustering technique that is not influenced by assumptions about structural features of different development stages. The SCs represent different stand structures that can be distinguished in current ageing Scots pine stands.

(ii) The construction of sequences with these SCs is based on the physiology and autecology of species, summarised in a process-based model. Within the framework of their assumptions, such models provide reliable and generally applicable predictions (Sharpe 1990). This approach provides a sound ecological basis for our results. The sequences of the SCs represent many different actual pathways of stand development in ageing Scots pine forests.

(iii) The four main pathways (Fig. 2.5) represent general patterns of structural development in ageing Scots pine forests. The basal area and mean DBH trends (Fig. 2.6) are realistic quantitative estimations of long-term structural development in these forests.

### 2.4.2 Limits and further research needs

Although the four main pathway patterns described clearly represent important development trends in ageing Scots pine stands, they are certainly not the only ones possible. This is illustrated by three facts:

(i) these pathway patterns are in themselves simplified syntheses of a larger amount of actual pathways in the simulation plots;

(ii) many predicted stand structures could not be approximated with our empirical SCs;

(iii) the model predictions are confined to small simulation plots, with light being the sole main driving force of stand dynamics.

Pathways that are not described in this study may, among other things, be linked to the dominance of bracken (*Pteridium aquilinum* (L.) Kuhn) (Den Ouden 2000), grazing and browsing (Engelmark *et al.* 1998, Blatt *et al.* 2001), exotic species (Maddelein *et al.* 1990), changing resources (Emmer 1995b), and/or pests (Jactel *et al.* 2002).

Other limitations of our study include the absence of information about successional time scales and spatial interactions between pathways. Moreover, we are inevitably limited by the assumption that the factors which operated during the 20 years of plot recording in the forest reserves, will be the only ones to operate in the long term. These are aspects that can only be studied when more and long-term development series become available.

### 2.4.3 Possible applications of the pathway concept in forestry

Conversion towards mixed broadleaved forests is a common current-day management goal in ageing Scots pine forests throughout Europe (Kenk & Guehne 2001). Since natural regeneration of broadleaved species establishes easily in these forests, the use of natural vegetation dynamics is often thought to be the best conversion method. This idea relates to the concept of close-to-nature forestry, which is characterised by a fundamental choice of working with and/or emulating natural vegetation dynamics (Lähde *et al.* 1999a).

Natural vegetation dynamics and forest management both act on stand structure and structural development. They influence each other through their direct impact on stand structure. Our main pathways actually describe patterns of stand structural development in ageing Scots pine forest resulting from natural vegetation dynamics. As such they can help to anticipate on natural vegetation dynamics and to incorporate them into management. Our results suggest that with moderate silvicultural treatments, homogeneous even-aged Scots pine plantations may be directed into different development pathways.

We suggest that the introduction of the pathway concept (as opposed to the climax concept) in close-to-nature forestry practice can encourage managers to deal with target forest structures in a more flexible manner. The pathway concept focuses on different development trajectories for a site rather than on a climax forest structure, and as such may help to diversify management. Moreover, with the estimations of basal area and mean DBH trends for the four main pathways described, new quantitative instruments for management planning have become available. Clearly other quantitative trends, e.g. of tree density or structure indices (Kint 2003), might also serve this purpose.

# 3 Spatial methods for quantifying forest stand structure development: a comparison between nearest-neighbour indices and variogram analysis

Kint, V., Van Meirvenne, M., Nachtergale, L., Geudens, G. & Lust, N.

Redrafted from: Forest Science (2003), 49(1), 36-49.

## Abstract

Insight into forest stand structure is of capital importance for understanding forest ecosystem structure and function. The ability of two spatial methods – based on (i) nearest-neighbour indices and (ii) geostatistical variogram analysis – to quantify forest stand structure and its development over short time periods was investigated in two mixed Scots pine stands. Results show that the two methods are complementary in quantifying spatial characteristics of forest stand structure: positioning, mixture and differentiation. The principal advantage of nearest-neighbour indices was their capacity for detecting subtle structure changes; moreover they are easy to calculate and interpret. Variograms of height and indicator variograms of presence/absence data were more complicated in their use and required more input data, but provided additional information on the number, impact and range of structure-determining factors such as competition and management. In this context the concept of the mark variogram is discussed.

## 3.1 Introduction

Quantitative data on forest stand structure are essential inputs for understanding ecosystem structure and functioning, and hence for sustainable forest management. The three-dimensional geometry of stands has both ecological and economic implications. The link between structure and biodiversity, ecological stability and future development of forest stands is widely recognized. The tree distribution pattern (further denoted as *positioning*) particularly determines different light regimes and regeneration patterns within the stand (Emborg 1998) and has a significant influence on growth and timber production (Pretzsch 1995). The number and distribution pattern of different tree species (*mixture*) determines light regime (Canham *et al.* 1994) and litter composition (Ferrari 1999), thus controlling a variety of biotic and abiotic processes. Vertical and horizontal size differentiation, resulting from positioning, mixture, age distribution and competition (*differentiation*), determines the spatial variation in microclimatic conditions, food supply and structural complexity, thus directly and indirectly affecting the presence and abundance of different animal and plant species (Spies 1998, Brokaw & Lent 1999).

Moreover, each management intervention is influenced by and in turn influences stand structure. Simulation or long-term monitoring of natural and human-driven stand structure development is therefore often used to evaluate the impact of current management practices (Buongiorno *et al.* 1994, Pretzsch 1996, Bailey & Tappeiner 1998).

Many methods for quantifying forest stand structure have been proposed. They can mainly be subdivided into two broad categories: (i) *non-spatial* and (ii) *spatial* methods. Spatial methods can further be distinguished as those using spatial indices on the one hand and those based on spatial statistical techniques on the other hand (Kint *et al.* 2000).

Non-spatial methods describe mean stand characteristics, independent of relative tree positions. Non-spatial indices quantify vertical structure, horizontal structure or species diversity. Examples are the Shannon-Wiener and Simpson indices (Magurran 1988 p.34-41), the 'Foliage Height Diversity' of MacArthur & MacArthur (1961), the 'Vertical Species Profile' of Pretzsch (1996) or the within-stand diversity index 'LLNS' of Lähde *et al.* (1999b). Stand structure however as we see it is an explicit spatial concept, whereas non-spatial indices neglect the spatial variation in tree size and the spatial distribution of tree species within the stand. Therefore in this chapter we will not consider this category of indices.

All spatial methods to describe stand structure take relative tree positions into account. A first category is based on the use of spatial indices. Many quadrant count and distance indices have already been summarised by Pielou (1977), Ripley (1981) and Upton & Fingleton (1985, 1989). Recently some new indices have been developed, all based on nearest-neighbour mathematics (Füldner 1995, Pretzsch 1997, Von Gadow & Hui 1999 p.131-140, Zenner & Hibbs 2000). These indices quantify each of the structural characteristics of forest stands – positioning, mixture and differentiation – separately, and should give a detailed insight into both stand structure and processes guiding its development.

A second category of spatial methods is based on spatial statistical techniques, such as point pattern analysis (Penttinen *et al.* 1992) and geostatistics (Goovaerts 1997). These are the most detailed methods for structure description, as distances between all pairs of trees within the stand are used to investigate the spatial pattern and autocorrelation of tree variables, such as dimensions or species. Results often reveal important spatial correlation within stands, thus improving the insight into stand structure and forest dynamics (Biondi *et al.* 1994, Kuuluvainen *et al.* 1996, 1998).

Each of the mentioned methods has been applied individually to characterise the structure of a stand and its development over time, but only few comparative studies have been conducted. In this chapter we will compare the performance of two spatial methods: (a) nearest-neighbour indices and (b) variogram analysis. More specifically, the objective of this chapter is threefold:

(i) Give a short description of each investigated method.
(ii) Present a case study in which results of both methods are interpreted in detail.
(iii) Address the ability of these approaches for answering two major questions: first whether the methods are effective (do they accurately quantify stand structure?) and secondly whether they are sensitive to changing structure (do they accurately quantify short-term stand structure development?).

## 3.2 Nearest-Neighbour indices

We chose to calculate a set of four spatial indices. According to Pielou (1977 p.226) and Gleichmar & Gerold (1998) distance indices are better suited for the description of (relative) spatial patterns than quadrant count indices. Therefore we focused on indices based on nearest-neighbour mathematics.

The primary criterion in defining the set of indices was that they should describe the three structural characteristics of forest stands: positioning, mixture and differentiation. For the description of (relative) spatial patterns and mixture, two commonly cited indices are selected, CE and S, along with the promising DM-index. For differentiation the only nearest-neighbour index known to us is T. Since vertical differentiation is of great ecological interest, we calculated T for height (TH).

### 3.2.1 The positioning index of Clark & Evans – CE

The *positioning index* CE, first described by Clark & Evans (1954), expresses the extent to which a forest stand deviates from the 'Poisson stand', i.e. a stand with a complete randomised spatial distribution of trees. The average distance between a tree and its nearest neighbour ($r_A$) is compared to the expected mean distance if trees were randomly positioned ($r_E$). With the edge effect correction of $r_E$ for compact unit areas by Donnelly (1978) this gives:

$$CE = \frac{r_A}{r_E} = \frac{\frac{1}{N}\sum_{i=1}^{N} r_i}{0.5 \cdot \left(\frac{A}{N}\right)^{1/2} + 0.0514 \cdot \frac{P}{N} + 0.041 \cdot \frac{P}{N^{3/2}}}$$

where $r_i$ is the distance between tree i and its nearest neighbour (in m), $N$ is the total number of trees in the sample plot, $A$ is the area of the plot (in m²) and $P$ its perimeter (in m). A Poisson stand has a CE value of 1. If clusters occur within the stand, CE will be smaller than 1. In regular positioned stands CE becomes larger than 1, with a maximum of 2.15 for a hexagonal arrangement of trees. The simplicity of calculation and the limited index range (between 0 and 2.15), simplifies the comparison between different stands.

In order to test the calculated CE values against a significant deviation of 1, the proposed statistic of Clark & Evans (1954) is applied. They test the null hypothesis ($H_0$: CE = 1 and $H_1$: CE ≠ 1) using a standard, normally distributed test value:

$$c = \frac{r_A - r_E}{\sigma_{r_E}} \qquad \text{with} \qquad \sigma_{r_E} = \frac{0.26136}{\sqrt{N \cdot \rho}}$$

where $\sigma_{rE}$ is the standard deviation of $r_E$ in a Poisson-forest of density $\rho$.

Pielou (1977 p.156) and Smaltschinski (1998) draw attention to shortcomings of CE in clustered stands. When clustering is likely to be present, other indices may be better suited if the purpose is to compare index values between stands (see Gleichmar & Gerold 1998 for examples). In most current managed stands in Western Europe – usually planted and uniformly treated – clustering is unlikely (Füldner 1995), so CE can be used.

### 3.2.2 The segregation index of Pielou – S

The *segregation index* S (Pielou 1977 p.226-229) quantifies the relative mixing of two species, independently of their spatial pattern, and supposes no other species are present in the stand. It is based on the comparison between the observed number of mixed pairs ($M_O$) and the expected number under random conditions ($M_E$).

Table 3.1 Contingency table, defining the values for the calculation of the segregation index of Pielou (S) for the species A and B.

| species | number of nearest neighbours of | | |
|---|---|---|---|
| | species A | species B | species A + B |
| species A | a | b | m |
| species B | c | d | n |
| species A + B | v | w | N |

Given a contingency table (Table 3.1), summarising the number of trees of both species with a nearest neighbour of their own species and of the other species, S is calculated as follows:

$$S = 1 - \frac{M_O}{M_E} = 1 - \frac{N \cdot (b + c)}{v \cdot n + w \cdot m}$$

Thus a distinction can be made between aggregation (association between species; $-1 < S < 0$), segregation (spatial separation; $0 < S < 1$) or neutral relation (random mixture; $S = 0$) between two tree species. A $\chi^2$-test may be used to judge whether the observed mixture departs significantly from that under random conditions ($H_0$: $S = 0$ and $H_1$: $S \neq 0$).

In mixed stands with more than two species, S does not necessarily describe competition effects between the two investigated species, as other species can also influence their relationship. Even in two-species stands, factors besides competition effects can affect S, e.g. seed tree position, past or present management and physical barriers. Therefore, 'segregation' and 'aggregation' shouldn't be understood in terms of competition, but are merely spatial pattern descriptions.

### 3.2.3 The mixture index of Von Gadow – DM

The *mixture index* DM, first introduced by Von Gadow (1993), for each individual tree i is defined as the probability that none of the three nearest neighbours is of the same species as tree i:

$$DM_i = \frac{1}{3} \cdot \sum_{j=1}^{3} V_{ij}$$

with

$$V_{ij} = \begin{cases} 0 \rightarrow \text{ tree i and neighbor j of the same species} \\ 1 \rightarrow \text{ tree i and neighbor j of different species} \end{cases}$$

It will be clear that $DM_i$ can take only four values: 0 – 0.33 – 0.66 – 1. The mean value for all trees represents the index value for the stand. Values can be calculated for each species separately or for all trees together. Depending on relative frequency and spatial pattern of a certain species within a stand, DM can take values between 0 and 1: strongly represented or segregated species will result in low DM values (indicating that homogeneous groups of tree species occur), whereas less frequent or regularly positioned species will have high DM values (indicating their complete mixture within the stand).

As no theoretical test exists to investigate significant differences between observed and under random mixture expected DM-values, a permutation approach has to be used (Lewandowski & Pommerening 1997). We generated 1000 permutations of the species distribution in the investigated stand (randomly re-assigning species-values to tree coordinates) and calculated for each permutation a DM-value. A two-sided test will indicate a significant difference from random mixture at an approximate level of $\alpha = 0.05$ (or 0.01) if the observed DM-value is within the 2.5% (or 0.5%) lowest or highest simulated DM-values.

S and DM are fundamentally different, both mathematically and with respect to interpretation, because of the number of nearest neighbours involved (one for S, three for DM) and the application possibilities (pairs of species for S, single species or groups for DM).

### 3.2.4 The height differentiation index of Von Gadow – TH

The *height differentiation index* TH (Von Gadow 1993) describes the difference (or similarity) in height between neighbouring trees. TH of a single tree i with height $H_i$ in relation to its three nearest neighbours is defined as:

$$TH_i = \frac{1}{3} \cdot \sum_{j=1}^{3} \left[ 1 - \frac{MIN\left(H_i, H_j\right)}{MAX\left(H_i, H_j\right)} \right]$$

where $H_j$ is the height of the $j^{th}$ nearest neighbour of any species (for total TH-values) or of the same species (for TH-values of that species). The mean value for all trees represents the index value for the stand. Values range between 0 and 1. Stands with almost no vertical structure differentiation will have a value close to 0, whereas highly differentiated stands will approach a value of 1. The same permutation approach as described for DM was used to decide on significant differences between observed and under random conditions expected TH-values, generating 1000 permutations of the height distribution in the investigated stand.

$DM_i$ and $TH_i$-values are calculated for every single tree and then averaged for the whole stand. A frequency distribution of these values can thus be calculated. This approach is especially useful for interpreting index-change over time. In this chapter we will illustrate the principle of calculating and interpreting frequency distributions using TH. For this purpose, we divided the TH-range into five equal classes. Note that for DM the same approach would result in four classes, as only four $DM_i$-values are possible.

## 3.3 Spatial statistics

Stand structure description based on spatial statistics can mainly be subdivided in two groups: (i) point pattern analysis and (ii) surface pattern analysis or geostatistics (Mateu & Ribeiro 1999). The first applies directly to spatial point processes and has therefore often been discussed in the context of forest stands (Penttinen *et al.* 1992, Moeur 1993, Chen & Bradshaw 1999). Most of the results of point pattern analysis can also be achieved by using geostatistical techniques, but the latter have some important advantages – such as the possibility of fitting a model to experimental second-order characteristics, kriging or stochastic simulation. We therefore chose to focus only on a geostatistical approach.

The use of geostatistics is not new in forest applications at the stand level. Kuuluvainen *et al.* (1996, 1998) calculated variograms of tree size in old growth and managed forest stands. Biondi *et al.* (1994) investigated the long-term change of variograms in a naturally evolving forest stand. Samra *et al.* (1989) used the technique in young plantations. Grushecky & Fajvan (1999) calculated indicator variograms of crown cover and regeneration data, measured on a regular grid. To our knowledge, the use of indicator variograms for the analysis of tree presence/absence data as we propose in this chapter has not yet been applied in the context of forestry.

### 3.3.1 Geostatistical theory of variograms

Geostatistics was developed to study variables that are distributed continuously in space, called '*regionalized variables*' (Isaaks & Srivastava 1989, Cressie 1991, Goovaerts 1997, Olea 1999). The basic principle of geostatistics is that correlation between values of a regionalized variable $Z$ will decrease as distance between the sample points increases. A Random Function (RF) expresses the spatial variation of $Z$, and its spatially autocorrelated component is mathematically described by a second-order characteristic. The latter can be estimated under assumption of second order stationarity, indicating that (i) the expected value of the RF exists and is independent of the location and (ii) the second-order characteristic of the RF exists and depends on the distance **h** (called the *lag*) between points. The most commonly used second order characteristic in forest applications is the variogram γ(**h**), as it is based on weaker stationarity assumptions:

$$\gamma(\mathbf{h}) = \frac{1}{2} Var\left[Z(\mathbf{x}) - Z(\mathbf{x}+\mathbf{h})\right] = \frac{1}{2} E\left[\left\{Z(\mathbf{x}) - Z(\mathbf{x}+\mathbf{h})\right\}^2\right]$$

The experimental value of *Z* in location **x**, *z*(**x**), is called a Random Variable (RV) of the RF. In order to estimate the variogram, the RF of *Z* is sampled at different points in space. A set of RV is used to calculate the experimental variogram:

$$\gamma(\mathbf{h}) = \frac{1}{2N(\mathbf{h})} \sum_{i=1}^{N(\mathbf{h})} \left[z(\mathbf{x_i}) - z(\mathbf{x_i}+\mathbf{h})\right]^2$$

where N(**h**) is the number of pairs of sample points that are separated by a lag **h**. The parameters of the theoretical variogram can be estimated by fitting a model to the experimental variogram. When spatial dependence is present and under assumption of second-order stationarity, the modelled variogram will generally increase with distance until a constant value is reached (called the *sill*). The distance at which the sill is reached is called the *range*. It is often observed that the modelled variogram for a distance approaching zero does not equal zero; this jump discontinuity for **h** > 0, called the *nugget*, is caused by spatial correlation at distances shorter that the smallest sampling distance (micro-scale variation) and by random sources of error (like measurement errors).

Since **h** is a distance vector, the variogram is a function of both distance and direction. To determine whether an anisotropy should be incorporated into the variogram model, directional experimental variograms are calculated.

### 3.3.2 Variograms of tree variables

Trees are discrete objects, so the variables associated with them are not strictly regionalized variables. Nevertheless, tree occurrence and size can be thought to be directly influenced by different spatially continuous variables, such as solar radiation, soil characteristics, and water and nutrient availability, thus allowing the use of variograms for characterising their spatial variation. It should however be borne in mind that variograms of tree variables in reality are *mark variograms*, i.e. second-order characteristics of a spatial point process (Mateu & Ribeiro 1999). Unlike regionalized variables, tree variables are not only characterised by a mean and two sources of variability (the spatial autocorrelation and a random error), but also a third source of spatial variation is introduced by the interaction between trees. Furthermore, human intervention (like thinning) also can influence directly or indirectly spatial variation of tree variables. The mark variogram also quantifies these effects of interaction between trees and human intervention, and as a result its form can deviate from that of the classical variogram. Theoretical variogram models do not always reflect these deviations, and their fitting to experimental mark variograms may require the exclusion of some experimental variogram points.

To investigate the size differentiation, we calculated experimental variograms $\gamma(\mathbf{h})$ of height for each tree species separately. Lag spacing was chosen as a function of pairs per lag distance. We found experimental variograms to behave in a stable way when at least 30 pairs for each plotted lag distance were available, often resulting in a lag spacing of 2 or 3m. Experimental variograms were calculated up to inter-tree distances of 90m. In some cases, the experimental variogram was clearly influenced by one or at most two outliers; these were identified through the calculation of the variogram cloud and the **h**-scatter-plots, and eventually masked. Variogram anisotropy, as investigated through the experimental variogram surface, was not found; consequently only omnidirectional experimental variograms were modelled.

To detect spatial patterns in the alternation of tree species we calculated an experimental indicator variogram $\gamma_I(\mathbf{h})$ for every species separately. In case of species A being investigated, a value equalling 1 was assigned to each tree if it was of species A and 0 if it was not. With this indicator value, the experimental variogram as defined above was calculated: it estimates how often two trees at distance **h** from each other have different indicator values. The smaller $\gamma_I(\mathbf{h})$, the greater the spatial connectivity of species A at distance **h** is (Goovaerts 1997 p.41).

### 3.3.3 Experimental variogram fitting

In order to estimate variogram parameters (range, sill and nugget), we used the combined visual and statistical fitting technique as integrated in the Variowin software (Pannatier 1996). In all cases, we found a (double) spherical model to give the best fit. This model is defined as:

$$\gamma(\mathbf{h}) = C_0 + \gamma_1(\mathbf{h}) + \gamma_2(\mathbf{h}) \quad \text{if} \quad \mathbf{h} > 0$$

with

$$\gamma_1(\mathbf{h}) = \begin{cases} C_1 \cdot \left( \dfrac{3 \cdot \mathbf{h}}{2 \cdot a_1} - \dfrac{1}{2} \cdot \left( \dfrac{\mathbf{h}}{a_1} \right)^3 \right) & \text{if} \quad 0 < \mathbf{h} \leq a_1 \\ C_1 & \text{if} \quad \mathbf{h} > a_1 \end{cases}$$

and

$$\gamma_2(\mathbf{h}) = \begin{cases} C_2 \cdot \left( \dfrac{3 \cdot \mathbf{h}}{2 \cdot a_2} - \dfrac{1}{2} \cdot \left( \dfrac{\mathbf{h}}{a_2} \right)^3 \right) & \text{if} \quad 0 < \mathbf{h} \leq a_2 \\ C_2 & \text{if} \quad \mathbf{h} > a_2 \end{cases}$$

where $C_0$ is the nugget, $a_1$ and $a_2$ are the ranges of the operating spatial factors and $C_1$ and $C_2$ the corresponding sills. Thus, for every variogram five parameters were estimated. The total sill $C_{tot}$ of the variogram is $C_0+C_1+C_2$.

## 3.4 Case Study

Our case study is of two planted Scots pine (*Pinus sylvestris* L.) stands that are being converted to mixed broadleaf stands: (i) parcel 10 of the state-owned forest in Ravels (UTM 31UFS3992 or 51°22'N; 5°00'E) and (ii) parcel 12a of the state-owned forest 'Gemeentebos' in Hechtel (UTM 31UFS6365 or 51°07'N; 5°20'E), both in the Campine region of Belgium. Soil texture at both sites is sand of aeolian origin. In Ravels a distinct micro-relief causes the soil moisture conditions to vary from moderately wet to wet, whereas in Hechtel dry land dunes characterise the landscape.

There are no significant climatic differences between both sites. Table 3.2 summarises tree demographics in both stands.

Table 3.2 Tree demographics in Ravels and Hechtel in 1992 and in 1998.

| stand | year | species[(a)] | tree density (/ha) | basal area (m²/ha) |
|---|---|---|---|---|
| Ravels | 1992 | Pi | 192 | 15.2 |
| | | Qu | 252 | 4.1 |
| | | Qr | 215 | 4.5 |
| | | Ps | 170 | 1.6 |
| | | total | 853 | 25.6 |
| | 1998 | Pi | 70 | 6.4 |
| | | Qu | 211 | 4.7 |
| | | Qr | 201 | 7.0 |
| | | total | 492 | 18.3 |
| Hechtel | 1992 | Pi | 42 | 5.9 |
| | | Qu | 367 | 9.6 |
| | | total | 426 | 16.1 |
| | 1998 | Pi | 40 | 6.2 |
| | | Qu | 321 | 11.1 |
| | | total | 376 | 18.0 |

(a) Pi *Pinus sylvestris*; Qu *Quercus robur*; Qr *Quercus rubra*; Ps *Prunus serotina*.

### 3.4.1 Stand description

In parcel 10 in Ravels (13.2 ha), Scots pine was planted in 1908. After partial harvesting of Scots pine trees during the Second World War, pedunculate oak (*Quercus robur* L.) was planted under the canopy. About 10 years later, an even-aged natural regeneration of red oak (*Quercus rubra* L.) established in patches where pedunculate oak had not survived, and a shrub layer consisting of black cherry (*Prunus serotina* Ehrh.) developed. Treatment was always intensive: e.g. between 1960 and 1992, on average 5 m³/ha of mainly pinewood were harvested yearly, thus giving form to a mixed stand (Fig. 3.1A). In 1993 a thinning to encourage release of pedunculate oak and red oak, removed more than 40% of the standing volume by cutting nearly 2/3 of the old Scots pine trees and all black cherries. Also on this occasion, a selective thinning of oak was carried out where red oak was removed preferably. In Fig. 3.1B the effect of the 1993 thinning is evident. As a result of the intensive treatment in this stand, it can be assumed that its development was guided predominantly by human intervention.

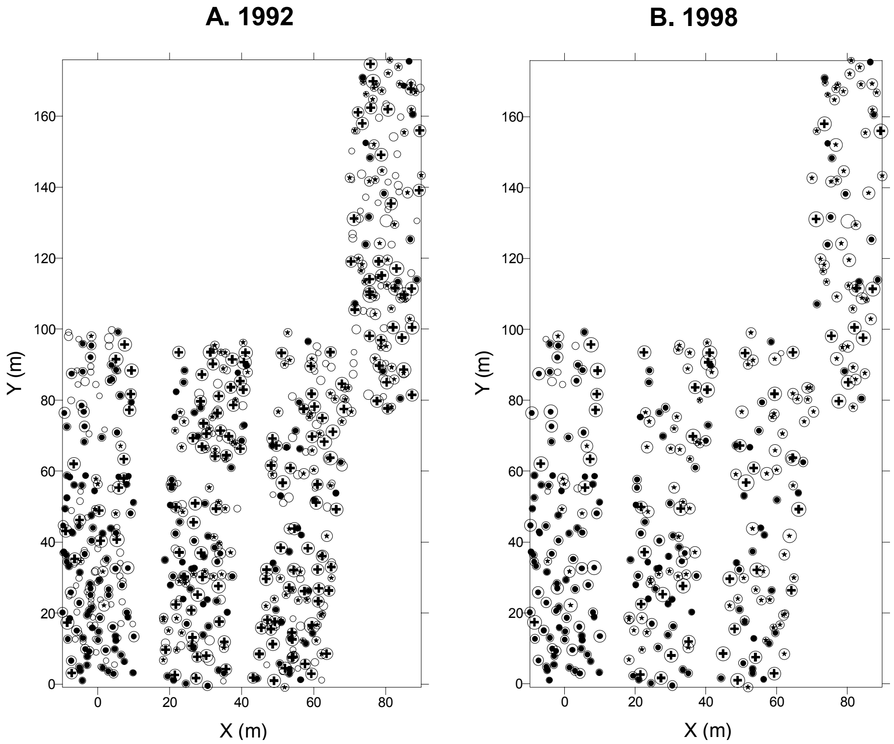


Figure 3.1 Position, from the left to the right, of the permanent sample plots A, B, C and E, and of the measured trees in compartment 10 in Ravels in 1992 and 1998. The radius of the circles is proportional to the circumference. Plot D is not shown because of its remote location. Legend: • = pedunculate oak; * = red oak; + = Scots pine; no indication = other.

Parcel 12a in Hechtel (4.2 ha) was planted as a homogeneous Scots pine stand, presumably in 1907. Approximately 15 years later, it transformed into a mixed stand with mainly pedunculate oak and some red oak. It is not known whether this was the result of oak planting or natural regeneration in the young pine plantation. Heavy thinnings in 1964 and 1973 removed almost all pines. Since then, no more thinnings have been carried out until the end of 1991, when the few remaining red oak trees were removed, resulting in a stand of pedunculate oak under a sparse canopy of old pines (Fig. 3.2A). In the six year time interval between measurements no intervention took place, as can be observed in Fig. 3.2A and 3.2B. As the stand has only been lightly thinned once between 1973 and 1998, it is assumed that stand structure in this period has been influenced also by competition between trees and the consequent self-thinning.

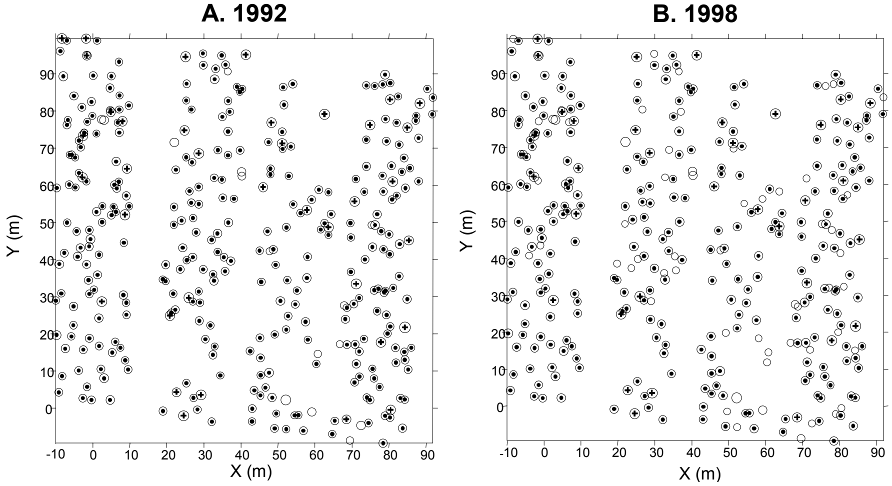


Figure 3.2 Position, from the left to the right, of the permanent sample plots E, D, C and B, and of the measured trees in compartment 12a in Hechtel in 1992 and 1998. The radius of the circles is proportional to the circumference. Plot A is not shown because of its remote location. Legend: • = pedunculate oak; + = Scots pine; no indication = other.

### 3.4.2 Measurements and sample plots

In both stands five permanent sample plots were laid out, each 100m by 20m, thus occupying a total area of 1 ha within each stand. For all trees with a diameter at breast height greater than approximately 4.7cm (i.e. circumference of 15cm) the following parameters were recorded in 1992 and in 1998: species, circumference, height and position.

Two major questions arise about the use of long and narrow plots in this analysis. First there is a problem of edge effects in calculating the indices. The calculated nearest neighbours for a tree standing near the edge of a plot are not necessarily the real nearest neighbours and as a result, a distortion of the correct index value can arise. A buffer is often used to eliminate edge effects, but due to the narrow plot shape we could not use this correction. To quantify the distortion of index values due to edge effects, we calculated the index values in Hechtel also on a larger 1998 data set, which comprises entirely four of our plots along with all intermediate trees. In this larger data set all edge effects were eliminated through a buffer. Height measurements are not available for this larger data set, so instead of TH we calculated TC (differentiation of circumference). These correct index values were only slightly different from those calculated in our plots (distortions between 0 and 9%) for all indices. For S, DM and TC all significance tests gave the same result. Only for CE we observed a significant overestimation of the correct value, resulting in a biased test that too often concluded regular positioning. These are strong indications that nearest-neighbour indices may also be calculated in plots without edge effect correction, under condition of cautious interpretation of CE significances.

Variogram analysis is not affected by this problem, as distances between trees rather than nearest neighbours are used. But a second problem linked to using long and narrow plots arises, since the narrowest dimension of the plots restricts lag distances. The available dataset has the potential to produce variograms over longer lag distances, provided that also exact distances between trees in different plots can be calculated. To obtain this, we measured the position and orientation of each plots relative to a common coordinate system and recalculated the coordinates of all trees (Fig. 3.1 and 3.2 show the stands after this conversion). In this way it became possible to characterise spatial phenomena related to the concepts of positioning, mixture and differentiation on a scale larger than the plot width.

### 3.4.3 Indices - results and discussion

Values for the spatial indices in 1992 and 1998 in Ravels and Hechtel are summarised in Table 3.3. CE, DM and TH were calculated for every tree species separately as well as for the whole stand. S was calculated for every pair of the major tree species.

#### 3.4.3.1 Positioning

The positioning index CE shows similar characteristics in both stands: tree species are either randomly positioned or show a tendency towards regularity, none of the species are clustered. The fact that Scots pine in Hechtel, although planted, is not regularly spaced, illustrates the long term randomising effect of thinning: even when uniformly thinned, the original regular pattern of a plantation is broken as a result of a stochastic thinning component.

Table 3.3 Values of spatial indices in Ravels and Hechtel in 1992 and in 1998.

| stand | year | species$^{(a)}$ | CE$^{(b)(e)}$ | S$^{(a)(c)(e)}$ | | DM$^{(d)(e)}$ | TH$^{(d)(e)}$ |
|---|---|---|---|---|---|---|---|
| | | | | Qu | Qr | | |
| Ravels | 1992 | Pi | 1.15** | 0.062 | -0.059 | 0.797 | 0.085**$^{<}$ |
| | | Qu | 1.00 | | 0.293** | 0.644**$^{<}$ | 0.175**$^{<}$ |
| | | Qr | 0.96 | | | 0.645**$^{<}$ | 0.159**$^{<}$ |
| | | Ps | 1.02 | | | 0.810 | 0.292**$^{<}$ |
| | | total | 1.07** | | | 0.722**$^{<}$ | 0.317 |
| | 1998 | Pi | 1.15** | 0.051 | 0.056 | 0.890 | 0.105*$^{<}$ |
| | | Qu | 1.02 | | 0.353** | 0.420**$^{<}$ | 0.190**$^{<}$ |
| | | Qr | 0.97 | | | 0.426**$^{<}$ | 0.120**$^{<}$ |
| | | total | 1.10** | | | 0.501**$^{<}$ | 0.203**$^{<}$ |
| Hechtel | 1992 | Pi | 1.10 | -0.080 | | 0.976 | 0.101*$^{<}$ |
| | | Qu | 1.11** | | | 0.141 | 0.251**$^{<}$ |
| | | total | 1.14** | | | 0.252 | 0.283**$^{<}$ |
| | 1998 | Pi | 1.10 | -0.090 | | 0.967 | 0.097 |
| | | Qu | 1.15** | | | 0.155 | 0.238**$^{<}$ |
| | | total | 1.16** | | | 0.270 | 0.270**$^{<}$ |

(a) Pi *Pinus sylvestris*; Qu *Quercus robur*; Qr *Quercus rubra*; Ps *Prunus serotina*.

(b) The hypothesis tested is $H_0$: CE = 1 and $H_1$: CE ≠ 1.

(c) The hypothesis tested is $H_0$: S = 0 and $H_1$: S ≠ 0.

(d) The hypothesis tested is $H_0$: DM (TH) = $DM_{ran}$ ($TH_{ran}$) and $H_1$: DM (TH) ≠ $DM_{ran}$ ($TH_{ran}$); where $DM_{ran}$ ($TH_{ran}$) is the expected value when species- (height-) values are randomly re-assigned to tree coordinates in a permutation approach.

(e) * indicates a significant difference at the $\alpha = 0.05$ level; ** idem at the $\alpha = 0.01$ level; for DM and TH a > or < sign indicates whether the observed value is greater or lesser than the expected value.

As values in 1998 seem consequently higher than those in 1992 (apart from Scots pine in Ravels, as a result of the randomising effect of the 1993 thinning), we can conclude that a slight shift towards more regularity in both stands occurred. The reason for this in Hechtel is probably the competition for space within the even-aged regeneration of oak, resulting in a more evenly distributed oak population. In Ravels, this illustrates the short-term effect of selective thinning in a randomly spaced population: it will tend to increase regularity by giving equal space to all individuals.

#### 3.4.3.2 Mixture

The segregation index S shows a very significant spatial separation between pedunculate oak and red oak in Ravels ($p < 0.01$). This seems logical since the red oaks are about 10 years younger than the pedunculate oaks and would therefore have mainly become established where the latter were less dense. In Hechtel, pines and oaks are randomly mixed. The presence of negative S values in our case should not be interpreted as a tendency towards aggregation of species (in the ecological sense of the word), but rather as an effect of thinning (we will discuss this in detail in the section about indicator variograms).

The change of S values between 1992 and 1998 was considered also. In Hechtel this change is negligible. In Ravels differences are clear: the spatial separation between species became more pronounced. This demonstrates that the 1993 thinning in Ravels mainly focused on liberating trees from competitors of a different species, thereby accentuating homogeneous patches within the stand.

The DM index in stands with intimate mixture is mainly determined by the relative abundances of the species. Strongly represented tree species will yield low DM values, as they probably have few neighbours of a different species. Consequently, in Hechtel we found a low DM value for pedunculate oak and a high value for Scots pine. Significance values indicate (as for S) that all species are randomly mixed. In Ravels in 1992, tree species abundances, and thus DM values, are rather similar. Pedunculate oak and red oak (and as a result also the total DM-value) have a very significantly lower value than expected in a random mixture, which again is consistent with S. Total DM values are weighted averages of species-specific values and give a general idea about mixture in a stand: low in Hechtel, high in Ravels.

Between 1992 and 1998, in Ravels we note a general decline in the mixing of species, which seems the logical consequence of the complete elimination of black cherry. Scots pine is the only exception to this: the heavy thinning of pine trees decreased its relative presence, augmenting the chance of finding other species as a neighbour. The overall result is a clear decrease of DM in the stand. In Hechtel, competition based mortality of pedunculate oak (reducing its relative abundance) results in a slight shift towards a higher DM value for the stand.

