# Forest components

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# Contents

# Foreword

Per 1986, the Dutch Minister of Agriculture and Fisheries approved the five-year financial protection of a research theme 'conservation and use of forest components'. This system of protected funding was meant to improve the quality of University research, in particular by stimulating researchers in related fields but from different University Departments to work on a common theme of their choice. Existing scientific lines of these researchers were thought to gain plus-value by intensifying contacts with others, by exposing them to discussions yielding new viewpoints, and finally to allow them to adjust their research more closely to a common goal. All those who know the busy University schedules and the growing restrictions on effective research time, i.e., time not limited to isolated half-hours between teaching and meetings, understood that the implementation of these splendid aims of oriented cooperation would cost time and go slowly. One of the ways in which Universities can correct this is the choice of appropriate subjects for graduate studies, and this has been systematically promoted for 'Forest Components' since years before the official programme was started.

The group that was responsible for the forest components theme decided to accelerate the process by starting an ambitious project, the writing of a common book. There is no way in which cooperation can be stimulated better, but this way has to be learned and practised too. The result is now before you. The book is not yet ideal in our opinion because it still contains too many traces of the old University tradition of researchers working, each apart, on such narrow subjects as they know best. This way of executing the research of course is necessary to reach sufficient depth. But it carries the risk of loss of vision of the whole system, parts of which are studied. Still a little bit unbalanced, but on its way to improve along lines that are more clear now, this presentation in a pluridisciplinary way is a first step, however, to overcome both the limits of individual researchers and the shallowness of groups.

We trust, however, that it is exactly this wrestling with integration of broad views versus the deepening of restricted views that may be as interesting to the reader as the facts, figures, conclusions and hypotheses on forests and their components which are presented in the following pages. On the brink of the last decennium of this century, it is hoped that this book may find its way to both specialists and generalists, and that most of its contents may also be of significance for the European forest managers.

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Coordinator of the 'Forest Components' team.

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# 1 Forest ecosystems and their components: an introduction

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## Summary

In the context of the problem of all forest researchers to delimit the systems they observe, three parallel hierarchies based on respectively architectural criteria (morphological, visible: forms to measure), population criteria (numerical, often invisible: numbers to count) and on production criteria (mass, invisible: masses to weigh) are described. The hierarchies show the same nested hierarchical levels, as a systems model in which at each level a system is conceived as a set of interacting subsystems, one level lower. Groups of subsystems are compartments. Components are the largest individual living systems in the hierarchy of cells, tissues, organs, organ complexes and organisms (components). Components, or compartments made up by components, form community systems by their interaction, respectively eco-units and forest mosaics. Moreover, a distinction is made between patterns and processes, the former guiding the latter, which in turn may change the former. The time dimension is considered too. The importance of using a clear and coherent image by all researchers is emphasized.

Important forest components, such as trees and man (*Homo sapiens*), have caught the attention of the researchers already for a long time, but the research of other forest subsystems such as the subterranean compartment, fungi or insects should be enhanced. A tendency is this direction is now perceptible.

## 1.1 Systems analysis, forests and nature

In the media, in political discussions or in management plans, forests often are mentioned in one breath with nature. Every forest researcher sooner or later has to face questions that are difficult to answer. Is a certain forest development or management system natural or not? Does human impact make a forest unnatural? Is a managed forest an ecosystem or not? It is appropriate to state from the outset that forest researchers, as scientists, cannot provide answers to such questions. The reason is, that such answers depend on a definition of 'nature', and that such definitions generally are axioms derived from philosophy (cf. Westhoff, 1977). In other words, they cannot be falsified by scientific data. But forest researchers have to adhere to scientific methods. These methods always use some system concept.

Systems usually are delimited by the researchers themselves. According to his or her perceptions and axioms, each researcher chooses a fragment of reality. This fragment is considered as a system. It then is divided in parts, its subsystems. Interaction between the subsystems explains the system. No scientific research escapes this approach. For example, many physicists choose a closed vessel with its contents as their system, and categories of physical matter in it as subsystems. The Linnean method views organisms as systems, to be described by their organs as subsystems. For the conceptual basis of methodological issues in botany,

the reader is referred to Sattler (1982).

How do forest researchers delimit their systems? It is often assumed that they do so according to 'natural limits', determining 'natural systems'. The term 'natural' here means nothing more than 'their own' limits, which can be seen by eye. If this is so, some approaches do not consider natural limits at all. Populations analysis, for instance, most often gives no spatial or temporal limits to ecosystems (but see Barkman, 1970) and considers sample areas of arbitrary size and shape which are judged to be representative for the dimensionless system studied. In structural analysis, forest vegetation layers have a remarkable analogy with man-made layers in rural 'coppice-with-standards' forests. Such layers may well have been delimited later in wild forests and interpreted as 'natural' phenomena (Westra, pers. comm., 1985). And ares, hectares or acres are clearly brought in from agricultural land-use patterns into forest analysis, just as the more recent pixel surfaces of satellite imagery are units in technological patterns. The image comes first, the forest second.

This state of affairs leaves a difficult kind of freedom to forest researchers for two reasons. The first one is, that they still have no scientific answer to questions such as those cited above. The second one is, that the closer they look, the more details they perceive that should be fitted into the image, and the further away a coherent and clear image seems to flee. Still, there are scientific tools to solve such dilemmas. Images can be constructed that fit facts that can be checked by others, while limiting the number of facts to be considered, so that the forest image becomes less like an impressionist painting. It is with such clear images that this introduction is concerned.

## 1.2 Concepts, criteria and hierarchies

Some broad concepts define the lines of approach chosen in this book, illustrated by its chapters in the form of case studies. The first postulate is that, whatever a forest ecosystem is, it cannot be characterized exclusively by its trees. Images of forests have to account for all organisms present, such as bacteria, fungi, insects, other animals, shrubs and herbs, and also trees. The second postulate is, that human impacts are always present in forests, be they small and irregular or heavy and frequent. Therefore, the human organism is included from the outset. This also allows us to consider management. The third postulate is, that no existing scientific approach is more than partial. None is more 'true' than another or more important than another. Only by respecting, harmonizing and interweaving the different approaches can an improved image be born. The fourth postulate is derived from the third one: because all forest images have some class of forest components in common, let us start modestly by giving the components a closer look.

The following concepts are operationally used.
- A model is a geometrical (graphical), verbal (described) or algebraic (calculated) representation of a chosen system.
- A component is an organism, or an abiotic system of the same order (e.g. a pedon, see Armson, 1977, p. 9), considered as a subsystem in a forest ecosystem.
- A compartment is a set of components that together, most often for simplification purposes, are chosen as one subsystem in a forest ecosystem (e.g. wood decomposers, Keizer & Arnolds; Vries, this vol.).

Given the huge number of component organisms if one includes all species, the necessity for the creation of compartments will be clear to every researcher and model-user who understands that a model has to remain manageable and show clear lines (e.g. Brünig & al., 1986). Too complicated models have received the surname of 'spaghetti models' from our colleagues in Hamburg (Brünig, pers. comm., 1983), because they are as difficult to follow as the lines of spaghetti strands interwoven in a dish. Figure 1.2 intentionally has such characteristics.

The basic criteria used in model building of all kinds seem to be only three. Verbal descriptions do not escape them, although human language is apt to mix them up:

- numbers are obtained by counting comparable objects and used in calculations: they are the central criterion in population models;
- forms are obtained by measuring objects and used in scale-drawings, maps in the broad sense: they are the central criterion in morphological and architectural analysis;
- masses are obtained by weighing objects or dosing substances, i.e. comparing their mass, a comparison that is expressed in numbers and used in calculations; they are the central criterion in ecological production models and most management models.

Modern computers can now translate nearly all criteria in numbers (digitalization) and retranslate them towards both other criteria in their outputs: plotters have maps, graphs and drawings as their outputs, and robots can produce specified masses.

The final scientific tool, after modelling and the application of well-chosen criteria, is hierarchization. The recent upsurge in interest in hierarchical systems theory is noteworthy (see bibliography).

Hierarchization serves to make manageable models by structuring the data sets in such a way that subsystems occur in the chosen system in such numbers and with such properties that models remain manageable. The most generally accepted hierarchy, however, has historically grown and incorporated successive methods using different criteria. Figure 1.1 separates the fragments that repose on each criterion and fills up the lacunae. This results in three parallel hierarchies, for architectural criteria (morphological, visible), for population criteria

| Architecture | Populations | Biomass |
|---|---|---|
| (Morphology, ect.) | (Syntaxonomy, ect.) | (Production, ect.) |

*site mosaics (maps)*

**POTENTIAL PRODUCTION** (resources)

| | | |
|---|---|---|
| *silvatic mosaic* *(transect, map)* *(cf. Koop, 1981)* | *COENON* *(dimensionless)* *(cf. Barkman, 1970)* | *gap mosaic* *(cf. Shugart, 1984)* |
| *ECO-UNIT* *(transect, map)* *(cf. Oldeman, 1983)* | *microcoenon* *(dimensionless)* *(cf. Barkman, 1970)* | *STAND PRODUCTION* *(cf. Mohren, 1987)* |

*compartments = auxiliary levels*

| | | |
|---|---|---|
| (e.g. structural sets, infrastructural sets, potential sets.. etc.) | (e.g. populations, species, synusiae, guilds, etc.; cf. Freysen & Wolden-dorp, 1978) | (e.g. stem mass, root mass, leaf mass, crop mass, weed mass, etc.) |

– – – – – – – *limit between organisms/communities* – – – – – – – –

| | | |
|---|---|---|
| ORGANISM (component, occupying spatio-temporal ecotope) (cf. Oldeman, 1974) | ORGANISM (Linnean individual, i.e. population of organs) (cf. Floras & Faunas) | SINGLE PLANT OR ANIMAL (mass, inputs, outputs,) (cf. Hari & al., 1981) |

*compartments = auxiliary levels*

| | | |
|---|---|---|
| (e.g. reiterated complex, model-conform complex, organ complex, etc.) | e.g. inflorescences, phyllotaxis, life form, seasonality, etc.) | (e.g. crown mass, root system mass, sap stream translocation, etc.) |
| ORGAN (subsystem in organism) (cf. Hallé & al., 1987) | ORGAN (member of organism) (cf. Handbooks botany, zoology) | ORGAN (function-bearer) (cf. De Wit & al., 1978) |

*lower levels (tissue, cell, subcellular) OMITTED*

Fig. 1.1. Three hierarchies of living systems, according to three basic criteria. Note that 'auxiliary levels' are main levels for some researchers. Such hierarchies are tools for research data structuring. See text.

**Architecture** (Morphology, ect.)   **Populations** (Syntaxonomy, ect.)   **Biomass** (Production, ect.)

POTENTIAL PRODUCTION (resources)

site mosaics (maps)

silvatic mosaic
(transect, map)
(cf. Koop, 1981)

COENON
(dimensionless)
(cf. Barkman, 1970)

gap mosaic
(cf. Shugart, 1984)

ECO-UNIT
(transect, map)
(cf. Oldeman, 1983)

microcoenon
(dimensionless)
(cf. Barkman, 1970)

STAND PRODUCTION
(cf. Mohren, 1987)

*Lieth in Douglas*

compartments = auxiliary levels

*Koop ● Virgin forest*
*Peters ● Japan ● Beech*
*Leersnijder, Boerboom ● Design*
*Rijssen, Schmidt ● Experiment*
*Van Baren ● Pergraon*
*Kuiper, Schoenmakers ● Thinning*

(e.g. structural sets,
infrastructural sets,
potential sets, etc.)