#### 3.4.3.3 Height differentiation

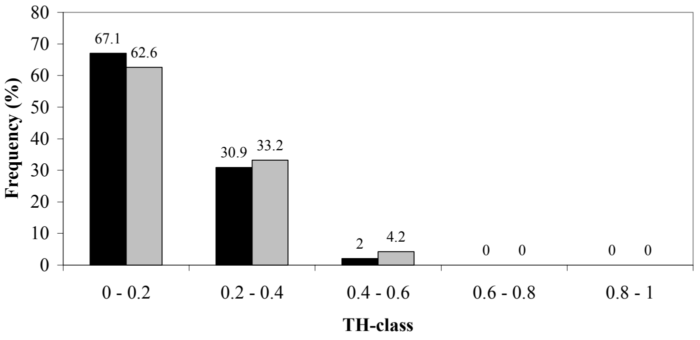
TH is very low in both stands, either for individual tree species or for the whole stand. This means that only limited height differences between neighbouring trees can be observed. Note that nearly all values are (very) significantly lower than the expected value when all observed heights are randomly re-assigned to tree coordinates. This is a clear indication of spatial autocorrelation.

Again we have a look at the change between 1992 and 1998. In Ravels it is rather complex. TH increases for Scots pine after thinning, indicating that distant pines seem to be more dissimilar than close standing pines (again an indication of spatial autocorrelation). For pedunculate oak TH increases: remaining dominant oaks after the 1993 selective thinning often have a much smaller oak from the shrub layer as nearest neighbour, rather than a competitor of similar dimensions. TH for red oak decreases probably due to the tree crowns expanding laterally and becoming flatter after the 1993 thinning, thus equalizing heights. The total TH value decreases dramatically, mainly as a result of the elimination of the low height-class of black cherry from the stand.

In Hechtel, the slight decrease of TH for all species is caused likely by competition: trees from the lowest height-classes are more likely to die of competition for light and space, thereby homogenizing the heights in the stand.

The analysis of the TH-change can be refined with the calculation of $TH_i$-distributions. They give information about the driving forces of the development. Fig. 3.3 for example shows the $TH_i$-distributions for pedunculate oak. In Ravels (Fig. 3.3A), the general shift towards higher TH classes indicates that only one process forced the TH to increase: the selective thinning mentioned above. The major trend in Hechtel (Fig. 3.3B) is a shift towards lower TH classes. Besides this, a minor trend is also present: the slight increase within the two highest TH classes (from 1.3 to 3.1% of the trees) indicates that some shorter oaks remained next to much taller ones, which is typically due to competition. This reveals that competition affects TH values in two opposite ways, which could not be detected by comparing the mean TH values.

**A. pedunculate oak in Ravels (TH: 0.175 - 0.190)**



**B. pedunculate oak in Hechtel (TH: 0.251 - 0.238)**

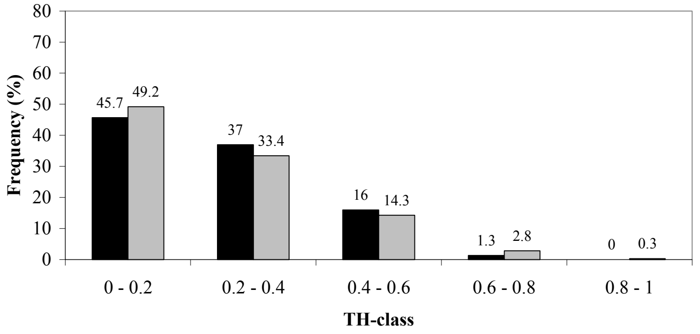


Figure 3.3 $TH_i$ distributions for pedunculate oak in Ravels and Hechtel in 1992 (black bars) and in 1998 (grey bars). The mean stand values are marked above the plots.

### 3.4.4 Variogram analysis – results and discussion

#### 3.4.4.1 Variograms of height

Experimental variogram plots and fitted models of height are shown in Fig. 4.4. It is clear that height is spatially autocorrelated for all tree species, indicating that neighbouring trees in general have similar heights. This was already indicated by the results of the height differentiation index; only TH for Scots pine in Hechtel in 1998 (Table 3.3) could not indicate autocorrelation.

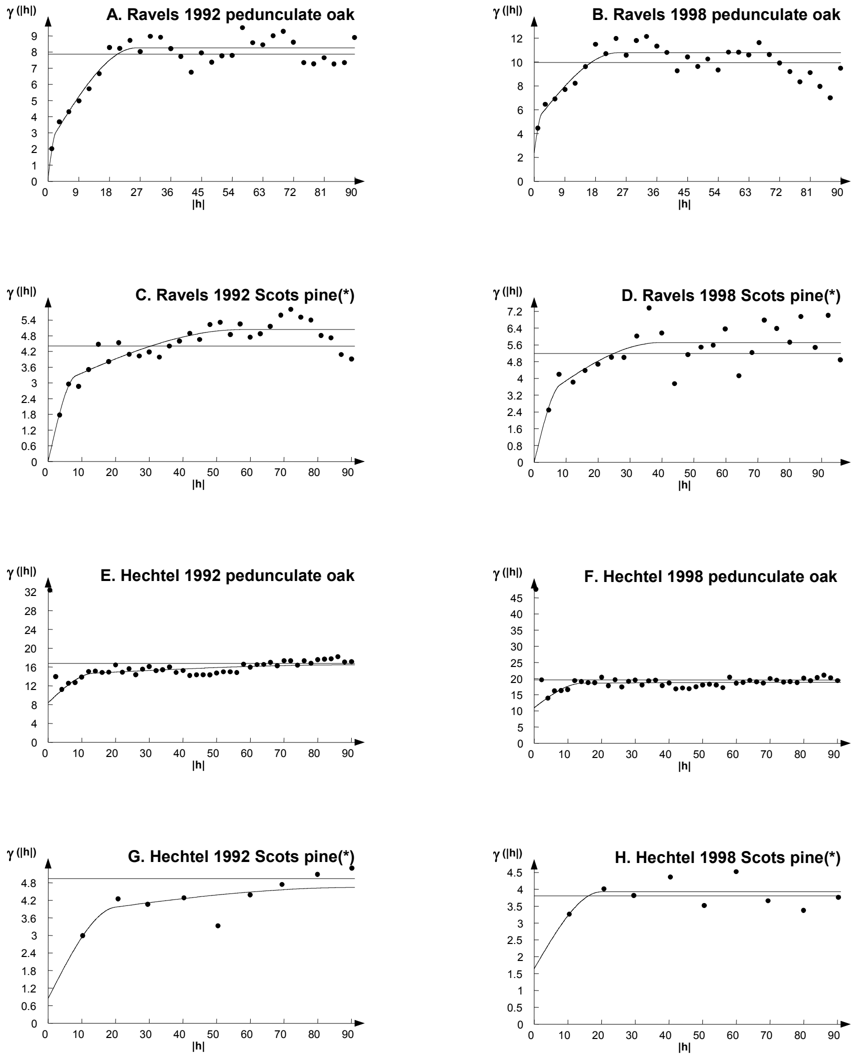


Figure 3.4 Experimental variograms and fitted models of height, for different species, in Ravels and Hechtel, in 1992 and 1998. (*) indicates that for the calculation of the first variogram point some data pairs were masked.

However, there is one important nuance in Hechtel where we found the experimental variograms for pedunculate oak to peak at 1m; at 4-5m lag distance the experimental variogram plot reaches a minimum (Fig. 3.4E and 3.4F). The peak at short distances suggests that close-standing oaks in Hechtel are very dissimilar in height. We already mentioned the possibility of finding unusual variogram forms for tree variables, as these are not strictly regionalized variables – see our discussion about mark variograms. Our findings of an experimental variogram peak at short distances for tree variables was also found by Biondi *et al.* (1994), Kuuluvainen *et al.* (1996, 1998) and Mateu & Ribeiro (1999). The deviation from the usual variogram form is explained by the interaction (mainly competition) between trees. Especially at short inter-tree distances, this introduces an important source of variability. Therefore, the short range of peaking of the experimental variogram can be interpreted as the range of asymmetric competition: in Hechtel, dominant oaks of the main canopy suppress small middle-storey oaks. We fitted a double-spherical model to the experimental variograms for pedunculate oak in Hechtel, excluding the first two experimental points. It will be clear that the resulting parameters (especially the nugget) are in some way affected also by competition, and thus do not purely reflect the effect of other factors.

In Ravels nearly all suppressed trees are removed because of repeated thinnings. Therefore, mainly symmetric competition between dominant trees is present, resulting in the pronounced autocorrelation at short distances, which ranges up to about 4-5m (Fig. 3.4A-D). This is an example where human intervention directly influences the spatial variation of tree variables.

Table 3.4 Parameters of the double-spherical model for the variograms of height, in Ravels and Hechtel, in 1992 and 1998, for the major tree species.

| stand | year | species[(a)] | nugget ($m^2$) | range (m) | | sill ($m^2$) | | $C_{tot}$ ($m^2$) |
|---|---|---|---|---|---|---|---|---|
| | | | $C_0$ | $a_1$ | $a_2$ | $C_1$ | $C_2$ | |
| Ravels | 1992 | Pi | 0.00 | 8.2 | 57.6 | 2.80 | 2.24 | 5.04 |
| | | Qu | 0.20 | 2.2 | 26.0 | 2.05 | 6.02 | 8.27 |
| | | Qr | 1.10 | 3.0 | 56.0 | 2.85 | 3.05 | 7.00 |
| | 1998 | Pi | 0.00 | 8.1 | 39.4 | 2.82 | 2.89 | 5.71 |
| | | Qu | 2.39 | 2.2 | 24.6 | 2.49 | 5.90 | 10.78 |
| | | Qr | 0.36 | 7.2 | 88.5 | 3.11 | 2.83 | 6.30 |
| Hechtel | 1992 | Pi | 0.85 | 20.0 | >90.0 | 2.80 | 0.99 | 4.64 |
| | | Qu | 8.43 | 13.6 | >90.0 | 5.78 | 2.28 | 16.49 |
| | 1998 | Pi | 1.65 | 20.0 | | 2.28 | | 3.93 |
| | | Qu | 11.01 | 14.3 | >90.0 | 7.49 | 0.39 | 18.89 |

(a) Pi *Pinus sylvestris*; Qu *Quercus robur*; Qr *Quercus rubra*.

Model parameters of the variograms are summarised in Table 3.4. Each variogram is characterised by five parameters, the first of which is the nugget ($C_0$). It quantifies the variability at near-zero distances due to micro-scale variation, random sources of error and – in the case of mark variograms – to some extent asymmetric competition; whereas the remaining part of the total sill ($C_{tot}$-$C_0$ = $C_1$+$C_2$) quantifies the variability due to measured spatial dependence. We found the relative nugget (ratio nugget to total sill) to be higher in Hechtel than in Ravels, which again reflects the effect of asymmetric competition.

Other parameters of the double-spherical model include the ranges $a_1$ and $a_2$. The presence of two ranges for all species indicates that two factors are operating at different spatial scales, each of which is responsible for a certain amount of spatial dependence, quantified by their respective sills ($C_1$ and $C_2$). However, the operating factors in our two stands are not necessarily the same. We speculate on three distinguishable factors that operate within a stand at increasing spatial scales:

(i) As already stated, at short inter-tree distances (ranging from 0 to about 10m, depending on species and development stage) the major factor is competition.

(ii) A second factor is related to site characteristics such as soil moisture, nutrient content and topography. Depending on the site, this factor can have a range between some meters and several tens of meters.

(iii) A third factor, which in some cases can be observed within a stand, is linked to soil parent material. Its range in soils of aeolian origin can be expected to be large (> 100m).

In Ravels, we clearly observe a first range due to symmetric competition (Table 3.4). The influence zone is larger for Scots pine (8m) than for the other species (2-3m) as pines are older and their crown and root system is further developed. The second range in Ravels is probably linked to soil moisture, which clearly varies throughout the stand. This second range has values between 25 and 88m, indicating a distinct reaction of different species to this factor. For Hechtel we already noted the presence of asymmetrical competition, which could not be reflected with a theoretical model. Therefore, we interpret the first modelled range in Hechtel (15-20m) to relate to the topography and consequent water availability, as land dunes are prominent in the stand. The second range (> 90m) could therefore indicate the influence of parent material. The corresponding sill is relatively low (4% of $C_{tot}$ on average), indicating that within the computed range of 90m this factor is only of limited importance. The relatively high total sill ($C_{tot}$) of pedunculate oak is a prominent feature within the model parameters in Hechtel, indicating an overall high variability of height for this species.

When comparing the parameter values of both stands between 1992 and 1998, only slight shifts are apparent – even if during the studied period clear changes in stand structure have occurred in Ravels (and to a less extent also in Hechtel), as demonstrated by the calculated spatial indices. The variogram modelling approach does not seem sensitive enough to reflect short-term structural changes.

#### 3.4.4.2 Indicator variograms of presence/absence data

The experimental variogram plots and fitted models for indicator coding of the presence/absence of tree species are shown in Fig. 3.5. They characterise the pattern of continuity (variability) of the major tree species in Ravels and Hechtel. In Hechtel, no spatial autocorrelation is detected. This indicates that species in Hechtel are randomly mixed, and that no spatial pattern in their alternation can be observed – which confirms the result of the segregation index S (Table 3.3). The experimental variograms in Hechtel were modelled as ‘pure nugget’ (Fig. 3.5G-H illustrates this for pedunculate oak; as pedunculate oak and Scots pine represent 96% of the trees within the stand, experimental indicator variograms for both species are calculated for nearly identical indicator coding and thus produce very similar results).

In Ravels, all species exhibit spatial autocorrelation: they are to some extent spatially connected; there is no random mixing. From the calculated S values (Table 3.3) we deduce that this is mainly due to the spatial separation of pedunculate oak and red oak. It is interesting to note that the calculation of DM for Scots pine could not detect the deviation from random mixture as indicated by the variogram.

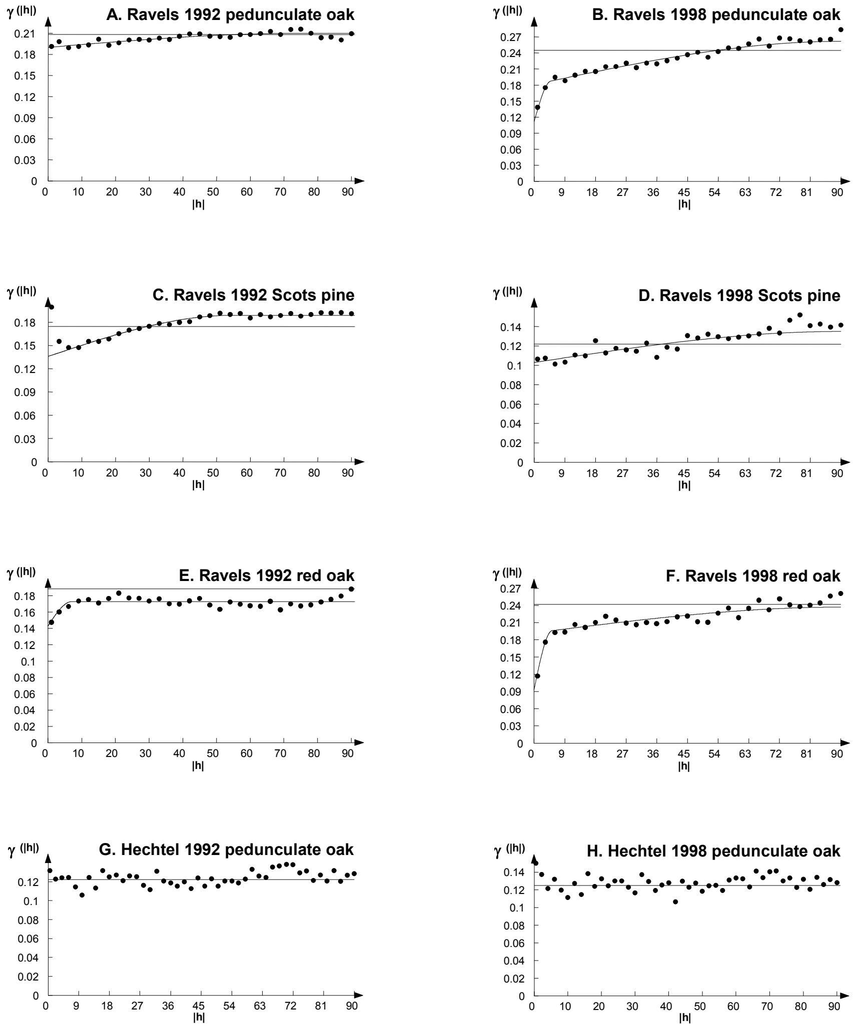


Figure 3.5 Experimental indicator variograms and fitted models of presence/absence data, for different species, in Ravels and Hechtel, in 1992 and 1998.

Again, one important point has to be made: for Scots pine in Ravels in 1992 a similar experimental variogram peak as discussed for the experimental variograms of height is observed (Fig. 3.5C). But the reason for its appearance is not linked to competition: in contrast to height, the indicator value for a tree during its lifetime does not change as an effect of competition. For Scots pine, the high indicator variability at short lags is due to thinnings before 1992: at short distances there are simply no neighbouring pines, thus leading to the systematic alternation of pines with other species. This explains why the negative S values in Table 3.3 shouldn't be interpreted as a tendency towards aggregation of species: the calculation of S is confined to one neighbour only for each tree, and therefore mainly reflects the experimental variogram peak at short distances, neglecting autocorrelation at larger distances. The reason for the experimental variogram peak of 1992 being absent in 1998 (Fig. 3.5D) is the heavy 1993 thinning, randomising the mixing (although not completely: a range of autocorrelation remains) of pines within the stand.

The experimental indicator variogram estimates how often trees at distance **h** from each other have different indicator values. The smaller $\gamma_I(\mathbf{h})$, the greater the degree of homogeneity of a tree species is within a distance **h**, indicating that areas exist where mainly trees with equal indicator value occur; for species A these areas could either be homogeneous clusters of species A, or areas without any tree of species A. The higher $\gamma_I(\mathbf{h})$, the more pairs with different indicator values appear within these areas. This is clearly the case in Ravels: we observe relatively high experimental variogram points, indicating that spatial connectivity of species is not clearly pronounced because of the intermingling of different species. The effect is less pronounced in 1998 for pedunculate oak and red oak (Fig. 3.5B and 3.5D) due to the 1993 intervention, which confirms the decrease of mixture as already demonstrated with both mixture indices.

Table 3.5 summarises all model parameters for the indicator variograms. In Ravels, we found one range in 1992 and two ranges (except for Scots pine) in 1998. Trees at shorter distances from each other than these ranges are more likely to have a same indicator value then would be the case under random mixing. The factors that determine the spatial connectivity of species can be very different. Many ranges in 1992 and 1998 are probably due to local site-suitability for the development of species or homogenizing management interventions. We already mentioned thinning to influence the spatial variability of Scots pine in Ravels in 1992, creating an experimental variogram peak. The short range of dependence for red oak (5-7m) is probably due to this species having established in patches where pedunculate oak was less dense. The 1993 thinning, resulting in the liberation of pedunculate oak from all competitors and the elimination of black cherry, created similar patches of pedunculate oak throughout the stand. The creation through human intervention of this new spatial structure is reflected in a new range (5m) for pedunculate oak in 1998.

Table 3.5 Parameters of the double-spherical model for the indicator variograms of presence/absence data, in Ravels and Hechtel, in 1992 and 1998, for the major tree species.

| stand | year | species[(a)] | nugget $C_0$ | range (m) | | sill | | $C_{tot}$ |
|---|---|---|---|---|---|---|---|---|
| | | | | $a_1$ | $a_2$ | $C_1$ | $C_2$ | |
| Ravels | 1992 | Pi | 0.136 | 54.9 | | 0.053 | | 0.189 |
| | | Qu | 0.190 | 74.8 | | 0.020 | | 0.210 |
| | | Qr | 0.143 | 7.1 | | 0.030 | | 0.173 |
| | 1998 | Pi | 0.103 | 89.4 | | 0.032 | | 0.135 |
| | | Qu | 0.112 | 4.9 | >90.0 | 0.069 | 0.081 | 0.262 |
| | | Qr | 0.093 | 5.3 | >90.0 | 0.099 | 0.045 | 0.237 |
| Hechtel | 1992 | Pi | 0.090 | | | | | 0.090 |
| | | Qu | 0.120 | | | | | 0.120 |
| | 1998 | Pi | 0.095 | | | | | 0.095 |
| | | Qu | 0.125 | | | | | 0.125 |

(a) Pi *Pinus sylvestris*; Qu *Quercus robur*; Qr *Quercus rubra*.

In classic variogram analysis such origination of new ranges is inconceivable, as this would mean the creation of previously absent spatial correlation for a regionalized variable. Mark variograms however reflect a spatial point process, where sudden pattern changes are possible. The indicator mark variogram therefore offers a new instrument for understanding the effect of different management interventions on species composition.

As for variograms of height, no quantitative trends in the change of parameter values between 1992 and 1998 were discerned.

## 3.5 Discussion

(1) A first major question is whether the methods are effective: do they accurately quantify stand structure? The spatial indices offer a meaningful description of forest stand structure: all structural characteristics (positioning, mixture and differentiation) are quantified and can be easily interpreted. For all indices used here statistical testing methods are available; in case of CE the test is subject to edge bias and a

supplementary correction should be applied. In most cases these tests seemed adequate, although not always sensitive enough (e.g. DM for Scots pine in Ravels; TH for Scots pine in Hechtel in 1998). Nevertheless there is one clear problem with using the spatial indices: they are single snapshots, and do not incorporate information about the driving forces of stand structure. Although Hechtel and Ravels have a different history in terms of management intensity, it is not clear from the 1992 indices which was intensively managed and which was more competition driven.

The calculation of experimental variograms and the estimation and interpretation of variogram parameters is more complex than for spatial indices, making them less suitable for every day applications. They provide a more detailed structure analysis, as structure is investigated as a function of distance between trees. Differentiation and mixture can be very well described; positioning is not explicitly quantified. But variograms do more than describe structure: they give a clear indication about the number, impact and range of structure-determining factors such as water availability and parent material. Moreover, all these variograms are in reality mark variograms (because tree variables are not exactly regionalized variables) that are shown to be very powerful for describing not only the classic sources of spatial variability but also those introduced by interaction between trees (e.g. asymmetrical competition in Hechtel) and human intervention (e.g. intensive management in Ravels).

Results from both methods are compatible and complementary. General conclusions of height differentiation and mixture indices are confirmed by variograms of height and indicator variograms of presence/absence data, respectively. Finally, variograms aid in avoiding misinterpretations of indices that are based on short distances only (e.g. negative S values).

(2) Another important question to address is the sensitivity of the methods to changing structure: do they accurately quantify short-term stand structure development? Spatial indices are capable of detecting even subtle structure changes, such as the competition-based shift of height differentiation in Hechtel. The change of index values over short time periods thus provides information on the effect of management and competition on stand structure. This makes this set of spatial indices very suitable for monitoring programs in both managed and natural forests.

For evaluating the short-term effect of management and competition on stand structure, variograms seem less suitable than spatial indices. In our study no quantitative trends in parameter change were discerned for variograms of height. The smoothing effect of modelling experimental variograms is probably too great to detect short-term development in differentiation. But when considered over longer time periods, trends in variogram parameter change are likely to occur (Biondi *et al.* 1994). Only indicator variograms of presence/absence data detected new ranges in Ravels after the heavy 1993 thinning, indicating the creation of new spatial patterns in tree mixture. The effect of management on species composition is reflected in this type of mark variogram.

(3) Apart from these questions, it may be of interest to compare both methods in terms of data requirements. Indices do not require individual tree mapped data. CE and S require only information about individual trees and their first nearest neighbour, but CE requires an additional distance measurement. The sampling effort is considerably higher for DM and TH, where three nearest neighbours are needed. When an appropriate sampling technique is used, sampling time may be considerably reduced (see Füldner 1995 for examples).

Variogram analysis requires the exact measurement of each tree position. Probably not all trees need to be mapped and only a subsample on a well-defined sampling scheme could be enough. In fact, the variogram analysis of height in Ravels is similar in 1992 and 1998. Since the 1998 measurement can be interpreted as a subsample of that in 1992 as a result of the 1993 thinning, we suggest that the assessment of spatial autocorrelation of height does not necessitate mapping the entire stand. It is however inevitable that a larger amount of data is needed for the variogram analysis as compared to the indices.

## 3.6 Conclusion

In this chapter we compared two spatial methods for quantifying forest stand structure, nearest-neighbour indices and variogram analysis. From the application of these methods in a case study of two stands we conclude:

(i) Both methods are effective in quantifying characteristics of forest stand structure. The calculation of spatial indices is straightforward, and results are easy to interpret. They mainly give a snapshot of a situation. Geostatistical analysis using mark variograms is more complex, but provides additional information on the number, the impact and the range of structure-determining factors such as competition and management. The two methods complement each other with respect to interpretation.

(ii) For the quantification of structure development, indices seem to be better suited than variograms. When available in a time series (even if only of two moments, as in our case study) indices provide information on the effect of management and competition on stand structure. Over such short time periods variograms did not demonstrate clear development trends; only indicator variograms of presence/absence data registered new ranges due to human intervention and therefore offer a new instrument for understanding the effect of management interventions on species composition.

The combined application of these methods in two stands with clearly different structure-determining factors (one managed and one more naturally developing) resulted in both cases in a truly better understanding of stand structure and of its short-term development. This is a clear indication that these methods may serve in a variety of stands, both managed and natural. We suggest that, for the purpose of evaluating the impact of management and/or competition on stand structure development, the use of indices in a monitoring program can give good results with a minimum of effort. To gain additional insight regarding structure-determining factors, such a monitoring program could be extended with an initial detailed variogram analysis, eventually repeated on a large time base to evaluate long-term changes of the range and impact of these factors.

This strategy would provide the most complete and accurate insight to both stand structure and its development over time. We propose to apply this strategy at first in unmanaged naturally evolving forest stands (such as forest reserves), to gain additional insight regarding natural processes, necessary as a reference for any nature-based forestry.

# 4 Forest stand structure assessment in forest reserves

Kint, V., De Wulf, R., & Lust, N.

Submitted for publication in an international forestry journal.

### Abstract

SIAFOR, a computer program for the quantification of the three-dimensional geometry of forest stands with nearest-neighbour indices, is presented and applied to: (i) stand structure assessment and interpretation in ageing Scots pine (*Pinus sylvestris* L.) stands in selected Dutch forest reserves and; (ii) the study of minimum sample size and optimal sample type for the estimation of stand structure with sampling techniques. The structure assessment in forest reserves was performed on three information levels. The first level (individual monitoring plots) and the second level (groups of similar plots) mainly provided information about local stand structures and structural types within the forest reserves, by describing tree positioning, mixture and size differentiation. The third level (approximations of long-term forest development) provided information about trends of structural development in ageing Scots pine stands, and the underlying competitive tree interactions involved. The use of sampling techniques to assess forest structure at reasonable accuracy levels often requires very large sample sizes. Minimum sample sizes to reach a certain accuracy level could not be related to basal area and tree density in the stands examined. Neighbour sampling was found to be more efficient than plot sampling in most cases. Different index estimates and statistical tests will vary in accuracy for a given sample size. It is concluded that moderate sample sizes combined with neighbour sampling will allow most index values (except for the segregation S) to be estimated with a reasonable degree of accuracy. To be reliable, statistical tests generally require larger sample sizes.

## 4.1 Introduction

Forest stand structure is a key element in understanding forest ecosystems. Horizontal and vertical stratification, the quantity and spatial distribution of living and dead biomass, vegetation composition and tree geometry, have often been related to biodiversity, ecological stability, competition processes and forest ecosystem functioning (Spies 1998, Naumburg & DeWald 1999, Zirlewagen & Von Wilpert 2001, Bobiec 2002, Jactel *et al.* 2002, Sallabanks *et al.* 2002). Structure assessment in forest stands is therefore an important ecological issue. Moreover, it is increasingly recognised that forest stand structure and structural development are of theoretical and practical importance in close-to-nature forest management (Hansen *et al.* 1991, Franklin *et al.* 2002, Palik *et al.* 2002).

A major component of stand structure is the three-dimensional geometry of forest stands, which is completely described by three spatial characteristics: tree positioning, distribution patterns of species, and size differentiation between trees (Von Gadow & Hui 1999 p.132). These characteristics have ecological relevance, can be used as references for management and are easy to quantify (Kint *et al.* 2003). This makes them particularly suitable for monitoring purposes. Different methods for quantifying the three-dimensional geometry of forest stands are compared by Biondi *et al.* (1994), Kuuluvainen *et al.* (1996), Pretzsch (1997), Gleichmar & Gerold (1998), Kint *et al.* (2000, 2003) and Pommerening (2002). All these methods, whether based on indices or on statistical techniques, are spatially explicit and therefore require information about relative tree positions.

Forest reserves networks have been established worldwide to investigate forest dynamics in different forest types, with a focus on silviculture and nature conservation (Norton 1999). Most European countries have established their own networks and efforts have been made to harmonise the network designs and monitoring methodologies (Hochbichler *et al.* 2000, Parviainen *et al.* 2000). Accordingly, standardised spatially-explicit data sets of long-term stand development under a minimum intervention scenario are being constructed in many different forest types and countries. The systematic analysis of stand structure and structural development in forest reserves will increase insights into forest ecosystem structure and functioning, and will provide quantitative references for close-to-nature forest management.

In managed forests, structure assessment may also be of interest for management evaluation or monitoring purposes. In most of these cases the collection of spatially explicit data throughout the whole stand will be considered too expensive and time-consuming. Instead appropriate sampling techniques should be used (e.g. Füldner 1995, Pommerening & Von Gadow 2000). However, clear guidance about the minimum sample size and the optimal sample type in stands of varying structural complexity is often lacking. This information can be obtained by performing virtual samplings in different completely stem-mapped forest stands, such as the forests reserves.

The purpose of this chapter is to present SIAFOR, a computer program for structure assessment, and to apply it in forest reserves. We have used SIAFOR to:

(i) describe and interpret stand structure and its development in ageing Scots pine (*Pinus sylvestris* L.) stands in selected Dutch forest reserves;
(ii) study minimum sample size and optimal sample type for the estimation of stand structure with sampling techniques.

## 4.2 Material and methods

In this chapter on 'structure assessment' we further develop the quantification of stand structure and structural development with nearest-neighbour indices. For an extended discussion on these indices and a comparison with other stand structure assessment methodologies we refer to Kint *et al.* (2003).

### 4.2.1 SIAFOR, a computer program for structure assessment

We developed a computer program (*SIAFOR:* Stand structure Index Assessment in FORests) for the purpose of calculating the structure indices for monitoring plots with stem-mapped data. The program eliminates edge effects and offers the possibility of virtual sampling. It is designed for use in forest reserves, but may also serve in other contexts. The software is written in the object-oriented language C++, which guarantees flexibility in maintaining and extending the source code. An executable version of SIAFOR 1.0 and the user guide (cf. Addendum B) are available free of charge for scientific and educational purposes. The authors welcome any suggestions about further development of the software and possible options to be included in future releases.

#### 4.2.1.1 Index calculations

SIAFOR calculates four nearest-neighbour indices, based on individual tree data in a monitoring plot (species, size(s) and spatial position) and plot characteristics (area and perimeter): the positioning index 'CE' (Clark & Evans 1954, Donnelly 1978), the relative mixture index 'S' (Pielou 1977 p.226-229), the mixture index 'DM' and the differentiation index 'T' (Von Gadow 1999). CE, DM and T are calculated for each species separately, and for all species together. S is calculated for each pair of species. Together these indices describe the three-dimensional geometry of forest stands, i.e. positioning, mixture and size differentiation (Kint *et al.* 2003). An overview of these indices, with their main characteristics and statistical tests, is given in Table 4.1.

Table 4.1 Characteristics and statistical tests of the four indices implemented in SIAFOR.

| index | range | description | statistical test |
|---|---|---|---|
| CE | 0 – 2.15 | *positioning* of trees within a plot: clustered (< 1), random (= 1) or regular (> 1) | z test<br>$H_0$: CE = 1<br>$H_1$: CE ≠ 1 |
| S | -1 – 1 | *relative mixture* of two species within a plot: aggregated-associated (< 0), neutral (= 0) or segregated-separated (> 0) | $\chi^2$ test<br>$H_0$: S = 0<br>$H_1$: S ≠ 0 |
| DM | 0 – 1 | *mixture* within a plot: degree of dissimilarity of species between neighbouring trees | permutation test$^{(b)}$<br>$H_0$: DM = $DM_{ran}$<br>$H_1$: DM ≠ $DM_{ran}$ |
| T$^{(a)}$ | 0 – 1 | *differentiation* within a plot: degree of dissimilarity of size between neighbouring trees | permutation test$^{(b)}$<br>$H_0$: T = $T_{ran}$<br>$H_1$: T ≠ $T_{ran}$ |

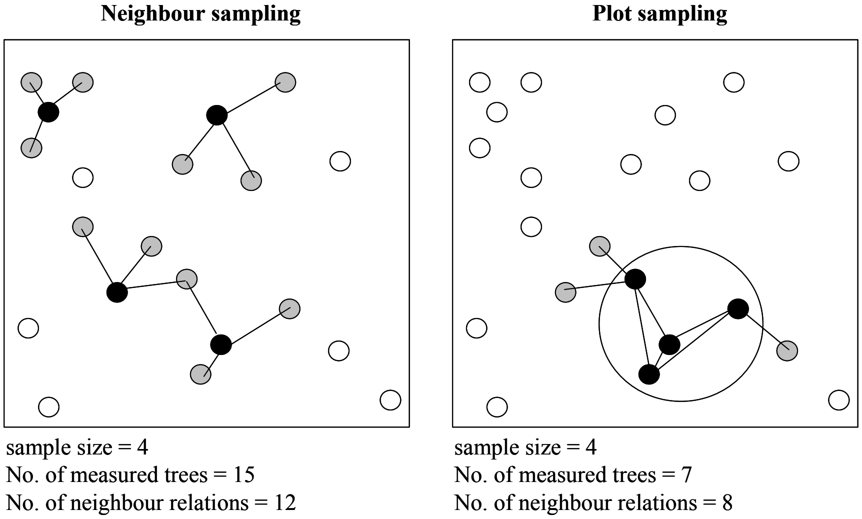
(a) T is calculated for a specific size: e.g. TD for diameter or TH for height.

(b) The permutation test for DM and T generates 1000 permutations, randomly reassigning species values or size values to tree coordinates. We used a two-sided test to indicate whether the real index value is significantly different from that under a random mixture or differentiation.

All indices are based on neighbour relations. The nearest neighbours for each tree are detected, based on information about tree positions in the monitoring plot. However, the detected nearest neighbours for a tree standing near the edge of a plot are not necessarily the real nearest neighbours and therefore a distortion of the correct index values can arise. To eliminate this error we implemented an edge effect correction within SIAFOR: trees that fall within a buffer following the plot border can only serve as nearest neighbour to other trees, but are themselves not considered in the calculation of the indices. Buffer width is a function of both the tree positions and the calculated index, and guarantees the elimination of all edge effects. Where plots have unsuitable shapes for this type of correction (e.g. long and narrow rectangular plots), the use of edge effect corrections can be restricted or disabled.

#### 4.2.1.2 Additional functionality

SIAFOR is furnished with an optional sampling module. This module repeatedly takes virtual samples of increasing size from a completely stem-mapped stand and calculates the index values for each sample. Sample size increment (in percent of tree density) and number of repetitions are user defined. This allows the user to determine, for the stand under investigation, the minimum sample size for index estimation at different levels of accuracy.



sample size = 4
No. of measured trees = 15
No. of neighbour relations = 12

sample size = 4
No. of measured trees = 7
No. of neighbour relations = 8

Figure 4.1 Examples of neighbour sampling and plot sampling with marking of sample trees (black circles), measured trees (grey circles) and neighbour relations (lines between trees).

Two sample types can be emulated within SIAFOR (Fig. 4.1): neighbour sampling and plot sampling (Pommerening & Von Gadow 2000). With *neighbour sampling* a number of sample trees are marked throughout a stand, and for each sample tree and its neighbour(s) appropriate variables are collected for the index to be estimated. If all four indices in Table 4.1 need to be estimated then these variables are the distance between the sample tree and its nearest neighbour as well as the species and sizes of the sample tree and of its three nearest neighbours. Note that in this case, the number of trees actually measured can become four times the sample size. With *plot sampling* a number of sample trees around a random point in the stand are marked, thus defining a group of neighbouring trees within a plot. Here the number of measured trees is only a fraction higher than the sample size (it is not equal to the sample size since sample trees at the edge of the plot may have neighbours outside of the plot that also need to be measured).

#### 4.2.1.3 The use of SIAFOR

SIAFOR can be used to calculate the aforementioned structure indices in most monitoring plots with stem-mapped data. There are, however, some plot requirements that may limit its use:

(i) plots should be circle plots, rectangular plots or convex tetragons;

(ii) there are no size limitations for plots, but the program is optimised for plots up to 5 ha;

(iii) small plots may have insufficient trees to calculate all indices: SIAFOR requires at least five trees (after edge effect correction) and their respective nearest neighbour(s) for an index to be calculated; the larger the number of trees in the analysis, the more representative results are for the whole stand.