*Ash mortality*
*insects*
*Non-polar*
*Nematodes*
*Aphyllophorales*

(e.g. populations,
species, syntaxae,
guilds, etc. cf.
Vesser & Wingen-
berg, 1978)

*Van Baren ● Kootwijk*
*Schoondewoerd, De Klein ● Labour*
*Staud*

(e.g. stem mass,
root mass, leaf mass,
crop mass, weed mass,
etc.)

*limit between organisms/communities*

ORGANISM
(component occupy-
ing spatio-temporal
ecotope)
(cf. Oldeman, 1974)

ORGANISM
(Linnean individual,
i.e. population of
organs)
(cf. Floras & Faunas)

*De Goede, Hanger*
*Arnolds, Kalzer*

SINGLE PLANT OR
ANIMAL
(mass, inputs, outputs,)
(cf. Hall & al., 1981)

*Mohren ● Douglas production*

compartments = auxiliary levels

(e.g. reiterated com-
plex, model-conform
complex, organ com-
plex, etc.)

e.g. inflorescences,
phyllotaxis, life
form, seasonality,
etc.

(e.g. crown mass, root
system mass, sap stream
translocation, etc.)

*Pollman ● Douglas wood*
*Van der Zwan ● Poplar wood*
*Olsthoorn ● Roots, acid rain*

ORGAN
(subsystem in organ-
ism)
(cf. Hallé & al., 1987)

ORGAN
(member of organ-
ism)
(cf. Handbooks bot-
any, zoology)

ORGAN
(function-bearer)
(cf. De Wit & al., 1978)

*lower levels (tissue, cell, subcellular) OMITTED*

Fig. 1.2. Methodological welter, appearing when approaches by authors in the present book and of related studies are approximately 'mapped' on the background of figure 1.1. The present figure should not be studied in detail and only illustrates the proliferation of methods. For many chapters, the author(s) can be found back here in one of the heavy black vertical lines, linking hierarchical levels (stars, balls). Levels may then be checked in figure 1.1. In conclusion, harmonization of methods is needed.

(numerical, often invisible) and for production criteria (mass, invisible).

On Figure 1.2, these hierarchies have been used as a map on which the chapters of the present book and other publications by team members are placed in the general field of study. This Figure should not be used in detail, except to find back a specific author.

### 1.3 Handling the hierarchies

Before considering the ecological implications of Figure 1.1, it is necessary to go into the distinction between 'pattern' and 'process'. It was the use of these concepts by Watt (1947) in the title of an article, that caught the minds of many researchers. In general, pattern and process may be distinguished but are inseparable. Patterns guide processes, that in their turn may change the patterns, in an ever-continuing feedback relationship. Confusion has arisen because the organized course of processes, made visible by the transcription of numerical data into graphs, also became identified with patterns (cf. Wit & al., 1978, p.3: 'structure'). This is also illustrated by the title of Rollet's book (1974), 'L'architecture des forêts denses...', in which 'architecture' denotes a set of relations between numbers, obtained from counts over thousands of hectares of tropical rain forests, and processed statistically into graphical images.

It is therefore proposed to reserve the notion of 'pattern' or in any case 'architecture' (Hallé & Oldeman, 1970) of systems to properties that can be directly seen and mapped, being linked to objects occupying a three-dimensional volume. Even if mapping or plotting are automatic, potential visibility by eye is a good criterion to end confusion. Architectural patterns, according to Hallé & al. (1978) are instant pictures. Their change may be indicated as dynamics (Hallé & al., 1978; Fanta, 1986). Dynamics are not processes, if the notion of process is reserved for underlying, organized movements at hierarchical levels deep within the system considered, such as energy and matter processing in photosynthesis or maintenance respiration (cf. Mohren, 1987).

Even if the above conventions were followed, a grey zone seems to persist between the notions of pattern and process. Phenomena such as a swarm of mosquitos in the forest (ten, a hundred, ten thousand) can both be seen and counted. The time dimension plays a role in this field of observation, because often fast dynamics which are denoted as phenological events, e.g. swarming, flowering, fruiting, flushing, are concerned. Biological architecture (Fig. 1.1) therefore not only is bound to space at some hierarchical level, but also has a time dimension. If time is taken into account and is clearly indicated in architectural, populational and ecophysiological studies, no confusion needs to arise. The grey zone, if it exists, is in the middle of Figure 1.1, in the population's hierarchy.

Good operational distinctions between pattern and process are important in models to be used by forest and nature managers. Many of their interventions first are visible as architectural change. This activates processes, resulting in

a new forest architecture that may or may not correspond to management aims. Things may also start with a process, e.g physiological processing of polluted air, leading to unwanted patterns.

Important ecological implications of the use of three hierarchies in forest ecosystems research are linked to the fact that these three, of course, are not independent. The populations hierarchy is placed in the centre because an organ, an organism, a population, each at their level, are the carriers of both architecture and processes. Horizontal studies, comparing architecture, population and biomass therefore are very useful for checking conclusions reached by explanatory models which mainly keep inside one of the vertical hierarchies and link two or three levels.

In the present book, some chapters present cases in which such transversal connections among hierarchies are clearly present (Peters, Japan; Leersnijder & Boeijink, application; both this vol.). All chapters have been 'mapped' on Figure 1.2 using the following population concept. If the notion of population is consistently used at every level, then each level contains a population of subsystems which are themselves populations at some lower level. An organism then is a linnean population of organs, a 'population (sensu stricto)' is a population of organisms, a microcoenon (Barkman, 1970) is a population of species (being themselves populations), and a coenon is a population of microcoena. Figure 1.1 shows the architectural and ecophysiological counterparts of these levels.

It is remarkable in ecosystems research, that studies emphasizing one of these hierarchies indeed have always needed the others. They usually have been added in simplified forms. Site data, as representing the resources and inputs for biological production, have been most thoroughly analysed in the ecophysiological production hierarchy, and are usually taken over as simplified site maps in the two others. Architectural patterns, at the ecosystem levels, in other studies have usually been simplified into normalized 'strata', 'stand surfaces' or other geometrically simple patterns, whereas they are fully taken into account at the levels of the organism and below (morphology). In production models and architectural models of forests, populations are most often represented only as species lists or by a more or less rough mapping of species groups. That such simplifications are not by definition harmful to model performance is proven by highly successful predictions, e.g. in the examples described by Shugart (1984) and those included by Fanta (1986).

## 1.4 Forest components

Now the reason to emphasize forest components in the present book and in the research theme mentioned in the foreword, is that plants, animals and humans do not conform so easily to our hierarchies which, as said above, are constructs of the human mind. The organisms which are the components of our forests very often do the unexpected with regard to the predictions based on scientific hierarchies. If this were not so, the occurrence of pests, diseases

(Hiemstra & al., this vol.), forest blow-downs, extinction of rare organisms in nature reserves and other usual events of this order would have long ended.

In such hierarchies, each species is a detail, with the exception of some highly visible ones such as trees. These master components therefore have all but fully monopolized the attention of researchers for a long time.

Books concerning other components (e.g. Brauns, 1976, or Szujecki, 1987, both on forest insects) are rare in comparison to all that is written on trees. Another highly visible component is *Homo sapiens*. It is the only one that can write down its strategies, determining its impact on and in forest ecosystems (Polman & Creemers, Leersnijder & Boeijink, this vol.).

Forest ecosystem models, built mainly with sites, trees and humans and rather neglecting an uncertain category of 'others', are only partially answering some questions raised on forests. The remaining uncertainties are so important, that no model could provide even the beginning of a coherent and acceptable explanation of the effects of major catastrophes like massive air pollution in Western Europe (Smits, 1984; Morselt & al., 1986) or forest fires (e.g. see Leffef, 1984), such as are scourging the Mediterranean regions. One thing became clear from the outset. This was, that the forest compartment below the ground had been too much neglected. Both new approaches to root studies and studies of plant and animal compartments such as chlorophyll-less plants (Keizer & Arnolds, this vol.) or soil animals were started.

As such things go, in the preceding decades the attention for certain components became successively fashionable. Soil biology made impressive headway, for instance in a Dutch priority research programme, organized by the Universities and organizations such as ZWO (BION) and NRLO in the 1980's. Like the chapters in the present book, however, this research is not yet fully integrated in a commonly accepted forest model, although publications like that by Kuiters (1987), on the biochemical guidelines given to herbaceous and seedling development through polyphenol decomposition chains in the litter, open perspectives to new explanations.

But in which compartment are such often indirect interactions between components to be grouped? And how indeed are optimal compartments to be distinguished at all in a forest ecosystem model? The very complex nature of the nematode community in forest soils illustrates this question. It also was illustrated by a preliminary project that preceded this research theme (Van Vuure, 1985). This author showed that the species composition of the mammal fauna is different in different development phases of eco-units (Fig. 1.1). Animals are among the forest components that most easily seem to escape sophisticated hierarchies in ecosystems research. Why is this? It is certainly linked to their mobility, which scarcely fits into the existing models, inspired by botanists and foresters. Is the animal compartment to be considered as a stochastic part of a stochastic forest model (Boyce, 1978; Shugart & Seagle, 1985)?

If one could follow the developments below the ground in vivo, some of the questions raised might be solved in this forest compartment. New methods are urgently needed to directly observe forest components in the rhizosphere. But

10

do such methods respect the integrity of this compartment and its components? The same question may be asked when considering canopy studies, which nowadays are further advanced in the tropics than in the temperate regions. And is the time ripe to include experimental results (Kuiper & Schoenmaker, this vol.), were it only for trees?

The creation of forest ecosystem models for the moment depends much on a deeper understanding of these questions, which require better knowledge of forest components, rather than the formulation of still more sophisticated, sweeping forest models. The importance and size of each component, and their grouping into functional, manageable compartments are absolutely essential knowledge for every researcher endeavouring to improve hierarchies and models. And this is a precondition for describing the whole model in mathematical terms.

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# 2 Modal transect construction for silvicultural design

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## Summary

Modal transects are scale-drawings of a forest ecosystem sample, that can be used to answer silvicultural questions with a previously determined degree of accuracy. They need to contain the necessary information in a directly visible or measurable form, that can be used either to insert more information or to abstract the information as necessary and within falsifiable limits. Contrary to a 'real' transect, where a narrow strip in a forest stand is drawn by ground-plan and profile diagram, a modal transect comprises information about the whole stand in a more or less abstracted profile diagram, but always representing the real stem number and canopy density. Simple examples are worked out, to explain the use of modal transects of different abstraction levels, for specified purposes.

## 2.1 Introduction and problem

The management requirements for forests, or forest stands, are usually described in terms of the silvicultural qualities of the mature growth.

In 1984, the Dutch State Forest Service formulated requirements for 'target forests', as the standard for the future. This long-term national plan was approved by parliament in 1986 (Anonymus, 1984, 1986).

On a well-defined site, the possible target forest area depends upon:
– the suitability of the site for tree species forming the skeleton of such projected stands;
– the management objectives.