Due to data limits, index values for single small monitoring plots are often of little interest. In SIAFOR this may be solved by grouping monitoring plots and calculating the index values of such a group. There are no limitations concerning the composition of groups (i.e. number and characteristics of plots) and this option may, for example, be used for performing a structure assessment of groups from similar monitoring plots in forest reserves.

The use of the sampling module is limited to one plot only; it does not function with groups of plots. Furthermore, the plot should be large enough to make virtual sampling meaningful. We advise a minimum plot area of 1 ha for using the sampling module.

### 4.2.2 Structure assessment on three information levels in forest reserves

The forest reserves programme in the Netherlands has been developed gradually since the early 1980s (Broekmeyer & Szabo 1993). No further management interventions are allowed in any of the reserves. In each reserve a core area (140 m x 70 m) and a series of circle plots (each 500 m²) on a regular grid-network are permanently marked and regularly monitored. Measured individual tree data for all living trees with a diameter at breast height (DBH) of at least 5cm, include the DBH, height, species, spatial position, crown length and tree vigour (Stuurman & Clement 1993).

We focus on forest ecosystems on oligotrophic and acidic sandy soils. The main tree species that are native to these sites are oak (*Quercus robur* L. and *Quercus petraea* (Mattuschka) Lieblein), birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.), common beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.). In nine forest reserves – former homogeneous Scots pine plantations with varying stand development since management stop – we selected only monitoring plots without a significant presence of exotic species. This resulted in seven core areas and 348 circle plots. Pine ages range from 55 to 160 years.

This data set has been previously analysed and interpreted by Kint (2003). Based on this work, we distinguished three information levels on which structure assessment with SIAFOR is meaningful:

(i) *core areas:* individual 0.98 ha monitoring plots, providing information about stand structure at different well-defined locations;

(ii) *structural classes:* groups of similar monitoring plots (core areas and circle plots), providing information about a particular stand structural type that can be distinguished in the data set;

(iii) *pathways:* sequences of structural classes, which are approximations of long-term stand structural development.

#### 4.2.2.1 Structure assessment in core areas

Table 4.2 summarises tree demographics in the seven core areas selected, three of which were surveyed twice. Most core areas are ageing Scots pine stands with pine ages between 100 and 160 years, and varying densities of birch and/or oak regeneration. Only *Lheebroeker Zand* and *Tongerense Hei* are relatively young pine stands of approximately 70 years. In *Noordhout,* beech is also important (basal area of 5.8 m²/ha in 1982 and 7.1 m²/ha in 1992). Finally, in *Stille Eenzaamheid* and *Zwarte Bulten* some pine regeneration is present. In each core area we calculated structure indices, as described in Table 4.1, for all trees together as well as for each species separately.

Table 4.2 Basal area and tree density in the core areas of selected reserves.

| reserve name & survey year | basal area (m²/ha) | | | | tree density (/ha) | | | |
|---|---|---|---|---|---|---|---|---|
| | total | pine | birch | oak | total | pine | birch | oak |
| Galgenberg 1986 | 21.2 | 19.4 | 0.4 | 1.0 | 483 | 272 | 62 | 129 |
| Galgenberg 1995 | 24.5 | 20.4 | 0.8 | 2.4 | 663 | 236 | 142 | 242 |
| Lheebroeker Zand 1987 | 19.4 | 16.9 | 0.0 | 2.5 | 383 | 299 | 8 | 70 |
| Lheebroeker Zand 1999 | 23.8 | 20.3 | 0.4 | 3.0 | 477 | 290 | 63 | 96 |
| Mattemburgh 1997 | 28.6 | 21.0 | 0.6 | 5.5 | 519 | 155 | 26 | 307 |
| Noordhout 1982 | 26.8 | 16.3 | 0.6 | 3.6 | 637 | 164 | 67 | 212 |
| Noordhout 1992 | 29.3 | 16.2 | 0.8 | 4.8 | 597 | 139 | 51 | 223 |
| Stille Eenzaamheid 2000 | 21.5 | 21.2 | 0.1 | 0.0 | 454 | 428 | 20 | 2 |
| Tongerense Hei 1996 | 25.0 | 25.0 | 0.0 | 0.0 | 454 | 454 | 0 | 0 |
| Zwarte Bulten 1991 | 20.5 | 17.9 | 2.5 | 0.0 | 1034 | 707 | 317 | 8 |

#### 4.2.2.2 Structure assessment in structural classes (SCs)

The selected monitoring plots (core areas and circle plots from all reserves and all surveys) were grouped by Kint (2003) into 19 different structural classes (SCs), using a series of hierarchical agglomerative cluster analyses based on basal area, tree density and mean tree sizes per species. Each SC describes a particular stand structural type that can be distinguished in the available data set. Table 4.3 summarises their species composition and density. The different SCs are labelled A to S. In D and E beech is also important (basal area of 6.3 and 6.7 m²/ha respectively). For each SC we calculated structure indices, as described in Table 4.1, for all trees together as well as for each species separately.

Table 4.3 Basal area and tree density of the structural classes.

| structural | basal area (m²/ha) | | | | tree density (/ha) | | | |
|---|---|---|---|---|---|---|---|---|
| class | total | pine | birch | oak | total | pine | birch | oak |
| A | 21.4 | 19.9 | 1.4 | 0.0 | 903 | 727 | 164 | 6 |
| B | 28.0 | 27.9 | 0.0 | 0.0 | 615 | 614 | 0 | 0 |
| C | 18.5 | 18.4 | 0.0 | 0.0 | 342 | 339 | 1 | 1 |
| D | 28.4 | 16.6 | 0.7 | 4.5 | 600 | 145 | 50 | 259 |
| E | 24.9 | 14.4 | 3.7 | 0.2 | 630 | 405 | 190 | 15 |
| F | 7.9 | 1.7 | 4.3 | 1.5 | 837 | 185 | 522 | 121 |
| G | 18.5 | 0.3 | 10.9 | 6.8 | 933 | 34 | 233 | 640 |
| H | 22.7 | 4.9 | 9.5 | 7.2 | 1119 | 52 | 386 | 616 |
| I | 21.1 | 4.1 | 10.9 | 5.9 | 2040 | 60 | 1510 | 440 |
| J | 22.2 | 0.5 | 19.9 | 0.4 | 1220 | 7 | 867 | 40 |
| K | 27.4 | 20.1 | 0.5 | 5.7 | 497 | 160 | 30 | 275 |
| L | 17.3 | 9.2 | 0.3 | 7.5 | 455 | 210 | 43 | 151 |
| M | 22.7 | 20.7 | 0.5 | 1.4 | 470 | 328 | 59 | 66 |
| N | 23.3 | 19.1 | 1.5 | 1.9 | 600 | 264 | 119 | 178 |
| O | 20.4 | 12.2 | 5.2 | 2.7 | 694 | 163 | 387 | 84 |
| P | 34.6 | 23.9 | 8.6 | 1.8 | 1020 | 460 | 500 | 40 |
| Q | 32.6 | 7.5 | 11.8 | 13.3 | 530 | 70 | 190 | 270 |
| R | 24.2 | 23.5 | 0.7 | 0.0 | 3215 | 3030 | 170 | 0 |
| S | 17.5 | 15.5 | 2.0 | 0.0 | 3900 | 3820 | 60 | 0 |

#### 4.2.2.3 Structure trends in main pathways of stand development

Kint (2003) also approximated long-term stand structural development in the selected forest reserves using sequences of the aforementioned SCs, that were constructed with the aid of model predictions. Four main stand development patterns (or pathways) in ageing Scots pine stands were distinguished: three linked to gap dynamics (‘gap pathways’) and one to major disturbance dynamics (‘disturbance pathway’).

The three gap pathways differ in light availability for regeneration and/or seed tree availability. All start form dense homogeneous pine stands with spontaneous regeneration of birch and oak. The first pathway is characterised by a rather abrupt decline of pine density, which facilitates birch regeneration, although oak continues to be present. The second pathway is characterised by a more gradual decline of pine density, and a development towards a relatively open canopy of old pines with an understorey of emerging oak and some birch. The third pathway is similar to the second, but with beech next to oak. The disturbance pathway is actually a group of pathways that involve major disturbances. It is illustrated here on a cleared storm area where a massive pine regeneration establishes, followed by self-thinning of pines and the suppression of broadleaved species. Other examples cover less radical circumstances that cause a more gradual but similar decline of broadleaves in favour of pine regeneration.

We visualise structure index trends for the four main pathways defined. Each of the SCs in the pathways is positioned at a discrete time stage (one point on the abscissa) and is represented on the ordinate by the index values of the monitoring plots it is composed of (i.e. either core areas or groups of similar circle plots within reserves) in order to obtain an idea about the variability of concrete field situations. A linear trend line is included for each structure index.

### 4.2.3 Minimum sample size and optimal sample type for structure assessment

Using the sampling module of SIAFOR, we compared two sample types (neighbour sampling and plot sampling) and searched for the minimum sample sizes needed in forest reserves to estimate the indices in Table 4.1 at different levels of accuracy. We did this using a completely stem-mapped stand in a Belgian forest reserve in the municipality of Liedekerke on the one hand, and the core areas in Dutch forest reserves on the other hand (see earlier). The stand in Liedekerke is the result of long-term development following spontaneous regeneration of mainly birch and oak on a cleared area. In 2000, *Liedekerke* had a mean basal area of 25.1 m²/ha (of which 14.4 for birch and 6.4 for oak) and a tree density of 709 trees per hectare (of which 517 for birch and 122 for oak). We selected this stand mainly because of its size (7.3 ha) and the structural difference with the core areas.

#### 4.2.3.1 Minimum sample size

In all of the stands we estimated the indices using both sample types, with increasingly larger sample sizes (in steps of 1% of tree density) and 1000 repetitions for each sample size. On the basis of these results we determined the minimum sample sizes that would result in a maximum deviation of 5%, 10% and 20% from the correct index values at the 90% and 95% probability levels. For CE and S it is not only important to estimate accurate index values, but also to determine whether they indicate a departure from random positioning or random mixture. Therefore, for these indices we also determined the minimum sample sizes needed to obtain correct outcomes of statistical tests at the 90% and 95% probability levels.

Our interpretation is limited to those cases where neighbour sampling requires less than 20% of the tree density or less than 20 sampled trees per species (further indicated by the term 'moderate sample size'). At the average tree density in the selected core areas (Table 4.2) and using the time estimation for neighbour sampling provided by Füldner (1995), it would take approximately four hours per hectare to complete this sample size. We consider this to be the maximum sample size that can be realistically used in forest stands. If the sample size required is larger then we assume that sampling will be abandoned and therefore the questions about minimal sample type and optimal sample type will become irrelevant.

#### 4.2.3.2 Optimal sample type

The optimal sample type for stand structure assessment is not necessarily the one requiring the lowest sample sizes. From the presentation of both implemented sample types (see earlier) it can be seen that there is a trade-off between two opposing factors: (i) the larger sample size probably required for plot sampling to obtain equal levels of accuracy and (ii) the considerably greater measurement effort for neighbour sampling at equal sample sizes.

The first factor, linked to sample design, is the consequence of the higher probability of obtaining accurate estimates for stand values when a sample is spread throughout the stand than when the sample is concentrated at one location in the stand. We term this the *Design Expansion Factor* (DEF). It can be estimated in the forest reserves stands by calculating the ratio of the sample size needed for plot sampling to that for neighbour sampling, at equal levels of accuracy.

The second factor, linked to measurement, is the consequence of data requirements for structure indices: these are not confined to sample trees but extend towards their immediate neighbours. Thus, at equal sample sizes the number of measured trees for neighbour sampling is a multiple of that for plot sampling. We term this the *Measurement Expansion Factor* (MEF). It can be estimated for each index separately and for groups of indices by calculating the ratio of the measurement effort needed for neighbour sampling to that for plot sampling, at equal sample sizes.

By comparing DEF and MEF we determined the optimal sample type in forest reserves stands. As long as DEF remains lower than MEF, the larger sample size required for plot sampling is compensated for by an even greater measurement effort for neighbour sampling, and plot sampling is the optimal sample type. Once DEF exceeds MEF, neighbour sampling becomes the optimal sample type.

## 4.3 Results

### 4.3.1 Structure assessment in core areas

The results of the structure index calculation with SIAFOR in the selected core areas are given in Table 4.4 for positioning (CE), segregation (S) and mixture (DM), and Table 4.5 for differentiation of diameter (TD), height (TH) and crown length (TCl). We limited the data in these tables to the main species pine, birch and oak, and to the aforementioned indices. Empty cells in Tables 4.4 and 4.5 indicate the absence of a species or that not all of the conditions for the calculation of the index were satisfied.

### 4.3.2 Structure assessment in structural classes

The results of the structure index calculation with SIAFOR for the SCs are summarised in Tables 4.6 and 4.7 in the same way as for the core areas. Note that empty cells in Tables 4.6 and 4.7 may also occur for species with elevated tree densities according to Table 4.3 (e.g. Q). This is because the values in Table 4.3 are standardised to one hectare, even though some SCs may be composed of only few monitoring plots which might have insufficient data to calculate all structure indices.

### 4.3.3 Structure trends in main pathways of stand development

Fig. 4.2 to Fig. 4.5 illustrate trends in the structure indices, given in Table 4.1, for the four main stand development patterns (pathways) in ageing Scots pine stands. Trends for basal area, tree density, mean DBH and mean height are also included in these figures to facilitate a better understanding of the pathways.

Table 4.4 Structure indices in core areas of the selected reserves: positioning (CE), segregation (S) and mixture (DM)(a).

| reserve name & | CE | | | | S | | | DM(b) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| survey year | total | pine | birch | oak | pine-birch | pine-oak | birch-oak | total | pine | birch | oak |
| Galgenberg 1986 | 1.13** | 1.19** | 0.62** | 1.06 | 0.211** | -0.239** | 0.323** | 0.598 | 0.458 | 0.685** | 0.816 |
| Galgenberg 1995 | 1.08** | 1.18** | 0.76** | 1.05 | 0.152* | -0.245** | 0.258** | 0.702 | 0.692 | 0.702** | 0.660 |
| Lheebroeker Zand 1987 | 1.22** | 1.19** | | 0.47** | | 0.677** | | 0.182** | 0.100** | | 0.375** |
| Lheebroeker Zand 1999 | 1.13** | 1.17** | 0.85 | 0.78* | -0.027 | 0.410** | 0.415** | 0.491** | 0.355 | 0.814 | 0.568** |
| Mattemburgh 1997 | 1.09** | 1.10 | 0.28** | 0.99 | 0.370** | 0.007 | 0.254 | 0.522 | 0.712 | 0.750** | 0.375 |
| Noordhout 1982 | 1.03 | 1.09 | | 0.73** | 0.228** | 0.118 | 0.476** | 0.648** | 0.779 | 0.722** | 0.489** |
| Noordhout 1992 | 1.05 | 1.06 | | 0.85 | 0.203* | 0.213** | 0.390** | 0.650** | 0.780 | 0.781** | 0.456** |
| Stille Eenzaamheid 2000 | 1.01 | 1.00 | | | | | | 0.057** | 0.032** | 0.583** | |
| Tongerense Hei 1996 | 1.08** | 1.08** | | | | | | | | | |
| Zwarte Bulten 1991 | 1.01 | 0.95* | 0.74** | | 0.493** | | | 0.301** | 0.217** | 0.457** | |

(a) Indices are explained in Table 4.1.

(b) The significant differences all indicate that the observed value is significantly less than under random mixture.

Table 4.5 Structure indices in core areas of the selected reserves: differentiation of diameter (TD), height (TH) and crown length (TCl)(a).

| reserve name & survey year | TD(b) | | | | TH(b) | | | | TCl(b) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | total | pine | birch | oak | total | pine | birch | oak | total | pine | birch | oak |
| Galgenberg 1986 | 0.450 | 0.167 | 0.261 | 0.339 | 0.365 | 0.077** | 0.209 | 0.309 | 0.299 | 0.300 | 0.245 | 0.335 |
| Galgenberg 1995 | 0.484 | 0.161 | 0.273 | 0.362 | 0.378 | 0.081 | 0.198 | 0.249 | 0.307 | 0.306 | 0.281 | 0.287 |
| Lheebroeker Zand 1987 | 0.237** | 0.159** | | | 0.175 | 0.102** | | | 0.318** | 0.292 | | |
| Lheebroeker Zand 1999 | 0.410 | 0.147** | 0.251 | 0.350* | 0.296 | 0.072** | 0.210 | 0.227** | 0.300** | 0.247** | 0.217 | 0.409 |
| Mattemburgh 1997 | 0.434 | 0.163* | | 0.265 | 0.324** | 0.098* | | 0.226** | 0.390 | 0.262** | | 0.317** |
| Noordhout 1982 | 0.425** | 0.181 | | 0.357 | 0.390** | 0.099 | | 0.376 | 0.478** | 0.366 | | 0.504 |
| Noordhout 1992 | 0.409** | 0.151* | | 0.370 | 0.370** | 0.105** | | 0.331 | 0.459** | 0.366** | | 0.466 |
| Stille Eenzaamheid 2000 | 0.347** | 0.339** | | | 0.286** | 0.275** | | | 0.367** | 0.372** | | |
| Tongerense Hei 1996 | 0.272** | 0.272** | | | 0.145** | 0.145** | | | 0.301** | 0.301** | | |
| Zwarte Bulten 1991 | 0.355** | 0.330** | 0.225** | | 0.249** | 0.226** | 0.151** | | 0.291** | 0.291** | 0.250** | |

(a) Indices are explained in Table 4.1.
(b) The significant differences all indicate that the observed value is significantly less than under random differentiation.

Table 4.6 Structure indices of the structural classes: positioning (CE), segregation (S) and mixture (DM)(a).

| structural | CE | | | | S | | | DM(b) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| class | total | pine | birch | oak | pine-birch | pine-oak | birch-oak | total | pine | birch | oak |
| A | 1.01 | 0.98* | 0.79** | | 0.265** | | | 0.232** | 0.147** | 0.462** | |
| B | 1.12** | 1.12** | | | | | | | | | |
| C | 1.22** | 1.23** | | | | | | | | | |
| D | 1.05** | 1.11* | 0.80 | 0.74** | 0.193** | 0.119** | 0.283** | 0.641** | 0.782 | 0.749** | 0.453** |
| E | 1.21* | 0.91 | 0.68 | | 0.635* | | | 0.098 | 0.022 | | |
| F | 0.97 | 0.71** | 0.87** | 0.96 | 0.609** | 0.033 | 0.310** | 0.406 | 0.545 | 0.263 | 0.769 |
| G | 1.03 | 0.63** | 1.15** | 1.02 | 0.142 | -0.053** | -0.026 | 0.450 | 0.889 | 0.670 | 0.311 |
| H | 1.04 | | 1.02 | 0.99 | | | 0.116* | 0.513 | | 0.620 | 0.377 |
| I | 1.03 | | 0.94 | 0.76 | | | 0.304** | 0.316 | | 0.202 | 0.769 |
| J | 1.04 | | 1.03 | | | | | 0.485 | | 0.297 | |
| K | 1.08** | 1.10* | 0.36** | 1.00 | 0.182** | -0.011 | 0.111** | 0.523 | 0.707 | 0.756** | 0.367 |
| L | 1.01 | 1.01 | 0.93 | 1.16* | 0.213** | 0.155 | | 0.298 | 0.212 | 0.600 | 0.256 |
| M | 1.19** | 1.22** | 0.70** | 0.66** | -0.010 | 0.468** | 0.388** | 0.349** | 0.223 | 0.766 | 0.499** |
| N | 1.12** | 1.20** | 0.79** | 1.08* | 0.118** | -0.188** | 0.101* | 0.671 | 0.581 | 0.706** | 0.722 |
| O | 0.98 | 1.22* | 0.83** | 1.06 | 0.119* | 0.359** | 0.334 | 0.453 | 0.682 | 0.288 | 0.648 |
| P | 1.07 | 0.80 | | | | | | 0.303** | 0.370* | 0.194** | |
| Q | 0.72* | | | | | | | | | | |
| R | 1.32** | 1.27** | 0.86 | | -0.065 | | | 0.089 | 0.053 | 0.413** | |
| S | 1.38** | 1.34** | | | | | | 0.019 | 0.010 | | |

(a) Indices are explained in Table 4.1.

(b) The significant differences all indicate that the observed value is significantly less than under random mixture.

Table 4.7 Structure indices of the structural classes: differentiation of diameter (TD), height (TH) and crown length (TCl)(a).

| structural | TD(b) | | | | TH(b) | | | | TCl(b) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| class | total | pine | birch | oak | total | pine | birch | oak | total | pine | birch | oak |
| A | 0.342** | 0.329** | 0.214** | | 0.241** | 0.227** | 0.148** | | 0.313** | 0.324** | 0.242** | |
| B | 0.267** | 0.267** | | | 0.148** | 0.149** | | | 0.301** | 0.302** | | |
| C | 0.344 | 0.344 | | | 0.177 | 0.177 | | | 0.332 | 0.332 | | |
| D | 0.418** | 0.167 | | 0.35 | 0.381** | 0.102 | | 0.323 | 0.465** | 0.366 | | 0.423 |
| E | 0.287 | 0.326 | | | 0.150 | 0.195* | | | 0.314 | 0.290 | | |
| F | 0.297 | 0.312 | 0.231 | | 0.184 | 0.134 | 0.140 | | 0.227 | 0.222 | 0.200 | |
| G | 0.405 | 0.252 | 0.264 | 0.323 | 0.324 | 0.220 | 0.117 | 0.208 | 0.297 | 0.252 | 0.201 | 0.283 |
| H | 0.413 | | 0.449 | 0.291 | 0.320 | | 0.292 | 0.158 | 0.322 | | 0.315 | 0.247 |
| I | 0.277 | | 0.243 | 0.364 | 0.175* | | 0.149* | 0.269 | 0.348** | | 0.316 | 0.433 |
| J | 0.399 | | 0.293 | | 0.404 | | 0.219 | | 0.334 | | 0.277 | |
| K | 0.434 | 0.163* | | 0.269 | 0.338** | 0.098* | | 0.242** | 0.397 | 0.262** | | 0.329** |
| L | 0.317** | 0.233* | | 0.436 | 0.231** | 0.134** | | 0.356 | 0.404 | 0.337 | | 0.494 |
| M | 0.350 | 0.180** | 0.275 | 0.337* | 0.259 | 0.106** | 0.226 | 0.239** | 0.311** | 0.283 | 0.239 | 0.366 |
| N | 0.474 | 0.168 | 0.287 | 0.357 | 0.381 | 0.081** | 0.208 | 0.267 | 0.300 | 0.295 | 0.274 | 0.303 |
| O | 0.409 | 0.282 | 0.288 | | 0.323 | 0.166 | 0.217 | | 0.293 | 0.215 | 0.254 | |
| P | 0.468 | | | | 0.374* | | | | 0.426 | | | |
| Q | | | | | | | | | | | | |
| R | 0.244 | 0.248 | 0.187 | | 0.131 | 0.114** | 0.127 | | 0.243 | 0.237 | 0.214 | |
| S | 0.183* | 0.182 | | | 0.124** | 0.117* | | | 0.186* | 0.181 | | |

(a) Indices are explained in Table 4.1.
(b) The significant differences all indicate that the observed value is significantly less than under random differentiation.

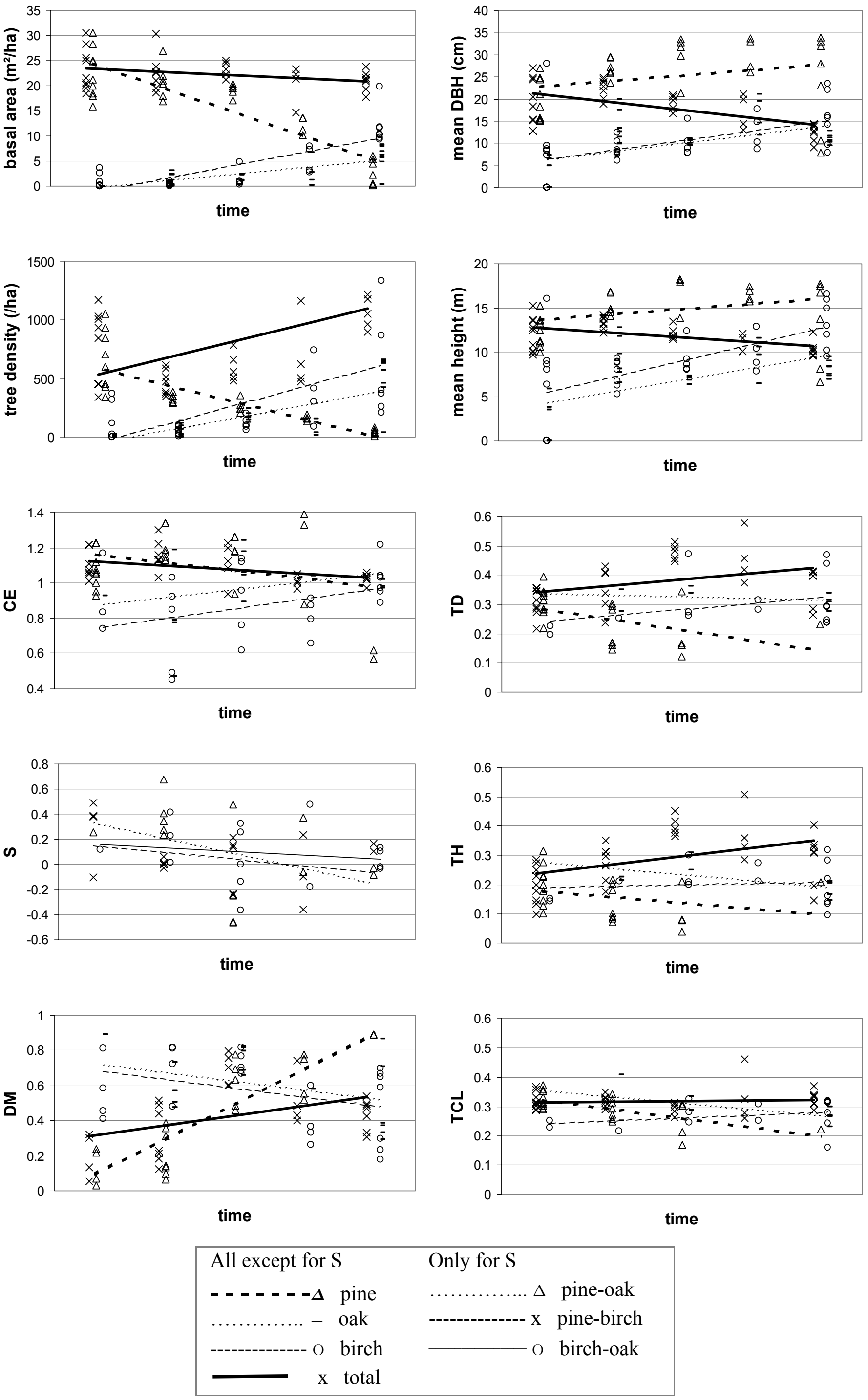


Figure 4.2 Structure trends for pathway one. Index explanation in Table 4.1.

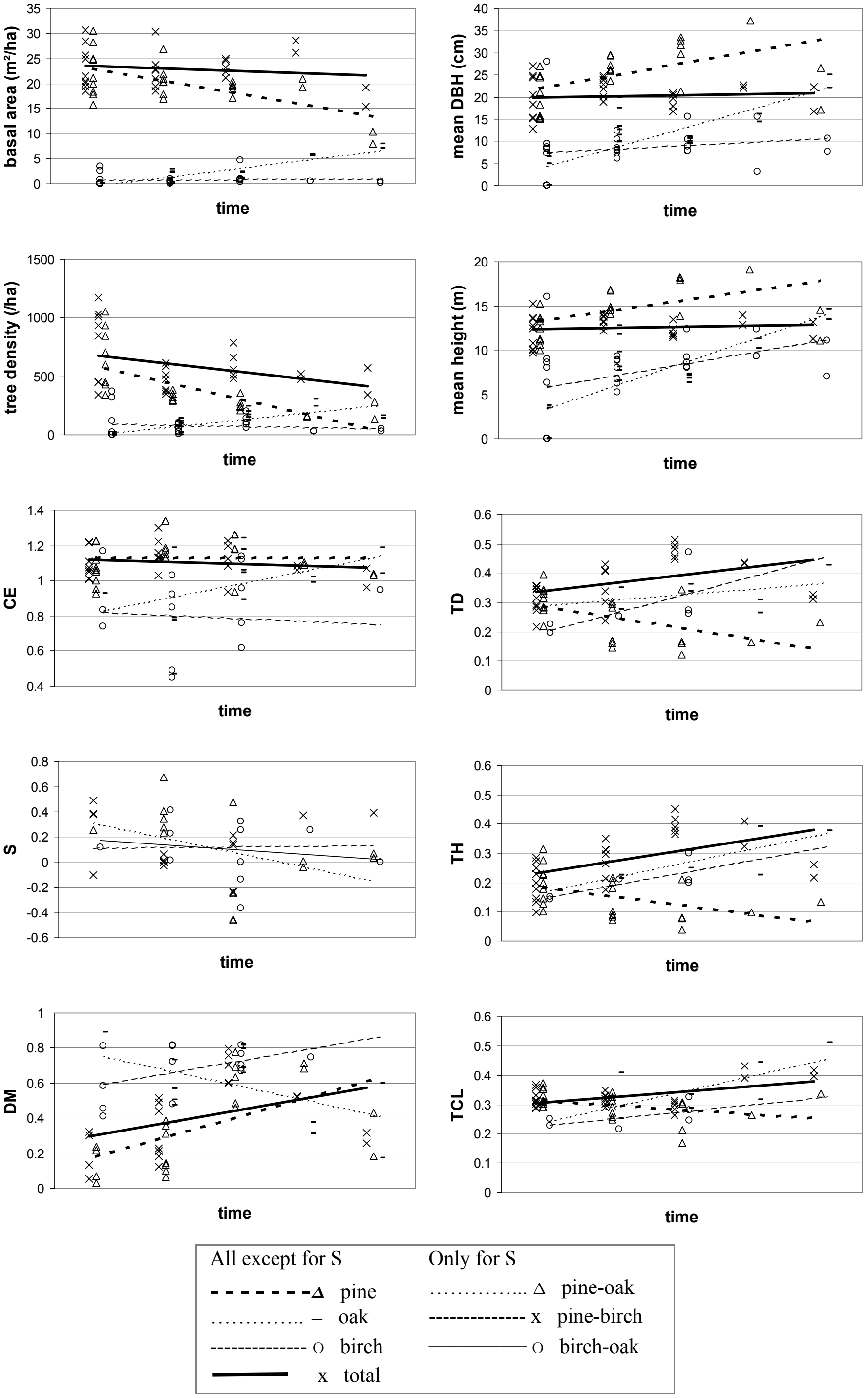


Figure 4.3 Structure trends for pathway two. Index explanation in Table 4.1.

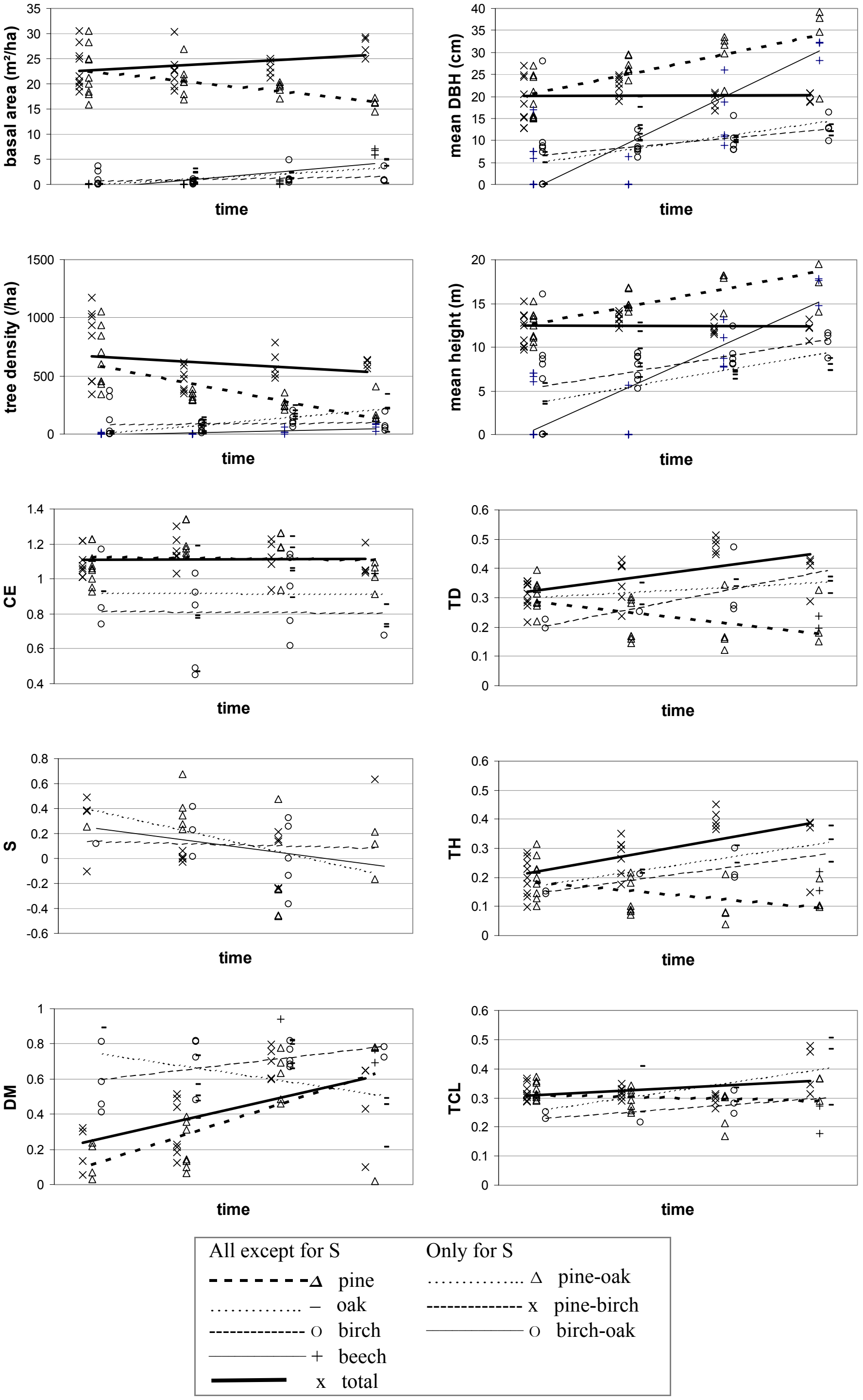


Figure 4.4 Structure trends for pathway three. Index explanation in Table 4.1.

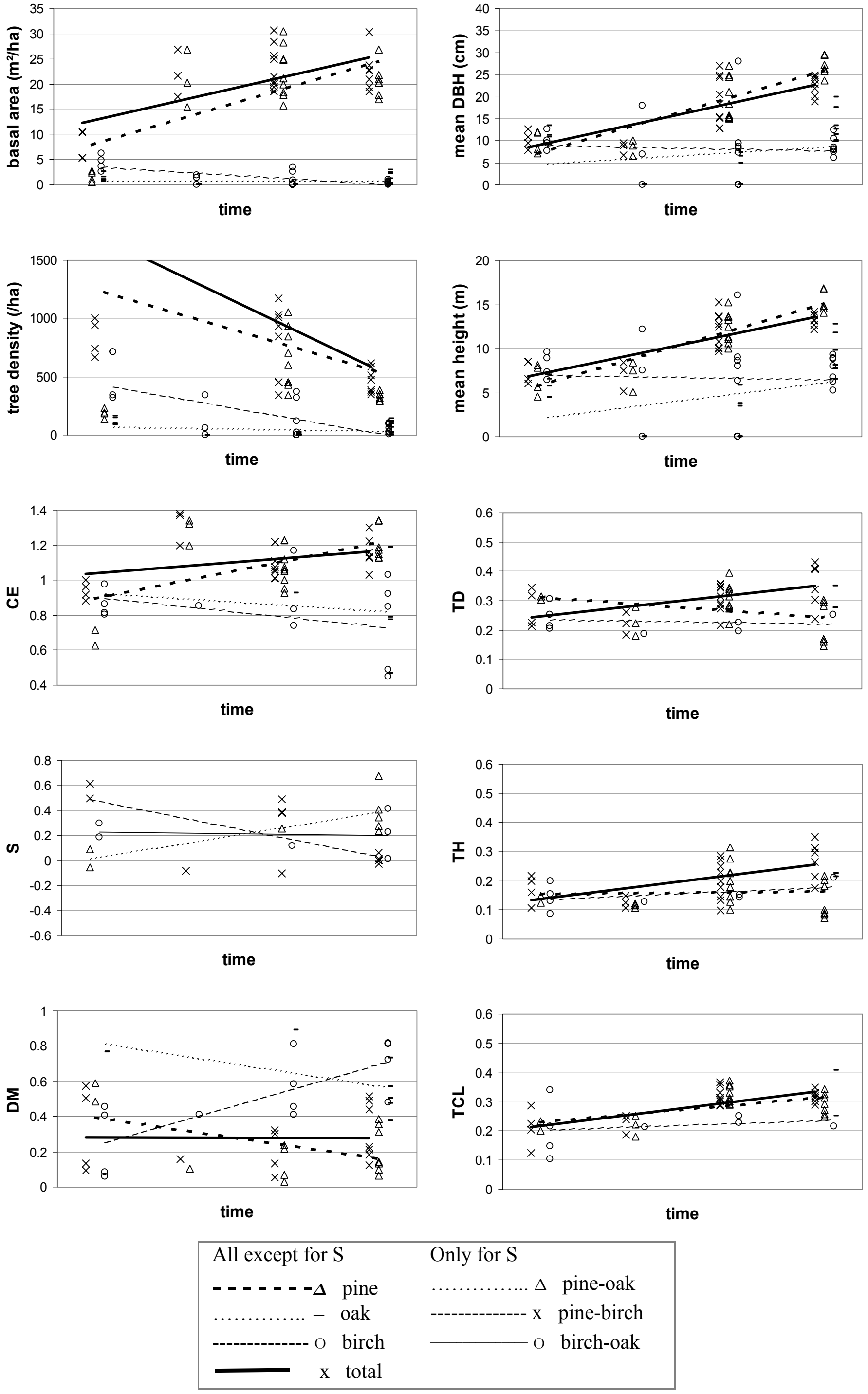


Figure 4.5 Structure trends for pathway four. Index explanation in Table 4.1.