Site factors can be classified into primary factors and secondary factors (Fanta, 1985). The primary factors, climate, topography, orography, geological material, ground and surface water, determine certain ecological properties of ecosystems but are themselves not a part of the ecosystem as are the secondary site factors. The secondary factors, forest climate, micro-relief, soil, humus and hydrology, arise from interaction between biotic and abiotic components of the ecosystem. Secondary site factors, lacking in young forest ecosystems, are very important in mature ones. Other factors, related to site factors and influencing growth, are pests and diseases, fire, fertilization practices and other stressors or facilitators.

To select the required possible forest target types and also to determine the most effective course from an existing to a target forest, presents the problem of going from the present status to the intended one, requiring a silvicultural system to be chosen. In addition to site factors, the dynamics of tree species on different sites must be understood to approach the problems. There are different courses leading to the goal as Leibundgut (1966) points out in a simple
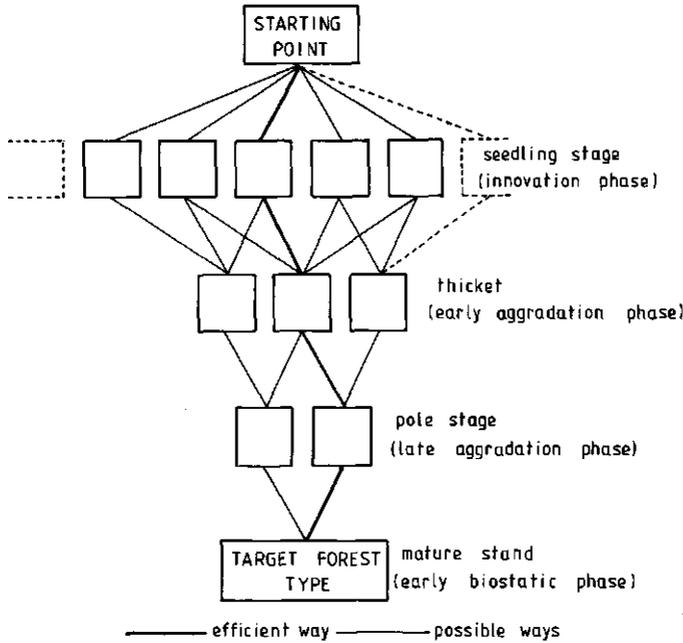
Fig. 2.1. Diagram to determine the intended forest management type and the most efficient silvicultural system, also indicating the crucial intermediate stages (Leibundgut, 1966; terms see Oldeman, 1983).

scheme (Fig. 2.1). Finding the best course is an optimalization problem involving all forestry disciplines. The potential consequences of different silvicultural interventions for the next development phase and for the mature stand on the site must be projected. In the case of deviations from the original program, the question arises whether it is still possible to implement the intended target or not and, if needed, how to alter the process from there on.

This paper intends to define a quantitative method to graphically represent important qualities of the different development stages and the changes, expected, or found to occur, due to growth and development of a stand as regulated by silvicultural interventions, with a previously determined degree of accuracy. With the method one should be able of anticipating on and checking of the consequences of a silvicultural system, to obtain and to pass on insight in the system, and have an aid in management.

## 2.2 Tree component dynamics

### 2.2.1 Analysis of tree dynamics

To study growth characters of tree species, the Department of Silviculture

and Forest Ecology uses transect analyses (e.g. Oldeman & al., 1983). A transect represents a narrow sample, selected within a forested area. There are different ways to draw a transect. For example, species, biomass or soil-profiles can be assessed along a line or strip through the landscape to inventory species or bio-mass-graphs or soil differences set out against one (length) coordinate. With a second coordinate one gets a surface and draws the results:
– height against length to give a profile diagram,
– width against length to give a ground-plan (Oldeman & al., 1983).

Transect drawings of forests usually are a combination of ground-plan and profile diagram. Examples of such transects, visualizing the actual situation as real as possible, can be found in Winckel (1980), Koop (1981) and in Greeven & Harmsel (1983) (Fig. 2.2).

By including dead trees, fallen trees, and tree stumps, it is possible to learn about the history of the stand structure. The architecture of trees can also con-tribute to historical diagnosis, such as diseases and crown development. To trace the contiguing development of trees, a new transect must be drawn after a number of years.

Because of the diversity of information that can be included, a transect draw-ing means to learn about relationships between forest components (Oldeman, this volume). Studying a transect is an unbiased, verifiable and repeatable way to get information about different aspects of a stand. The method has some pitfalls to be avoided:
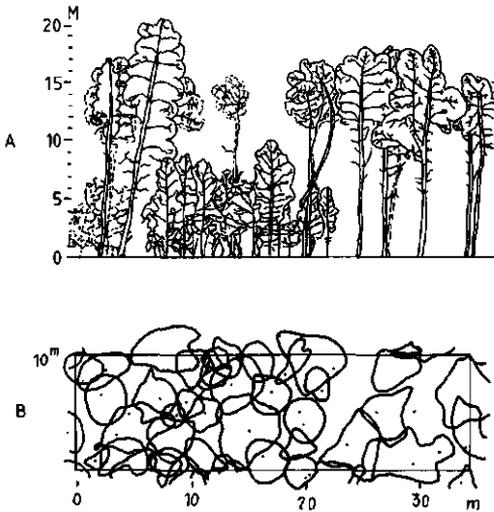


Fig. 2.2. Real transect of a representative part of a stand in the 'Zeisterbos' in Utrecht, The Nether-lands (e.g. Greeven & Harmsel, 1983): A: profile diagram; upper storey existing of *Pinus sylvestris* L.; under storey existing of *Betula pubescens* Ehrh. and *Quercus* spp.
B: ground-plan.

- All the work of gathering and processing data is done between the start of the field work and the finishing of the scale-drawing. No time should be spent in later calculations. If no selection is made of the number and nature of data to be included, this method may become time-consuming.
- A choice has to be made, whether to gather many data per $m^2$ on a small surface, or few data per $m^2$ on a large surface. Architectural analysis can provide a high density of information. If one takes small samples in a stand, representativity for that stand should always be considered.
- If the information density is too high, the resulting scale-drawings become cluttered because in a two-dimensional projection, all measured features become superposed. The separation in a side-view and a ground-plan is prefered above the complications of a projection of one stand picture in three-dimensional perspective. If the sample area chosen is too large for the information density, and too much data are gathered, unreadable and useless documents can result.

### 2.2.2 Dynamics of representative trees on representative sites

Dynamics of tree species and provenances are related to site factors. However, exact prediction of these dynamics on a given site is impossible because of unknown and unpredictable factors, such as fluctuating weather conditions or attacks by pests and diseases. In older forests the secondary site factors, varying over short distances can be very important and also change with time. They are dynamic, compared to the more static primary site factors.

To establish patterns in dynamics of tree species and provenances, as related to the site, one has to find representative trees on well defined, representative sites in different developmental stages. The dynamics of these trees are used to model the dynamics of similar trees in the target stand. On extreme sites with regard to properties such as soil chemistry, hydrology, climate and forest history, one should look for special stand and tree qualities such as stand structure in relation to dimensions of mean and crop trees, plustrees, border trees and trees with undesirable characters. Such stand and tree qualities should be known in all developmental stages of a stand (Fig. 2.1).

Within certain limits, as explained above, the understanding of tree response makes it possible to foresee developments in a stand on a specific site. An efficient silvicultural system can be chosen to convert the present stand into one of the target stands and designing a development course with economically and ecologically acceptable phases.

### 2.2.3 Silvicultural design

Long-term national Dutch aims in forestry require a multiple-use silviculture. Therefore silvicultural systems cannot be built exclusively around the production of wood crops. The study of the dynamics of representative trees on representative sites may be narrowed down to few relevant criteria as long as the management aims are limited. The implementation of the new plans requires in many cases the conversion of present-day stands to very different future

16                                              

stands. First it is necessary to define the parameters for designing conversions, and to gather information needed for implementation, in close connection with teaching these principles to future foresters who will have to deal with the national plan and its implementation. The Dutch Forest Service has coined the word 'forest image' (bosbeeld) to indicate the observed or depicted image of an existing or planned forest, in every development phase (Fig. 2.1). Most often, a forest image concerns a stand (eco-unit level, Oldeman, 1983, this vol.) or sometimes a mosaic of stands (silvatic mosaic level). In this chapter, only the stand-level will be considered.

A population of stands with the same architecture, species composition and production characteristics, but in all development phases (age classes) could be exemplified by pine stands with normal age class distribution. They are all of the same 'kind' but differ in maturity, whereas stands of the same kind can also be found elsewhere. Such a population was termed a 'bossoort' by Westra (1983), a Dutch term that litterally means 'species of forest', in analogy to a population of organisms of the same kind, a species. Oldeman (pers. comm.) proposes to use the term 'sylvon' to denote such populations of stands, and to define it as follows: A sylvon is a population of eco-units with the same architecture, species composition and production processes, in all their possible development phases. For a definition of an eco-unit, see Oldeman (1983).

In the following section, the foreseen development of a member of a simple sylvon (Fig. 2.3), with or without silvicultural intervention, and on the basis of knowledge of the main components, will be examined. It is thought, that a simple start is more suitable to establish methods, and test principles, than a more complicated one that might introduce problems difficult to solve prior to establishment of basic approaches.

## 2.3  Construction and use of modal transects

### 2.3.1  Representation of forest images by modal transects

According to the Oxford Dictionary, 'modal', means 'involving affirmation of possibility, necessity, or contingency'. Transects that are used in silvicultural design should be just that. They must contain information for a precise aim, and have the ability to answer questions by including or excluding extra information. Definition: a modal transect is a scale-drawing of a forest ecosystem sample that can be used to answer silvicultural questions with a previously determined degree of accuracy. It needs to contain the necessary information in a directly visible or measurable form, that can be used either to insert more information or to abstract its information as necessary within falsifiable limits.

Generally the modal transect as used here, will consist of a profile diagram, representing the real number of trees per ha, compared to the profile diagram from 'real' transect drawings, described in chapter 2.2.1.

The modal transect can be at any point between an extreme with a very low degree of abstraction with very high information density, and an extreme with

a very high degree of abstraction. The highest degree of information density is reached when a three- or four-level model is made (Oldeman, this vol., his Fig. 1.1). The last ones include data at the level of organs, organisms and ecosystem(s). For instance it can include:
- number of trees per ha and tree species
- canopy density per ha and tree species
- variation in crown width and depth per tree species
- variation in tree height per tree species
- variation in tree architecture per tree species with detailed tree drawings and data about diameters and quality aspects.
- distribution of dead wood on the forest floor
- distribution, height and density of shrubs and herbaceous plants
- soil data.
The following aspects of modal transects must be considered:
- The need for a ground-plan depends upon the questions asked. Abstraction can often include this ground-plan.
- The dilemma of dense information on a small surface against sparse information on a large area, given the same investment of time, manpower and means, must be resolved at all intermediate points.
- A well-chosen modal transect should be adapted to show clear relationships between site qualities and tree development.
- Finally silvicultural interventions and their results should be shown with great simplicity in modal transects. This is only possible if reactions of tree species and other forest components on the sites are understood.
  Leaving out unknown facts is not abstraction in the constructive sense, and may lead to lack of relation to the real forest situation, as well as make the model unfalsifiable.