Note that in Fig. 4.4 structure index trends for beech could not be included. Only in the last development stage of this third pathway is the density of beeches large enough for a structure calculation to be performed. The results should be interpreted with caution, as only a few field cases of this pathway are available in the data set and there is no certainty as to the representativeness of these.

### 4.3.4 Minimum sample size and optimal sample type

We estimated index values using both sample types, with increasing large sample sizes and 1000 repetitions for each sample size. The resulting probability intervals are illustrated in Fig. 4.6 for the case of the estimation of positioning (CE) in Liedekerke with neighbour sampling.

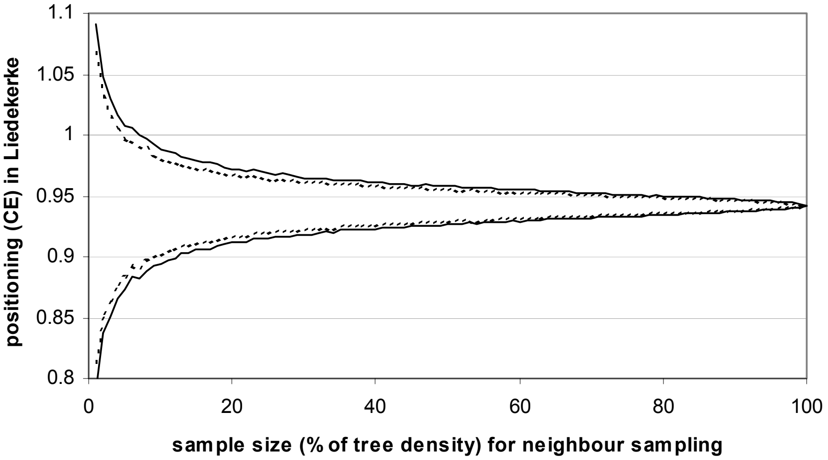


Figure 4.6 90% (dotted line) and 95% (full line) probability intervals for estimated values of CE in *Liedekerke* with neighbour sampling.

Similar figures were constructed for all of the indices, stands and sample types investigated. Based on these, Tables 4.8 to 4.11 summarise the minimum sample sizes in the selected forest stands (in percent of tree density) for the estimation of CE, S, DM and TD respectively, for the main species (i.e. with tree density greater than 10% of total tree density), both sample types and different levels of accuracy.

Table 4.8 Minimum sample sizes in forest reserves (in percent of tree density) that, at the 90% and 95% probability levels, result in maximum deviations of 5%, 10% and 20% from the correct positioning value (CE) and a correct statistical test.

| reserve name | species | tree density (/ha) | neighbour sampling | | | | | | | | plot sampling | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 90% probability | | | | 95% probability | | | | 90% probability | | | | 95% probability | | | |
| | | | max. deviation | | | stat. test | max. deviation | | | stat. test | max. deviation | | | stat. test | max. deviation | | | stat. test |
| | | | 20% | 10% | 5% | | 20% | 10% | 5% | | 20% | 10% | 5% | | 20% | 10% | 5% | |
| Liedekerke | total | 709 | 1 | 2 | 8 | 7 | 1 | 3 | 10 | 10 | 8 | 26 | 63 | 51 | 12 | 41 | 64 | 51 |
| | birch | 517 | 1 | 3 | 11 | 1 | 1 | 4 | 16 | 1 | 8 | 36 | 60 | 1 | 12 | 40 | 67 | 11 |
| | oak | 122 | 3 | 12 | 34 | 12 | 4 | 16 | 42 | 17 | 30 | 68 | 87 | 74 | 34 | 74 | 90 | 75 |
| Galgenberg | total | 483 | 5 | 11 | 29 | 9 | 5 | 14 | 37 | 14 | 5 | 18 | 34 | 21 | 8 | 22 | 37 | 23 |
| | pine | 272 | 5 | 11 | 34 | 5 | 5 | 16 | 42 | 7 | 5 | 16 | 41 | 5 | 5 | 24 | 45 | 9 |
| | birch | 62 | 45 | 76 | 92 | 66 | 53 | 81 | 94 | 74 | 71 | 86 | 95 | 76 | 74 | 90 | 97 | 79 |
| | oak | 129 | 12 | 36 | 69 | 54 | 17 | 44 | 76 | 64 | 18 | 33 | 53 | 75 | 21 | 45 | 54 | 80 |
| Lheebr. Zand | total | 383 | 5 | 7 | 22 | 5 | 5 | 9 | 28 | 5 | 5 | 13 | 31 | 7 | 5 | 16 | 34 | 12 |
| | pine | 299 | 5 | 8 | 23 | 5 | 5 | 11 | 31 | 5 | 5 | 11 | 63 | 5 | 5 | 16 | 71 | 5 |
| | oak | 70 | 51 | 81 | 96 | 16 | 60 | 87 | 97 | 23 | 81 | 93 | 96 | 4 | 84 | 94 | 97 | 4 |
| Mattemburgh | total | 519 | 5 | 10 | 29 | 28 | 5 | 13 | 36 | 38 | 5 | 16 | 41 | 51 | 5 | 20 | 44 | 55 |
| | pine | 155 | 8 | 27 | 56 | 79 | 11 | 30 | 66 | 87 | 12 | 27 | 47 | 83 | 14 | 36 | 79 | 85 |
| | oak | 307 | 5 | 16 | 42 | 37 | 7 | 22 | 51 | 46 | 8 | 16 | 41 | 31 | 10 | 20 | 45 | 40 |
| Noordhout | total | 637 | 5 | 14 | 40 | 89 | 6 | 18 | 48 | 93 | 37 | 81 | 93 | 98 | 42 | 86 | 94 | 99 |
| | pine | 164 | 7 | 21 | 54 | 43 | 10 | 29 | 62 | 60 | 11 | 27 | 46 | 43 | 15 | 32 | 81 | 45 |
| | oak | 212 | 19 | 49 | 79 | 17 | 24 | 58 | 85 | 25 | 67 | 76 | 93 | 63 | 69 | 79 | 96 | 65 |
| | beech | 86 | 15 | 45 | 77 | 97 | 21 | 52 | 81 | 99 | 41 | 65 | 78 | 70 | 49 | 69 | 81 | 78 |
| Stille Eenz. | total | 454 | 5 | 15 | 43 | 99 | 7 | 21 | 52 | 100 | 16 | 56 | 88 | 99 | 19 | 60 | 91 | 99 |
| | pine | 428 | 5 | 17 | 47 | 87 | 8 | 24 | 55 | 92 | 16 | 58 | 85 | 94 | 20 | 64 | 91 | 94 |
| Tonger. Hei | pine | 454 | 5 | 13 | 35 | 48 | 5 | 17 | 44 | 60 | 10 | 48 | 64 | 64 | 17 | 53 | 67 | 67 |
| Zwarte Bulten | total | 1034 | 5 | 8 | 23 | 87 | 5 | 10 | 31 | 92 | 55 | 79 | 89 | 93 | 65 | 83 | 90 | 94 |
| | pine | 707 | 5 | 12 | 36 | 98 | 5 | 16 | 43 | 99 | 61 | 77 | 86 | 99 | 68 | 79 | 87 | 100 |
| | birch | 317 | 14 | 41 | 72 | 12 | 19 | 50 | 79 | 25 | 35 | 66 | 92 | 33 | 43 | 82 | 93 | 41 |

Table 4.9 Minimum sample sizes in forest reserves (in percent of tree density) that, at the 90% and 95% probability levels, result in maximum deviations of 5%, 10% and 20% from the correct relative mixture value (S) and a correct statistical test.

| reserve name | pair of species | joint tree density (/ha) | neighbour sampling | | | | | | | | plot sampling | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 90% probability | | | | 95% probability | | | | 90% probability | | | | 95% probability | | | |
| | | | max. deviation | | | stat. test | max. deviation | | | stat. test | max. deviation | | | stat. test | max. deviation | | | stat. test |
| | | | 20% | 10% | 5% | | 20% | 10% | 5% | | 20% | 10% | 5% | | 20% | 10% | 5% | |
| Liedekerke | birch-oak | 639 | 16 | 43 | 75 | 4 | 21 | 53 | 81 | 5 | 66 | 71 | 94 | 16 | 69 | 72 | 95 | 19 |
| Galgenberg | pine-birch | 334 | 90 | 96 | 98 | 92 | 92 | 97 | 99 | 95 | 96 | 98 | 99 | 97 | 96 | 98 | 99 | 99 |
| | pine-oak | 401 | 78 | 93 | 97 | 70 | 83 | 95 | 97 | 74 | 66 | 94 | 97 | 63 | 69 | 95 | 97 | 64 |
| | birch-oak | 191 | 84 | 95 | 98 | 79 | 87 | 96 | 98 | 83 | 82 | 87 | 96 | 71 | 83 | 88 | 97 | 73 |
| Lheebr. Zand | pine-oak | 369 | 34 | 67 | 90 | 15 | 42 | 75 | 92 | 18 | 50 | 85 | 92 | 42 | 52 | 87 | 95 | 44 |
| Mattemburgh | pine-oak | 462 | 99 | 100 | 100 | 5 | 99 | 100 | 100 | 5 | 100 | 100 | 100 | 26 | 100 | 100 | 100 | 31 |
| Noordhout | pine-oak | 376 | 88 | 96 | 98 | 95 | 91 | 97 | 98 | 97 | 85 | 97 | 98 | 99 | 93 | 98 | 99 | 100 |
| | pine-beech | 250 | 95 | 97 | 98 | 56 | 96 | 98 | 99 | 90 | 76 | 96 | 98 | 87 | 94 | 97 | 98 | 88 |
| | oak-beech | 298 | 47 | 77 | 93 | 23 | 54 | 83 | 95 | 27 | 53 | 64 | 95 | 47 | 55 | 71 | 96 | 50 |
| Zwarte Bulten | pine-birch | 1024 | 18 | 48 | 77 | 8 | 25 | 55 | 82 | 9 | 19 | 43 | 65 | 11 | 24 | 47 | 69 | 13 |

Table 4.10 Minimum sample sizes in forest reserves (in percent of tree density) that, at the 90% and 95% probability levels, result in maximum deviations of 5%, 10% and 20% from the correct mixture value (DM).

| reserve name | species | tree density (/ha) | neighbour sampling | | | | | | plot sampling | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 90% probability max. deviation | | | 95% probability max. deviation | | | 90% probability max. deviation | | | 95% probability max. deviation | | |
| | | | 20% | 10% | 5% | 20% | 10% | 5% | 20% | 10% | 5% | 20% | 10% | 5% |
| Liedekerke | total | 709 | 2 | 7 | 21 | 2 | 9 | 29 | 57 | 76 | 93 | 65 | 79 | 95 |
| | birch | 517 | 4 | 13 | 38 | 5 | 17 | 45 | 70 | 91 | 96 | 76 | 93 | 97 |
| | oak | 122 | 2 | 7 | 23 | 3 | 10 | 30 | 19 | 50 | 62 | 23 | 55 | 63 |
| Galgenberg | total | 483 | 5 | 12 | 37 | 5 | 17 | 44 | 9 | 17 | 60 | 10 | 22 | 82 |
| | pine | 272 | 9 | 28 | 60 | 12 | 34 | 68 | 14 | 36 | 82 | 16 | 46 | 84 |
| | birch | 62 | 16 | 45 | 76 | 21 | 53 | 81 | 50 | 71 | 90 | 58 | 84 | 92 |
| | oak | 129 | 5 | 15 | 41 | 7 | 20 | 50 | 9 | 16 | 46 | 9 | 23 | 49 |
| Lheebroeker Zand | total | 383 | 31 | 60 | 86 | 37 | 70 | 90 | 77 | 88 | 94 | 80 | 90 | 95 |
| | pine | 299 | 41 | 73 | 92 | 48 | 80 | 94 | 86 | 96 | 98 | 89 | 96 | 98 |
| | oak | 70 | 49 | 79 | 93 | 56 | 84 | 96 | 33 | 83 | 96 | 34 | 83 | 97 |
| Mattemburgh | total | 519 | 5 | 19 | 47 | 7 | 23 | 55 | 16 | 58 | 76 | 22 | 62 | 78 |
| | pine | 155 | 7 | 23 | 52 | 10 | 30 | 63 | 13 | 30 | 78 | 15 | 41 | 81 |
| | oak | 307 | 12 | 34 | 65 | 15 | 42 | 75 | 33 | 68 | 83 | 46 | 72 | 85 |
| Noordhout | total | 637 | 5 | 11 | 33 | 5 | 15 | 42 | 37 | 63 | 73 | 44 | 66 | 75 |
| | pine | 164 | 5 | 15 | 40 | 6 | 19 | 49 | 7 | 21 | 34 | 10 | 24 | 38 |
| | oak | 212 | 18 | 47 | 76 | 23 | 56 | 83 | 68 | 74 | 87 | 69 | 75 | 90 |
| | beech | 86 | 5 | 29 | 62 | 13 | 35 | 69 | 47 | 66 | 76 | 54 | 69 | 78 |
| Stille Eenzaamheid | total | 454 | 49 | 78 | 94 | 56 | 84 | 95 | 55 | 89 | 97 | 61 | 92 | 97 |
| | pine | 428 | 54 | 83 | 95 | 64 | 87 | 96 | 59 | 91 | 97 | 65 | 94 | 97 |
| Zwarte Bulten | total | 1034 | 9 | 28 | 59 | 13 | 37 | 68 | 22 | 46 | 85 | 25 | 57 | 87 |
| | pine | 707 | 17 | 44 | 77 | 22 | 53 | 83 | 41 | 63 | 95 | 46 | 72 | 96 |
| | birch | 317 | 12 | 34 | 69 | 16 | 43 | 76 | 21 | 46 | 63 | 25 | 52 | 79 |

Table 4.11 Minimum sample sizes in forest reserves (in percent of tree density) that, at the 90% and 95% probability levels, result in maximum deviations of 5%, 10% and 20% from the correct diameter differentiation value (TD).

| reserve name | species | tree density (/ha) | neighbour sampling | | | | | | plot sampling | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 90% probability max. deviation | | | 95% probability max. deviation | | | 90% probability max. deviation | | | 95% probability max. deviation | | |
| | | | 20% | 10% | 5% | 20% | 10% | 5% | 20% | 10% | 5% | 20% | 10% | 5% |
| Liedekerke | total | 709 | 1 | 1 | 4 | 1 | 1 | 6 | 1 | 4 | 19 | 1 | 7 | 37 |
| | birch | 517 | 1 | 2 | 5 | 1 | 2 | 7 | 1 | 4 | 16 | 1 | 7 | 20 |
| | oak | 122 | 1 | 4 | 16 | 2 | 6 | 21 | 3 | 10 | 26 | 4 | 13 | 35 |
| Galgenberg | total | 483 | 5 | 8 | 24 | 5 | 10 | 33 | 5 | 13 | 32 | 6 | 15 | 42 |
| | pine | 272 | 7 | 23 | 53 | 10 | 30 | 63 | 15 | 47 | 69 | 21 | 53 | 72 |
| | birch | 62 | 23 | 57 | 84 | 31 | 68 | 89 | 27 | 89 | 94 | 40 | 90 | 95 |
| | oak | 129 | 9 | 27 | 61 | 12 | 35 | 69 | 23 | 57 | 72 | 31 | 61 | 74 |
| Lheebroeker Zand | total | 383 | 8 | 25 | 57 | 10 | 33 | 64 | 15 | 28 | 58 | 18 | 31 | 64 |
| | pine | 299 | 8 | 22 | 54 | 10 | 29 | 61 | 25 | 58 | 67 | 35 | 61 | 69 |
| | oak | 70 | 17 | 44 | 76 | 21 | 54 | 83 | 46 | 67 | 77 | 51 | 70 | 81 |
| Mattemburgh | total | 519 | 5 | 8 | 23 | 5 | 11 | 32 | 5 | 15 | 59 | 6 | 24 | 61 |
| | pine | 155 | 11 | 32 | 65 | 14 | 39 | 73 | 29 | 48 | 64 | 35 | 52 | 67 |
| | oak | 307 | 5 | 16 | 44 | 7 | 21 | 52 | 18 | 36 | 63 | 22 | 41 | 67 |
| Noordhout | total | 637 | 5 | 9 | 27 | 5 | 12 | 33 | 8 | 21 | 52 | 11 | 27 | 57 |
| | pine | 164 | 14 | 40 | 71 | 20 | 47 | 77 | 59 | 75 | 87 | 66 | 79 | 89 |
| | oak | 212 | 9 | 25 | 58 | 11 | 32 | 67 | 16 | 29 | 53 | 18 | 32 | 56 |
| | beech | 86 | 26 | 57 | 83 | 31 | 65 | 87 | 67 | 81 | 95 | 71 | 92 | 97 |
| Stille Eenzaamheid | total | 454 | 5 | 17 | 42 | 6 | 22 | 51 | 9 | 18 | 47 | 10 | 21 | 51 |
| | pine | 428 | 5 | 17 | 44 | 7 | 23 | 53 | 9 | 19 | 31 | 10 | 23 | 61 |
| Tongerense Hei | pine | 454 | 5 | 13 | 35 | 5 | 18 | 45 | 11 | 30 | 75 | 15 | 56 | 80 |
| Zwarte Bulten | total | 1034 | 5 | 8 | 24 | 5 | 10 | 30 | 7 | 21 | 50 | 10 | 29 | 56 |
| | pine | 707 | 5 | 12 | 34 | 5 | 16 | 43 | 48 | 75 | 88 | 54 | 79 | 90 |
| | birch | 317 | 6 | 19 | 50 | 9 | 27 | 58 | 28 | 61 | 82 | 38 | 66 | 84 |

We determined the *design expansion factor* DEF using the data in Tables 4.8 to 4.11. The only cases used were those where neighbour sampling with moderate sample sizes were sufficient for index estimation. The minimum sample size with plot sampling is always higher than that for neighbour sampling (i.e DEF > 1). The average DEF values are 4.3 for CE, 3.3 for S, 5.6 for DM and 2.7 for TD. In most cases DEF values tend to increase with accuracy. Moreover, average DEF values for *Liedekerke* (on average 8.0 for CE, 4.0 for S, 13.4 for DM and 2.9 for TD) are systematically higher than for core areas (3.0 for CE, 3.0 for S, 2.9 for DM and 2.7 for TD).

Table 4.12 Measurement Expansion Factors (MEF) for structure indices.

| index | MEF | measurement effort(a) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | on sample trees | | | | on neighbour(s) | | | |
| | | identify neighbour(s) | species | DBH | height | distance | species | DBH | height |
| CE(b) | 1.18 | n<br>p | | | | n<br>0.7*p | | | |
| S(c) | 1.50 | n<br>p | n<br>p | | | | n | | |
| DM(c) | 1.75 | 3*n<br>3*p | n<br>p | | | | 3*n | | |
| TD(c) | 1.75 | 3*n<br>3*p | | n<br>p | | | | 3*n | |
| TH(c) | 3.31 | 3*n<br>3*p | | | 10*n<br>10*p | | | | 30*n |
| all but TH | 2.11 | 3*n<br>3*p | n<br>p | n<br>p | | n<br>0.7*p | 3*n | 3*n | |
| all | 3.31 | 3*n<br>3*p | n<br>p | n<br>p | 10*n<br>10*p | n<br>0.7*p | 3*n | 3*n | 30*n |

(a) ‘n’ and ‘p’ indicate a unity of measurement effort for neighbour sampling and plot sampling respectively. All measurement actions require the same effort, with the exception of height measurements which require ten times this effort. MEF is defined by the ratio of summed n and p.
(b) Estimate based on a forest with random positioning of trees, in which approximately 60% of the nearest neighbour relations are mutual (Pielou 1977) and therefore only need to be measured once in a plot sample. Deviations from random positioning result in slightly different MEF values (theoretically between 1 and 1.33).
(c) Estimate does not take into account the measurement effort for plot sampling on neighbours that fall outside the plot, which results in a slight overestimation of values.

Table 4.12 provides some of the calculated *measurement expansion factors* MEFs for the structure indices. They are based on the counting of measurement actions for each sample type. It was assumed that all measurement actions required the same effort, with the exception of height measurements that required ten times as much, and that for plot sampling all of the trees within the plot were numbered (to indicate neighbour relations and avoid double measurements). The values in Table 4.12 are approximations, since they depend on assumptions about measurement efforts and do not take into account some factors that are difficult to quantify (cf. notes b and c to Table 4.12).

## 4.4 Discussion

### 4.4.1 Structure assessment in core areas

Structure assessment in a core area provides information about the structure of a particular stand at a particular moment in time. The seven core areas investigated represent different ageing Scots pine stands, with varying densities of birch and/or oak regeneration (cf. Table 4.2). Since pine is the dominant species in all core areas, we observed some similar patterns in the calculated structure values.

*CE:* Positioning of ageing pine trees (Table 4.4) is regular (CE significantly greater than 1) or random (CE not significantly different from 1), the latter only in cases where tree density of pine is low. This is an artefact of the regular grid used at the time of planting and the management history (Gleichmar & Gerold 1998). Two exceptions are *Stille Eenzaamheid* and *Zwarte Bulten*, where clustered pine regeneration is present, and the overall positioning of pines, overstorey trees and regeneration combined, is random or clustered (CE significantly smaller than 1). Birch is clustered in nearly all cases.

*S:* The relative mixture (Table 4.4) between pine and a regenerating species indicates segregation in most cases (S significantly greater than 0). Birch and oak are thus often spatially separated from pine, indicating that both species emerge in canopy gaps of pine. In *Galgenberg* the relative mixture between pine and oak indicates aggregation (S significantly smaller than 0) between both species. For a similar case, Kint *et al.* (2003) proved how such negative S values are not linked to any ecological process of attraction between species, but rather to former selective thinnings of pine. Finally, in most cases birch and oak are segregated, indicating that both species occur more or less spatially-separated from each other.

*DM:* Mixture (Table 4.4) is in all cases consistent with former results, indicating a significantly lower DM value for clustered or segregated species than would be the case under random mixture (cf. permutation test in Table 4.1). In general, mixture values tend to be higher for species with lower relative tree densities and vice versa.

*T:* Differentiation values (Table 4.5) range from very low (minimum observed T value of 0.072; relative difference in size between neighbouring trees is negligible) to extremely high (maximum observed T value of 0.504; average relative difference in size between neighbouring trees of 50%). For pine, differentiation of height (TH) is always lower than that of diameter (TD), which in turn is lower than that of crown length (TCl). With some exceptions, the same relationships also hold for birch and oak. Since in most reserves many T values are significantly lower than would be the case under random conditions (cf. permutation test in Table 4.1), we can assume that autocorrelation of tree sizes is commonly present (Kuuluvainen *et al.* 1998).

### 4.4.2 Structure assessment in structural classes

An SC groups similar monitoring plots, and hence represents a particular stand structural type that can be distinguished in the forest reserves. Structure assessment of an SC provides information about the specific characteristics that distinguish it from other SCs, and helps to give an impression of the actual appearance of the stand structural type. Some SCs are similar with respect to species composition, which makes it possible to discuss them together. We discuss three groups of SCs, based on Tables 4.3, 4.6 and 4.7, which represent markedly different stand structures from those already discussed in the core areas.

#### 4.4.2.1 Birch stands with oak regeneration

Four SCs (G, H, I and J) represent stands of emerging birch with oak regeneration and very few remaining old pine trees. These SCs are characterised by a random or regular distribution of birch and oak, but both species are also segregated. Only in the case of G are sufficient pine trees available to calculate positioning and segregation;

this indicates that remaining pines occur in clusters that are slightly associated with oak trees. This association might be due to chance, given the limited number of pine trees in the calculation. However, other plausible explanations, e.g. the ability of oak (in contrast to birch) to emerge at locations with prolonged pine cover, should not be excluded. There are no common patterns in mixture or differentiation values for these four SCs.

#### 4.4.2.2 Regenerations after a storm

F represents mixed regenerations of birch, pine and oak on an open area after a storm. Stand structure indices in this particular SC reveal that birch, the main species in the regeneration, and pine occur in segregated clusters. Oak is more randomly spread throughout the stand, although segregation from birch suggests a preferential mixture with pine. Mixture values reflect the species proportions: low for birch, high for pine and oak. Differentiation seems to be similar for birch and pine, and in all cases it is low. Not enough oak trees were available to calculate oak differentiation.

#### 4.4.2.3 Dense pine regenerations

R and S are SCs that represent very dense pine regenerations on open areas, with possibly a fraction of birch. The high density of pines is such that no empty places remain, which results in a regular positioning. Where birch is present, it occurs randomly throughout the stand. Mixture values reflect the species proportions: very low for pine, much higher for birch. Pine differentiation is very low.

### 4.4.3 Structure trends in main pathways of stand development

A pathway consists of a sequence of SCs. Structure assessment within these sequences (Fig. 4.2 to 4.5) provides information about trends of stand structural development in ageing Scots pine stands, and the underlying competitive tree interactions. The decline of pine density and the regeneration of broadleaved species in canopy gaps (for the three gap pathways) as well as the massive regeneration and self-thinning of pines and the suppression of broadleaved species (for the disturbance pathway) are reflected in the structural trends. We discuss these trends for each index separately.

#### 4.4.3.1 Positioning (CE)

In all three gap pathways, the positioning of ageing pines is initially regular: an artefact of planting and management history. In the first pathway it tends towards random distribution as fewer pine trees remain (CE decreases towards 1). In the second and third pathways the decline of pine density is apparently not strong enough to have the same effect.

In the first pathway, birch establishes in canopy gaps of pine and hence starts clustered. As more gaps become available and birch density increases, the species tends towards random positioning (CE increases towards 1). This is consistent with the regeneration strategy of birch (Perala & Alm 1990, Atkinson 1992). In the second and third pathways birch is suppressed by oak or beech, and only survives in a few clusters.

Oak regeneration tends from clustered towards random positioning in the first and second pathways. The regeneration strategy of oak, however, is not directly linked to gap formation. Oak is mainly dispersed by blue jays (*Garrulus glandarius* L.) and small rodents (*Apodemus sylvaticus* L. and *Clethrionomys glareolus* Schreber), and can survive for prolonged periods under a pine canopy (Van Hees 1997, Larsen & Johnson 1998, Mosandl & Kleinert 1998, Frost & Rydin 2000). We therefore presume that oaks randomly establish and survive under pine canopies prior to gap formation, and that they gradually grow up to measurement size (minimum DBH of 5cm) as more light becomes available in the gaps. This would explain the initial oak clustering. In the third pathway oak is suppressed by beech, and only survives in a few clusters.

The disturbance pathway is characterised by a massive regeneration of pine that develops from clustering towards regularity due to self-thinning (Warrington 1994). Together with pine, oak and birch establish in clusters. Broadleaved species are gradually suppressed and their density decreases. They survive in a few clusters or as individual trees.

#### 4.4.3.2 Mixture (S and DM)

In the gap pathways, broadleaved species initially emerge in canopy gaps of pine and hence start segregated from pine. But as pine density decreases, they tend towards a random mixture with remaining pine trees (S decreases towards 0). In the second and third pathways, birch survives in clusters that remain segregated from pine. Birch and oak also establish segregated from each other: in large gaps, birch regeneration may prevent the advance regeneration of oak from maturing, whereas in small gaps the advance regeneration of oak may prevent birch from establishing (Coates & Burton 1997). There is however a slight tendency towards decreasing segregation between birch and oak, indicating that they gradually become randomly mixed. Increasing relative tree density of species results in decreasing mixture (DM) and vice versa.

In the disturbance pathway, birch establishes segregated from pine, whereas oak and pine are initially randomly mixed. As broadleaved species are suppressed and their density decreases, the few remaining birch trees become randomly mixed with pine, and oaks survive in clusters segregated from pine. Birch and oak establish and remain segregated from each other. The increasing isolation of oak from other species explains its decreasing mixture, even though its relative tree density decreases.

#### 4.4.3.3 Differentiation (T)

It has often been demonstrated that under conditions of competition for light (asymmetric competition), and as long as no major mortality occurs, tree size variation at small inter-tree distances increases (Biodi *et al.* 1994, Kuuluvainen *et al.* 1998, Mateu & Ribeiro 1999). This explains the increasing differentiation of birch in the first pathway, and of birch and oak in the second and third pathways. According to Cannell & Grace (1993), a decrease of differentiation, as for oak in the first pathway, is due to symmetric competition which acts to slow down the growth of all plants and so decreases the divergence in plant size. Oaks in the first pathway are gradually suppressed by birches, which make it plausible to assume symmetric competition between oaks.

Meyer & Pogoda (2001) found that once competition leads to mortality, there is a decreasing differentiation due to the loss of lower size classes. This is observed for pine in all gap pathways, indicating that neighbouring remaining old pines tend to be increasingly similar. In the disturbance pathway this decrease was only observed for diameter differentiation of pine. Further research is needed to establish the reasons for the increasing height and crown length differentiation of pine in this pathway; here we suggest that in cases of strong self-thinning it could be linked to a trade-off between the loss of lower size classes on the one hand and the ongoing competition for released growing space and light on the other.

### 4.4.4 Minimum sample size and optimal sample type for structure assessment

Many of the minimum sample sizes in Tables 4.8 to 4.11, particularly for S and for high accuracy estimates, amply exceed the limit of 20% that we set as the highest feasible sample size in normal situations. This is in contrast with the results of Pommerening & Von Gadow (2000), who concluded that sampling techniques imply only small errors in most cases, even at relatively low sample sizes. We were not able to relate the minimum sample sizes to basal area and tree density in the stands examined. This is illustrated in *Tongerense Hei* where, in spite of the structural simplicity of the stand (homogeneous pine), minimum sample sizes for CE are considerably higher than in *Lheebroeker Zand* (mixed stand of pine and oak). Hence, the results in our stands (Tables 4.8 to 4.11) are merely indicative for similar stands. When more detail about minimum sample sizes is needed in a given situation, a preliminary study with SIAFOR on a representative plot can be performed.

We focussed on those cases where moderate sample sizes are sufficient for index estimation at a given accuracy level. A comparison of DEF values and MEF values clearly indicates that for the estimation of CE, S, DM and TD, neighbour sampling is more interesting than plot sampling in both *Liedekerke* and all core areas (DEF > MEF for every index singularly and for all together). For some individual cases, plot sampling may be more interesting still (e.g. low accuracy estimates for most indices in *Galgenberg*), but it is difficult to relate these cases to stand structure. However, if TH should be estimated (and assuming that TH and TD have equal DEF values), the effort needed for height measurements makes plot sampling more interesting in both *Liedekerke* and all core areas (DEF < MEF). If in addition to TH all other indices need to be estimated as well, plot sampling remains more interesting in the core areas; only at larger stand sizes is neighbour sampling again more efficient. Since in most cases T values for different sizes give similar results, the estimation of TD will often suffice and neighbour sampling should be chosen whenever the stand size is 1 ha or larger.

For neighbour sampling, certain trends seem to emerge from our results, namely that at a given sample size (i) accuracy of estimates is highest for TD, and gradually decreases for CE, DM and S; (ii) accuracy is less for statistical tests than for index estimates; (iii) accuracy is often less for species with low tree densities; and (iv) accuracy is greater in large stands.

Our study indicates that with moderate sample sizes and neighbour sampling, most CE, DM and TD values can be estimated with an accuracy of 20% maximum deviation at the 90% or 95% probability levels, and that many can be estimated to an even greater degree of accuracy. For S, moderate sample sizes are almost never sufficient to reach this accuracy level. Also the statistical tests for CE and S generally require larger sample sizes to be reliable. At a sample size of 10%, only TD and CE can be estimated with an accuracy of 20% maximum deviation. At a sample size of 5%, this is only the case for total TD and total CE values.

## 4.5 Conclusion

SIAFOR, a computer program for the quantification of the three-dimensional geometry of forest stands with nearest-neighbour indices, has been successfully used for (1) stand structure assessment and interpretation in ageing Scots pine stands in selected Dutch forest reserves and; (2) the determination of minimum sample size and optimal sample type for the estimation of stand structure with sampling techniques.

(1) The structure assessment in forest reserves was performed on three information levels. The first level (individual monitoring plots) and the second level (groups of similar plots) mainly provide information about local stand structures and structural types within the forest reserves, by describing tree positioning, mixture and size differentiation. Together these indices proved to give a detailed insight of forest stand structure. The third level (approximations of long-term forest development) provides information about trends of structural development and the underlying competitive

tree interactions involved. From the structure assessment in ageing Scots pine stands the following conclusions about structural development can be formulated:

(i) As pine density decreases, pines tend from regular positioning towards random positioning.

(ii) Regeneration of birch establishes in canopy gaps of pine. Regeneration of oak establishes prior to gap formation under a canopy of pine, and gradually grows up as more light becomes available in the gaps. This means that both species initially occur in clusters that are segregated from all other species. If they are not suppressed, birch and oak tend towards random positioning and random mixture.

(iii) Massive regeneration of pine on open areas after a storm is initially clustered. Due to self-thinning, pine develops towards regular positioning. Birch and oak survive as individual trees or in isolated clusters.

(iv) With asymmetric competition, and as long as no major mortality occurs, the differentiation of species increases. With symmetric competition, e.g. when oak is suppressed by birch, it decreases.

(v) Once competition leads to mortality, differentiation generally decreases, except in cases of strong self-thinning where a trade-off between the loss of lower size classes on the one hand and the ongoing competition for released growing space and light on the other, may lead to both decreasing or increasing differentiation.

(vi) Structural development at the stand level in ageing Scots pine stands is characterised by a tendency towards random positioning, increasing mixture and increasing differentiation. On open areas after a storm it is characterised by a tendency towards regularity, a status quo for mixture and increasing differentiation.

(2) The use of sampling techniques to assess forest structure at reasonable accuracy levels often requires very large sample sizes. Moreover, we were not able to relate the minimum sample sizes to basal area and tree density in the stands examined. Therefore, our results are merely indicative for similar stands. Some general conclusions can be formulated, based on those cases in our study where moderate sample sizes were sufficient for index estimation:

(i) Neighbour sampling should be preferred over plot sampling, except for the estimation of height differentiation on small areas (< 1 ha).

(ii) At a given sample size the accuracy of different index estimates and statistical tests will vary. It will be highest for TD, and gradually decreases for CE, DM and S; lower for statistical tests than for index estimates; lower for species with low tree densities; higher in large stands.

(iii) Using neighbour sampling, most CE, DM and TD values can be estimated with a minimum accuracy level, defined by a maximum deviation of 20% from the correct index value at the 90% probability level. For S, moderate sample sizes are almost never sufficient to reach this accuracy level. Also the statistical tests for CE and S generally require larger sample sizes to be reliable.

## Chapter five

# 5 Close-to-nature forestry in ageing Scots pine forests in Western Europe

Kint, V., Geudens, G., Mohren, G.M.J., De Wulf, R., Goris, R. & Lust, N.

Submitted for publication in an international forestry journal.

### Abstract

Conversion towards mixed broadleaved forests is a common management goal in ageing Scots pine (*Pinus sylvestris* L.) forests throughout Europe. Since naturally regenerated broadleaved species establish easily in these forests, conversion based on natural vegetation dynamics is often recommended. This idea relates to the concept of close-to-nature forestry, which is characterised by a fundamental choice of working with and/or emulating natural vegetation dynamics. Conceptual models of natural vegetation dynamics describe patterns of stand structural development within forest ecosystems. As such, they can help forest managers to anticipate natural vegetation dynamics and incorporate them into their management. We review two existing conceptual models of natural vegetation dynamics in ageing Scots pine stands, i.e. a climax model and a recently developed pathway model. We argue that the pathway model is more suitable for guiding close-to-nature forest management in ageing Scots pine stands than the climax model, based on the level of detail in describing stand structural development, the representation of major disturbances and structural diversity, and the flexibility in use. We provide a framework for management implementation based on the pathway model. At the stand level, our framework considers the choice of a target pathway, the regeneration methods used and the silvicultural treatment. Some thoughts about management practices at the landscape level, management planning and management evaluation are offered. We explore the prospects for close-to-nature forestry in ageing Scots pine forests and show the value of our framework in this context. Finally, we discuss the relationship between our framework and the German concept of forest development types.

## 5.1 Introduction

From the end of the 18th century until far into the 20th century, Scots pine was systematically planted on poor sandy soils throughout Western Europe. Short-rotation silviculture (40-50 years) in these homogeneous plantations was predominantly focused on the production of mine props and construction timber. As a result of the diminishing economic return (partly induced by the closing of the coal mines) and an increased social demand for more nature values and biodiversity in recent decades, the management of these forests has gradually become focused on multifunctionality (Mason & Alía 2000) and short rotations have been abandoned. In ageing Scots pine stands (50 years and over) natural regeneration of broadleaved species is often observed, mainly of silver birch (*Betula pendula* Roth), downy birch (*Betula pubescens* Ehrh.), pedunculate oak (*Quercus robur* L.), sessile oak (*Quercus petraea* (Mattuschka) Lieblein), and common beech (*Fagus sylvatica* L.), in addition to natural regeneration of Scots pine itself.

Nowadays, conversion towards mixed broadleaved forests is a common management goal in ageing Scots pine plantations throughout Europe. The reasons for this conversion include the increase of ecosystem stability, biodiversity, amenity purposes, economic flexibility, sustained soil fertility and the reduction of soil nutrient leaching (Mosandl & Küssner 1999, De Schrijver *et al.* 2000, 2002, Kenk & Guehne 2001). Since naturally regenerated broadleaved species establish easily in these forests, conversion based on natural vegetation dynamics is often recommended (Kuper 1994, Mosandl & Kleinert 1998, Zerbe 2002). This idea is related to the concept of close-to-nature forestry. However, a framework for its implementation, based on thorough insight into natural vegetation dynamics, has yet to be provided. As a result, most attempts at close-to-nature forest management are based on limited experience or lack coherence.

Even though close-to-nature forestry has only become widely adopted in recent times, the concept had already been proposed and elaborated a long time ago, for example, Cotta (1816), Gayer (1880), Köstler (1950), Tschermak (1950), Leibundgut (1951) and Mayer (1977). Close-to-nature forestry is characterised by the attempt to somehow incorporate natural vegetation dynamics within forest management (Lähde *et al.* 1999a, Führer 2000, Nabuurs *et al.* 2001). Different approaches to close-to-nature forestry may attribute different degrees of importance to natural vegetation dynamics. The often cited ‘Pro Silva’ approach, for example, focuses on timber production and economic yield, and considers natural vegetation dynamics as a means to this end (Kuper 1994, Anonymous 1999). Other approaches may consider natural vegetation dynamics as a worthwhile objective in its own right (Coates & Burton 1997).

In this chapter we consider close-to-nature forestry in its broadest sense: i.e. a framework for forest management that is characterised by a fundamental choice of working with and/or emulating natural vegetation dynamics. Hence, instead of assuming that a forest can be completely controlled, close-to-nature forestry adopts the principle that management should be guided by natural vegetation dynamics to achieve its goals. Although, 'close-to-nature forestry', 'nature-oriented forestry' and 'diversity-oriented forestry' are often used as synonyms in the literature, we distinguish between these terms. The second two terms semantically imply that management should be focused ('oriented') on nature conservation. Close-to-nature forestry, however, may be adopted under varying management goals.

After a brief introduction to natural vegetation dynamics and their representation through conceptual models, our purposes are to:

(i) present two existing conceptual models of natural vegetation dynamics in ageing Scots pine stands, i.e. a climax and a pathway model, and discuss their suitability for use in close-to-nature forest management;

(ii) provide a framework for the implementation of close-to-nature forestry in ageing Scots pine stands, based on the pathway model.

## 5.2 Natural vegetation dynamics in forest ecosystems

Natural vegetation dynamics encompasses all spontaneous vegetation processes and patterns, i.e. occurring without direct anthropogenic influence and involving species native to a site. Knowledge of natural vegetation dynamics is the basis for close-to-nature forestry (Fig. 5.1).

Gaining an understanding of natural vegetation dynamics in forests is difficult due to the lack of forests without direct anthropogenic influence, and because of the complexity involved. Vegetation dynamics is dependent on biotic factors (competitive tree interactions, pests and diseases, grazing and browsing), disturbances (varying in scale, intensity, frequency, spatial pattern and type) and environmental conditions (soil type, water and nutrient availability and climate). Many attempts have been made, for different forest ecosystems, to express prevailing insights into natural vegetation dynamics in the form of conceptual models. We distinguish two types of conceptual models for natural vegetation dynamics, namely those based on the climax concept and those based on the pathway concept. Climax and pathway models both have merits and limitations, and should be regarded as complementary.

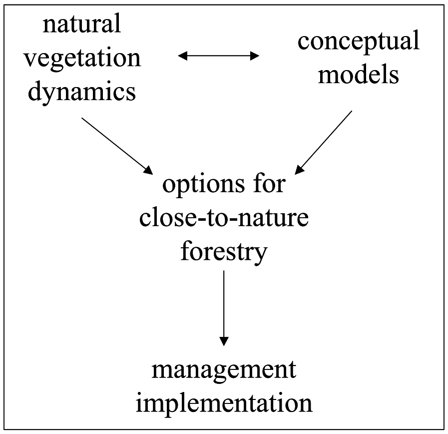


Figure 5.1 Knowledge of natural vegetation dynamics, expressed in conceptual models, is the basis for close-to-nature forestry and its management implementation.

The concept of natural vegetation dynamics being a unidirectional deterministic development towards a stable terminal stage (climax) following a disturbance, was first formulated by Clements (1916). Since many of the assumptions in the original climax concept have been questioned, it is now widely used in adapted forms. Over the course of time, the static Clementsian concept has gradually given way to a more dynamic view. The unique and stable climax has now been replaced by a range of possible climaxes, dependent on site characteristics, each of which are part of a cyclical process of degradation and directional development (Cook 1996, Peterken 1996 p.128-131, Kimmins 1997 p.403-406). Climax models generally represent natural vegetation dynamics as a fixed sequence of developmental stages (i.e. succession) following a disturbance (e.g. storm or fire). In this approach, the fact that the climax vegetation may not always be reached due to stochastic factors is considered irrelevant. In this sense the climax vegetation is related to the concept of potential natural vegetation (Van Der Werf 1991, Leuschner 1997).

The observation that natural vegetation dynamics can have multiple endpoints and can be stochastic, has led to the pathway concept. Multiple development pathways may exist for a single site type, each depending on biotic factors, disturbances and environmental conditions (Cattelino *et al.* 1979, Pickett *et al.* 1987). Different pathways can occur simultaneously within a forest, can operate at different spatial and temporal scales, and may or may not lead to similar structures (Cook 1996, Spies & Turner 1999, Frelich 2002). In this sense, "the general pattern of succession is more analogous to a braided river, where individual channels split and recombine in a variety of configurations, than to a single channel" (Peterken 1996 p.138).

Natural vegetation dynamics and forest management both affect stand structure and structural development. They influence each other through their direct impact on stand structure. Conceptual models describe patterns of stand structural development within forest ecosystems in relation to biotic factors, disturbances and/or environmental conditions. As such they can help to anticipate natural vegetation dynamics and to incorporate them into management. Accordingly, conceptual models of natural vegetation dynamics may be used as guides for close-to-nature forest management that influence both planning and practice (Fig. 5.1).

## 5.3 Conceptual models of natural vegetation dynamics in ageing Scots pine stands

Ageing Scots pine stands in Western Europe often occur on oligotrophic and acidic sandy soils. In nearly all cases, Scots pine has been planted. Natural plant associations on these sites are *Betulo-Quercetum roboris, Fago-Quercetum* and *Deschampsio-Fagetum* (Stortelder *et al.* 1999). The main tree species native to these sites are Scots pine, silver birch, downy birch, pedunculate oak, sessile oak and common beech. In the following sections we present and compare existing climax and pathway models of natural vegetation dynamics, starting from homogeneous Scots pine stands. We also discuss their suitability for use in close-to-nature forest management. These models presuppose that seed trees for all species are present and that the impact of herbivores impeding natural regeneration processes is not excessive. Where these conditions are not met, adequate corrections should be incorporated.

### 5.3.1 Climax models in ageing Scots pine stands

Climax models of natural vegetation dynamics on oligotrophic and acidic sandy soils in North-western Europe have been elaborated by Fanta (1982, 1986, 1995) and Leuschner (1991, 1994). Their models describe similar long-term development patterns from homogeneous Scots pine forests towards a site-specific climax. A synthesis of these models is presented in Fig. 5.2. It is characterised by directional development, first towards an oak-birch forest and further towards an oak-beech forest.

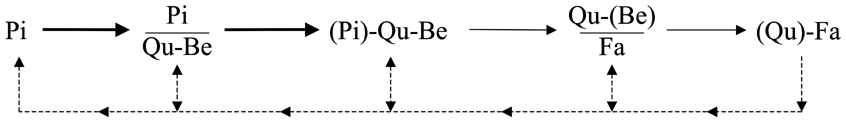


Figure 5.2 A synthesis of the climax models of Fanta (1982, 1986, 1995) and Leuschner (1991, 1994), which describes succession from homogeneous Scots pine forests towards oak-birch (thick full arrows) or oak-beech (thin full arrows) forests. Dashed arrows indicate disturbances. Pi = Scots pine, Be = birch, Qu = oak, Fa = beech. Fractions indicate differences between the overstorey and the understorey.

Fanta (1982, 1986, 1995) discriminates between the primary succession towards a climax (see also Prach 1989), and the subsequent cycles of secondary succession. The latter are characterised by three possible succession strategies towards the climax following a disturbance: (i) the ‘iterative strategy’, where the climax is immediately repeated; (ii) the ‘alternative strategy’ where the succession towards the climax passes through transient stages and; (iii) the ‘deflective strategy’ which leads to a prolonged treeless stage. Only the alternative strategy is represented in Fig. 5.2 (dashed arrows). The climax itself is completely determined by soil texture: oak-birch on poor sandy soils and oak-beech on somewhat richer sandy soils.

A similar model is presented by Leuschner (1991, 1994). He describes secondary succession towards oak-beech forests on all types of sandy soils based on resource availability. The oak-birch forest is not considered as a separate climax, but rather as a developmental stage towards the oak-beech climax. Disturbances, both natural and anthropogenic, set back succession towards previous developmental stages.

Finally, Clerkx *et al.* (2002) and Zerbe (2002) distinguish general development scenarios of ageing Scots pine stands towards oak or oak-beech forests, based on the current vegetation community. Their findings, although much less detailed, are consistent with the aforementioned models.

### 5.3.2 Pathway model in ageing Scots pine stands

Recently, Kint (2003) developed a pathway model of natural vegetation dynamics on oligotrophic and acidic sandy soils, The development in various ageing Scots pine stands was approximated, based on an extensive data set in forest reserves and a process-based gap model. This yielded four main pathways (Fig. 5.3). Three of these were linked to gap dynamics, and one to major disturbance dynamics.

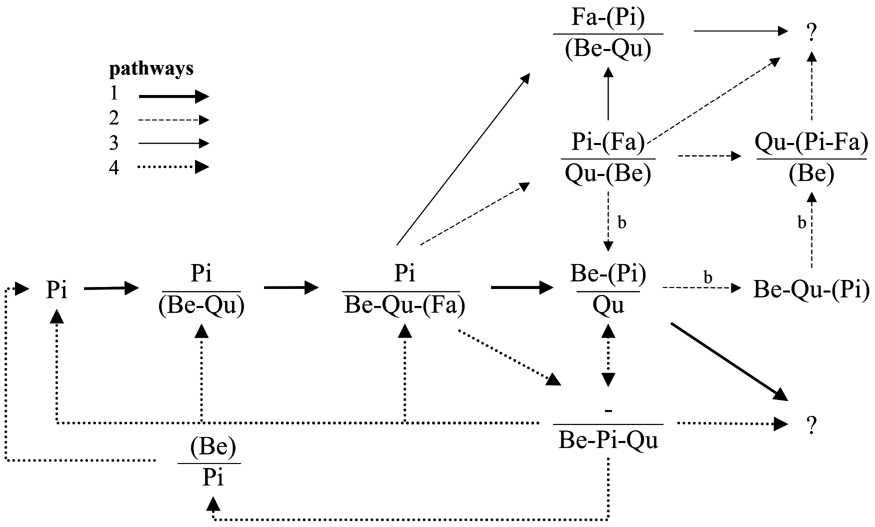


Figure 5.3 The pathway model (after Kint 2003) describes different development patterns in ageing Scots pine stands. Pathways 1 to 3 are linked to gap dynamics and pathway 4 to major disturbance dynamics. Pi = Scots pine, Be = birch, Qu = oak, Fa = beech. Fractions indicate differences between the overstorey and understorey.

Kint (2003) only described pathways that could be approximated with existing observed stand structures in forest reserves. As a consequence, the suggested pathways often end up in undefined stand structures (the question marks in Fig. 5.3), i.e. structures that are not yet observed in the forest reserves simply because the development time has not yet been long enough. That these undefined structures might to a certain extent approximate to the climaxes of Fig. 5.2, cannot be excluded. If this were the case, the pathway model could be interpreted as an elaborated version of the first development steps of the climax model. However further research is needed to establish whether the pathways in ageing Scots pine stands really do converge towards a climax, and if so to which and to what extent.

#### 5.3.2.1 Pathways linked to gap dynamics

Gap dynamics are characterised by small-scale, low-intensity but high frequency disturbances (Coates & Burton 1997, Wohlgemuth *et al.* 2002). The three pathways linked to gap dynamics in ageing Scots pine stands differ in light availability for regeneration (depending on gap origin and gap size) and/or seed tree availability. All start from dense homogeneous Scots pine stands with spontaneous regeneration of birch and oak.

The first pathway (thick arrows in Fig. 5.3) is characterised by a rather abrupt decline of Scots pine density and the creation of large canopy gaps, which facilitates birch regeneration although oak remains present. Gap origin is probably linked to minor disturbance events (such as storms), causing the death and toppling of groups of trees. The second pathway (dashed arrows in Fig. 5.3) is characterised by a more gradual decline of pine density, and a development towards a relatively open canopy of old pines with an understorey of emerging oak and some birch. A variant of this second pathway (dashed arrows marked with ‘b’ in Fig. 5.3) passes through stages where birch and oak compete. Goris (2002) showed that the gap origin in the second pathway is also linked to minor disturbances, rather than to biotic factors. Therefore differences with the first pathway are mainly due to the intensity and/or frequency of a disturbance which causes smaller gap sizes. The third pathway (thin arrows in Fig. 5.3) is similar to the second but with beech next to oak. The presence of beech is closely related to the availability of seed trees.

#### 5.3.2.2 Pathways linked to major disturbance dynamics

Major disturbance dynamics are characterised by large-scale, high-intensity and low-frequency disturbance events (Wohlgemuth *et al.* 2002). In West-European forests, most major disturbances are caused by storm events (Pontailler *et al.* 1997, Bengtsson *et al.* 2000, Fischer *et al.* 2002). The pathway research confirms the importance of major disturbances in natural forest dynamics in ageing Scots pine stands. The fourth pathway is actually a group of pathways that involve major disturbances, which lead to large cleared areas within the forest. The pathway model in Fig. 5.3 shows many different development patterns following a major disturbance (dotted arrows). Many of these join one of the gap pathways and others lead to undefined structures. However, another possible development pattern is towards a new generation of Scots pine.

### 5.3.3 Suitability of the climax and pathway models as guides for close-to-nature forest management in ageing Scots pine forests

Not all conceptual models of natural vegetation dynamics are equally suitable for guiding close-to-nature forest management. In our view the presented pathway model is more suitable for ageing Scots pine forests than the climax model because of its: (i) level of detail in describing stand structural development; (ii) representation of major disturbances and structural diversity; and (iii) flexibility in use.

We want to stress, however, that our arguments in favour of the pathway model are confined to the particular model as described in Fig. 5.3, and to its application in a context of close-to-nature forestry. Hence, they do not intend to formulate a depreciation of the presented climax model, neither of climax models in general. These models have indeed proven their merits for many purposes.

#### 5.3.3.1 Level of detail in describing stand structural development

As conceptual models of natural vegetation dynamics describe patterns of stand structural development within forest ecosystems, they can help to anticipate natural vegetation dynamics and to incorporate these into management practice. Thus, their usefulness in close-to-nature forest management is mainly determined by their representation of stand structural development. The more detailed this description, the more useful the model is for management. In the climax model the description of structural development is limited to a sequence of species compositions. However, in the pathway model, trends of basal area, tree density, mean tree sizes and of three-dimensional geometry of stands have been provided for each pathway (Kint 2003). The three-dimensional geometry of stands encompasses tree positioning, distribution patterns of species and size differentiation of trees. The pathway model undoubtedly provides more insights into stand structure and structural development in ageing Scots pine forests than the climax model.

#### 5.3.3.2 Representation of major disturbances and structural diversity

There is an increasing consensus among forest ecologists about the importance of incorporating major disturbances and structural diversity into close-to-nature forest management. Major disturbances, such as storms, fire, insect outbreaks or other large-scale events, are natural components of a forest ecosystem which influence forest structure and functioning (Pickett & White 1985, Turner *et al.* 1998, Bengtsson *et al.* 2000, Frelich 2002). Their impact can have a high ecological value. The diversity of forest structures and development patterns is a consequence of the many endogenous and exogenous factors involved in natural vegetation dynamics (Oliver & Larson 1996, Peterken 2001). This diversity is found on both a stand and a landscape level (Axelsson & Östlund 2001, Jasinski & Angelstam 2002). A conceptual model of natural vegetation dynamics should help managers to integrate these two aspects into forest management.

We recognise that both of these aspects are represented in the climax and pathway models. However, the two models differ in how they achieve this. Climax models focus on one final development stage, the climax. As disturbances divert from the climax, these are represented as retrogressive. Diversity of stand structures is represented by the different developmental stages on the way towards the climax. This focus on a climax vegetation means that forest managers generally associate it with the potential natural vegetation and interpret it as a management goal (e.g. Mosandl & Küssner 1999). Therefore, the use of the climax model in a forest management context may lead to:

(i) the avoidance of major disturbances or minimising their impact under all circumstances, even in cases where they do not directly endanger or even can help to reach specific management goals;

(ii) the preferential treatment and/or planting of desired, mostly late-successional species, and an underrating of other species. This

> inevitably leads to a deficit of important natural forest structures, at both the stand and landscape levels (Bengtsson *et al.* 2000, Axelsson & Östlund 2001).

The pathway model, on the other hand, represents major disturbances as one of the main pathways of natural stand development, which is equivalent to other pathways without disturbances. Hence, the management opportunities that arise due to major disturbances are explicitly considered. As in the climax model, the diversity of stand structures is represented by different developmental stages. However, as the emphasis is on the different routes of vegetation development rather than on a climax vegetation, the diversity of development patterns is also explicitly considered.

#### 5.3.3.3 Flexibility in use

The pathway concept is inherently flexible. Forest managers using the pathway model have the opportunity to continuously evaluate their management and, by switching between pathways, to adapt it to changing conditions. Under changing climate and/or growth conditions – e.g. fluctuating herbivore densities, dominance of bracken (*Pteridium aquilinum* (L.) Kuhn) – new pathways can be described and easily added to the existing model. In this sense, the current pathway model is not yet complete, and probably does not even cover some important development patterns in ageing Scots pine stands. However, the essence of the model is not the description of the four pathways – these are merely summaries of prevailing development patterns – but rather the principle that every site has its own specific development pattern, which is dependent on a range of deterministic and stochastic factors.

It is clear that the climax model does not offer the same flexibility. It only describes one development pattern, from which managers will need to deviate whenever they are confronted with stochastic factors. Moreover, there is a risk that the climax model will easily become outdated when major changes in the environment occur (e.g. climatic change), so that new models with modified climax vegetations will need to be developed.

## 5.4 Close-to-nature forest management in ageing Scots pine stands based on the pathway model

Our intention is not to provide a particular management recipe. Rather our aim is to indicate how the pathway model can guide close-to-nature forest management in ageing Scots pine stands, by providing a framework for management implementation.

### 5.4.1 Practice at the stand level

At the stand level, the pathway model has consequences for: (i) the choice of a target pathway; (ii) the used regeneration methods and; (iii) the silvicultural treatment (Fig. 5.4).

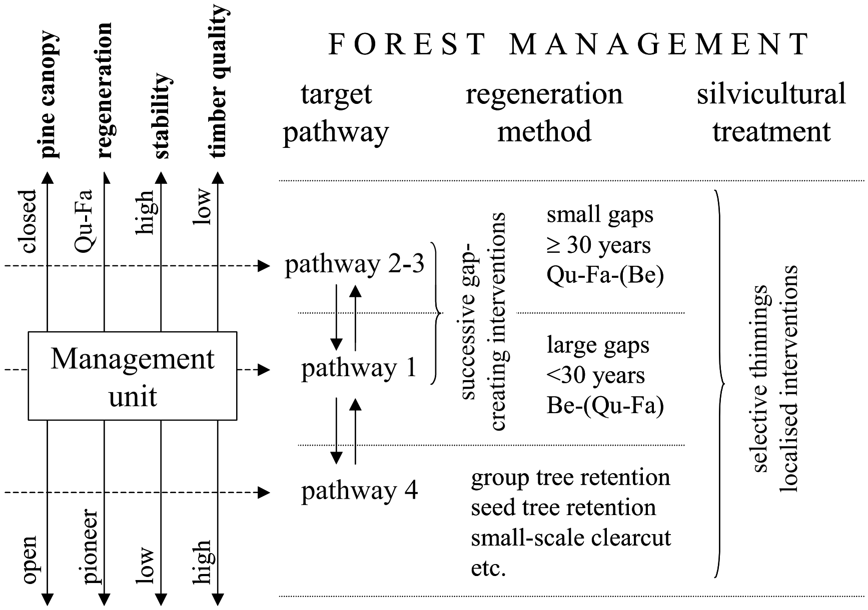


Figure 5.4 Framework for the implementation of close-to-nature forest management in ageing Scots pine stands, based on the pathways concept. Pi = Scots pine, Be = birch, Qu = oak, Fa = beech.

#### 5.4.1.1 Target pathway

The first management step is to define a target pathway for each stand. The target pathway should not be confused with a management goal. It defines the expected development route, and as such may help to decide which management goals are feasible and provide guidance for management practices. The most appropriate pathway can be chosen (Fig. 5.4) on the basis of stand characteristics (e.g. pine age and cover, composition of regeneration, stability). For example, a pathway towards oak (second pathway) is plausible if the pine canopy is still rather closed, no massive birch regeneration is yet present, and no major hazard of large-scale storm damage is imminently expected. In some cases the definition of the target pathway may also be inspired by factors related to a specific management goal (e.g. timber production). The high timber quality of Scots pine in a stand may be an economic argument for large-scale interventions, emulating a major disturbance and inducing a pathway of high competition within an even-aged mixed regeneration (fourth pathway).

Traditionally, forest stands are defined more or less arbitrarily and considered as independent management units. However, natural vegetation dynamics does not stop at stand borders. In the context of close-to-nature forestry based on the pathway concept, the management units should, where possible, be defined by the scale of natural processes within pathways. This means that, based on the spatial extent of observed vegetation developments, different stands may be pooled into one management unit or that one stand may be divided into two or more management units. In such cases the forest manager's ecological knowledge about micro-sites could play a leading role. This flexibility in dealing with stand borders optimises the integration of natural vegetation dynamics into forest management.

The definition of target pathways (possibly accompanied by a redefinition of stand borders) results in a patchwork structure, similar to that described by Peterken (1996 p.168-174). Due to the many stochastic factors in a forest, this patchwork may change considerably over time. For example, if a pathway towards oak was chosen for a certain stand, factors such as storm or mast-year occurrence might alter this choice by inducing a development towards other species. This is illustrated in Fig. 5.4 by the switch arrows between the target pathways. The availability of adapted management planning tools for these situations is discussed below.

#### 5.4.1.2 Regeneration methods

Natural regeneration of broadleaved species in ageing Scots pine stands has been reported by many authors (Kuper 1994, Leuschner 1994, Lust *et al.* 1998, Zerbe 2002). It is easy to induce and its use in close-to-nature management is feasible, as both the quantity and quality of regeneration obtained are often good. Planting, e.g. for provision of seed trees at specific locations, is only occasionally necessary. Natural regenerations, however, may be very diverse, and management interventions will generally be focused at guiding them in the desired direction by controlling the density of the Scots pine canopy. The scale, intensity and frequency of the management interventions will vary, dependent on the target pathway chosen (Fig. 5.4).

For gap pathways, successive gap-creating interventions can create uneven-aged mixed regenerations of birch, oak and/or beech as major tree species. The shelterwood system is less suited for this purpose, as it is designed to spatially homogenise the treated forest (Franklin *et al.* 2002). The composition of mixtures can be guided by choosing proper gap sizes, according to the species' light demands, and regeneration periods. Goris (2002) found age differences of up to 30 years in a natural oak regeneration under Scots pine canopy, which may serve as a reference regeneration period for oak. Regeneration of beech occurs only sporadically and so even longer periods are probably needed here. For birch regeneration these periods will generally be much shorter, due to the species ability to rapidly invade a gap.

The emulation of major disturbances by managers, should certainly not just be seen as a synonym to clearcutting (Bengtsson *et al.* 2000, Franklin *et al.* 2002). Very little is known about the scale of major disturbances in ageing Scots pine stands, or about possible stand structures and development patterns following major disturbance. The pathway model suggests that different stand structures and developmental patterns may be present in a disturbance area. Therefore, the use of similar interventions over large areas should be avoided and instead a variety of possible techniques should be combined, such as group tree retention with variable densities, seed tree retention, and small-scale clearcutting.

#### 5.4.1.3 Silvicultural treatment

With successive gap-creating interventions, the number of regeneration clusters increases as more gaps become available. This results in mixed uneven-aged regenerations. At the level of individual gaps, a gradual development towards the dominance of one species, or even towards homogeneity, is observed in many cases (Vercammen 2001). If the gap is small and/or advance oak or beech regeneration is present, birch will probably disappear. In larger gaps, where light characteristics are optimal for birch, oak and beech may be suppressed but continue to be present. Major disturbances, on the other hand, will probably result in massive even-aged mixed regenerations with intensive competitive interactions. Just as with the development in individual gaps, a gradual shift towards the dominance of one species is observed in many cases (Vandewiele 2001).

These phenomena are also observed within the pathways (Kint 2003). However, they should not lead to homogeneity at the stand level: neither of the pathways features one species only. In all cases the dominating species is accompanied by other species, which occur in separate clusters or in random mixtures. Furthermore, Kint (2003) also reported a tendency towards increasing short-distance tree size variation for most species in all pathways. These structural features within stands are preserved or even stimulated by selective thinnings (Füldner 1995, Pretzsch 1999). In these cases, we recommend localised as opposed to stand interventions, as this best emulates the natural mortality process of individual trees. Thinnings from below should be avoided, as they generally divert from the pathway trends described.

In some cases, e.g. where one pathway tends to dominate or management goals are not met on very large areas, more drastic interventions in favour of other stand structures may be desirable. This can be realised by redefining the target pathway and starting a new regeneration period.

### 5.4.2 Practice at the landscape level

There is no knowledge about the spatial or temporal distribution of different pathways on a landscape level (sum of the management units in a forest). We propose a pragmatic solution, i.e. to strive towards an equal distribution of pathways throughout the forest or at the very least to create the conditions that will make this possible in the future (e.g. by planting seed trees where necessary).

This may have implications for the definition of target pathways at the stand level. Since switching between pathways due to stochastic factors mainly depends on disturbances, it seems logical that pathways requiring more and stronger management interventions (e.g. pathways 1 and 4, Fig. 5.4) are not considered as much in the initial distribution of pathways throughout the forest. It is presumed that the influence of natural disturbances on pathways will automatically increase over time.

### 5.4.3 Considerations for management planning and evaluation

The adoption of the pathway model in forest management has implications for management planning. Classically adopted management plans, with fixed management units, regular cutting cycles and rotations, should be revised. The most important consequences of the proposed management approach on management planning are: (i) flexibility in dealing with stand borders to adapt management units to the spatial and temporal scale of natural vegetation dynamics and (ii) thinking not merely in terms of goals but also in terms of opportunities during development. To solve such management planning problems, flexible algorithms that continuously try to generate and evaluate alternative management options for changing management units are needed. Heuristic methods such as genetic algorithms, simulated annealing or tabu search can be considered for performing this task (Ducheyne *et al.* 2001, Chen & Von Gadow 2003).

A related aspect is management evaluation. Evaluating whether or not the interventions used achieved the planned goals and where necessary making adjustments, is part of a sound management practice. For this purpose, it is necessary to define evaluation criteria and establish a monitoring programme. The adoption of the pathway model opens new challenges for both:

(i) Evaluation criteria are generally quantitative measures, e.g. diameter or age distributions and mixtures. In the context of close-to-nature forestry using pathways, quantitative development trends can also be used in addition to these fixed targets. As previously mentioned, trends of basal area, tree density, mean tree sizes and three-dimensional geometry of stands have been defined for each pathway (Kint 2003) and can be used for evaluation purposes.

(ii) Many methods are readily available for monitoring basal area, tree density and mean tree sizes, the most obvious example of which are permanent sample plots. A more detailed management evaluation based on the development of the three-dimensional geometry of stands, is also possible. Sampling techniques for its estimation are reviewed by Kint (2003).

## 5.5 Discussion

### 5.5.1 Close-to-nature forestry in ageing Scots pine forests

The integration of natural vegetation dynamics into forest management is often recommended in ageing Scots pine stands, mainly because naturally regenerating broadleaved species establish easily in these forests. Alternatives and compromises to such a close-to-nature approach may exist in other forest ecosystems or in relation to specific management goals, (e.g. Quine *et al.* 1999, Palik *et al.* 2002). Furthermore, some factors may hamper or even impede natural vegetation dynamics in ageing Scots pine stands, therefore making it difficult to implement a close-to-nature approach. Examples are the presence of invasive exotic species (Maddelein *et al.* 1990), excessive browsing by herbivores (Van Hees *et al.* 1996, Kuiters & Slim 2002) or the absence of seed trees (Geudens *et al.* 2002). In most ageing Scots pine stands, however, close-to-nature forest management seems feasible.

As well as helping to realise one of the major current-day management goals in these forests, i.e. conversion towards mixed broadleaved forests, close-to-nature forest management also has some intrinsic positive aspects. One of these is biodiversity (in the sense of species and habitat diversity). It is widely recognised that promoting ecosystem structure and functioning resulting from natural vegetation dynamics is one of the possible approaches to biodiversity conservation (Hansen *et al.* 1991, Larsson 2001, Harvey *et al.* 2002, Wohlgemuth *et al.* 2002). Moreover, a management approach that maximises the use of natural processes has clear economic advantages, as many costly interventions (such as planting or fertilising) can often be omitted (Lähde *et al.* 1999a, Wieman 1999).

### 5.5.2 A framework for management implementation based on the pathway model

Close-to-nature forestry has been associated with a range of management principles, such as preferring natural regeneration, applying smaller clearcuts or group and selective fellings, concentrating on individual tree development for optimal value of timber, exercising a preference for indigenous species, leaving more dead wood in the forest, allowing for more natural mortality through major disturbances, using longer rotations, aiming for uneven-aged or mixed species stands with more vertical diversity, protecting valuable habitats, etc. (Lust *et al.* 1998, Kenk & Guehne 2001, Nabuurs *et al.* 2001). As valuable as these principles might be, they cannot guarantee that the resulting management is close-to-nature. The extent to which these principles are compatible with natural vegetation dynamics and how they should be combined and implemented is determined by the forest ecosystem.

Our framework for management implementation, based on the pathway model, indicates how the aforementioned management principles can be combined to maximise the incorporation of natural vegetation dynamics into forest management. It provides a sound ecological basis for management practice.

We are not aware of other attempts to formulate a framework for management implementation in ageing Scots pine stands, based on a conceptual model of vegetation dynamics. However, many authors have proposed specific silvicultural measures within the context of close-to-nature forestry that are consistent with our results (Koop & Siebel 1993, Kuper 1994, Lust *et al.* 1998, 1999, 2000, Van Der Jagt *et al.* 2000). In summary, some of their practical recommendations which can be considered as useful supplements to our framework are:

(i) *Successive gap-creating interventions:* Gaps should initially cover 10-15% of the surface (including existing gaps). This may gradually increase towards 50% at the end of the regeneration period. Gap size distribution should approximate that in natural stands: only few large gaps (e.g. 25-30 ares) and progressively more smaller gaps (minimal 1-2 ares). Silviculturists tend to prescribe larger gap sizes for varying reasons (e.g. minimal 5-10 ares), and this would probably favour birch.

(ii) *Herbivore impact:* The spreading of regeneration gaps throughout the forest generally decreases herbivore impact. In exceptional cases (e.g. starting conversion management in homogeneous forests) fencing or the control of herbivore density may be necessary.

(iii) *Exotic species control:* Black cherry (*Prunus serotina* Ehrh.) and American red oak (*Quercus rubra* L.) should be removed prior to gap formation, if their dominance in the regeneration is not wanted.

(iv) *Selective thinning:* Working with 'future trees' (sensu Van Der Jagt *et al.* 2000) has proven to be a flexible and feasible way to guide selective thinnings.

### 5.5.3 Forest development types

Our framework is related to the German concept of 'Waldentwicklungstypen' or *forest development types* (FDTs), which is being developed for use in the whole country (Perpeet 2000). FDTs comprise forest stands with similar initial silvicultural conditions and similar management goals, and describe the most appropriate procedures and techniques to reach these goals whilst taking multiple forest functions into consideration (Von Teuffel 1999). They explicitly rely on natural vegetation dynamics to achieve this, and therefore an adaptive management strategy is proposed rather than a prescriptive one (Otto 1995). In practice, each FDT is named after the major tree species aimed for and in the case of conversion management by the current species as well (e.g. 'pine, aim oak') (Ministerium Ländlicher Raum Baden-Württemberg, 1999). The FDT approach is assumed to result in much lower risks and costs than classical approaches (e.g. *forest goal types*), especially in countries where labour is extremely expensive.

Our framework is complementary to the FDT approach and is in essence a guide for incorporating natural vegetation dynamics into forests management, independent of the management goals. It provides general guides for management practice, without specifying the silvicultural actions to be carried out. Therefore these guides should be properly interpreted and applied by managers in accordance with local field situations and specific management goals. For this purpose, FDTs can be further elaborated to indicate how specific silvicultural measures during forest development can lead to the achievement of certain management goals.

Based on the results of this study, the elaboration of FDTs in ageing Scots pine stands would provide a useful and indispensable tool for implementing close-to-nature forest management in these forests. In Fig. 5.5 we propose some of the possible FDTs that could be defined in ageing Scots pine stands, together with their possible connections. The further elaboration should be regional, since forest history, soil types, climate, policy priorities and/or other factors – and hence appropriate silvicultural measures – may differ between regions.

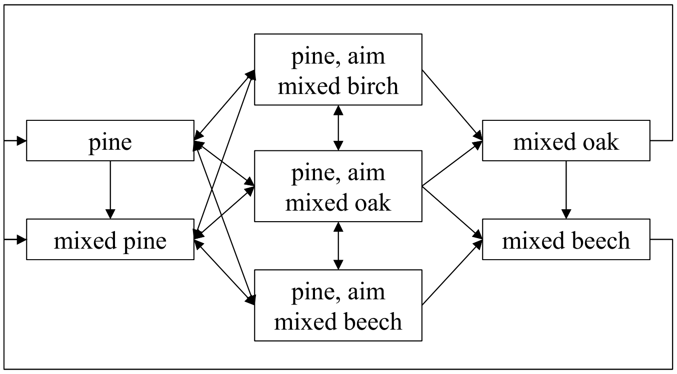


Figure 5.5 Some of the possible FDTs that could be defined in ageing Scots pine stands, together with their possible connections.

## 5.6 Conclusion

Conceptual models of natural vegetation dynamics may be used as guides for both the planning and practice of close-to-nature forest management. We have compared a pathway model of natural vegetation dynamics in ageing Scots pine forests with conceptual models that use a climax approach, and have discussed the suitability of both for guiding close-to-nature forest management in these forests. We conclude that the pathway model is more suitable than the climax model for this purpose, based on the level of detail in describing stand structural development, the representation of major disturbances and structural diversity, and the flexibility in use.

Close-to-nature forestry is characterised by working with and/or emulating natural vegetation dynamics. The framework provided for the implementation of close-to-nature forest management in ageing Scots pine stands based on the pathway model, is in essence a guide for incorporating natural vegetation dynamics into forest management, independent of the management goals. It provides a sound ecological basis for management practice.

Forest development types (FDTs) should be elaborated in accordance with local field situations and specific management goals for the purpose of choosing appropriate silvicultural measures. FDTs encompass forest stands with similar initial silvicultural conditions and management goals, and describe the most appropriate procedures and techniques to reach these, whilst explicitly relying on natural vegetation dynamics. Based on the results of this study, the elaboration of regional FDTs in ageing Scots pine stands would provide a useful and indispensable tool for implementing close-to-nature forest management in these forests.

### Purpose one

"The construction of a conceptual model of natural vegetation dynamics in ageing Scots pine forests, describing stand structures and stand structural development."

Our study is, as far as we know, the only attempt to construct a conceptual model of vegetation dynamics in ageing Scots pine forests using the pathway concept. With the aid of long-term predictions of FORGRA (a process-based gap model of forest development on poor sandy soils) and of data from Dutch forest reserves, we distinguished four main pathways of natural vegetation dynamics in these forests. Three of these are linked to gap dynamics, and lead towards dominance of birch, oak and beech respectively. They differ in light availability for regeneration (depending on gap origin and gap size) and/or seed tree availability. The fourth pathway is linked to major disturbance dynamics, and shows many different development patterns after major disturbances. Many of these join one of the gap pathways; others lead towards a new generation of Scots pine. We are not aware of other research in these forests where the empirical strength of forest reserves data and the predictive ability of process-based models are combined.