### 2.3.2 Modal transects: construction and abstraction

The construction of modal transects at different abstraction levels is demonstrated here for an existing 35-year-old forest stand in which a real transect with ground-plan and profile diagram has been drawn (Fig. 2.3-A). The forest stand is situated near Wageningen, Gelderland, The Netherlands.

The tree component population contains 420 trees/ha, with a mean tree distance of 5.24 m, consisting of 90% Scots pine (*Pinus sylvestris* L.), 5% oak (*Quercus robur* L.), 5% birch (*Betula pendula* Roth.) and Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco). Canopy closure is about 65%.

a. First abstraction level (Fig. 2.3-B).
  This level is close to the real transect. On a line transect of 90 m long, 17 trees $(90*(5.24)^{-1})$ have to be drawn. In this case there are 16 pines (90%) and 1 oak (5%) and no birch and Douglas fir. In addition to tree number and tree species, variation in tree height, stem form, crown width, depth, architecture and variation in stem distances remain. This level is very well suited to foresee the consequences of silvicultural interventions in detail.

18

b. Second abstraction level (Fig. 2.3-C).

This level resembles the first one, but for the crown characters: only crown width, depth and (a)symmetry, i.e. Koop's 'crown coordinates' have been precisely indicated (cf. Koop's computer model, 1987). Crown form and architecture are only roughly shown, but the contents of crown volumes are left out.

This level can be used if only crown coordinates are available without complete tree drawings. Stand structure can be shown, but not tree architecture. In the two-level model (Oldeman, this vol., his Fig. 1.1), only the volumes or spatial niches of the tree components are introduced as subsystems at the eco-unit level (also cf. Kuiper & Schoenmakers, this vol.).

c. Third abstraction level (Fig. 2.3-D).

This level gives tree species distribution, stem number per ha, mean tree height, mean crown depth and width. It can be used to indicate the development of these features and may be considered to visualize some aspects of stand yield tables.
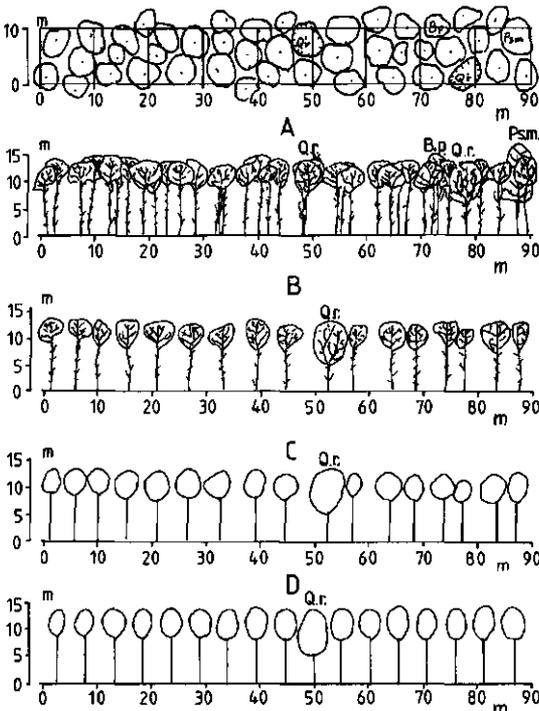


Fig. 2.3. Four examples of different abstraction levels for the respresentation of a forest image of Scots pine (*Pinus sylvestris* L.) with some oak (Q.r.: *Quercus robur* L.), birch (B.p.: *Betula pendula* Roth.) and Douglas fir (Ps.m.: *Pseudotsuga menziesii* (Mirbel) Franco). Canopy closure is ca 65%. A: ground-plan and profile diagram of the 'real' transect; B: modal transect with a low abstraction level (level 1); C: modal transect with an intermediate abstraction level (level 2); D: modal transect with a high abstraction level (level 3).

More abstraction levels can be used. To follow the development of other forest components, for example, the shrub and herb compartments (for definition of compartment, see Oldeman, this vol.), the scale of the transect has to be adapted to the dimensions of the components. For a good architectural drawing of shrubs, a scale of about 1:50 will be needed, whereas for the above third abstraction level a scale of 1:500 will serve. Generally speaking, the less interest there is in individual tree characteristics, the higher the degree of abstraction of the modal transect can be.

### 2.3.3 Examples and use of modal transects of different abstraction levels

To construct a modal transect one has to know the intended purpose in order to include necessary data. From there, the most useful scale and the length of the transect can be defined.

**Example 1** (Fig. 2.4a).
Use: prediction of stand structure and of tree architecture of a stand after a 30-year-management period according a yield table. Scale: 1:500 (1:200 might be better). Length: 90 m.
– Present situation (Fig. 2.4a-A; compare the transect in Fig. 2.3B):

| Tree sp. | Age (Years) | Stemnum-ber/ha =420 | Canopy closure 65% | Crown width (m) | Crown depth (m) | Tree height (m) |
|---|---|---|---|---|---|---|
| Pinus sylvestris; | 35 | 376 | 53.5 | 3-6 | 3-6 | 12-15 |
| Quercus robur; | 35 | 23 | 6.5 | ± 6 | ± 8 | ± 13 |
| Pseudotsuga menziesii; | 35 | 11 | 3.0 | ± 6 | ± 11 | ± 17 |
| Betula pendula; | 35 | 10 | 2.0 | ± 4 | ± 6 | ± 16 |

As already mentioned in 2.3.2, a stem number of 420/ha results in a mean distance between trees of 5.24 m. In a transect of 90 m long, a total of 17 trees have to be drawn. The tree canopy closure of 65% (ground-plan) has to be transformed for the profile-diagram into a canopy closure of about 80% ($\sqrt{0.65}$ * 100%) and this leads to a mean distance between crowns of 1.05m (0.2 * 5.24m).
Attention: The trees theoretically have a triangular espacement. This means that crowns have a sixangular surface. The crown of one tree therefore has a surface of $0.5*a^2\sqrt{3}$ and not $0.25*\Pi a^2$ (Fig. 2.4b). Variation in tree architecture and relative distance between the trees can be read from the 'real' transect.
– Situation after 10 years (age 45; Fig. 2.4a-B): Because of the very low stem number at age 35, the next 10 years no thinnings are to be performed. Height growth of Scots pine in this period would be about 3 m (according to the yield table of Grandjean & Stoffels, 1955, site index II). The mean canopy

20    *Wageningen Agric. Univ. Papers 90-6 (1990)*
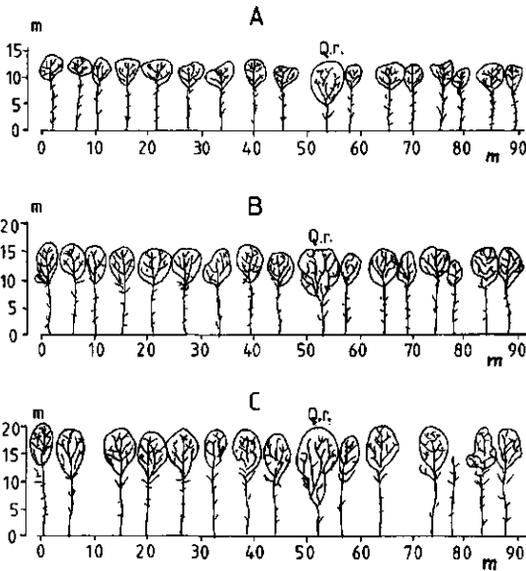
Fig. 2.4a. Prediction of growth of trees in a stand, under conditions defined in the text, with the help of a modal transect of abstraction level 1. A: 35 years old (compare Fig. 2.3-B); B: 10 years later (45 years old); the arrows show the trees removed; C: 30 years later (65 years old). Height development from yield table (Grandjean & Stoffels, 1955).
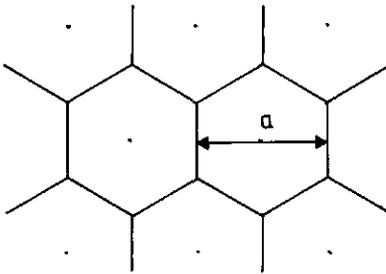


Fig. 2.4b. Tree in a triangular espacement and their theoretically crown $0.5a^2\sqrt{3}$. In a profile diagram in principle crown diameter a will be drawn.

closure would increase to 80%. Tree architecture at age 35 can still be recognized at age 45. Supposing that during the next 20 years about 25% of the stem number will be removed, 320 trees/ha remain, with a mean stem distance of about 6 m. In a transect of 90 m, 15 trees will have to be drawn. Assuming a selective thinning procedure in the upper story favouring oaks, the trees to be removed can be indicated (see arrows Fig. 2.4a-B). After thinning the canopy closure is about 65%.

– Situation after 30 years (age 65; Fig. 2.4a-C): The mean tree height is 19 m
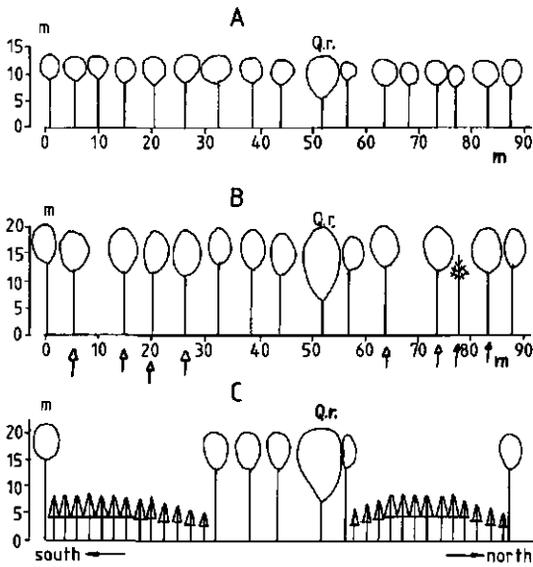
Fig. 2.5. Prediction of tree behaviour in a stand, under conditions indicated in the text, with the help of a modal transect of abstraction level 2. A: 35 years old (compare Fig. 2.3-C); B: after 30 years (compare Fig. 2.4-C). The arrows show the trees removed; C: after 45 years (Scots pine 80 years old and Douglas fir 15 years old).

and crown closure is about 70% (Grandjean & Stoffels, 1955; Schütz & Tol, 1982). In this case 40 trees are presumed to have died due to lack of vitality, leaving a stem count of 280 trees/ha.

**Example 2** (Fig. 2.5).
Use: design of stand structure after multiple strip felling in a 65 year old Scots pine stand to establish Douglas fir, a current Dutch silvicultural system ('coulissenkap'). Scale: 1:500 (1:200 might be better). Length: 90 m.
– Present situation (Fig. 2.5-A): as in example 1, but instead of 'real'-trees, model trees are used, indicating crowns only by crown volumes as defined by coordinates (Fig. 2.3-C).
– Situation after 30 year (age Scots pine stand 65; Fig. 2.5-B): Silvicultural interventions and stand development were exactly as in example 1. Now 30 m wide strips are cleared with 30 m wide intervals between them. Cleared strips are planted with Douglas fir, 4.000 plants per ha, with a mean stem distance of 1.70 m.
– Situation after 45 year (age Scots pine 80, age Douglas fir 15, Fig. 2.5-C): The Scots pine stand has not been thinned in the past periode. In the Douglas fir stand, one release cutting has been performed. The stem number is now 2.200/ha (mean stem distance 2.29 m). Northern border trees have a growth
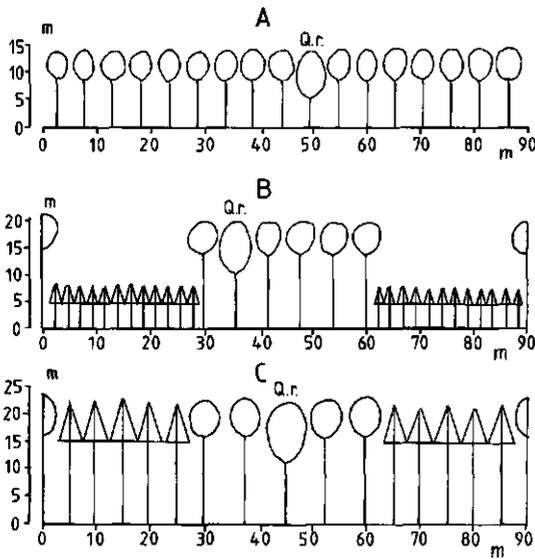
Fig. 2.6. Prediction of growth of trees in a stand, under conditions indicated in the text, with the help of a modal transect of abstraction level 3, containing less information, but in another hierarchy (Oldeman, this vol.), than yield tables. A: 35 years old (compare Fig. 2.3-D); B: Scots pine 80 years old and Douglas fir 15 years old (compare Fig. 2.5-C); C: Scots pine 110 years old and Douglas fir 45 years old. Note the variable position of the oak in this modal transect, indicating that its exact position is unimportant for this abstraction level.

delay due to exposition (cf. Koks & Leersnijder, 1984). Border trees can have a growth delay due to competition. In this case we presume some competition with oak.

Probably there is no competition with old Scots pine (van Goor, pers. comm.; Sevenster, pers. comm.).

**Example 3** (Fig. 2.6).

Use: design of progressive conversion of a Scots pine stand into a Douglas fir stand (within about 50 years). Scale: 1:500. Length: 90 m.

– Present situation (Fig. 2.6-A): as in example 1. Known data are only tree number/ha and therefore the mean stem distance, mean canopy closure, mean tree height and crown depth (compare Fig. 2.3-D) can only be presumed.

– Situation after 45 years (age Scots pine 80, age Douglas fir 15; Fig. 2.6-B): as in example 2.

– Situation after 75 years (age Scots pine 110, age Douglas fir 45; Fig. 2.6-C): Number of trees in the Scots pine strips has decreased to 210/ha with a mean stem distance of 7.5 m. The number of trees in the Douglas fir strips has decreased to 460/ha with a mean stem distance of ca. 5 m. The site index for the Douglas fir stand is about IV (yield tabel of Bastide & Faber, 1972).

**2.4 Preliminary conclusions**

Models (cf. Oldeman, this vol., his Fig. 1.2) are tools to arrange information, to get new information and /or insight in processes. With the construction of modal transects the optimal input of information, the information density for a given forest area, depends upon the complexity of the forest cover, and the specific purpose of the model. Examples of different aims of modal transects, requiring different input of information, are given in paragraph 2.3. The information density is unfluenced both by the number of hierarchical levels involved and the quality of the information included: population data, architectural data and/or production data. A conscious choice of the model criteria as linked to other models and in view of furthering the understanding of specific problems, is necessary if the method will be used for designing future forests. For example, the forests with far-reaching multiple-use principles as stated in the national forest plan. The method requires an investment in research and testing in many different forest situations of increasing complexity before it can be fully operational in silviculture.

The testing in simple situations presented here, allows the following preliminary conclusions to be drawn:
1. Production parameters, such as diameter, heigth/diameter ratio or basal area cannot be included in architectural, graphical models. They are part of an indispensable model along another line (biomass accumulation, cf. Bormann & Likens, 1979) that has to be represented by another area of research.
2. If the abstraction level is well-chosen, modal transects are a powerful tool for the delimitation of functional compartments. They also can be used in population and production research, as illustrated by the borderzone aspects between eco-units on Fig. 2.5-C. This requires more special compartmentalisation if eco-units become smaller and the relative weight of borders become more important in a target forest. The modal transect gives a quantitative, geometrical criterium for delimitation.
3. Leaving out component architecture, as was gradually done (Fig. 2.3), makes the model more abstract to show more clearly some aspects of the stand, but less about stand dynamics. This is acceptable only in global planning. As soon as special aims are to be implemented, and the silvicultural methods are designed to produce them, component architecture and build-up become more important. Examples are nesting space for birds (Komdeur & Vestjens, 1982), establishemt of special plants in target stands with nature conservation aims, crooked trees may be of interest for recreation stands, or minor forest products linked to components such as fungi (cf. Keizer & Arnolds, this vol.) or blueberries (*Vaccinium myrtillus*, Ericaceae).
4. A modal transect can be influenced vertically, considering the number of hierarchical system levels to be included, or horizontally, considering the number of data per system level. It seems prudent to limit most modal transects to two levels, as illustrated by Fig. 2.3-A (component architecture/mosaic architecture), respectively corresponding to stand management questions and conversion questions.

5. Contrarily to a weighted choice of the distribution of needed data over the different hierarchical system levels chosen, the reduction of the number of data makes the whole model weaker in information, especially about relationships in and between different components and about dynamics of components. Fig. 2.6 is at the limit of this case, the situation depicted seeming self-evident to all involved and the model only depicting properties of systems and components that can be arguably represented better by tabulated numerical data concerning population or production ecology.

6. Relations have been principally established in this paper between architectural and production criteria, but links at the stand level could be sought with population criteria. These links may be found by using the microcoenon concept of Barkman (1970), as exemplified in Koop (1981).

7. The concept of modal transect as developed in these pages is to serve as a tool for architectural model optimalization in silviculture and forest ecology.

## Acknowledgments

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# 3 Regeneration units in natural beech forest in Shirakami Mountains (Japan)

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## Summary

In Shirakami, Northern Japan, the architecture of natural *Fagus crenata* forest was analysed by means of the belt transect method. This beech forest is a representative of the Japanese Lindero membranaceae – Fagetum crenatae association (Sasaki, 1970). Beech is dominating the forest canopy at about 26 m height, while shrubs and low trees form a second layer at about 2 m height. Two regeneration units were distinguished by comparing size and growth development of dominant beech trees. The architecture of each regeneration unit is described by its components, and this model is used to describe the spatial ecological volumes occupied by the components. Analysis of the architecture and development of the regeneration units and their components makes it possible to both describe and explain history and future of the unit.

## 3.1 Introduction

In the mountainous area of Shirakami, *Fagus crenata* Bl. forests can be found to cover a vast area, being the dominant forest type. These beech forests remain in a fairly natural condition, although the human use and influences in the last century are obvious. The beech forest found here is representative for Northern Honshu, Japan. Thus in Shirakami a beech forest stand was selected for analysis.

This study aims at describing the forest by architecture and form of individual trees and regeneration units. A regeneration unit (eco-unit) is a vegetation unit which started to grow and develop at the same time at the same surface (Oldeman, 1983; this vol.). Both in trees and in regeneration units, different phases of development are distinguished. Trees of the future have not yet attained their maximum size but have the potential to become part of the forest canopy, which consists of trees of the present. Trees of the past are senescent and about to disappear from the forest. Note that small trees and shrubs develop in the same way. The tall trees of the present form a structural emsemble, a compartment which architecturally dominates the regeneration unit. Small trees or shrubs of the present can form a second, lower structural ensemble.

After the zero event (tree fall, standing dead), the regeneration unit can pass through the phases of innovation (no persistent architecture found, comparable with seedling phase in forestry), aggradation (canopy closed, more persistent architecture), biostasis (architecturally most organized), and degradation (architecture falls apart) (Oldeman, 1986).

This study is part of a research project which concerns the ecology and silviculture of the beech forests in the temperate zone of the Northern Hemisphere. Hence, the local situation will be described by an architectural model, that makes international comparison possible.

Fig. 3.1. Location of the study area in Japan (*)

## 3.2 Study area

The Shirakami Mountains are located in Northern Honshu, Japan, at a latitude of 40°30′ N and longitude 140° E (Fig. 3.1). Here a beech forest stand was selected, situated on an East-facing slope of 18 to 21°, at an altitude of about 500 m above sea level.

The climate was classified as Dfb after Köppen (Strahler & Strahler, 1979), with a maximum snow depth of ca. 2 m. Climatically, 1986 was an average year. The soil was classified as a wet humus podzol, $P_{w(h)III}$ (sensu Forest Soil Division, 1976).

Till the end of the last century, whole families would move into isolated areas of the Shirakami Mountains and remain there for the summer. Beech was used for fuelwood, charcoal and tools or utensils. Where forests were located near streams, wood could be transported to more inhabited areas. The present study site was located near a rather big stream. In recent years, the human influence has been very slight, and the forest could develop spontaneously.

## 3.3 Method

In the beech forest stand, a site with a structure characteristic for the stand was selected. In August 1986, a belt transect of 30 x 10 m$^2$ was established. All trees and shrubs of 0.5 m and higher were recorded in a crown projection map and profile diagram. Their height (H) and diameter at breast height (DBH) were measured, and crown density was estimated for each individual. The trunk forms and leaf densities in the top of the crown were described for trees higher

28

than 5 m. From these trees an increment core was taken and year-ring width was measured. Thus growth could be described. The age of a tree was estimated by adding a calculated number to the number of visible year-rings. This number was obtained from the calculated missing radius, dividing it by:

A. the average year-ring width of the first visible 20 years (if less than 20 years were missing), or

B. the average year-ring width of all visible years (if more than 20 years were missing).

The vegetation under the 0.5 m height limit was recorded by the Braun-Blanquet method. The height and sprouts of 1986 of the beech saplings in this layer were measured, while their age was recorded.

The canopy structure of the beech forest stand was studied by means of aerial photographs, with a scale of 1:10.000, recorded on September 8, 1984, by the National Soil and Geography Institute (numbers TO-84-IX CI 9 and 10).

## 3.4 Results

*Architecture*

The aerial photographs showed that the plot was situated in a forest stand of about 3 ha, which was structurally distinct from the surrounding forest stands. The stand had a more closed canopy structure, formed by crowns of different size and height.

Figure 3.2 shows the belt transect of a multilayered forest stand. The canopy layer has a height of 24 to 27 m and is dominated by beech, with an occasional *Acer mono*. A shrub and small tree layer of 2 m height is found to consist of *Lindera umbellata* var. *membranacea, Cephalotaxus harringtonia, Clethra barbinervis, Acer japonica* and *Acanthopanax sciadophylloides*. Between these two layers many potential, suppressed beech trees are visible.

The belt transect and the vegetation below 0.5 m (Table 3.1) indicate that the forest belongs to the association of Lindero membranaceae – Fagetum crenatae (Sasaki, 1970). The presence of some moisture indicating plants (*Anthyrium vidalii, Dryopteris austriaca, D. africana*) show the mesic to moist qualities of the site. Note the presence of seedlings and saplings of tall trees, e.g. beech, *Acer mono, Acanthopanax sciadophylloides* and *Magnolia obovata*. The maximum age of a beech sapling in this layer was 25 years, while most of the saplings were found to be 3 years old (mast year 4 years ago). Growth was very different among the saplings when current year growth of the top shoot was compared with the total height of saplings, e.g. 1.5 cm and 40 cm (25 years), 5.5 cm and 55 cm (20 years), 3 cm and 17 cm (3 years).