### Purpose two

"The development of a methodology to quantify spatial characteristics of forest stand structure, and its implementation in a computer programme."

Two methods for quantifying forest stand structure, based on nearest-neighbour indices and geostatistical variogram analysis respectively, resulted complementary in quantifying spatial characteristics of forest stand structure. The principal advantage of nearest-neighbour indices was their capacity for detecting subtle structure changes; moreover they were easy to calculate and interpret. Variograms of tree variables were more complicated in their use and required more input data, but provided additional information on the number, impact and range of structure-determining factors such as competition and management. Variograms also aided in avoiding misinterpretations of indices that are based on short distances only. The computer programme SIAFOR, designed to calculate a set of four nearest-neighbour indices in monitoring plots with stem-mapped data, eliminates edge effects and offers the possibility of virtual sampling.

### Purpose three

“The quantification and interpretation of spatial characteristics of stand structure and structural development in ageing Scots pine forests.”

SIAFOR was successfully applied for stand structure assessment in ageing Scots pine stands. We concluded that (i) as pine density decreases, pines tend from regular positioning towards random positioning; (ii) regeneration of broadleaved species under pine canopy often establishes in segregated clusters, and gradually develops towards random positioning and random mixture; (iii) massive regeneration of pine on open areas after storm develops from clustering towards regular positioning due to self-thinning; (iv) with asymmetric competition, and as long as no major mortality occurs, size differentiation of species increases; with symmetric competition it decreases; (v) once competition leads to mortality, differentiation generally decreases. Also the minimum sample size and optimal sample type for the estimation of stand structure with sampling techniques were determined using SIAFOR. Neighbour sampling was found to be more efficient than plot sampling in most cases. Different index estimates and statistical tests will vary in accuracy for a given sample size. It is concluded that moderate sample sizes combined with neighbour sampling will allow most index values to be estimated with a reasonable degree of accuracy. To be reliable, statistical tests generally require larger sample sizes.

### Purpose four

“The providing of a framework for the implementation of close-to-nature forestry in ageing Scots pine forests.”

The pathway model, developed under purpose two, is more suitable for guiding close-to-nature forest management in ageing Scots pine stands than models using a climax approach, due to the level of detail in describing stand structural development, the representation of major disturbances and structural diversity, and the flexibility in use. The provided framework for the implementation of close-to-nature forest management in ageing Scots pine stands, based on the pathway model, is in essence a guide for incorporating natural vegetation dynamics into forests management, independent of management goals. It provides a sound ecological basis for management practice. Based on the results of this study, the elaboration of regional 'forest development types' in ageing Scots pine stands would provide a useful and indispensable tool for implementing close-to-nature forest management in these forests.

### Research priorities

Forest dynamics research requires, if it is to make a meaningful contribution to forest management, long-term interdisciplinary studies. Our application of the pathway model is an illustration of the interaction between research on natural vegetation dynamics and forest management. There are however some important issues in our study that require further elaboration, or remain unanswered. Within the approach of combining forest reserves data and model predictions, we distinguish three main research priorities:

(i) Further development of the pathway model. Definition of pathways linked to exotic tree species, dominant herbal vegetation, elevated impact of herbivores. Reconstruction of the spatial and temporal distribution of different pathways on a landscape level. Investigation of the possible convergence of pathways, and of the impact of changing climate and/or growth conditions.

(ii) Exploration of the different pathways with respect to feasible management goals. Elaboration of adapted 'forest development types'. Further development and diffusion of adapted management planning and evaluation tools.

(iii) Extension of the research to aspects of forest dynamics other than structural development, and to other forest ecosystems.

# Summary

With an estimated area of three-and-a-half million hectares, homogeneous even-aged Scots pine (*Pinus sylvestris* L.) plantations constitute one of Western Europe's most important forest types. Nowadays, most of these forests are managed for multiple purposes, and conversion towards mixed broadleaved forests is a common management goal. Since natural regeneration of broadleaved species establishes easily in many ageing Scots pine stands (50 years and over) there is a growing interest in forest management that makes use of natural vegetation dynamics. This idea relates to the concept of close-to-nature forestry, which is characterised by a fundamental choice of working with and/or emulating natural vegetation dynamics.

Natural vegetation dynamics and forest management both affect stand structure and structural development. They influence each other through their direct impact on stand structure. Hence, the description of stand structure and structural development within forest ecosystems in relation to biotic factors, disturbances and/or environmental conditions, can help to anticipate natural vegetation dynamics and to incorporate them into management. The purpose of this study was to investigate the stand structure and structural development in ageing Scots pine stands resulting from natural vegetation dynamics, as a means to guide close-to-nature forest management in these stands. We could take advantage of an extensive forest reserves data set and a process-based model of forest development. The four main steps of our study are summarised subsequently.

## A pathway model of natural vegetation dynamics in ageing Scots pine forests

Many attempts have been made, for different forest ecosystems, to formulate prevailing insights in natural vegetation dynamics with conceptual models. Long-term stand development in forest ecosystems on oligotrophic and acidic sandy soils is generally described as a fixed sequence of development stages towards a climax. However, stand development is not necessarily directional, but rather multiple development pathways may exist for a single site type. Our study is, as far as we know, the only attempt to construct a conceptual model of vegetation dynamics in ageing Scots pine forests using the pathway concept.

For this purpose we selected ageing Scots pine stands with varying stand development since management stop in nine Dutch forest reserves on poor sandy soils. We used agglomerative cluster analysis on these data to define 19 empirical structural classes, which represent different stand structures in ageing Scots pine forests. With the aid of long-term predictions of FORGRA, a process-based gap model of forest development on poor sandy soils, we constructed sequences of these structural classes. The used methodology can be interpreted as an attempt to construct long-term empirical data series from the readily available short-term data, by using a predictive model as the upscaling criterion. We are not aware of other research in these forests where the empirical strength of forest reserves data and the predictive ability of process-based models are combined.

Sequences of structural classes, representing different actual pathways of stand development, show similar patterns. We distinguish four main pathway patterns: three presumably linked to gap dynamics and one to major disturbance dynamics. The three pathways linked to gap dynamics lead towards dominance of birch, oak or beech. They differ in light availability for regeneration (depending on gap origin and gap size) and/or seed tree availability. The pathway linked to major disturbance dynamics shows many different development patterns after major disturbances. Many of these join one of the gap pathways; others lead towards a new generation of Scots pine. For each of the main pathway patterns, trends of basal area and mean diameter are visualised. Our findings are consistent with results from previous research in similar forests.

### Quantification of spatial characteristics of forest stand structure

Quantitative data on forest stand structure are essential inputs for understanding ecosystem structure and functioning, and hence for sustainable forest management. The link between the three-dimensional geometry of forest stands and species diversity, habitat diversity, ecological stability and competition processes is widely recognized. Moreover, forest stand structure and structural development are increasingly considered as being of theoretical and practical importance in close-to-nature forest management.

We compared two methods for quantifying spatial characteristics of forest stand structure. These characteristics are tree positioning, distribution patterns of species and size differentiation between trees. The first method calculates a set of four nearest-neighbour indices to describe spatial structural characteristics in forest stands: CE to determine tree positioning, S and DM to determine (relative) mixture and T to determine size differentiation. The second method calculates mark variograms of tree height and mark indicator variograms of presence/absence data. Both methods are applied in a case study of two mixed Scots pine stands with different management history. We compared their ability to accurately quantify stand structure and short-time structural development, and their data requirements.

The two methods resul complementary in quantifying spatial characteristics of forest stand structure. The principal advantage of nearest-neighbour indices is their capacity for detecting subtle structure changes; moreover they are easy to calculate and interpret. Variograms of tree variables are more complicated in their use and require more input data, but provide additional information on the number, impact and range of structure-determining factors such as competition and management. Variograms also aid in avoiding misinterpretations of indices that are based on short distances only.

The quantification of spatial characteristics of forest stand structure is implemented in a computer programme, SIAFOR, designed to calculate the aforementioned set of four nearest-neighbour indices in monitoring plots with stem-mapped data. The programme eliminates edge effects and offers the possibility of virtual sampling.

### Spatial characteristics of stand structure and structural development in ageing Scots pine forests

We applied SIAFOR for (i) stand structure assessment and interpretation in ageing Scots pine stands in selected Dutch forest reserves and (ii) the determination of minimum sample size and optimal sample type for the estimation of stand structure with sampling techniques.

The structure assessment in ageing Scots pine forests encompasses the quantification of spatial characteristics of stand structure and structural development. With SIAFOR we calculate CE, S, DM and T, using data from Dutch forest reserves at three information levels. The first level (individual monitoring plots) and the second level (structural classes) mainly provide information about local stand structures and structural types within the forest reserves. The third level (pathways of stand development) provides information about trends of structural development, and the underlying competitive tree interactions involved. We conclude that (i) as pine density decreases, pines tend from regular positioning towards random positioning; (ii) regeneration of broadleaved species under pine canopy often establishes in segregated clusters, and gradually develops towards random positioning and random mixture; (iii) massive regeneration of pine on open areas after storm develops from clustering towards regular positioning due to self-thinning; (iv) with asymmetric competition, and as long as no major mortality occurs, size differentiation of species increases; with symmetric competition it decreases; (v) once competition leads to mortality, differentiation generally decreases, although exceptions are observed.

In most of the cases where structure assessment is useful, the collecting of spatially explicit data throughout the whole stand will be considered too expensive and time-consuming. Instead appropriate sampling techniques should be used. With SIAFOR we simulated two sample types, neighbour sampling and plot sampling, in ageing Scots pine stands of varying structural complexity, and determined the minimum sample sizes needed to reach different levels of accuracy. The use of sampling techniques to assess forest structure at reasonable accuracy levels often requires very high sample sizes. Moreover, we were not able to relate the minimum sample sizes to basal area and tree density in the stands examined. Hence, our results are merely indicative for similar stands. Neighbour sampling is found to be more efficient than plot sampling in most cases. Different index estimates and statistical tests will vary in accuracy for a given sample size. It is concluded that moderate sample sizes combined with neighbour sampling will allow most index values (except for the segregation S) to be estimated with a reasonable degree of accuracy. To be reliable, statistical tests generally require larger sample sizes.

## A framework for the implementation of close-to-nature forestry in ageing Scots pine forests

Close-to-nature forestry has the potentiality to realise one of the most common current-day management goals in ageing Scots pine forests, i.e. conversion towards mixed broadleaved forests. It is also one of the possible approaches to biodiversity conservation and has clear economic advantages. Conceptual models of natural vegetation dynamics may be used as guides for close-to-nature forest management that influence both planning and practice. We compared our pathway model of natural vegetation dynamics in ageing Scots pine forests with conceptual models that use a climax approach, and discussed their suitability for guiding close-to-nature forest management in these forests. We argue that the pathway model is more suitable for guiding close-to-nature forest management in ageing Scots pine stands than the climax model, based on the level of detail in describing stand structural development, the representation of major disturbances and structural diversity, and the flexibility in use.

We provide a framework for the implementation of close-to-nature forest management in ageing Scots pine stands, based on the pathway model. At the stand level, our framework considers the choice of a target pathway, the used regeneration methods and the silvicultural treatment. Some thoughts about management practices at the landscape level, management planning and management evaluation are offered. The provided framework is in essence a guide for incorporating natural vegetation dynamics into forests management, independent of management goals. It provides a sound ecological basis for management practice. Finally, we discuss the relationship between our framework and the German concept of forest development types.

# Samenvatting

Met een geschatte oppervlakte van drie miljoen vijfhonderdduizend hectare vormen homogene gelijkjarige aanplantingen van grove den (*Pinus sylvestris* L.) een van de belangrijkste bostypes van West-Europa. Tegenwoordig is multifunctioneel bosbeheer in deze bossen gebruikelijk, en in veel gevallen is bosomvorming naar gemengde loofbossen een doelstelling. Vaak komt in oudere bestanden van grove den (50 jaar en ouder) spontane verjonging van loofboomsoorten voor, wat de interesse voor bosbeheer op basis van natuurlijke vegetatiedynamiek stimuleert. Het concept van natuurgetrouwe bosbouw, gekenmerkt door een fundamentele keuze om met natuurlijke vegetatiedynamiek te werken en/of deze na te bootsen, is hiermee verwant.

Natuurlijke vegetatiedynamiek en bosbeheer werken allebei in op de bestandsstructuur en de structuurontwikkeling. Ze beïnvloeden elkaar wederzijds door hun rechtstreekse impact op de bestandsstructuur. De beschrijving van de structuur in bosecosystemen, in relatie tot biotische factoren, verstoringen en/of omgevingsfactoren, is dus een instrument om op de natuurlijke vegetatiedynamiek te anticiperen en deze in het bosbeheer te verwerken. Deze studie onderzoekt de bestandsstructuur en de structuurontwikkeling in oudere bestanden van grove den ten gevolge van natuurlijke vegetatiedynamiek, met als doel natuurgetrouw bosbeheer in deze bestanden te gidsen. Hiervoor konden we gebruik maken van een uitgebreide dataset uit bosreservaten en een procesgebaseerd bosontwikkelingsmodel. We vatten de vier stappen uit ons onderzoek samen.

## Pathways van natuurlijke vegetatiedynamiek in oudere bestanden van grove den

Gangbare inzichten in natuurlijke vegetatiedynamiek, voor verschillende bosecosystemen, werden reeds vaak verwerkt in conceptuele modellen. Langetermijn bestandsontwikkeling in bosecosystemen op arme zure zandbodems werd vaak beschreven als een vaste sequentie van ontwikkelingsstadia tot aan een climax. De bestandsontwikkeling is echter niet noodzakelijk gericht; er kunnen meerdere ontwikkelingspaden (‘pathways’) voor eenzelfde standplaats bestaan. Voor zover wij weten is onze studie de enige om het pathway concept te gebruiken bij de bouw van een conceptueel model van vegetatiedynamiek in oudere bestanden van grove den.

In negen Nederlandse bosreservaten op arme zandbodems selecteerden we oudere bestanden van grove den, gekenmerkt door verschillende bestandsontwikkelingen sinds de stopzetting van het bosbeheer. Met agglomeratieve clusteranalyse vonden we 19 structuurklassen binnen deze dataset, vertegenwoordigers van verschillende bestandsstructuren. Met behulp van langetermijn voorspellingen van FORGRA, een procesgebaseerd gapmodel van bosontwikkeling op arme zandbodems, werden deze structuurklassen in sequenties geplaatst. De gebruikte methode is een poging om langetermijn empirische datareeksen te bouwen uit beschikbare kortetermijn reeksen, door gebruik te maken van een voorspellingsmodel. Wij kennen geen ander onderzoek in gelijkaardige bossen waarbij empirische gegevens uit bosreservaten werden gecombineerd met voorspellingen van een procesgebaseerd model.

De verschillende sequenties van structuurklassen, die reële pathways van bestandsontwikkeling benaderen, vertonen gelijklopende patronen. We onderscheiden vier hoofdpathways: drie die vermoedelijk verband houden met bosdynamiek in openingen in het kronendak (‘gapdynamiek’) en een met bosdynamiek na grote verstoringen (‘verstoringdynamiek’). De drie hoofdpathways met gapdynamiek leiden naar dominantie van berk, eik of beuk. Ze verschillen onderling in lichtbeschikbaarheid voor verjonging (afhankelijk van de oorzaak en grootte van openingen in het kronendak) en/of beschikbaarheid van zaadbomen. De hoofdpathway met verstoringdynamiek toont verschillende ontwikkelingspatronen na grote verstoringen. Deze kunnen terugleiden naar een van de pathways met gapdynamiek, of naar een nieuwe generatie van grove den. Voor elk van deze hoofdpathways zijn trends van grondvlak en gemiddelde diameter gevisualiseerd. Onze resultaten stroken met eerder onderzoek in gelijkaardige bossen.

### Kwantificering van ruimtelijke kenmerken van de bestandsstructuur

Om inzicht in een bosecosysteem te verwerven zijn kwantitatieve gegevens over de bestandsstructuur noodzakelijk. Het verband tussen de driedimensionale geometrie van een bosbestand enerzijds, en soortendiversiteit, habitatdiversiteit, ecologische stabiliteit en competitieprocessen anderzijds, is algemeen erkend. Ook wordt steeds vaker aandacht geschonken aan het theoretisch en praktisch belang van de bosstructuur en de structuurontwikkeling voor natuurgetrouw bosbeheer.

We vergeleken twee methodes om ruimtelijke kenmerken van de bosstructuur te kwantificeren. Deze kenmerken zijn de positionering van bomen, het verspreidingspatroon van soorten, en de differentiatie tussen bomen. De eerste methode berekent vier indices, gebaseerd op buurrelaties tussen bomen, om de ruimtelijke kenmerken van bosbestanden te beschrijven: CE voor de positionering, S en DM voor de (relatieve) menging en T voor de differentiatie. De tweede methode berekent variogrammen van de boomhoogte en indicatorvariogrammen. Beide methodes werden toegepast in een gevallenstudie van twee gemengde bestanden van grove den met verschillende beheersgeschiedenis. We vergeleken hun vermogen om de bestandsstructuur en de kortetermijn structuurontwikkeling accuraat te kwantificeren, alsook hun gegevensbehoeften.

De twee methodes zijn complementair wat betreft de kwantificering van ruimtelijke kenmerken van bosbestanden. Het voornaamste voordeel van de indices is hun capaciteit om subtiele structuurveranderingen te detecteren. Bovendien zijn ze eenvoudig te berekenen en te interpreteren. Variogrammen van boomvariabelen zijn moeilijker in gebruik en behoeven meer inputgegevens, maar verschaffen bijkomende informatie over het aantal, de impact en de reikwijdte van structuurbepalende factoren zoals competitie en beheer. Variogrammen helpen ook in het vermijden van interpretatiefouten bij indices die enkel op korte afstanden gebaseerd zijn.

De kwantificering van ruimtelijke kenmerken van de bestandsstructuur werd geïmplementeerd in SIAFOR, een computerprogramma voor de berekening van de vier vermeldde indices in opnameplots met gekende boomlocaties. Het programma elimineert randeffecten en biedt de mogelijkheid voor het uitvoeren van virtuele steekproeven.

**Ruimtelijke kenmerken van de bestandsstructuur en de structuurontwikkeling in oudere bestanden van grove den**

We gebruikten SIAFOR voor (i) de structuurbepaling en -interpretatie in oudere bestanden van grove den in geselecteerde Nederlandse bosreservaten en (ii) de studie van de minimale steekproefgrootte en het optimale steekproeftype bij de schatting van de bestandsstructuur met steekproeftechnieken.

De structuurbepaling in oudere bestanden van grove den omvat de kwantificering van ruimtelijke kenmerken van de bestandsstructuur en de structuurontwikkeling. Met SIAFOR berekenden we CE, S, DM en T, op drie informatieniveaus in de Nederlandse bosreservaten. Het eerste niveau (individuele opnameplots) en het tweede niveau (structuurklassen) geven voornamelijk informatie over lokale bestandsstructuren en structuurtypes binnen de bosreservaten. Het derde niveau (pathways van bestandsontwikkeling) geeft informatie over trends van structuurontwikkeling, en over de onderliggende competitie. Uit deze analyse blijkt: (i) dennen evolueren van regelmatige naar random positionering naargelang hun dichtheid afneemt; (ii) verschillende loofboomsoorten verjongen vaak in ruimtelijk gescheiden clusters onder scherm van grove den; de verjonging ontwikkelt doorgaans in de richting van random positionering en random menging; (iii) massale verjonging van den op stormvlaktes evolueert van clustering naar regelmatige positionering als gevolg van zelfdunning; (iv) onder asymmetrische competitie, en zolang geen belangrijke mortaliteit voorkomt, vergroot de differentiatie tussen bomen; onder symmetrische competitie vermindert ze; (v) van zodra competitie aanleiding geeft tot mortaliteit, vermindert de differentiatie meestal, al zijn er uitzonderingen.

In de meeste gevallen waar structuurbepaling nuttig is, zal het verzamelen van ruimtelijk expliciete gegevens in volledige bestanden te duur en te tijdrovend bevonden worden. Dan kunnen steekproeftechnieken gebruikt worden. Met SIAFOR simuleerden we twee steekproeftypes, een gebruik makend van metingen tussen buurbomen en een van metingen in groepen, in oudere bestanden van grove den met verschillende structuurcomplexiteit. We bepaalden de minimale steekproefgrootte die nodig was om verschillende nauwkeurigheden te bereiken. Doorgaans zijn hoge steekproefgroottes nodig om de bosstructuur met redelijke nauwkeurigheid te kunnen bepalen. Bovendien konden we de minimale steekproefgrootte niet in verband brengen met het grondvlak en het stamtal in de onderzoeksbestanden. Onze resultaten zijn bijgevolg slechts richtinggevend voor gelijkaardige bestanden. Het steekproeftype op basis van metingen tussen buurbomen is bijna altijd efficiënter dan dat op basis van metingen in groepen. Bij een gekozen steekproefgrootte is de nauwkeurigheid van de indexschattingen, evenals van hun statistische testen, verschillend. We besluiten dat matige steekproefgroottes volstaan om de meeste indexwaarden (met uitzondering van S) met een minimale nauwkeurigheid te kunnen schatten. Voor een betrouwbare schatting van de uitkomst van statistische testen met steekproeftechnieken zijn doorgaans hogere steekproefgroottes nodig.

### Een kader voor de implementatie van natuurgetrouwe bosbouw in oudere bestanden van grove den

Met natuurgetrouwe bosbouw is het mogelijk een tegenwoordig vaak voorkomende beheersdoelstelling in oudere bestanden van grove den te verwezenlijken, nl. omvorming naar gemengde loofbossen. Het is ook een van de mogelijke benaderingen voor het behoud van biodiversiteit, en heeft duidelijke economische voordelen. Conceptuele modellen van natuurlijke vegetatiedynamiek kunnen gebruikt worden als gidsen voor natuurgetrouw bosbeheer, zowel bij de planning als de praktijk. We vergeleken ons pathway model van natuurlijke vegetatiedynamiek in oudere bestanden van grove den met conceptuele modellen die een climaxbenadering gebruiken, en besproken hun geschiktheid als gidsen voor natuurgetrouw bosbeheer in deze bossen. We besluiten dat het pathway model geschikter is voor deze taak dan het climax model, gebaseerd op de graad van detail in de beschrijving van de structuurontwikkeling, de voorstelling van grote verstoringen en van structuurdiversiteit, en de flexibiliteit in het gebruik.

We verschaffen een kader voor de implementatie van natuurgetrouw bosbeheer in oudere bestanden van grove den, gebaseerd op het pathway model. Op bestandsniveau behandelt dit de keuze van een doelpathway, de gebruikte verjongingsmethode en het bosbouwkundig beheer. De gevolgen voor het beheer op landschapsniveau, de beheersplanning en de beheersevaluatie worden besproken. Dit kader is wezenlijk een gids om natuurlijke vegetatiedynamiek in het bosbeheer te verwerken, onafhankelijk van beheersdoelstellingen. Het biedt een degelijke ecologische basis voor het praktijkbeheer. We bespreken de relatie met het concept van bosontwikkelingstypes.

# References

Afdeling Bos en Groen (2001). Beheervisie voor openbare bossen. Ministerie van de Vlaamse Gemeenschap, Brussel, België, 98p.

Andersson, F.O., Feger, K., Hüttl, R.F., Kräuchi, N., Mattsson, L., Sallnäs, O. & Sjöberg, K. (2000). Forest ecosystem research - priorities for Europe. Forest Ecology and Management, 132, 111-119.

Anonymous (1999). Pro Silva. Pro Silva Europe information brochure. 36p.

Arntzen, M. (1997). Algemene informatie van het bosreservaat - Dwingeloo "Lheebroeker Zand". Report W-114. IKC Natuurbeheer, Wageningen, the Netherlands, 23p.

Atkinson, M.D. (1992). *Betula pendula* Roth. (*B. verrucosa* Ehrh.) and *B. pubescens* Ehrh. Journal of Ecology, 80, 837-870.

Axelsson, A. & Östlund, L. (2001). Retrospective gap analysis in a Swedish boreal forest landscape using historical data. Forest Ecology and Management, 147, 109-122.

Badeck, F., Lischke, H., Bugmann, H., Hickler, T., Hönninger, K., Lasch, P., Lexer, M.J., Mouillot, F., Schaber, J. & Smith, B. (2001). Tree species composition in European pristine forests: comparison of stand data to model predictions. Climatic Change, 51, 307-347.

Bailey, D. & Tappeiner, J.C. (1998). Effects of thinning on structural development in 40- to 100-year-old Douglas-fir stands in western Oregon. Forest Ecology and Management, 108, 99-113.

Bartelds, G. (1997a). Algemene informatie van het bosreservaat - Saasveld "Het Molenven". Report W-121., Wageningen, the Netherlands, 20p.

Bartelds, G. (1997b). Algemene informatie van het bosreservaat - Rozendaal "Zwarte Bulten". Report W-120. IKC Natuurbeheer, Wageningen, the Netherlands, 20p.

Bartelink, H.H., Kramer, K. & Mohren, G.M.J. (1997). Applicability of the radiation-use efficiency concept for simulating growth of forest stands. Agricultural and Forest Meteorology, 88(1-4), 169-179.

Battaglia, M. & Sands, P.J. (1998). Process-based forest productivity models and their application in forest management. Forest Ecology and Management, 102, 13-32.

Bengtsson, J., Nilsson, S.G., Franc, A. & Menozzi, P. (2000). Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management, 132, 39-50.

Biondi, F., Myers, D.E. & Avery, C.C. (1994). Geostatistically modeling stem size and increment in an old-growth forest. Canadian Journal of Forest Research, 24, 1354-1368.

Blatt, S.E., Janmaat, J.A. & Harmsen, R. (2001). Modelling succession to include a herbivore effect. Ecological modelling, 139, 123-136.

Bobiec, A. (2002). Living stands and dead wood in the Bialowieza forest: suggestions for restoration management. Forest Ecology and Management, 165, 125-140.

Bossel, H. (1991). Modelling forest dynamics: moving from description to explanation. Forest Ecology and Management, 42, 129-142.

Botkin, D.B. (1993). Forest dynamics: an ecological model. Oxford University Press, 309p.

Brock, T.C.M., Van Der Hammen, T., Van Der Molen, P.C., Ram, E.T.H., Van Reenen, G.B.A. & Wijnstra, T.A. (1989). An account of the history, flora and vegetation of nature reserve "Het Molenven". Acta Bot. Neerl. ser. C.

Brocke, E. & Zonderwijk, M. (1982). Bosreservaat Noordhout - Inventarisatie april 1982. Stichting Utrechts Landschap, the Netherlands.

Broekmeyer, M.E.A. (1995). Bosreservaten in Nederland. Report 133. IBN-DLO, Wageningen, the Netherlands, 87p.

Broekmeyer, M.E.A. & Clerkx, A.P.P.M. (1997). Vegetatie en bosstructuur van het bosreservaat Zwarte Bulten. Report 257. IBN-DLO, Wageningen, the Netherlands, 77p.

Broekmeyer, M.E.A. & Szabo, P.J. (1993). The Dutch forest reserves programme. In: Broekmeyer *et al.* (Eds.) European forest reserves. Pudoc Scientific Publishers, Wageningen, the Netherlands, 75-85p.

Broekmeyer, M.E.A., Vos, W. & Koop, H.E. (1993). European forest reserves. Pudoc Scientific Publishers, Wageningen, 306p.

Brokaw, N.V.L. & Lent, R.A. (1999). Vertical structure. In: Hunter (Ed.) Maintaining biodiversity in forest ecosystems. Cambridge University Press, 373-399.

Bücking, W. (1997). Naturwald, Naturwaldreservate, Wildnis in Deutschland und Europa. Forst und Holz, 52, 515-522.

Bücking, W. (2003). Dynamik in Bannwäldern - Erkenntnisse für eine naturnahe Waldwirtschaft. FVA, Freiburg, 67p.

Bugmann, H. (2001). A review of forest gap models. Climatic Change, 51, 259-305.

Bugmann, H., Fischlin, A. & Kienast, F. (1996). Model convergence and state variable update in forest gap models. Ecological Modelling, 89, 197-208.

Buongiorno, J., Dahir, S., Lu, H. & Lin, C. (1994). Tree size diversity and economic returns in uneven-aged forest stands. Forest Science, 40(1), 83-103.

Busing, R.T. (1991). A spatial model of forest dynamics. Vegetatio, 92, 167-179.

Canham, C.D., Finzi, A.C., Pacala, S.W. & Burbank, D.H. (1994). Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Canadian Journal of Forest Research, 24, 337-349.

Cannell, M.G.R. & Grace, J. (1993). Competition for light: detection, measurement, and quantification. Canadian Journal of Forest Research, 23, 1969-1979.

Cattelino, P.J., Noble, I.R., Slatyer, R.O. & Kessell, S.R. (1979). Predicting the multiple pathways of plant succession. Environmental Management, 3, 41-50.

Chave, J. (1999). Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. Ecological modelling, 124, 233-254.

Chen, B. & Von Gadow, K. (2003). A case study of simulated annealing, genetic algorithm, tabu search and linear programming for solving forest planning problems. Forstarchiv, 74, 26-31.

Chen, J. & Bradshaw, G.A. (1999). Forest structure in space: a case study of an old growth spruce-fir forest in Changbaishan Natural reserve, PR China. Forest Ecology and Management, 120, 219-233.

Chertov, O.G., Komarov, A.S. & Karev, G.P. (1999). Modern approaches in forest ecosystem modelling. European Forest Institute, 116p.

Clark, P.J. & Evans, F.C. (1954). Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology, 35, 445-453.

Clements, F.E. (1916). Plant succession: an analysis of the development of vegetation. Report 242. Carnegie Institute, Washington DC.

Clerkx, A.P.P.M. (2001). Bosreservaat De Heul: bosstructuur en vegetatie bij aanwijzing tot bosreservaat. Report 371. Alterra, Wageningen, the Netherlands, 49p.

Clerkx, A.P.P.M. & Broekmeyer, M.E.A. (1997). Bosdynamiek in Noordhout: tien jaar monitoring van een Wintereiken-Beukenbos. Report 279. IBN-DLO, Wageningen, the Netherlands, 95p.

Clerkx, S. & Van Hees, A. (1999). Natuurlijke verjonging in bos op de arme zandgronden. De Levende Natuur, 100(5), 158-162.

Clerkx, A.P.P.M., Broekmeyer, M.E.A., Szabo, P.J., Van Hees, A.F.M., Van Os, L.J. & Koop, H.G.J.M. (1996). Bosdynamiek in bosreservaat Galgenberg. Report 217. IBN-DLO, Wageningen, the Netherlands, 137p.

Clerkx, A.P.P.M., Schelhaas, M.J. & Sanders, M.E. (2001). Bosreservaat Mattemburgh - Bosstructuur en vegetatie bij aanwijzing tot bosreservaat. Report 223. Alterra, Wageningen, the Netherlands, 47p.

Clerkx, A.P.P.M., Wijdeven, S.M.J. & Sanders, M.E. (2002). Bosdynamiek in bosreservaat Lheebroeker Zand. Report 537. Alterra, Wageningen, the Netherlands, 55p.

Coates, K.D. & Burton, P.J. (1997). A gap-based approach for development of silvicultural systems to address ecosystem management objectives. Forest Ecology and Management, 99, 337-354.

Cook, J.E. (1996). Implications of modern successional theory for habitat typing: a review. Forest Science, 42(1), 67-75.

Cotta, H. (1816). Anweising zum Waldbau. Dresden.

Cressie, N.A.C. (1991). Statistics for spatial data. Wiley, New York, 900p.

De Schrijver, A., Van Hoydonck, G., Nachtergale, L., De Keersmaeker, L., Mussche, S. & Lust, N. (2000). Comparison of nitrate leaching under silver birch (*Betula pendula*) and Corsican pine (*Pinus nigra ssp. laricio*) in Flanders (Belgium). Water air and soil pollution, 122, 77-91.

De Schrijver, A., Kint, V., Geudens, G. & Lust, N. (2002). Bosomvorming - noodzaak en praktijk van een effectgerichte maatregel tegen verzuring en vermesting.

Academia Press, Ghent, 93p.

De Waal, R. & Winteraeken, R. (1999). Humus en natuurlijke verjonging van Zomer-en Wintereik. De Levende Natuur, 100(5), 163-167.

Den Ouden, J. (2000). The role of bracken (*Pteridium aquilinium*) in forest dynamics. Ph.D. Wageningen University, the Netherlands, 218p.

Donnelly, K.P. (1978). Simulation to determine the variance and edge-effects of total nearest neighbour distance. In: Hodder (Ed.) Simulation methods in archaeology. Cambridge University Press, London, 91-95p.

Ducheyne, E.I., De Wulf, R.R. & De Baets, B. (2001). Bi-objective genetic algorithm for forest management: a comparative study. In: Proceedings of the 2001 genetic and evolutionary computation conference, San Francisco, 63-66.

Eisenhauer, D. (1994). Eichennaturverjüngung unter Kiefer. Beitrage für Forstwirtschaft und Landschaftsökologie, 28(2), 53-61.

Emborg, J. (1998). Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. Forest Ecology and Management, 106, 83-95.

Emmer, I.M. (1995a). Humus form and soil development during a primary succession of monoculture *Pinus sylvestris* forests on poor sandy substrates. Ph.D. University of Amsterdam, the Netherlands, 135p.

Emmer, I.M. (1995b). Humus form development and succession of dwarf shrub vegetation in grass dominated primary *Pinus sylvestris* forests. Annals of Forest Science, 52, 561-571.

Engelmark, O., Hofgaard, A. & Arnborg, T. (1998). Successional trends 219 years after fire in an old *Pinus sylvestris* stand in northern Sweden. Journal of Vegetation Science, 9(4), 583-592.

Fanta, J. (1982). Natuurlijke verjonging van het bos op droge zandgronden. Report 301. Rijksinstituut voor onderzoek in de bos- en landschapsbouw "De Dorschkamp", Wageningen, the Netherlands, 236p.

Fanta, J. (1986). Forest site as a framework for forest succession. In: Fanta (Ed.) Forest dynamics research in Western and Central Europe, Wageningen, the Netherlands, 58-65.

Fanta, J. (1995). Walddynamik in Flugsandgebieten des niederländischen Teiles des nordwesteuropäischen Diluviums. Forstarchiv, 66, 128-132.

Ferrari, J.B. (1999). Fine-scale patterns of leaf litterfall and nitrogen cycling in an old-growth forest. Canadian Journal of Forest Research, 29, 291-302.

Fischer, A., Lindner, M., Abs, C. & Lasch, P. (2002). Vegetation dynamics in central European forest ecosystems (near-natural as well as managed) after storm events. Folia Geobotanica, 37(1), 17-32.

Franc, A., Gourlet-Fleury, S. & Picard, N. (2000). Une introduction à la modélisation des fôrets hétérogènes. ENGREF, Nancy, 312p.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K. & Chen, J. (2002). Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management, 155, 399-423.

Frelich, L.E. (2002). Forest dynamics and disturbance regimes - studies from temperate evergreen-deciduous forests. Cambridge University Press, 266p.

Friend, A.D., Shugart, H.H. & Running, S.W. (1993). A physiology-based gap model for forest dynamics. Ecology, 74, 792-797.

Frost, I. & Rydin, H. (2000). Spatial pattern and size distribution of the animal-dispersed tree *Quercus robur* in two spruce-dominated forests. Ecoscience, 7, 38-44.

Führer, E. (2000). Forest functions, ecosystem stability and management. Forest Ecology and Management, 132, 29-38.

Füldner, K. (1995). Zur Strukturbeschreibung in Mischbeständen. Forstarchiv, 66, 235-240.

Gayer, K. (1880). Der Waldbau. Wiegandt, Hempel & Parey, Berlin.

Geudens, G., Kint, V. & Vercammen, P. (2002). Structuur in natuurlijke verjongingen van berk en den: ontwikkeling in menging en ongelijkjarigheid. In: De Schrijver *et al.* (Eds.) Bosomvorming - noodzaak en praktijk van een effectgerichte maatregel tegen verzuring en vermesting. Academia Press, Ghent, 49-57.

Gleichmar, W. & Gerold, D. (1998). Indizes zur Charakterisierung der horizontalen Baumverteilung. Forstwissenschaftliches Centralblatt, 117, 69-80.

Good, R. (2001). Forest reserves, parks and wilderness: an Australian perspective. In: Evans (Ed.) The forests handbook, volume 2. Blackwell Science, 27-52.

Goovaerts, P. (1997). Geostatistics for natural resources evaluation. Oxford University Press, New York, 483p.

Goreaud, F., Loreau, M. & Millier, C. (2002). Spatial structure and survival of an inferior competitor: a theoretical model of neighbourhood competition in plants. Ecological Modelling, 158, 1-19.

Goris, R. (2002). Dendrochronologische analyse van spontane verjonging van zomereik onder grove den in het bosreservaat Mattemburgh. Master thesis. Ghent University, Belgium, 121p.

Griese, F. (1994). Waldentwicklung in Naturwäldern auf Sandstandorten der Lüneburger Heide. Allgemeine Forst Zeitschrift, 49(11), 576-579.

Grushecky, S.T. & Fajvan, M.A. (1999). Comparison of hardwood stand structure after partial harvesting using intensive canopy maps and geostatistical techniques. Forest Ecology and Management, 114, 421-432.

Hansen, A.J., Spies, T.A., Swanson, F.J. & Ohmann, J.L. (1991). Conserving biodiversity in managed forests - lessons from natural forests. BioScience, 41(6), 382-392.