Among the individual trees higher than 5 m, four groups of trees were distinguished. Table 3.2 shows these groups as the set of suppressed trees of the future, the set of free trees of the future, the set of trees of the present and the set of trees of the past. They were recognized respectiveley as trees under canopy, trees
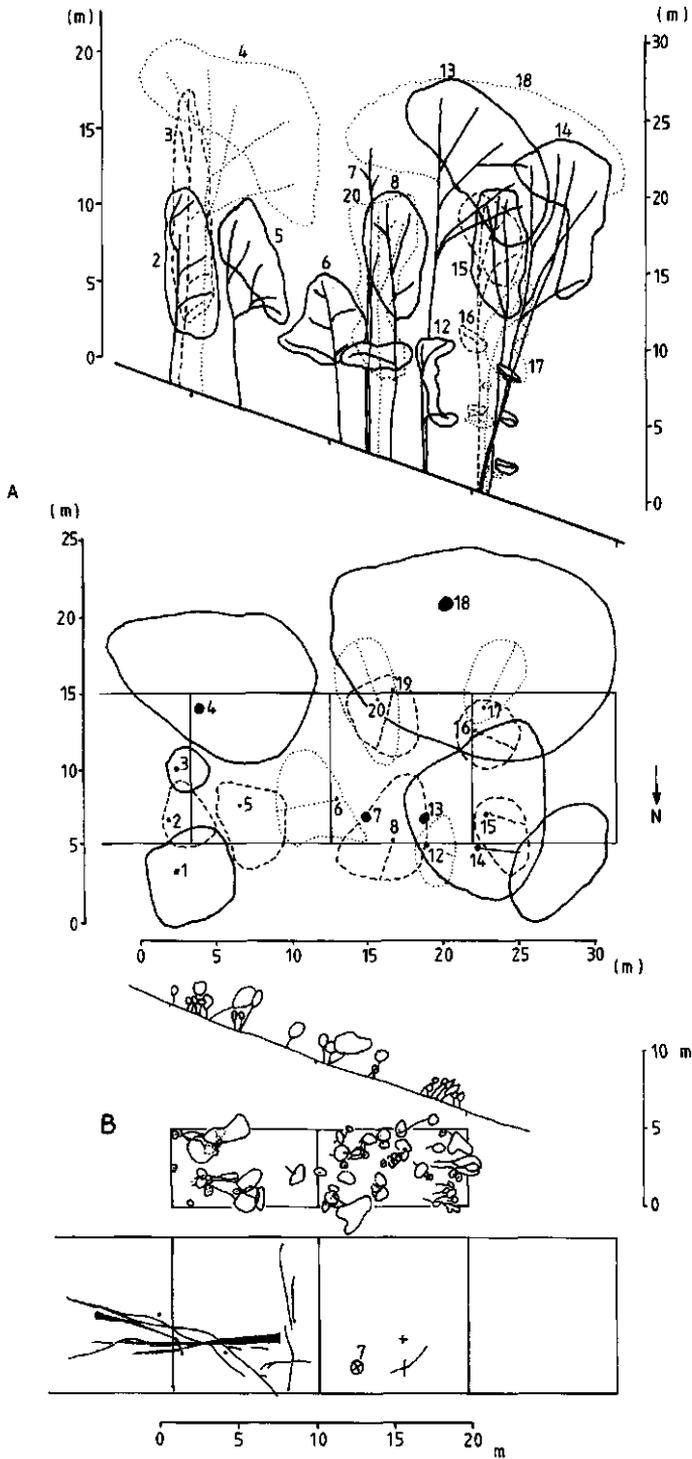
Fig. 3.2. Belt transect in Shirakami Mts., Honshu

A. Trees higher than 5 m. Trees are beech, except for nr. 14 which is *Acer mono*;
B. Trees and shrubs below 5 m high. Thick lines indicate trees in front or on top of the transect, while thin, broken or dotted lines indicate those in the background or underneath.

Table 3.1. The coverage and density of the vegetation under 50 cm recorded by the Braun-Blanquet method.

| | |
|---|---|
| *Viburnum furcatum* Blume | 1.1 |
| *Lindera umbellata* Thunb. var. *membranacea* | 1.1 |
| *Magnolia salicifolia* Maxim. | +.+ |
| *Rhus ambigua* Zav. | 1.1 |
| *Hydrangea petiolaris* Sieb. et Zucc. | 1.1 |
| *Schizophragma hydrangeoides* Sieb. et Zucc. | 1.1 |
| *Fagus crenata* Blume | +.+ |
| *Acer mono* Maxim. | +.+ |
| *Acanthopanax sciadophylloides* Franch. et Sav. | +.+ |
| *Magnolia obovata* Thunb. | +.+ |
| *Plagiogyria matsumureana* Makino | +.+ |
| *Anthyrium vidalii* Nakai | +.+ |
| *Vitis coignetiae* Pulliat | +.+ |
| *Dryopteris austriaca* Woynar | +.+ |
| *Sasa kurilensis* Makino et Shibata | +.+ |
| *Clethra barbinervis* Sieb. et Zucc. | +.+ |
| *Acer japonicum* Thunb. | +.+ |
| *Dryopteris miqueliana* C.Chr. | +.+ |
| *Acer tenuifolium* Koidz. | +.+ |
| *Cephalotaxus harringtonia* K. Koch | +.+ |
| *Dryopteris africana* C.Chr. | +.+ |
| *Chimaphila japonica* Miq. | +.+ |

in canopy gap, tall trees forming the canopy and senescent or standing dead trees.

Although the trees of the present attained their maximum height, this height was not the same for all these trees. On the slope, however, the canopy showed to be rather horizontal (Fig. 3.2). The trees of the present had a straight trunk and a good DBH increment over the last 10 years, while suppressed trees of the future showed a bent trunk and a weak growth. The trees of the present and the future had similar ages. The trees above the 5 m level originated within a period of 100 years, while most are found to be between 120 and 160 years old (Fig. 3.3). The variation of growth rate with time of the individual trees (Fig. 3.4) suggests, that regeneration and growth of this forest stand started ca 130 years ago. Figure 3.4 also illustrates that about 30 years ago trees 1, 6 and 8 suddenly came into favourable growth conditions.
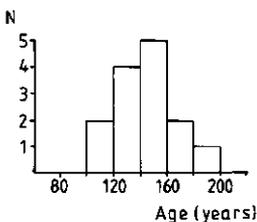


Fig. 3.3. Age distribution of trees higher than 5 m.

Table 3.2. Characteristics of four different groups of trees (above 5 m in height). All trees are *Fagus crenata*, except tree nr. 14 which is *Acer mono*.

| | trees of the future | | | | | | | | | | | | trees of the present | | | trees of the past | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | suppressed | | | | | | free | | | | | | | | | | |
| tree number | 12 | 15 | 16 | 17 | 19 | 20 | 1 | 2 | 3 | 5 | 6 | 8 | 4 | 13 | 18 | 7 | 14 |
| height (m) | 9.5 | 21 | 18.5 | 14.5 | 21 | 18 | 21 | 13 | 20 | 14 | 12 | 18.5 | 24 | 27 | 30 | 20 | 24 |
| DBH (cm) | 12.0 | 28.5 | 20.5 | 18.0 | 21.5 | 14.5 | 40 | 24 | 29 | 25 | 18 | 25 | 74 | 61 | 111 | 75 | 44 |
| bole form** | b | b | b | b | b | b | rs | rs | rs | rs | rs | rs | s | s | s | s/b | s/b |
| top of crown* | dm | m | dm | m | m | dm | d | m | d | ms | d | d | d | m | ms | – | ms |
| crown density (%) | 90 | 90 | 90 | 90 | 90 | 70 | 70 | 90 | 90 | 50 | 50 | 90 | 90 | 70 | 70 | 0 | 50 |
| age (years) at 50 cm height | 133 | 157 | 130 | 110 | 150 | 165 | 196 | – | 149 | 130 | 125 | 160 | 117 | 145 | – | – | 148 |
| average diameter growth in the last 10 years (mm) | 0.4 | 1.3 | 0.2 | 0.9 | 1.8 | 0.8 | 2.3 | – | 2.6 | 1.5 | 3.6 | 2.2 | 5.0 | 6.7 | – | – | 0.6 |

\* d = densely leaved; m = medium leaved; s = sparsely leaved.
\*\* b = bent; rs = rather straight; s = straight; s/l straight or bent.
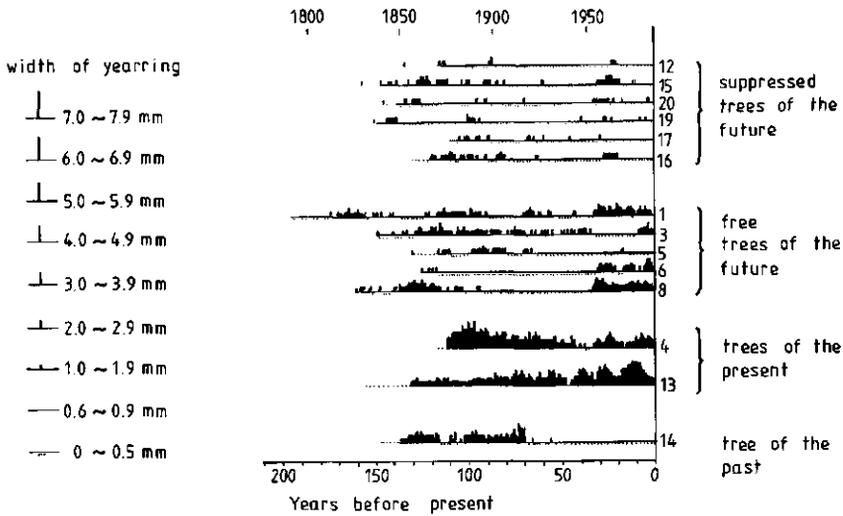
Fig. 3.4. Growth of trees higher than 5 m. Horizontal lines indicate increment cores taken at 50 cm height, while the width of the year-rings is shown vertically above the lines.
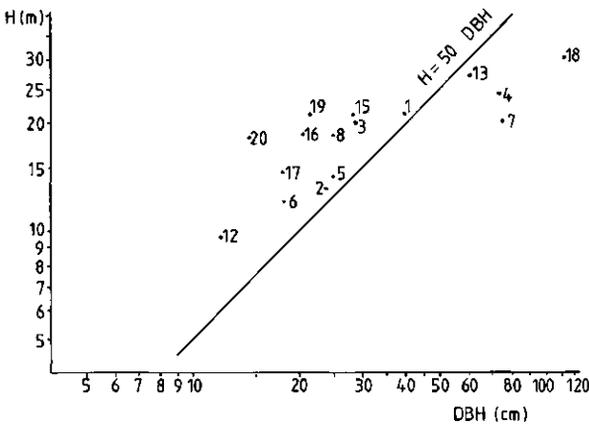


Fig. 3.5. H – DBH relation for beech trees higher than 5 m (log/log scale).

Figure 3.5 shows the height – diameter relationship for the beech trees. Note that the trees of the present and the trees of the future are separated by the reference line H = 50 DBH. This is unlike European beech (*Fagus sylvatica* L.), where according to Alfen (1981) the reference line H = 100 DBH had the same quality. Contrary to Alfen, however, the reference line in the Japanese forest was not checked with a formal analysis of tree model conformity (cf. Hallé & al., 1978).

*Regeneration Units*

The size, growth, and development of the tallest trees were the criteria for distinguishing different regeneration units. In this stand, age was not a useful criterion. In the belt transect (Fig. 3.1), two regeneration units were distinguished, i.e. unit A in the aggradation phase, and unit B in the biostatic phase. Note that the border of the belt transect is not the border of the regeneration units. The transect shows parts of the regeneration units. Hence, their absolute sizes are unknown. The trees of the future 1, 2, 3, 5, 6 and 8 belong to unit A. They have ages between 125 and 195 years but were suppressed up to 30 years ago (Fig. 3.4). The trees of the present 4, 13 and 18 and the suppressed trees of the future 12, 15, 16, 17, 19 and 20 belong to unit B. This unit orginated about 130 years ago, although tree 18 may be much older (compare sizes). As tree 7 has a diameter similar to trees 4 and 13, and the trees in both units have similar ages, it is assumed that before the death of tree 7, unit B occupied the whole surface of A and B. In other words, a larger former B-like eco-unit fragmented in the actual A and B.

Table 3.3 shows the importance of the different sets of trees and shrubs in a regeneration unit as expressed in wood volumes per are (10x10 m) and in coverage of the soil surface under the regeneration unit. All trees and shrubs above 50 cm high are included in the table. Note how above 5 m the set of the future increases, and below 5 m the second structural ensemble increases when going from B to A. The data in Table 3.3 were used to construct Figure 3.6, in which the vertical height of different sets is indicated and the horizontal coverage, expressed in percentages. Thus the regeneration units are described as spatial ecological volumes occupied by the sets of trees and shrubs, which are eco-unit compartments (Oldeman, this vol., his Fig. 1.1). The ecological volumes referred to here are not niches according to the accepted definition (cf. Bakker, in Bakker & al., 1985, p.5). As the height of the trees seems to be related to their position on the slope (Fig. 3.1A), this slope is also indicated in Figure 3.6. Note the importance and scale of the different structural ensembles. Two layers can be distin-

Table 3.3. The coverage and the wood volumes of the different sets of trees and shrubs in the regeneration units. Note that amounts per are may not be extrapolated to hectares, because they represent real, not average values.

| | | unit B | | unit A | |
|---|---|---|---|---|---|
| | | coverage (%) | wood vol. ($m^3$/are) | coverage (%) | wood vol. ($m^3$/are) |
| above 5 m in height: | first structural ensemble | 100 | 7.04 | 0 | 0 |
| | trees of the future | 30 | 0.45 | 69 | 0.98 |
| | trees of the past | 0 | 0 | 0.6 | 3.94 |
| below 5 m in height: | second structural ensemble | 0 | 0 | 11 | 0.0065 |
| | shrubs and trees of the future | 24 | 0.0027 | 27 | 0.0058 |
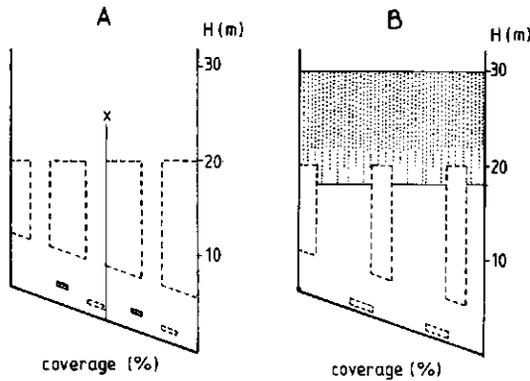
Fig. 3.6. The regeneration units, evaluated in side-view as spatial niches occupied by the set of the present (solid lines, surrounding dotted areas), the set of the future (broken lines) and the set of the past (x). Schematical.

guished in the set of trees and shrubs of the future, i.e. trees above 5 m and trees and shrubs below 2 m in height.

## 3.5 Conclusion and discussion

The results of the analysis leave without answer the question of the different ages and temporal variations in growth of the canopy trees 4 and 13, and therefore the origin of regeneration unit B remains unclear. Considering the area of the belt transect alone, the zero-event must have involved several big trees and may have been caused by either cutting or a natural factor (typhoon).

1. Cutting probably took place 150 to 160 years ago. Because they are used for fuelwood or charcoal preparation, no small (beech) trees would have been left. Tree 13 had to compete with trees 8, 12, 14 and 15. Tree 13 appears to have been strongest and showed an increase in growth, while the others remained behind. About 30 years later, tree 4 appeared on a spot where no competing trees were present as yet. Hence it showed a fast growth, and soon it formed one unit with the surrounding trees. Tree 18 is standing 4 m lower on the other side of the small ridge formed by this slope. When logging took place on the front side of the transect via the valley, tree 18 was left out for convenience, thus accounting for its larger size.
2. A strong natural impact would have occurred about 120 years ago, felling the (over)mature trees, and leaving sites with saplings (e.g. trees 8, 12, 13, 14 and 15) or sites ready for regeneration (4). Tree 18 might have been spared because of its low position on the slope.
3. Thirty years ago, the structure of the regeneration unit changed again by the death of tree 7, causing increased growth of trees 1, 6 and 8 (Fig. 3.4), and creating unit A which from now on has an architecture and a development differing from unit B.

4. In the future, trees 4 and 13 may expand their crowns into the canopy gap (cf. crown size tree 18). Trees 1, 3 and 8 with increased growth and considerable height may become part of the canopy soon, while tree 5 with poor growth and tree 6 with small size will remain behind. A new biostatic phase will be formed in unit A, with a smaller set of trees of the future than in unit B. The suppressed trees of the future may remain behind in size, with a poor growth.

5. Considering the lack of beech saplings between 0.5 and 5 m, it is not expected that saplings under 0.5 m will survive much longer than 25 years and proceed upward. Thus, within one regeneration unit the age gap between the upper beech trees and the beech saplings will increase. If the present situation of this shrub and small tree layer is maintained, then after the next zero-event the available young beech saplings will grow up and form the new generation of beeches of the present.

6. It may be concluded that within one regeneration unit of beech, the beech trees of the present and the suppressed beech trees of the future are of the same generation. The suppressed beech trees in a remarkable fashion can retain their potential to resume growth and to become a canopy tree, after release from a long perod (e.g. 70 years for tree 8) of suppression. In beech, seedlings do not become a new, suppressed generation, as they do not survive much longer than 25 years.


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# 4 Dying of ash in the Netherlands

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## Summary

Around 1985 growing concern about a previously unknown disorder in common ash (*Fraxinus excelsior L.*) instigated a preliminary inventory. The disorder was reported from all parts of The Netherlands, with the notable exclusion of Limburg, from different soil types and from all kind of ash plantations. In some plantations up to 20% of the trees were affected.

The first and most important symptom is wilting of (part of) the crown, combined with premature leaf fall; other symptoms may follow. The wilting process can be very quick, a few days till a few weeks, and may lead to complete dead of the tree, which may take less than one till several years. Normal growth till the moment of symptom expression can occur.

Various fungi were isolated, one not yet identified fungus relatively often. Wood anatomical investigations showed dark colourations and many tyloses in both early and late wood vessels. A comparison with dying of ash in other countries gave also no definite solution. More research is needed.

## 4.1 Introduction

The importance of ash (*Fraxinus excelsior* L.) in Dutch forestry has increased considerably since 1950 as a result of the availability of better sites, the planting of more broadleaved forests and the occurrence of such problems as Dutch elm disease in elms and watermark disease in tree willows.

The increased use of ash in roadside, recreational and amenity plantations, and in the newly established forests in the IJsselmeerpolders has resulted in approximately 5000 ha ash forest (CBS, 1985) and about 5000 km roadside and line plantations (SBB, not publ.) by 1980. As foreseen in the long term planning of the Dutch government (Anonymus, 1986), this area will be doubled by the year 2050.

However, since the end of the 1970's a previously unknown disorder of ash – commonly called 'essensterven' (dying of ash) – has been observed at several places in the country. The rapid increase of this disorder instigated a preliminary investigation during the summer of 1986. This article deals with the results of that survey and with some of the provisional results of a more comprehensive investigation started in the summer of 1987.

## 4.2 Methods

A questionnaire was sent to all district officers of the State Forest Service in order to obtain more detailed information about the distribution and the seriousness of the disorder and the symptoms occurring. Several questions aimed

at tracing possible relations with abiotic factors as soiltype and groundwater level while relations with management practices were also included.

Based on the results of this inquiry two permanent plots were selected: one near Zeewolde, the other near Heiligerlee. In order to obtain a detailed description of the development of the disorder these plots have been assessed several times during the summer of 1986. Two affected trees and one apparently healthy tree have been felled to enable initial anatomical examinations of the wood to be undertaken.

In the same year five other trees were felled for initial phytopathological examinations. Observations were continued in 1987. The permanent plots have been described again several times and phytopathological examinations have been repeated with some affected trees from other locations.

## 4.3 Results

*Distribution of the disorder*

Dying of ash occurs in a large part of the country. Only in very few cases could a directly demonstrable cause e.g. a strong rise of the groundwater level or a site not suitable for ash, be indicated. A vast part of the reported dying of ash seems to be due to a so far unknown factor.

Figure 4.1 shows the places where dying ash trees have been reported up to September 1987. Although this map certainly is not complete, the absence of reports on dying ash in the province of Limburg is conspicuous because of the considerable amount of ash in this province (557 ha closed ash forest or 11% of the total area in the country; CBS, 1985).

The disorder has been found in all kinds of ash plantations: roadside, amenity and recreational plantations as well as forest stands, both pure and mixed stands. Only coppice seems to escape. The disorder affects *F. excelsior L.* and several cultivars ('Westhof's glorie', 'Diversifolia', 'Atlas'). No reports of the disorder in *F. ornus L.* and other *Fraxinus*-species have been received. The age of the affected trees was less than 30 years. In most affected areas, however, older ash stands are rare. Very young trees also are affected. In 1987 the disorder has been found in some nursery beds with saplings between 4 and 6 years old.