Harvey, B.D., Leduc, A., Gauthier, S. & Bergeron, Y. (2002). Stand-landscape integration in natural disturbance-based management of the southern boreal forest. Forest Ecology and Management, 155, 369-385.

Hasenauer, H., Burgmann, M. & Lexer, M.J. (2000). Konzepte der Waldökosystemmodellierung. Centralblatt für das Gesamte Forstwesen, 117, 137-164.

Hochbichler, E., O'Sullivan, A., Van Hees, A. & Vandekerkhove, K. (2000). Recommendations for data collection in forest reserves, with an emphasis on regeneration and stand structures. In: Parviainen (Ed.) COST action E4 - Forest reserves research network. European commission, 135-181.

Huberty, C.J. (1994). Applied discriminant analysis. John Wiley & sons, 466p.

Isaaks, E.H. & Srivastava, R.M. (1989). An introduction to applied geostatistics. Oxford University Press, 561p.

Jactel, H., Goulard, M., Menassieu, P. & Goujon, G. (2002). Habitat diversity in forest plantations reduces infestations of the pine stem borer *Dioryctria sylvestrella*. Journal of Applied Ecology, 39, 618-628.

Jansen, J.J., Sevenster, J. & Faber, P.J.E. (1996). Opbrengsttabellen voor belangrijke boomsoorten in Nederland. IBN-DLO, Wageningen, 202p.

Jasinski, K. & Angelstam, P. (2002). Long-term differences in the dynamics within a natural forest landscape - consequences for management. Forest Ecology and Management, 161, 1-11.

Johnsen, K., Samuelson, L., Teskey, R., McNulty, S. & Fox, T. (2001). Process models as tools in forestry research and management. Forest Science, 47(1), 2-8.

Jorritsma, I.T.M., Mohren, G.M.J., Van Wieren, S.E., Van Hees, A.F.M., Bartelink, H.H., Nabuurs, G.J. & Slim, P.A. (1997a). Bosontwikkeling in aanwezigheid van hoefdieren: een modelbenadering. In: Van Wieren *et al.* (Eds.) Hoefdieren in het boslandschap. Backhuys Publishers, Leiden, 147-164.

Jorritsma, I.T.M., Mohren, G.M.J., Van Hees, A.F.M. & Seigers, G. (1997b). Bosontwikkeling onder invloed van hoefdieren: scenario-analyses. In: Van Wieren *et al.* (Eds.) Hoefdieren in het boslandschap. Backhuys Publishers, Leiden, 165-191.

Jorritsma, I.T.M., Van Hees, A.F.M. & Mohren, G.M.J. (1999). Forest development in relation to ungulate grazing: a modeling approach. Forest Ecology and Management, 120, 23-34.

Judson, O.P. (1994). The rise of the individual-based model in ecology. Trends in Ecology and Evolution, 9, 9-14.

Kauppi, A. & Kiviniitty, M. (1988). Growth habits and crown architecture of *Betula pubescens* Ehrh. of seed and sprout origin. Canadian Journal of Forest Research, 18, 1603-1613.

Keane, R.E., Ryan, K.C. & Running, S.W. (1996). Simulating effects of fire on northern Rocky Mountain landscapes with the ecological process model FIRE-BGC. Tree Physiology, 16, 319-331.

Keane, R.E., Austin, M., Field, C., Huth, A., Lexer, M.J., Peters, D., Solomon, A. & Wyckoff, P. (2001). Tree mortality in gap models: application to climate change. Climatic Change, 51, 509-540.

Kellomäki, S. & Väisänen, H. (1997). Modelling the dynamics of the forest ecosystem for climate change studies in the boreal conditions. Ecological modelling, 97, 121-140.

Kemmers, R.H. & Mekkink, P. (1999). Humusprofielen in de bosreservaten Lheebroek en Mattemburgh. Report 686. Alterra, Wageningen, the Netherlands.

Kenk, G. & Guehne, S. (2001). Management of transformation in central Europe. Forest Ecology and Management, 151, 107-119.

Kimmins, J.P. (1990). Modeling the sustainability of forest production and yield for a changing and uncertain future. Forestry Chronicle, 66, 271-280.

Kimmins, J.P. (1997). Forest ecology - A foundation for sustainable management. Prentice Hall, New Jersey, 596p.

Kint (2003). Structural development in ageing Scots pine (*Pinus sylvestris* L.) stands in western Europe. Ph.D. Ghent University, Belgium.

Kint, V., Lust, N., Ferris, R. & Olsthoorn, A.F.M. (2000). Quantification of forest stand structure applied to Scots pine (*Pinus sylvestris* L.) forests. Investigación Agraria: Sistemas y Recursos Forestales, special issue 1, 147-163.

Kint, V., Geudens, G. & Jorristma, I.T.M. (2002). Spontane ontwikkeling van bossen na omvorming: projecties over langere termijn. In: De Schrijver *et al.* (Eds.) Bosomvorming - noodzaak en praktijk van een effectgerichte maatregel tegen verzuring en vermesting. Academia Press, Ghent, 59-68.

Kint, V., Van Meirvenne, M., Nachtergale, L., Geudens, G. & Lust, N. (2003). Spatial methods for quantifying forest stand structure development: a comparison between nearest-neighbor indices and variogram analysis. Forest Science, 49(1), 36-49.

Knoppersen, G. (1995). Algemene informatie van het bosreservaat - Amerongen "Galgenberg". Report W-90. IKC Natuurbeheer, Wageningen, the Netherlands, 17p.

Koop, H.G.J.M. (1987). Het RIN bosecologisch informatiesysteem: achtergronden en methoden. Report 87/4. Rijksinstituut voor Natuurbeheer, Leersum, the Netherlands, 47p.

Koop, H.G.J.M. (1989). Forest dynamics - SILVI-STAR: A comprehensive monitoring system. Springer-Verlag, Berlin, 229p.

Koop, H.G.J.M. & Boddez, P. (1991a). Galgenberg, Amerongen: bosstructuur kernvlakte. Report 91/13. Rijksinstituut voor Natuurbeheer, Leersum, the Netherlands, 19p.

Koop, H.G.J.M. & Boddez, P. (1991b). Lheebroek, Dwingelo: bosstructuur kernvlakte. Report 91/12. Rijksinstituut voor Natuurbeheer, Leersum, the Netherlands, 15p.

Koop, H.G.J.M. & Clerkx, A.P.P.M. (1995a). De vegetatie van bosreservaten in Nederland, deel 3: bosreservaat Galgenberg, Amerongen. Report 140. IBN-DLO, Wageningen, the Netherlands, 25p.

Koop, H.G.J.M. & Clerkx, A.P.P.M. (1995b). De vegetatie van bosreservaten in Nederland, deel 2: bosreservaat Lheebroek, Dwingeloo. Report 139. IBN-DLO, Wageningen, the Netherlands, 25p.

Koop, H.G.J.M. & Siebel, H.N. (1993). Conversion management towards more natural forests: evaluation and recommendations. In: Broekmeyer *et al.* (Eds.)

European forest reserves. Pudoc Scientific Publishers, Wageningen, 199-204.

Korzukhin, M.D., Ter-Mikaelian, M.T. & Wagner, R.G. (1996). Process versus empirical models: which approach for forest ecosystem management? Canadian Journal of Forest Research, 26, 879-887.

Köstler, J. (1950). Waldbau. Parey, Berlin, 418p.

Kuiters, A.T. & Slim, P.A. (2002). Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities. Biological Conservation, 105, 65-74.

Kuper, J.H. (1994). Sustainable development of Scots pine forests. Ph.D. Wageningen University, the Netherlands, 317p.

Kuuluvainen, T., Penttinen, A., Leinonen, K. & Nygren, M. (1996). Statistical opportunities for comparing stand structural heterogeneity in managed and primeval forests: an example from boreal spruce forest in southern Finland. Silva Fennica, 30(2-3), 315-328.

Kuuluvainen, T., Järvinen, E., Hokkanen, T.J. , Rouvinen, S. & Heikkinen, K. (1998). Structural heterogeneity and spatial autocorrelation in a natural mature *Pinus sylvestris* dominated forest. Ecography, 21, 159-174.

Kwakkel, M. (2001). Boshistorie van bosreservaten Grote Weiland en Stille Eenzaamheid. Eindwerk. Wageningen-UR, the Netherlands, 23p.

Larsen, D.R. & Johnson, P.S. (1998). Linking the ecology of natural oak regeneration to silviculture. Forest Ecology and Management, 106, 1-7.

Larsson, T.B. (Ed.) (2001). Biodiversity evaluation tools for European forests. Ecological Bulletins, 50, 236.

Lasch, P. & Lindner, M. (1995). Application of two forest succession models at sites in north east Germany. Journal of Biogeography, 22, 485-492.

Legendre, P. & Legendre, L. (1998). Numerical ecology. Elsevier, Amsterdam, 853p.

Leibundgut, H. (1951). Der wald, eine lebensgemeinschaft. Büchergilde Gutenberg, Zürich, 222p.

Leibundgut, H. (1959). Über Zweck und Methodik der Struktur- und Zuwachsanalyse von Urwäldern. Schweizerische Zeitschrift für Forstwesen, 110(3), 111-124.

Leibundgut, H. (1966). Waldreservate. Schweizerische Zeitschrift für Forstwesen, 117, 900-907.

Leibundgut, H. (1990). Über den Sinn und die Bedeutung von Waldreservaten. Österreichische Forstzeitung, 101(7), 16-17.

Leuschner, C. (1991). Driving forces and limiting factors in long-term dynamics of forest ecosystems on sandy soils. University of Göttingen, Germany, 172p.

Leuschner, C. (1993). Resource availability at three presumed stages of a heathland succession on the Lüneburger Heide, Germany. Journal of Vegetation Science, 4, 255-262.

Leuschner, C. (1994). Walddynamik auf Sandböden in der Lüneburger Heide (NW-Deutschland). Phytocoenologia, 22, 289-324.

Leuschner, C. (1997). Das Konzept der potentiellen natürlichen Vegetation (PNV): Schwachstellen und Entwicklungsperspektiven. Flora, 192, 379-391.

Lewandowski, A. & Pommerening, A. (1997). Zur Beschreibung der Waldstruktur - Erwartete und beobachtete Arten-Durchmischung. Forstwissenschaftliches Centralblatt, 116, 129-139.

Lexer, M.J. & Hönninger, K. (2001). A modified 3D-patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes. Forest Ecology and Management, 144, 43-65.

Lindner, M. (1998). Wirkung von Klimaveränderungen in mitteleuropäischen Wirtschaftswäldern. Report 46. PIK, Potsdam, Germany, 109p.

Lindner, M. (2000). Developing adaptive forest management strategies to cope with climate change. Tree Physiology, 20, 299-307.

Liu, J. & Ashton, P.S. (1995). Individual-based simulation models for forest succession and management. Forest Ecology and Management, 73, 157-175.

Lust, N. (1982). Vergelijkende studie van bosreservaten in Europa. Groene Band, 47, 1-20.

Lust, N., Muys, B. & Nachtergale, N. (1998). Increase of biodiversity in homogeneous Scots pine stands by an ecologically diversified management. Biodiversity and Conservation, 7, 249-260.

Lust, N., Maddelein, D., Neirynck, J. & Nachtergale, L. (1999). Management of uneven-aged mixed stands originating from regeneration under Scots pine cover. In: Olsthoorn *et al.* (Eds.) Management of mixed-species forests: silviculture and economics. IBN Scientific Contributions 15, Wageningen, 199-207.

Lust, N., Geudens, G. & Olsthoorn, A.F.M. (2000). Scots pine in Belgium and the Netherlands. Investigación Agraria: Sistemas y Recursos Forestales, special issue 1, 213-231.

Lähde, E., Laiho, O. & Norokorpi, Y. (1999a). Diversity-oriented silviculture in the boreal zone of Europe. Forest Ecology and Management, 118, 223-243.

Lähde, E., Laiho, O., Norokorpi, Y. & Saksa, T. (1999b). Stand structure as the basis of diversity index. Forest Ecology and Management, 115, 213-220.

Maas, G.J. & Van der Werff, M.M. (1990). De bodemgesteldheid van bosreservaten in Nederland, deel 1: bosreservaat Lheebroek. Report 98.1. DLO-Staring Centrum, Wageningen/Oosterbeek, the Netherlands, 29p.

MacArthur, R.H. & MacArthur, J.W. (1961). On bird species diversity. Ecology, 42(3), 594-598.

Maddelein, D. & Neirynck, J. (1995). Omvorming van Kempische dennenbossen naar gemengde bestandstypes op basis van inlandse eik. Groene Band, 97, 1-29.

Maddelein, D., Lust, N., Meyen, S. & Muys, B. (1990). Dynamics in maturing Scots pine monocultures in North-east Belgium. In: IUFRO XIX World Congress, proceedings volume 1, Montréal, Canada, 95-106.

Maddelein, D., Meyen, S. & Lust, N. (1991). Driving forces and limiting factors in long-term dynamics of forest ecosystems on sandy soils. Ghent University, Belgium, 223p.

Magurran, A.E. (1988). Ecological diversity and its measurement. Princeton university press, New Jersey, 179p.

Mailly, D., Kimmins, J.P. & Busing, R.T. (2000). Disturbance and succession in a coniferous forest of northwestern North America: simulations with DRYADES, a spatial gap model. Ecological modelling, 127, 183-205.

Mäkelä, A., Landsberg, J., Ek, A.R., Burk, T.E., Ter-Mikaelian, M., Ágren, G.I., Oliver, C.D. & Puttonen, P. (2000). Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. Tree Physiology, 20, 289-298.

Mason, W.L. & Alía, R. (2000). Current and future status of Scots pine (*Pinus sylvestris* L.) forests in Europe. Investigación Agraria: Sistemas y Recursos Forestales, special issue 1, 317-335.

Mateu, J. & Ribeiro, P.J. (1999). Geostatistical data versus point process data: analysis of second-order characteristics. In: Proceedings of the second European conference on geostatistics for environmental applications, Valencia, Spain, 213-224.

Mayer, H. (1977). Waldbau. Gustav Fischer Verlag, Stuttgart, 483p.

Mekkink, P. (1993). De bodemgesteldheid van bosreservaten in Nederland, deel 12: bosreservaat Zwarte Bulten. Report 98.12. DLO-Staring Centrum, Wageningen, the Netherlands.

Mekkink, P. (1995). De bodemgesteldheid van bosreservaten in Nederland, deel 17: bosreservaat Galgenberg. Report 98.17. DLO-Staring Centrum, Wageningen, the Netherlands, 44p.

Mekkink, P. (1996a). De bodemgesteldheid van bosreservaten in Nederland, deel 21: bosreservaat Het Molenven. Report 98.21. DLO-Staring Centrum, Wageningen, the Netherlands.

Mekkink, P. (1996b). De bodemgesteldheid van bosreservaten in Nederland, deel 19: Tongerense Hei. Report 98.19. DLO-Staring Centrum, Wageningen, the Netherlands, 45p.

Mekkink, P. (1998). De bodemgesteldheid van bosreservaten in Nederland, deel 30: bosreservaat Mattemburgh. Report 98.30. Staring Centrum, Wageningen, the Netherlands.

Mekkink, P. (2000). De bodemgesteldheid van bosreservaten in Nederland, deel 1: bosreservaat De Heul. Report 60-1. Alterra, Wageningen, the Netherlands.

Ménard, A., Dubé, P., Bouchard, A., Canham, C.D. & Marceau, D.J. (2002). Evaluating the potential of the SORTIE forest succession model for spatio-temporal analysis of small-scale disturbances. Ecological Modelling, 153, 81-96.

Meyer, P. & Pogoda, P. (2001). Entwicklung der räumlichen Strukturdiversität in nordwestdeutschen Naturwäldern. Allgemeine Forst und Jagdzeitung, 172, 213-220.

Meyer, P., Unkrig, W. & Griese, F. (2000). Dynamik der Buche (*Fagus sylvatica* L.) in nordwestdeutschen Naturwäldern. Forst und Holz, 55, 470-477.

Ministerie LNV (2000). Natuur voor mensen, mensen voor natuur - nota natuur, bos en landschap in de 21e eeuw. The Netherlands, 58p.

Ministerium Ländlicher Raum Baden-Württemberg (1999). Richtlinie Landesweiter

Waldentwicklungstypen. Landesforstverwaltung Baden-Württemberg, Germany, 54p.

Mlinšek, D. (1993). Forestry and society-oriented research on the history of virgin forests and their future needs. In: Broekmeyer *et al.* (Eds.) European forest reserves. Pudoc Scientific Publishers, Wageningen, 29-33.

Moeur, M. (1993). Characterizing spatial patterns of trees using stem-mapped data. Forest Science, 39, 756-775.

Mohren, G.M.J. & Burkhart, H.E. (1994). Contrasts between biologically-based process models and management-oriented growth and yield models. Forest Ecology and Management, 69, 1-5.

Mohren, G.M.J., Van Hees, A.F.M. & Bartelink, H.H. (1991). Succession models as an aid for forest management in mixed stands in the Netherlands. Forest Ecology and Management, 42, 111-127.

Mosandl, R. & Kleinert, A. (1998). Development of oaks (*Quercus petraea* (Matt.) Liebl.) emerged from bird-dispersed seeds under old-growth pine (*Pinus sylvestris* L.) stands. Forest Ecology and Management, 106, 35-44.

Mosandl, R. & Küssner, R. (1999). Conversion of pure pine and spruce forests into mixed forests in eastern Germany: some aspects of silvicultural strategy. In: Olsthoorn *et al.* (Eds.) Management of mixed-species forests: silviculture and economics. IBN Scientific Contributions 15, Wageningen, 208-218.

Muys, B., Maddelein, D. & Lust, N. (1992). Ecology, practice and policy of black cherry (*Prunus serotina* Ehrh.) management in Belgium. Silva Gandavensis, 57, 28-45.

Nabuurs, G.J., Päivinen, R., Schelhaas, M.J., Pussinen, A., Verkaik, E., Lioubimow, A. & Mohren, F. (2001). Nature-oriented forest management in Europe - Modeling the long-term effects. Journal of Forestry, 99(7), 28-33.

Nansen, C., Tchabi, A. & Meikle, W.G. (2001). Succession sequence of forest types in a disturbed dry forest reserve in southern Benin, West Africa. Journal of Tropical Ecology, 17, 525-539.

Naumburg, E. & DeWald, L.E. (1999). Relationships between Pinus ponderosa forest structure, light characteristics, and understory graminoid species presence and abundance. Forest Ecology and Management, 124, 205-215.

Norby, R.J., Ogle, K., Curtis, P.S., Badeck, F., Huth, A., Hurtt, G.C., Kohyama, T. & Peñuelas, J. (2001). Aboveground growth and competition in forest gap models: an analysis for studies of climatic change. Climatic Change, 51, 415-447.

Norton, D.A. (1999). Forest reserves. In: Hunter Jr. (Ed.) Maintaining Biodiversity in forest ecosystems. Cambridge University Press, 525-555.

Olea, R.A. (1999). Geostatistics for engineers and earth scientists. Kluwer Academic Publishers, Boston, 303p.

Oliver, C.D. & Larson, B.C. (1996). Forest stand dynamics. John Wiley & Sons, New York, 520p.

Otto, H. (1995). Zielorientierter Waldbau und Schutz sukzessionaler Prozesse. Forst und Holz, 50, 203-209.

Pacala, S.W. & Deutschman, D.H. (1995). Details that matter: The spatial distribution of individual trees maintains forest ecosystem function. Oikos, 74, 357-365.

Pacala, S.W., Canham, C.D. & Silander, J.A.Jr. (1993). Forest models defined by field measurements: I. The design of a northeastern forest simulator. Canadian Journal of Forest Research, 23, 1980-1988.

Palik, B.J., Mitchell, R.J. & Hiers, J.K. (2002). Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation. Forest Ecology and Management, 155, 347-356.

Pannatier, Y. (1996). Variowin - Software for spatial data analysis in 2D. Springer Verlag, Berlin, 91p.

Parviainen, J., Bücking, W., Vandekerkhove, K., Schuck, A. & Päivinen, R. (2000). Strict forest reserves in Europe: efforts to enhance biodiversity and research on forests left for free development in Europe (EU-COST-Action E4). Forestry, 73(2), 107-118.

Peng, C. (2000). Growth and yield models for uneven-aged stands: past, present and future. Forest Ecology and Management, 132, 259-279.

Penttinen, A., Stoyan, D. & Henttonen, H.M. (1992). Marked point processes in forest statistics. Forest Science, 38(4), 806-823.

Perala, D.A. & Alm, A.A. (1990). Reproductive ecology of birch: a review. Forest Ecology and Management, 32, 1-38.

Perpeet, M. (2000). Zur Anwendung von Waldentwicklungstypen (WET). Forstarchiv, 71, 143-152.

Peterken, G.F. (1996). Natural woodland - ecology and conservation in Northern temperate regions. Cambridge University Press, 522p.

Peterken, G.F. (2001). Structural dynamics of forest stands and natural processes. In: Evans (Ed.) The forests handbook, volume 1. Blackwell Science, 83-104.

Pickett, S.T.A. & White, P.S.E. (1985). The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, 472p.

Pickett, S.T.A., Collins, S.L. & Armesto, J.J. (1987). Models, mechanisms and pathways of succession. The Botanical Review, 53, 335-371.

Pielou, E.C. (1977). Mathematical ecology. Wiley, 385p.

Pommerening, A. (2002). Approaches to quantifying forest structures. Forestry, 75(3), 305-324.

Pommerening, A. & Von Gadow, K. (2000). Zu den Möglichkeiten und Grenzen der Strukturerfassung mit Waldinventuren. Forst und Holz, 55, 622-631.

Pontailler, J., Faille, A. & Lemée, G. (1997). Storms drive successional dynamics in natural forests: a case study in Fontainebleau (France). Forest Ecology and Management, 98, 1-15.

Porté, A. & Bartelink, H.H. (2002). Modelling mixed forest growth: a review of models for forest management. Ecological Modelling, 150, 141-188.

Prach, K. (1989). Primary forest succession in sand dune areas. Report 544. Research Institute for Forestry and Landscape Planning "De Dorschkamp", Wageningen, the Netherlands, 117p.

Prentice, I.C. & Leemans, R. (1990). Pattern and process and the dynamics of forest structure: a simulation approach. Journal of Ecology, 78, 340-355.

Pretzsch, H. (1995). Zum Einfluss des Baumverteilungsmusters auf den Bestandeszuwachs. Allgemeine Forst und Jagdzeitung, 166(9/10), 190-201.

Pretzsch, H. (1996). Strukturvielfalt als Ergebnis waldbaulichen Handelns. Allgemeine Forst und Jagdzeitung, 167(11), 213-221.

Pretzsch, H. (1997). Analysis and modeling of spatial stand structures. Methodological considerations based on mixed beech-larch stands in Lower Saxony. Forest Ecology and Management, 97, 237-253.

Pretzsch, H. (1999). Structural diversity as a result of silvicultural operations. In: Olsthoorn *et al.* (Eds.) Management of mixed-species forests: silviculture and economics. IBN Scientific Contributions 15, Wageningen, 157-174.

Pretzsch, H. (2001). Modellierung des Waldwachstums. Parey Buchverlag, 341p.

Pretzsch, H., Biber, P. & Durský, J. (2002). The single tree-based stand simulator SILVA: construction, application and evaluation. Forest Ecology and Management, 162, 3-21.

Price, D.T., Zimmermann, N.E., Van Der Meer, P.J., Lexer, M.J., Leadley, P., Jorritsma, I.T.M., Schaber, J., Clark, D.F., Lasch, P., McNulty, S., Wu, J. & Smith, B. (2001). Regeneration in gap models: priority issues for studying forest responses to climate change. Climatic Change, 51, 475-508.

Quine, C.P., Humphrey, J.W. & Ferris, R. (1999). Should the wind disturbance patterns observed in natural forests be mimicked in planted forests in the British uplands? Forestry, 72, 337-358.

Reynolds, J.F., Bugmann, H. & Pitelka, L. (2001). How much physiology is needed in forest gap models for simulating long-term vegetation response to global change? Challenges, limitations, and potentials. Climatic Change, 51, 541-557.

Ripley, B.D. (1981). Spatial statistics. John Wiley & Sons, 252p.

Rode, M.W. (1999a). The interaction between organic layer and forest growth and forest development on former heathland. Forest Ecology and Management, 114, 117-127.

Rode, M.W. (1999b). Influence of forest growth on former heathland on nutrient input and its consequences for nutrition and management of heath and forest. Forest Ecology and Management, 114, 31-43.

Rogister, J.E. (1978). Het Quercion rob.-petr. (Malc. 1929) Br.-Bl. 1932 in België als ekologische en floristische gemeenschap. Report reeks A nr 17. Proefstation van Waters en Bossen, Groenendaal, België, 175p.

Rots, A.J.G. (1997). Algemene informatie van het bosreservaat - Vierhouten "Tongerense heide". Report W-151. IKC Natuurbeheer, Wageningen, the Netherlands, 25p.

Rykiel, E.J., Jr. (1996). Testing ecological models: the meaning of validation. Ecological Modelling, 90, 229-244.

Sallabanks, R., Riggs, R.A. & Cobb, L.E. (2002). Bird use of forest structural classes in grand fir forests of the Blue Mountains, Oregon. Forest Science, 48(2), 311-321.

Samra, J.S., Gill, H.S. & Bhatia, V.K. (1989). Spatial stochastic modeling of growth and forest resource evaluation. Forest Science, 35(3), 663-676.

Schelhaas, M.J. & Van Dort, K.W. (2003). Bosreservaat De stille Eenzaamheid: bosstructuur en vegetatie bij aanwijzing tot bosreservaat. Report. Alterra, Wageningen, the Netherlands.

Seagle, S.W. & Liang, S. (2001). Application of a forest gap model for prediction of browsing effects on riparian forest succession. Ecological Modelling, 144, 213-229.

Seidling, W. & Von Lührte, A. (1996). Spontane Gehölzentwicklung in wenig gepflegten Kiefernbeständen. Forstarchiv, 67, 147-159.

Sharpe, P.J.H. (1990). Forest modeling approaches: compromises between generality and precision. In: Dixon *et al.* (Eds.) Process modeling of forest growth responses to environmental stress. Timber press, Portland, 180-190.

Shugart, H.H. (1984). A theory of forest dynamics - The ecological implications of forest succession models. Springer Verlag, New York, 278p.

Smaltschinski, T. (1998). Charakterisierung von Baumverteilungen. Forstwissenschaftliches Centralblatt, 117, 355-361.

Smit, R. (2002). The secret life of woody species - A study on wood species establishment, interactions with herbivores and vegetation succession. Ph.D. Wageningen University, the Netherlands, 139p.

Sougnez, N. (1974). Les chenaies silicicoles de Belgique (*Quercion robori-petraeae* (Malc. 1929) Br.-Bl. 1932). Colloques Phytosociologiques, III, 183-249.

Spies, T.A. (1998). Forest structure: a key to the ecosystem. Northwest Science, 72(2), 34-39.

Spies, T.A. & Turner, M.G. (1999). Dynamic forest mosaics. In: Hunter Jr. (Ed.) Maintaining Biodiversity in forest ecosystems. Cambridge University Press, Cambridge, 95-160.

Stortelder, A.F.H., Schaminée, J.H.J. & Hommel, P.W.F.M. (1999). De vegetatie van Nederland, Deel 5 - ruigten, struwelen, bossen. Opulus Press, Leiden, 376p.

Stuurman, F.J. & Clement, J. (1993). The standardized monitoring programme for forest reserves in the Netherlands. In: Broekmeyer *et al.* (Eds.) European forest reserves. Pudoc Scientific Publishers, Wageningen, 99-108.

Tschermak, L. (1950). Waldbau auf pflanzengeographisch-ökologischer Grundlage. Wien.

Turner, M.G., Baker, W.L., Peterson, C.J. & Peet, R.K. (1998). Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems, 1, 511-523.

Upton, G.J.G. & Fingleton, B. (1985). Spatial data analysis by example, volume 1 - Point pattern and quantitative data. John Wiley and Sons, Oxford, 410p.

Upton, G.J.G. & Fingleton, B. (1989). Spatial data analysis by example, volume 2 - Categorical and directional data. John Wiley & Sons, Oxford, 414p.

Urban, D.L., Bonan, G.B., Smith, T.M. & Shugart, H.H. (1991). Spatial applications of gap models. Forest Ecology and Management, 42, 95-110.

Van Der Jagt, J.L., Paasman, J.M., Klingen, L.A.S., Houtzagers, M.R. & Konings, C.J.F. (2000). Geintegreerd bosbeheer - praktijk, voorbeelden en achtergronden. Expertisecentrum LNV, Wageningen, 214p.

Van Der Meer, P.J., Jorritsma, I.T.M. & Kramer, K. (2002). Assessing climate change effects on long-term forest development: adjusting growth, phenology, and seed production in a gap model. Forest Ecology and Management, 162, 39-52.

Van Der Werf, S. (1991). Natuurbeheer in Nederland, deel 5 - Bosgemeenschappen. Pudoc, Wageningen, 375p.

Van Ham, W.A. (1985). De Mattemburgh, "Een landgoed en zijn bewoners". Publikaties van het archiviaat "Nassau-Brabant", the Netherlands, 91p.

Van Hees, A.F.M. (1997). Growth and morphology of pedunculate oak (*Quercus robur* L) and beech (*Fagus sylvatica* L) seedlings in relation to shading and drought. Annals of Forest Science, 54, 9-18.

Van Hees, A.F.M. & Clerkx, A.P.P.M. (2003). Shading and root-shoot relations in saplings of silver birch, pedunculate oak and beech. Forest Ecology and Management, 176, 439-448.

Van Hees, A.F.M., Kuiters, A.T. & Slim, P.A. (1996). Growth and development of silver birch, pedunculate oak and beech as affected by deer browsing. Forest Ecology and Management, 88, 55-63.

Van Oene, H., Berendse, F. & De Kovel, C.G.F. (1999). Model analysis of the effects of historic CO2 levels and nitrogen inputs on vegetation succession. Ecological Applications, 9(3), 920-935.

Vanclay, J.K. (1994). Modelling forest growth and yield: applications to mixed tropical forests. CAB International, Wallingford, 312p.

Vanclay, J.K. (1995). Growth models for tropical forests: a synthesis of models and methods. Forest Science, 41, 7-42.

Vandekerkhove, K. (1998). Criteria voor de selectie van bosreservaten in functie van een betere kadering van de Vlaamse bosreservaten in een Europees netwerk. Mededelingen van het Instituut voor Bosbouw en Wildbeheer, 3, 113.

Vandekerkhove, K. (2001). Bosreservaten in Vlaanderen: aanknopingspunten en verschillen met de Nederlandse situatie. Nederlands Bosbouwtijdschrift, 73(6), 7-10.

Vandekerkhove, K. (2003). Bosreservaten-Nieuws 3. IBW, Belgium, 16p.

Vandekerkhove, K. & Van Den Meersschaut, D. (1999). Bosreservaten in Vlaanderen. De Levende Natuur, 100, 179-182.

Vandewiele, S. (2001). Spontane evolutie van de bosstructuur en effect van brand op de bosontwikkeling in de Withoefse Heide. Master thesis. Ghent University, Belgium, 141p.

Vercammen, P. (2001). Competitie in natuurlijke verjongingen van berk in bestanden van grove den: studie van groei en ruimtelijke patronen. Master thesis. Ghent University, Belgium, 117p.

Von Gadow, K. (1993). Zur Bestandesbeschreibung in der Forsteinrichtung. Forst und Holz, 48, 602-606.

Von Gadow, K. (1999). Waldstruktur und Diversität. Allgemeine Forst und Jagdzeitung, 170(7), 117-122.

Von Gadow, K. & Hui, G. (1999). Modelling forest development. Kluwer Academic Publishers, Dordrecht, 213p.

Von Teuffel, K. (1999). Waldentwicklungstypen in Baden-Württemberg. Allgemeine Forst Zeitschrift, 13, 672-676.

Warrington, S. (1994). Field evidence for intra-specific competition between trees. Journal of Biological Education, 28(3), 186-190.

Weishampel, J.F. & Urban, D.L. (1996). Coupling a spatially-explicit forest gap model with a 3-D solar routine to simulate latitudinal effects. Ecological modelling, 86, 101-111.

Wieman, E.A.P. (1999). Kosten en doelrealisatie van omvorming naar kleinschalig gestructureed bos - bedrijfseconomische consequenties van omvorming van vlaktegewijze opstanden aan de hand van scenario's. Report 430. IBN-DLO, Wageningen, the Netherlands.

Wijdeven, S.M.J., Oosterbaan, A., Van De Berg, C. & Van Jole, M. (2000). Groei van ongelijkjarige mengingen van grove den en berk op arme zandgronden. Report 014. Alterra, the Netherlands, 33p.

Williams, M. (1996). A three-dimensional model of forest development and competition. Ecological Modelling, 89, 73-98.

Wohlgemuth, T., Bürgi, M., Scheidegger, C. & Schütz, M. (2002). Dominance reduction of species through disturbance - a proposed management principle for central European forests. Forest Ecology and Management, 166, 1-15.

Wullschleger, S.D., Jackson, R.B., Currie, W.S., Friend, A.D., Luo, Y., Mouillot, F., Pan, Y. & Shao, G. (2001). Below-ground processes in gap models for simulating forest response to global change. Climatic Change, 51, 449-473.

Zenner, E.K. & Hibbs, D.E. (2000). A new method for modeling the heterogeneity of forest structure. Forest Ecology and Management, 129, 75-87.

Zerbe, S. (2002). Restoration of natural broad-leaved woodland in Central Europe on sites with coniferous forest plantations. Forest Ecology and Management, 167, 27-42.

Zirlewagen, D. & Von Wilpert, K. (2001). Modeling water and ion fluxes in a highly structured, mixed-species stand. Forest Ecology and Management, 143, 27-37.

Zukrigl, K. (1990). Wozu brauchen wir Naturwaldreservate? Österreichische Forstzeitung, 101(7), 27-28.

# A FORGRA – Process implementation

## A.1 Growth

### A.1.1 Light extinction

Light falls in vertically on top of a simulation plot. The canopy is divided in horizontal layers of 1m. The vertical exponential extinction of incoming PAR within a canopy layer X is proportional to leaf density:

$$E_X = PAR_X \cdot \exp\left( -k \cdot \frac{A_{l,X}}{A_{c,p}} \right) \qquad [\mathrm{MJ}]$$

with $E_X$ the remaining part of $PAR_X$ after extinction in crown layer X, k the extinction coefficient for diffuse light (set at 0.5 for all species), $A_{l,X}$ the total leaf area within crown layer X and $A_{c,p}$ the total crown area within the simulation plot p. Leaves are assumed to be black (no reflection) and horizontal. Leaf area is calculated from leaf biomass [kg] and Specific Leaf Area (SLA, cf. Table A.1) [m²/kg].

### A.1.2 Biomass production and allocation

Light extinction within canopy layers is converted to light absorption by individual trees. Biomass increase of a single tree is obtained by multiplying the amount of light absorbed with a species-specific radiation-use efficiency (RUE, cf. Table A.1) [kg/MJ], thereby implicitly accounting for limitations in water and nutrient supply.

Biomass allocation occurs only during the growing season. Biomass is initially subdivided in below-ground biomass (35%) and above-ground biomass (65%). The latter is allocated to stem, branches and foliage according to a seasonal species-specific pattern, derived from observed biomass distributions.

### A.1.3 individual tree growth

Height increment of individual trees is imposed, using the Chapmann-Richards equation:

$$\frac{dH}{dt} = H \cdot h_1 \cdot h_2 \cdot \left( \frac{H_{\max}^{\frac{1}{h_2}} - H^{\frac{1}{h_2}}}{H^{\frac{1}{h_2}}} \right) \qquad [\mathrm{m}]$$

with $H_{max}$ the maximal tree height and $h_1$ and $h_2$ empirical parameters (cf. Table A.1). Height increment is reduced when too little biomass is partitioned to the stem to meet the imposed height increment. DBH increment is derived from stem biomass and tree height, assuming a species-specific cone-shaped stem form.

## A.2 Regeneration

Seed production is calculated for a single tree, the amount depending on species, age and mast year (all data from literature). Incoming seeds in a simulation plot mainly come from trees in the plot, although seeds can immigrate from neighbouring plots (the ‘blue jay effect’).

The number of germinating seeds results from the number of sound seeds in a plot (a fraction of all available seeds FG, cf. Table A.1), the light availability at the forest floor and the cover of the forest floor.

Seedling growth is depending on a species-specific relative growth rate (RGR, cf. Table A.1), which is reduced when light availability decreases. As with adult trees, newly formed biomass of the seedlings is partitioned to the plant organs according to a species-specific pattern, and height increment is imposed. Initially, new seedlings are not described as individuals, bus as cohorts. When height or age of a cohort exceeds a critical value, new individuals are added to the plot.

## A.3 Mortality

Mortality of trees can be caused by age (species-specific maximal tree age $AGE_{max}$, cf. Table A.1), instability (depending on height-diameter ratio) or competition. The latter is related to diameter growth rate, accounting for different minimum growth rates at different tree ages. In this way it is implicitly assumed that when growth rate is below a certain threshold level, maintenance costs exceeds the amount of sugar produced by the foliage, and the tree dies.

Table A.1 Some parameter values used by FORGRA for the main tree species (all data from literature).

| **species** [a] | **SLA** [$m^2$/kg] | **RUE** [kg/MJ] | **h1** | **h2** | **$H_{max}$** [m] | **FG** | **RGR** | **$AGE_{max}$** [yr] |
|---|---|---|---|---|---|---|---|---|
| Be | 15 | 0.7 | 0.01252 | 0.9504 | 20 | 0.73 | 0.7 | 120 |
| Qu | 8 | 1.35 | 0.01336 | 0.96667 | 26 | 0.75 | 0.2 | 700 |
| Fa | 13 | 1.35 | 0.02688 | 1.957 | 30 | 0.45 | 0.3 | 350 |
| Pi | 4.1 | 1 | 0.035 | 1.5998 | 24 | 0.4 | 0.45 | 200 |
| Fr | 12 | 0.8 | 0.09 | 1.515 | 6 | 0.4 | 0.35 | 60 |
| So | 15 | 0.8 | 0.056 | 1.4579 | 7 | 0.4 | 0.42 | 60 |

(a) Be *Betula spp.*, Qu native *Quercus spp.*, Fa *Fagus sylvatica*, Pi *Pinus sylvestris*, Fr *Frangula alnus*, So *Sorbus aucuparia*.

## A.4 Additional literature

Jorritsma, I.T.M., Mohren, G.M.J., Van Wieren, S.E., Van Hees, A.F.M., Bartelink, H.H., Nabuurs, G.J. & Slim, P.A. (1997a). Bosontwikkeling in aanwezigheid van hoefdieren: een modelbenadering. In: Van Wieren *et al.* (Eds.) Hoefdieren in het boslandschap. Backhuys Publishers, Leiden, 147-164.

Jorritsma, I.T.M., Van Hees, A.F.M. & Mohren, G.M.J. (1999). Forest development in relation to ungulate grazing: a modeling approach. Forest Ecology and Management, 120, 23-34.

Kint, V., Geudens, G. & Jorristma, I.T.M. (2002). Spontane ontwikkeling van bossen na omvorming: projecties over langere termijn. In: De Schrijver *et al.* (Eds.) Bosomvorming - noodzaak en praktijk van een effectgerichte maatregel tegen verzuring en vermesting. Academia Press, Ghent, 59-68.

# Addendum B

# B SIAFOR – User guide

## B.1 Introduction

The computer program SIAFOR (Stand structure Index Assessment in FORests) calculates a set of four structure indices in forest monitoring plots with stem-mapped data. The program eliminates edge effects and offers the possibility of virtual sampling. It is designed for use in forest reserves, but may also serve in other contexts. The software is written in the object-oriented language C++, which guarantees flexibility in maintaining and extending the source code. An executable version of SIAFOR 1.0 is available free of charge for scientific and educational purposes. The authors welcome any suggestions about further development of the software and possible options to be included in future releases.

## B.2 Index calculation

SIAFOR calculates four nearest-neighbour indices, based on individual tree data in a monitoring plot (species, size(s) and spatial position) and plot characteristics (shape and dimensions): the positioning index ‘CE’, the relative mixture index ‘S’, the mixture index ‘DM’ and the differentiation index ‘T’. CE, DM and T are calculated for each species separately, and for all species together. S is calculated for each pair of species. Together these indices describe the three-dimensional geometry of forest stands, i.e. positioning, mixture and size differentiation. An overview of these indices, with their main characteristics and statistical tests, is given in Table B.1.

Table B.1 Characteristics and statistical tests of the four indices implemented in SIAFOR.

| index | range | description | statistical test |
|---|---|---|---|
| CE | 0 – 2.15 | *positioning* of trees within a plot: clustered (< 1), random (= 1) or regular (> 1) | z-test<br>$H_0$: CE = 1<br>$H_1$: CE $\neq$ 1 |
| S | -1 – 1 | *relative mixture* of two species within a plot: aggregated-associated (< 0), neutral (= 0) or segregated-separated (> 0) | $\chi^2$-test<br>$H_0$: S = 0<br>$H_1$: S $\neq$ 0 |
| DM | 0 – 1 | *mixture* within a plot: degree of dissimilarity of species between neighbouring trees | permutation test<br>$H_0$: DM = $DM_{ran}$<br>$H_1$: DM $\neq$ $DM_{ran}$ |
| T | 0 – 1 | *differentiation* within a plot: degree of dissimilarity of size between neighbouring trees | permutation test<br>$H_0$: T = $T_{ran}$<br>$H_1$: T $\neq$ $T_{ran}$ |

### B.2.1 The positioning index of Clark & Evans – CE

The *positioning index* CE, first described by Clark & Evans (1954), expresses the extent to which a forest stand deviates from the 'Poisson stand', i.e. a stand with a complete randomised spatial distribution of trees. The average distance between a tree and its nearest neighbour ($r_A$) is compared to the expected mean distance if trees were randomly positioned ($r_E$). With the edge effect correction of $r_E$ for compact unit areas this gives:

$$CE = \frac{r_A}{r_E} = \frac{\frac{1}{N}\sum_{i=1}^{N} r_i}{0.5 \cdot \left(\frac{A}{N}\right)^{1/2} + 0.0514 \cdot \frac{P}{N} + 0.041 \cdot \frac{P}{N^{3/2}}}$$

where $r_i$ is the distance between tree i and its nearest neighbour (in m), $N$ is the total number of trees in the sample plot, $A$ is the area of the plot (in m²) and $P$ its perimeter (in m). A Poisson stand has a CE value of 1. If clusters occur within the stand, CE will be smaller than 1. In regular positioned stands CE becomes larger than 1, with a maximum of 2.15 for a hexagonal arrangement of trees.

In order to test the calculated CE values against a significant deviation of 1, the proposed statistic of Clark & Evans (1954) is implemented. They test the null hypothesis ($H_0$: CE = 1 and $H_1$: CE ≠ 1) using a standard, normally distributed test value:

$$c = \frac{r_A - r_E}{\sigma_{r_E}} \qquad \text{with} \qquad \sigma_{r_E} = \frac{0.26136}{\sqrt{N \cdot \rho}}$$

where $\sigma_{rE}$ is the standard deviation of $r_E$ in a Poisson-forest of density ρ.

### B.2.2 The segregation index of Pielou – S

The *segregation index* S (Pielou 1977) quantifies the relative mixture of two species, independently of their spatial pattern, and supposes no other species are present in the stand. It is based on the comparison between the observed number of mixed pairs ($M_O$) and the expected number under random conditions ($M_E$).

Table B.2 Contingency table, defining the values for the calculation of the segregation index of Pielou (S) for the species A and B.

| species | number of nearest neighbours of | | |
|---|---|---|---|
| | species A | species B | species A + B |
| species A | a | b | m |
| species B | c | d | n |
| species A + B | v | w | N |

Given a contingency table (Table B.2), summarising the number of trees of both species with a nearest neighbour of their own species and of the other species, S is calculated as follows:

$$S = 1 - \frac{M_O}{M_E} = 1 - \frac{N \cdot (b + c)}{v \cdot n + w \cdot m}$$

Thus a distinction can be made between aggregation (association between species; -1 < S < 0), segregation (spatial separation; 0 < S < 1) or neutral relation (random mixture; S = 0) between two tree species. A $\chi^2$-test may be used to judge whether the observed mixture departs significantly from that under random conditions ($H_0$: S = 0 and $H_1$: $S \neq 0$). The $\chi^2$-test is performed with the Yates-correction. Where appropriate the testing procedure by Fisher is used.

### B.2.3 The mixture index of Von Gadow – DM

The *mixture index* DM, first introduced by Von Gadow (1993), for each individual tree i is defined as the fraction of the three nearest neighbours that is of a different species as tree i:

$$DM_i = \frac{1}{3} \cdot \sum_{j=1}^{3} V_{ij}$$

with

$$V_{ij} = \begin{cases} 0 \rightarrow \text{ tree i and neighbor j of the same species} \\ 1 \rightarrow \text{ tree i and neighbor j of different species} \end{cases}$$

It will be clear that $DM_i$ can take only four values: 0 – 0.33 – 0.66 – 1. The mean value for all trees represents the index value for the stand. Values can be calculated for each species separately or for all trees together. Depending on relative frequency and spatial pattern of a certain species within a stand, DM can take values between 0 and 1: strongly represented or segregated species will result in low DM values (indicating that homogeneous groups of tree species occur), whereas less frequent or regularly positioned species will have high DM values (indicating their complete mixture within the stand).

As no theoretical test exists to investigate significant differences between observed and under random mixture expected DM-values, a permutation approach is used. SIAFOR generates 1000 permutations of the species distribution in the investigated stand (randomly re-assigning species-values to tree coordinates) and calculates for each permutation a DM-value. A two-sided test will indicate a significant difference from random mixture at an approximate level of $\alpha = 0.05$ (or 0.01) if the observed DM-value is within the 2.5% (or 0.5%) lowest or highest simulated DM-values.

### B.2.4 The differentiation index of Von Gadow – T

The *differentiation index* T (Von Gadow 1993) describes the degree of dissimilarity of size (height, diameter, crown length, etc.) between neighbouring trees. T of a single tree i with size $S_i$ in relation to its three nearest neighbours is defined as:

$$T_i = \frac{1}{3} \cdot \sum_{j=1}^{3} \left[ 1 - \frac{MIN\left(S_i, S_j\right)}{MAX\left(S_i, S_j\right)} \right]$$

where $S_j$ is the size of the $j^{th}$ nearest neighbour of any species (for total T-values) or of the same species (for T-values of that species). The mean value for all trees represents the index value for the stand. Values range between 0 and 1. Stands with almost no size differentiation will have a value close to 0, whereas highly differentiated stands will approach a value of 1. Again a permutation approach is used to decide on significant differences between observed and under random conditions expected T-values, generating 1000 permutations of the size distribution in the investigated stand. SIAFOR offers the possibility to calculate T-values for four different tree sizes simultaneously.

### B.2.5 Additional calculations

Next to the four described indices, SIAFOR calculates some additional values that may be helpful in interpreting results.

S describes the spatial pattern between two species only, even if more than two species are present (i.e. partial segregation). However, in SIAFOR both partial and total segregation between species are tested by:

1. The performance of a $\chi^2$-test between two categories (‘species 1’ and ‘species 2’), as explained in §B.2.2. The degree of segregation is expressed by the deviation of S from 0 within the range [-1;1]. In the output this is mentioned as ‘partial segregation’.
2. The performance of a $\chi^2$-test between three categories: ‘species 1’, ‘species 2’ and ‘all other species’. The degree of total segregation is expressed by S’ (cf. further). In the output this is mentioned as ‘total segregation’.

3. The performance of a $\chi^2$-test between x categories, one for each species in the stand. The degree of total segregation is expressed by S’ (cf. further). In the output this is mentioned as ‘general dependency between x categories’.

For both total segregation tests (2. and 3.) the degree of segregation is expressed by the index S’:

$$S' = \frac{\chi^2}{N \cdot (d-1)}$$

with $\chi^2$ the test-value of the performed $\chi^2$-test, N the total number of trees considered in the test and d the dimension of the test (i.e. three for case 2. and x for case 3.). S’ can reach values between 0 to 1; the higher S’, the less species are randomly mixed. Note that S’ cannot make a distinction between segregation and aggregation.

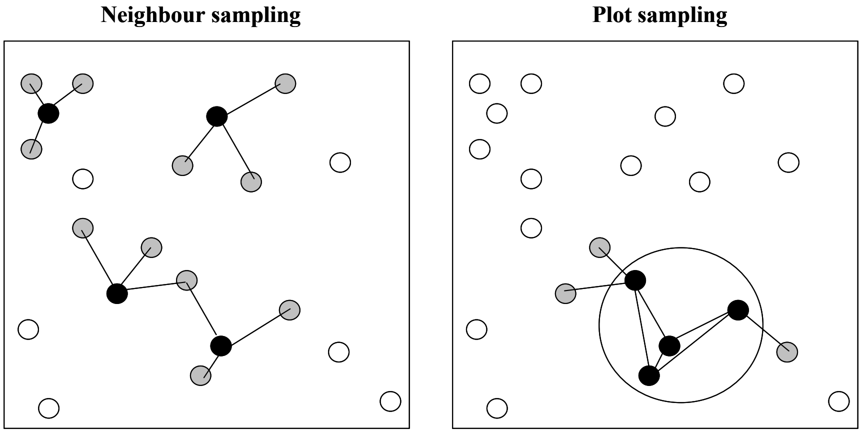
Finally, as $DM_i$ and $T_i$-values are calculated for every single tree and then averaged for the whole stand, frequency distributions of the single tree values are calculated. This is especially useful for interpreting index-change over time. For this purpose, SIAFOR divides the T-range into five equal classes. For DM only four classes are used, as only four $DM_i$-values are possible.

## B.3 Edge effect correction

All indices are based on neighbour relations. The nearest neighbours for each tree are detected, based on information about tree positions in the monitoring plot. However, the detected nearest neighbours for a tree standing near the edge of a plot are not necessarily the real nearest neighbours and therefore a distortion of the correct index values can arise. To eliminate this error an edge effect correction is implemented within SIAFOR: trees that fall within a buffer following the plot border can only serve as nearest neighbour to other trees, but are themselves not considered in the calculation of the indices. Buffer width is a function of both the tree positions and the calculated index, and guarantees the elimination of all edge effects. Where plots have unsuitable shapes for this type of correction (e.g. long and narrow rectangular plots), the use of edge effect corrections can be restricted or disabled.

## B.4 Sampling module

SIAFOR is furnished with an optional sampling module. This module repeatedly takes virtual samples of increasing size from a completely stem-mapped stand and calculates the index values for each sample. Sample size increment (in percent of tree density) and number of repetitions are user defined. This allows the user to determine, for the stand under investigation, the minimum sample size for index estimation at different levels of accuracy.



sample size = 4
No. of measured trees = 15
No. of neighbour relations = 12

sample size = 4
No. of measured trees = 7
No. of neighbour relations = 8

Figure B.1 Examples of neighbour sampling and plot sampling with indication of sample trees (black circles), measured trees (grey circles) and neighbour relations (lines between trees).

Two sample types can be emulated within SIAFOR (Fig. B.1): neighbour sampling and plot sampling. With *neighbour sampling* a number of sample trees are marked throughout a stand, and for each sample tree and its neighbour(s) appropriate variables are collected for the index to be estimated. With *plot sampling* a number of sample trees around a random point in the stand are marked, thus defining a group of neighbouring trees within a plot.

## B.5 Practical use of SIAFOR

### B.5.1 Plot requirements

SIAFOR can be used to calculate the aforementioned structure indices in most monitoring plots with stem-mapped data. There are, however, some plot requirements that may limit its use:

(iv) plots should be circle plots, rectangular plots or convex tetragons;

(v) there are no size limitations for plots, but the program is optimised for plots up to 5 ha;

(vi) small plots may have insufficient trees to calculate all indices: SIAFOR requires at least five trees (after edge effect correction) and their respective nearest neighbour(s) for an index to be calculated; the larger the number of trees in the analysis, the more representative results are for the whole stand.

Due to data limits, index values for single small monitoring plots are often of little interest. In SIAFOR this may be solved by grouping monitoring plots and calculating the index values of such a group. There are no limitations concerning the composition of groups (i.e. number and characteristics of plots) and this option may, for example, be used for performing a structure assessment of groups from similar monitoring plots in forest reserves.

The use of the sampling module is limited to one plot only; it does not function with groups of plots. Furthermore, the plot should be large enough to make virtual sampling meaningful. We advise a minimum plot area of 1 ha for using the sampling module.

### B.5.2 Command line

SIAFOR is a command line programme. This makes it particularly suitable to be run in batch-mode. The command line should have the following format for the programme to run correctly. Any deviation from this format will cause the programme to stop and generate an error message.

```
[path]\SIAFOR [infile] [outfile] [sample step]
[repetitions] [sample type] [buffer use] [buffer level]
```

with:

- `[path]` indicates the path towards the local folder (e.g. C:\siafor) containing both the executable file (siafor.exe) as well as the input file (see further). The output file will be saved in this folder;
- `[infile]` and `[outfile]` are the names of the input and output files respectively. The extension should be .txt in both cases;
- `[sample step]` is an integer between 1 and 100, defining the sample size increment (in percentage of tree density). Hence, a value of 5 will result in samples of 5%, 10%, 15%, …, 100% of the tree density. If no sampling is required, a value of 100 should be used.
- `[repetitions]` is a positive integer value, defining the number of times each sample should be taken. If `[sample step]` is set to 100 (i.e. no sampling is required), any value for `[repetitions]` will automatically be interpreted as 1.
- `[sample type]` can take two values: 1 and 2. A value of 1 stands for neighbour sampling, and 2 for group sampling.
- `[buffer use]` can take three values: 0, 1 and 2. A value of 0 disables the edge effect correction. A value of 1 enables the standard edge effect correction, guaranteeing the total elimination of all edge effects. A value of 2 enables the custom edge effect correction, and requires a value for `[buffer level]`.
- `[buffer level]` is only required when `[buffer use]` is set to 2. It can take three values (1, 2 and 3), indicating the number of nearest neighbours for which all edge effects should be eliminated.

Hence the following command at the command line prompt >

```
C:\siafor\siafor f_in.txt f_out.txt 30 1000 1 1
```

will run the SIAFOR software with the file f_in.txt (both in the folder c:\siafor), at samples of 30%, 60%, 90% and 100% of the tree density, with 1000 repetitions for each sample (except for 100%), using neighbour sampling and with a standard edge effect correction. The results will be written to f_out.txt in the folder c:\siafor.

### B.5.3 Input file format

The input file contains all information about the monitoring plot(s) and the trees. It should be an ASCII-file (extension .txt) to be placed in the same folder as the executable file (siafor.exe). It is important that the correct format is used: incorrect formats may cause the programme to stop or to generate wrong results. The input file contains two separate parts: first a description of the different monitoring plots and their characteristics, and subsequently a listing of all individual trees per plots. Plots and trees are listed on one line each, with tabs between the different variables. An example of an input file with three plots, limited to five trees per plot, could be:

```
1  2  12.616
2  1  140   70
3  3  100   121.9 95.92 113.7 148.1
1  1  5     18    9.5   1     0     1     2.16  11.09
1  2  5     28    14.5  3.5   0     1     0.97  5.01
1  3  5     31    15    5     0     1     1.95  3.38
1  4  5     26    15.5  3.5   0     1     7.39  9.46
1  5  5     25    16    5     0     1     8.86  6.68
2  1  5     5     5.5   1     1.21  2     1.1   2.1
2  2  5     8     7.5   3.5   1.73  1     4.3   1.7
2  3  5     7     6     6     0     7     5.6   0.7
2  4  5     6     6     1     1.97  1     5.6   4.4
2  5  5     24    12.5  5     2.66  1     6.2   3.1
3  1  1     35.65 0     0     0     1     0.70  3.3
3  2  1     12.73 0     0     0     1     1.40  2.6
3  3  1     17.19 0     0     0     1     2.80  5.1
3  4  1     10.19 0     0     0     1     0.80  7.6
3  5  1     13.69 0     0     0     1     1.10  7.75
```

#### B.5.3.1 Plot description

SIAFOR distinguished between thee monitoring plot types, depending on their shape: circle plots, rectangular plots and convex tetragons. The first lines of an input file list the different plots for which structure indices should be calculated. For each plot three types of information are required, separated by tabs: (i) the plot number, (ii) the plot shape and (iii) the plot dimensions.

(i) The plot number is an integer value, starting with 1, and increasing with one unit for each additional plot. Plots should be listed in ascending order, with the plot number at the start of a line.

(ii) Rectangular plots are indicated with a value 1, circular plots with 2 and convex tetragons with 3.

(iii) The plot dimensions depend on the plot shape (Fig. B.2). For rectangular plots the length in meters of the sides along the abscissa (a) and ordinate (o) are required (plot 2 in the example: 140m and 70m respectively). For circle plots only the radius (r) in meters is required (plot 1 in the example: 12.616m). Convex tetragons are characterised by five dimensions: the length in meters of the four sides (L1 to L4) and of the diagonal from above left towards below right (d) (plot 3 in the example: 100m, 121.9m, 95.92m, 113.7m and 148.1m respectively). Note that the correct order of dimensions is important.

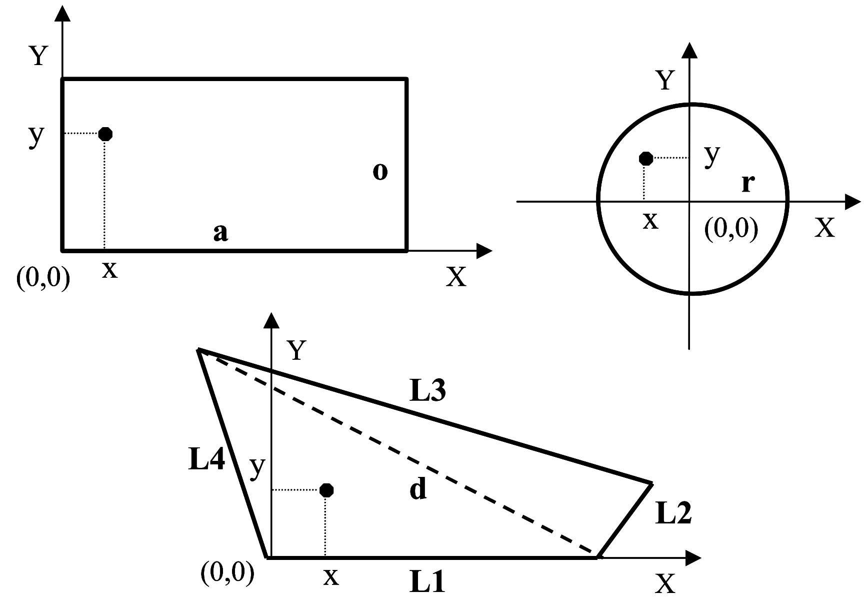


Fig. B.2 Definition of monitoring plot characteristics and of the co-ordinate system for input file construction.

### B.5.3.2 Tree description

After the plot description, and without leaving a blank line, the listing of all trees can start (one line for each tree). Trees are characterised by five types of information, again always separated by tabs: (i) the tree code, (ii) species, (iii) size(s), (iv) vigour and (v) location.

(i) A tree code consists out of a unique combination of two succeeding variables: the number of the plot in which the tree is found, and an arbitrary tree number. The plot number must correspond to the used numbers in the plot description at the start of the input file. Trees must be listed in ascending order of plot numbers; within a plot, tree order is arbitrary.

(ii) The tree species is characterised by a user defined coding. Species codes should be positive integer values, and may not be 0. In the example only two species, represented by the codes 1 and 5, are present. SIAFOR allows a maximum of 11 species.

(iii) Four tree sizes can be provided with the programme. SIAFOR interprets the subsequent variables as diameter (in cm), height, crown length and crown radius (in m); the user is however free to enter different variables. If less than four size variables are known, the remaining places in the input file should be filled out with 0.

(iv) Tree vigour is indicated by codes 1 or 2 (for living trees) and codes 6 to 9 (for dead trees). The differentiating within one category (e.g. difference between 1 and 2) may be useful for a more detailed description of tree vigour, but is neglected by SIAFOR. Dead trees are only used by SIAFOR to calculate plot statistics, and are omitted for structure index calculation.

(v) Tree location is defined by the position of trees on the abscissa (x) and ordinate (y) within the co-ordinate system as defined in Fig. B.2. SIAFOR will check, based on the given tree co-ordinates and the plot characteristics, whether all of the listed trees fall within the plot borders.

### B.5.4 Output file format

The output file is an ASCII-file (extension .txt). It is build at the end of the calculation, and consists out of three parts: (i) a header, (ii) a short description of the input data and (iii) the results of the structure index calculation. Depending on the number of plots and on the use of subsampling, the output may be slightly different. The examples below all refer to the calculations for one plot with subsampling every 25%. The main difference with multiple plots is that in those cases no subsampling is possible, and that instead separate results for each plot as well as for all plots together will be listed.

#### B.5.4.1 The header

The header of the output file contains the following elements:

- used SIAFOR version and exact time of output generation;
- number of plots in the calculation, with their dimensions and derived variables;
- total number of trees and of dead trees in the input file;
- user defined settings of subsampling and edge effect correction.

```
RESULTS OF THE STRUCTURE CALCULATION - SIAFOR Version 1.0
- unique plot
Wed Jun 04 15:02:55 2003

RECTANGULAR PLOT:
width: 140 m height: 60 m surface: 0.84 ha

STAND CHARACTERISTICS:
Total number of trees:    523
Dead trees:               72

NEIGHBOUR SAMPLE:
Step size subsamples:     25 %
Number of repetitions:    10

Buffer:                   standard
```

#### B.5.4.2 Data description

The data description is a short summary over all plots of stem density and basal area per species:

```
I. DENSITY VALUES OF LIVING TREES FOR THE PLOT
Species      Stem density             Basal area
             (#)    (#/ha) (%)        (m2/ha)      (%)
1            38     45     8.43       0.701        2.42
2            5      6      1.11       0.0854       0.295
3            59     70     13.1       6.2          21.5
5            115    137    25.5       16.2         55.9
8            1      1      0.222      0.0374       0.129
9            162    193    35.9       5.22         18.1
10           2      2      0.443      0.0244       0.0845
11           66     79     14.6       0.441        1.53
TOTAL:       451    537    100        28.9         100
```

### B.5.4.3 Results of the index calculation

The following is just an excerpt of the total output. For all indices the buffer width (in m), the number of trees that are remain after buffer setting ('marked' trees), the sample size (in %) and the number of sampled trees are indicated. For each subsample the calculated index value as well as the 95% probability interval are given. Finally the results of the statistical testing are represented by the percentage of repetitions resulting in the acceptance of the null hypothesis (%-), and those resulting in its rejecting at a 0.05 (%*) and 0.01 (%**) significance level. In all cases a value of –999 indicates that not all conditions for the calculation were satisfied (e.g. to few trees).

For DM and T some additional information is included. The last row of the last column (unnamed) indicates the mean index-value of all permutations (in the example 0.917 and 0.477 for DM and TD respectively). From the comparison of this value with the real index value one can decide whether the observed mixture or differentiation is lesser or bigger than the one under random conditions. Also a distribution of tree values over four (DM) or five (T) categories is included (cf. §B.2.5). Finally, next to the S-value itself (which is a partial segregation) also a total segregation value S' is calculated (cf. §B.2.5).

```
II. INDEX CE OF CLARK AND EVANS
-----------> TOTAL:
buffer #marked sample #used index +/-95% %-  %* %**
6.5    298     25     75   1.008 0.125  70  10 20
6.5    298     50     149  1.019 0.102  70  20 10
6.5    298     75     224  1.039 0.034  90  10 0
6.5    298     100    298  1.045 0      100 0  0
```

```
III. SEGREGATION
-----------> (code 1) - (code 5) > TOTAL:
buffer  #marked sample #used index  +/-95% %-   %*   %**
6.5     298     25     75    -999   0     -999 -999 -999
6.5     298     50     149   -999   0     -999 -999 -999
6.5     298     75     224   -999   0     -999 -999 -999
6.5     298     100    298   0.0952 0     0    0    100

-----------> (code 1) - (code 5) > PARTIAL (Pielou):
buffer #marked sample #used index +/-95% %-  %*   %**
6.5    298     25     29   0.341 0.437  60  30   10
6.5    298     50     56   0.389 0.278  20  20   60
6.5    298     75     82   0.365 0.0969 0   10   90
6.5    298     100    110  0.359 0      0   0    100

IV. INDEX DM OF VON GADOW
-----------> unknown (code 1):
buffer #marked sample #used index +/-95% %-  %*  %**
9.99   25      25     6   0.706 0.206 -999 -999 -999 -999
9.99   25      50     13  0.713 0.118 -999 -999 -999 -999
9.99   25      75     19  0.709 0.0746-999 -999 -999 -999
9.99   25      100    25  0.707 0     0    0    100 0.917

sample f(0) +/-95% f(.33) +/-95% f(.66) +/-95% f(1)  +/-95%
25     0    0      33.33 15.4   21.67 37.88  45    48.82
50     0    0      26.92 20.41  32.31 13.85  40.77 17.48
75     0    0      28.95 11.14  29.47 7.213  41.58 12.35
100    0    0      28    0      32    0      40    0

V. INDEX TD OF VON GADOW
-----------> TOTAL:
buffer #marked sample #used index +/-95% %-  %*  %**
9.99   240     25     60   0.385 0.0509 -999-999-999-999
9.99   240     50     120  0.391 0.0264 -999-999-999-999
9.99   240     75     180  0.393 0.0156 -999-999-999-999
9.99   240     100    240  0.393 0      0    0   100 0.477

sample f(.20) +/-95% f(.40) +/-95% f(.60) +/-95% f(.80) +/-95%
25     18.33 8.574  35.5  10.45  30.67 12.62  14.17 11.02
50     16.67 5.222  37.5  4.87   30.25 6.258  13.75 3.289
75     16.94 2.96   36.06 2.689  31.61 2.59   13.33 3.63
100    16.67 0      36.67 0      31.25 0      13.33 0

sample f(1)  +/-95%
25     1.333 2.066
50     1.833 2.284
75     2.056 0.8965
100    2.083 0
```

## B.6 References

Clark, P.J. & Evans, F.C. (1954). Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology, 35, 445-453.

Pielou, E.C. (1977). Mathematical ecology. Wiley, 385p.

Von Gadow, K. (1993). Zur Bestandesbeschreibung in der Forsteinrichtung. Forst und Holz, 48, 602-606.

## B.7 Additional literature

Kint, V., Van Meirvenne, M., Nachtergale, L., Geudens, G. & Lust, N. (2003). Spatial methods for quantifying forest stand structure development: a comparison between nearest-neighbor indices and variogram analysis. Forest Science, 49(1), 36-49.

Kint (2003). Structural development in ageing Scots pine (*Pinus sylvestris* L.) stands in western Europe. Ph.D. Ghent University, Belgium. ISBN 90 382 0504 X.

# Addendum C

## Acronyms and notations

| | |
|---|---|
| $AGE_{max}$ | maximal tree age (FORGRA parameter) |
| Be | silver birch (*Betula pendula* Roth) and downy birch (*Betula pubescens* Ehrh.) |
| BQ | natural plant association *Betulo-Quercetum roboris* |
| BQm | natural plant association *Betulo-Quercetum roboris*, subassociation *molinietosum* |
| CE | nearest-neighbour index of Clark & Evans |
| DBH | diameter at breast height (at 1.3m height) |
| DEF | design expansion factor |
| DM | nearest-neighbour index ‘Durchmischung’ of Von Gadow |
| $DM_i$ | DM for a single tree I |
| $DM_{ran}$ | expected value of DM when species values are randomly re-assigned to tree coordinates in a permutation approach |
| Fa | common beech (*Fagus sylvatica* L.) |
| FDT | forest development type |
| FG | fraction of sound seeds (i.e. that can germinate) (FORGRA parameter) |
| FORGRA | used process-based gap model |
| FQ | natural plant association *Fago-Quercetum* |
| FQm | natural plant association *Fago-Quercetum*, subassociation *molinietosum* |
| Fr | alder buckthorn (*Frangula alnus* Mill.) |
| **h** | lag; distance vector (geostatistics) |
| $H_0$ | null hypothesis (statistics) |
| $H_1$ | alternative hypothesis (statistics) |
| $H_{max}$ | maximal tree height [m] (FORGRA parameter) |
| La | larch (*Larix* spp.) |
| MEF | measurement expansion factor |
| $MP_p$ | model prediction for a simulation plot p |
| $OV_{p,t}$ | output vector at time t of $MP_p$ |
| PAR | photosynthetic active radiation |
| Pc | spruce (*Picea* spp.) |
| Pi | Scots pine (*Pinus sylvestris* L.) |
| Pm | Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) |

| | |
|---|---|
| PNV | potential natural vegetation |
| Ps | black cherry (*Prunus serotina* Ehrh.) |
| Qr | American red oak (*Quercus rubra* L.) |
| Qu | pedunculate oak (*Quercus robur* L.) and/or sessile oak (*Quercus petraea* (Mattuschka) Lieblein) |
| RF | random function (geostatistics) |
| RGR | relative growth rate (FORGRA parameter) |
| RUE | radiation use efficiency [kg/MJ] (FORGRA parameter) |
| RV | random variable (geostatistics) |
| S | nearest-neighbour index ‘segregation’ of Pielou |
| SC | structural class |
| SCO | structural class object |
| SIAFOR | computer programme for structure assessment |
| SLA | specific leaf area [$m^2$/kg] (FORGRA parameter) |
| So | rowan (*Sorbus aucuparia* L.) |
| T | nearest-neighbour index ‘differentiation’ of Von Gadow |
| $T_{ran}$ | expected value of T when values are randomly re-assigned to tree coordinates in a permutation approach |
| TC | T of circumference |
| TCl | T of crown length |
| TD | T of diameter |
| TH | T of height |
| $TH_i$ | TH for a single tree I |
| $TH_{ran}$ | expected value of TH when height values are randomly re-assigned to tree coordinates in a permutation approach |
| $\alpha$ | level of significance (statistics) |
| $\gamma(\mathbf{h})$ | variogram |
| $\gamma_I(\mathbf{h})$ | indicator variogram |

SI-units are used

# Curriculum vitae

Vincent Kint (°1973, Ghent, Belgium) finished his secondary school at Sint-Barbara-college in Ghent. After an additional year of scientific formation, he started his studies in 1992 at the Faculty of Agricultural and Applied Biological Sciences, Ghent University. He interrupted his studies for a two years international experience in Italy and Switzerland, where he graduated in social and religious sciences. After his return to Belgium he continued his studies at Ghent University, and had the opportunity to fulfil part of his study curriculum at the University of Natural Resources and Applied Life Sciences, Vienna. He specialised in forest ecology and management, and made his master thesis on the quantification of spatial structural characteristics of forest stands. He graduated as a Master in Engineering in Land and Forest Management in 1999. In October of that same year he was employed at the Laboratory of Forestry and the Laboratory of Forest Management and Spatial Information Techniques at Ghent University. Ever since he focused on his Ph.D. study programme and research, in close collaboration with his colleagues at Wageningen-UR, the Netherlands. He is author or co-author of the following publications:

De Schrijver, A., Kint, V. & Lust N. (eds.) (2002). Comparison of ecosystem functioning and biogeochemical cycles in temperate forests in Southern Chile and Flanders. Academia Press, Ghent, 129p.

De Schrijver, A., Kint, V., Geudens, G. & Lust, N. (eds.) (2002). Bosomvorming – noodzaak en praktijk van een effectgerichte maatregel tegen verzuring en vermesting. Academia Press, Ghent, 93p. (in Dutch)

Geudens, G., Kint, V. & Lust, N. (2002). Early below ground interaction among seedlings in natural regeneration of Scots pine. In: Proceedings of the IUFRO conference on restoration of boreal and temperate forests, April 2002, Vejle, Denmark, 177-178.

Geudens, G., Kint, V. & Vercammen, P. (2002). Structuur in natuurlijke verjongingen van berk en den: ontwikkeling in menging en ongelijkjarigheid. In: Proceedings van de studiedag 'bosomvorming', November 2001, Ghent University, 49-57. (in Dutch)

Geudens, G., Staelens, J., Kint, V., Goris, R. & Lust, N. (submitted). Allometric biomass equations for high density Scots pine natural regeneration in the first years of establishment.

Kint, V., De Wulf, R., Lust, N. & Mohren, G.M.J. (2000). A gap model for simulating conversion of Scots pine stands: methodological considerations. In: Proceedings of the conference on forest ecosystem restoration, April 2000, Vienna, 340-343.

Kint, V., Lust, N., Ferris, R. & Olsthoorn, A.F.M. (2000). Quantification of forest stand structure applied to Scots pine (*Pinus sylvestris* L.) forests. Investigación Agraria: Sistemas y Recursos Forestales, special issue 1, 147-163.

Kint, V., Van Meirvenne, M., Nachtergale, L., Geudens, G. & Lust, N. (2000). Spatial methods for describing forest stand structure evolution in intensively and extensively managed mixed Scots pine forests. In: Proceedings of the conference on forest ecosystem restoration, April 2000, Vienna, 143-150.

Kint, V. (2001). Spontane bosontwikkeling en beheer: de intuïtie voorbij. Nederlands Bosbouwtijdschrift, 73(2), 33-38. (in Dutch)

Kint, V., Geudens, G. & Jorritsma, I. (2002). Spontane ontwikkeling van bossen na omvorming: projecties over langere termijn. In: Proceedings van de studiedag 'bosomvorming', November 2001, Ghent University, 59-68. (in Dutch)

Kint, V., Geudens, G. & Lust, N. (2002). Long-term stand structure development in forest reserves on poor sandy soils: implications for restoration management. In: Proceedings of the IUFRO conference on restoration of boreal and temperate forests, April 2002, Vejle, Denmark, 175-176.

Kint, V., Van Meirvenne, M., Nachtergale, L., Geudens, G. & Lust, N. (2003). Spatial methods for quantifying forest stand structure development: a comparison between nearest-neighbor indices and variogram analysis. Forest Science 49(1), 36-49.

Kint, V., Mohren, G.M.J., Geudens, G., De Wulf, R. & Lust, N. (submitted). Pathways of stand development in ageing Scots pine forests.

Kint, V., De Wulf, R. & Lust, N. (submitted). Forest stand structure assessment in forest reserves.

Kint, V., Geudens, G., Mohren, G.M.J., De Wulf, R., Goris, R. & Lust, N. (submitted). Close-to-nature forestry in ageing Scots pine forests in Western Europe.