*Symptoms*

The first and only symptom which is always present is wilting of the entire crown or part of it, followed by necrosis and premature leaf fall from the wilted parts of the crown (Figs. 4.2 and 4.3). Later on symptoms can include:
– appearence of reduced new shoots with very small pale green till chlorotic leaves and very short internodes (Fig. 4.4);
– dying (partially or completely) of the crown;
– appearence of a dead and discoloured sector in the stem;
– appearence of epicormic shoots on the still living parts of the tree, often followed by a partial dieback of these shoots;
– dying of the whole tree.
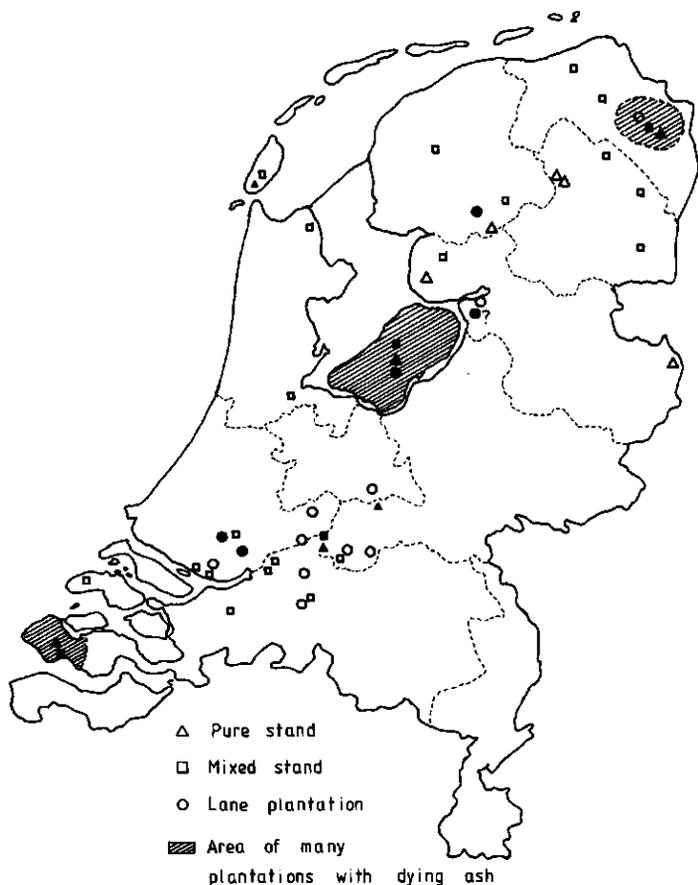
Fig. 4.1. Reports of dying ash (*F. excelsior L.*) in the Netherlands till September 1987. Open signs represent individual plantations with dying ash, dark signs represent several plantations with dying ash.

Other symptoms which have been observed are:
- partial dying of the bark of stem and branches;
- discolourations as browning of the pith of one and two year old twigs, small brown streaks at various places in the wood and a caramel discolouration in the cambial zone or the outer wood of the stem;
- the appearence of long cracks in the bark.

*Development of the disorder*
The above described symptoms manifest themselves in the growing season, quite often after a period of normal growth. In 1986 and 1987 especially in the months August and September many newly affected trees were observed. The

Fig. 4.2. Development of the disorder.
Left: Healthy ash tree. Note the regularly outspread position of the leaves and leaflets in the upper crown. Middle: A tree with early wilting symptoms. Particularly in the upper crown all leaves droop. Right: A tree which lost almost all leaves after wilting. The trees are 12 years old and have been removed from the stand carefully to enable a picture to be taken. (Horsterwold afd. Pz5-a1, 1 September 1987).



Fig. 4.3. Detail from the crown of a severely wilted ash tree. The plantation has been established in 1977, picture taken 1 September 1987 (Horsterwold Pz5-a1).



Fig. 4.4. Detail of regrowth after wilting and leaf fall. Reduced new shoots with very small pale green till chlorotic leaves and very short internodes. (1 September 1987, Horsterwold Pz5-a1).

40

wilting process takes place within a few weeks and sometimes even within a few days and can lead to complete death of the tree within the same year. Sometimes the trunk and the lower parts of the crown of affected trees die only after several years of lingering including the generation of epicormic shoots and a gradual dieback. So far, complete recovery has not been observed.

Especially in young trees (up to 15 or 20 years old) the process of wilting and loss of the foliage can occur very suddenly. In these trees no signs of a decreased growth before the wilting symptoms appear, have been found. Measurement of the shoots of some affected trees showed normal growth until the moment of symptom expression (Table 4.1).

It would appear that in trees of 20 years and older, as well as this acute process, a more chronic process can occur. These trees do not show the sudden complete wilting and leaf fall as described earlier. Instead a much more gradual decline happens. In 1987 in the city of Rotterdam some 20 year old trees were reported

Table 4.1. Shoot length (cm) of leader and topmost branches – in order of affection – of tree 7 (reduced new shoots after wilting and complete leaf fall), 1 (almost bare after wilting), 2 (wilted, early leaf fall), 6 (early wilting), and 5 (appearently healthy); and rainfall between 1.VI and 31.VIII in 1985-1987. For description of symptoms see text. Location: Horsterwold.

| tree number, (date) | shoot length (cm) | | | | | |
| | leader | | | topmost branches | | |
| | 1985 | 1986 | 1987 | 1985 | 1986 | 1987 |
|---|---|---|---|---|---|---|
| 7, (1.IX) | 114 | 84 | 81 | 63 | 96 | 72 |
| | | | | 57 | 57 | 34 |
| 1, (6.VIII) | – | 56 | 71 | 63 | 53 | 34 |
| | | | | 46 | 38 | 30 |
| | | | | 47 | 38 | 23 |
| 2, (6.VIII) | – | 55 | 90 | – | 40 | 70 |
| 6, (1.IX) | – | 77 | 144 | 67 | 42 | 53 |
| | | | | 58 | 46 | 60 |
| 5, (1.IX) | 110 | 56 | 209 | 73 | 55 | 147 |
| | | | | 84 | 62 | 174 |
| | | | | – | 24 | 110 |
| | | | | – | 40 | 113 |

| period | Rainfall (mm) | | | | | |
| | total | | | deviation to the mean | | |
| | 1985 | 1986 | 1987 | 1985 | 1986 | 1987 |
|---|---|---|---|---|---|---|
| 1.VI till 1.IX | 370 | 225 | 362 | +76 | –69 | +68 |

showing a gradual decline including early leaf fall in 1986, extremely late flushing in 1987, sparse and light- coloured foliage, gradual wilting, partial leaf fall and a partial dieback of the topmost twigs during the growing season of 1987. More recently this kind of dieback has been reported in other parts of the country too.

Especially in plantations where the disorder has been present for several years, the dying of ash seems to occur more or less in groups.

*Seriousness of the disorder*

The percentage of affected trees per plantation varies from a few trees per plantation up to 20% of the trees in some plantations in the province of Flevoland.

The disorder is widespread, the number of affected plantations is still growing and the percentage of affected trees in those plantations is still increasing. The disorder, therefore, seems to have become a serious threat, especially as it already occurs frequently in some areas where many ash plantations are to be found (e.g. Flevoland, Eastern-Groningen).

*Results of the phytopathological examinations*

In 1986 samples were taken from five affected trees (Hiemstra, 1987): three with a crown partially died back and a stained sector in the wood of the stem (trees probably affected in 1985 or even earlier) and two showing severe wilting (first affected in 1986). From the discoloured sector in the stem of the first three trees two *Fusarium* sp. and two *Phoma* sp. were isolated. All isolations from the wood outside this sector were negative. From the twigs and small branches of the trees with severe wilting almost every attempt led to the isolation of the same, *Cephalosporium* - like fungus. The places of isolation and the results are summarized in Table 4.2.

In 1987 the isolation experiments were repeated with samples from four recently wilted trees from three different locations. Isolations from wood samples taken from the stems of these trees (even when the stem contained a discoloured sector) in almost all cases proved to be negative. From one and two year old twigs of these trees however, one fungus was very consistently isolated. This fungus has not yet been identified properly but it shows a great resemblance to the fungus that has been isolated from the twigs of affected trees in 1986.

*Results of the wood anatomical investigations*

For this purpose three ash trees were felled:
(1) A tree (probably affected first in 1985) with the crown partly dead and the other part completely wilted. The bark of the stem was partly dead and sunken. The living part of the bark on the stem was adjacent to the wilted part of the crown.
(2) A tree (affected first in 1986) dying with severe wilting.
(3) A healthy looking tree.
Macroscopical, microscopical and SEM examinations of wood samples from

Table 4.2. Results of the 1986 isolation experiments with 5 affected ash trees (*Fraxinus excelsior* L.) from Horsterwold.

| nr. tree | condition of the tree | | |
|---|---|---|---|
| | place of isolation; number of isolations, results | | |
| I | Crown partly dead, stained sector in the stem, bark on that sector dead. (Affection probably started in 1985). | | |
| | discoloured wood sector; | 6, | 6 pos.: Fusarium sp. I |
| | margin of this sector; | 6, | -- |
| | not discoloured wood; | 6, | -- |
| | dark spots in wood; | 9, | -- |
| | twig partly dead, dead part; | 3, | -- |
| | margin living/dead; | 3, | -- |
| | living part; | 3, | -- |
| II | As tree I | | |
| | discoloured wood sector; | 6, | 6 pos.: Fusarium sp. 1, 2x<br>Fusarium sp. 1, 3x<br>Phoma sp.1 |
| | margin of this sector<br>wood not discoulored; | 6, | -- |
| III | As tree I | | |
| | spots in wood small branch; | 6, | 1 pos.: Phoma sp. 2 |
| | 'normal' wood same branch; | 6, | -- |
| IV | Completely bare after wilting (affection started in 1986) | | |
| | wood of small branch; | 6, | 4 pos: Cephalosporium - like sp. |
| V | As IV, twigs partly dead | | |
| | twigs, superficial; | 3, | 2 pos.: 1 Schizothyrella sp.<br>1 Cephalosporium- like sp. |
| | just under the woodsurface; | 3, | 3 pos.: Cephalosporium - like sp. |
| | deeper in the wood; | 3, | 3 pos.: Cephalosporium - like sp. |

these trees led to the following results (Miller & Hiemstra, 1987): In tree nr. 1 many vessels showed dark colourations caused by a considerable tylose activity. These thick-walled tyloses most frequently were found in the early wood but were often present in the late wood. The vessels in the late wood also often contained granulated deposits.

In tree nr. 2 tyloses were much less abundant and appeared to be limited to the last growth rings. Unlike the tyloses found in tree nr. 1 these tyloses, which were found in a few of the early wood vessels, were thin-walled. Wood

samples from the healthy tree appeared to be free of tyloses.

In addition to this, the part of the stem with sunken bark of tree nr. 1 was further examined. This revealed that a large part of the secondary wood growth had ceased to develop during the summer of 1985. At this side of the stem the bark was dead and therefore appeared sunken (in comparison with the still living and growing part of the stem). At the other side of the stem, where wood growth had continued, a disturbance in the late wood of 1985, characterized by large groups of parenchymatous cells, followed by a continuation of normal wood growth, could be shown. The cause of the zonal colouration in the sector where radial growth ceased in 1985 is not known, but dead or dying tissue can be stained by certain fungi (Hibben & Silverborg, 1978).

## 4.4 Discussion

One of the primary goals of the 1986 investigation was to collect more information on possible causes of the problem. Hence, some questions on possible causes such as site (soil type and groundwater level), climate (dry periods), management practices and the involvement of pathogenic organisms were included in the inquiry. The answers received lead to the following presumptions, but it should be remembered that the data resulting from this inquiry are incomplete and not detailed.

### Site
The disorder seems to occur on sites with very different soil types. Affected trees were reported on clay, loam, sand and even peat soils. The groundwater level may vary from high to very low. Some of the sites with affected trees are known to be unsuitable for ash, but the vast majority of affected trees grow on sites regarded as suitable. A site unsuitable for ash trees as a general cause of the current problem therefore is unlikely.

### Climate
As the ash is known to be a species with a high water requirement and because wilting appears to be the primary symptom of the disorder, the occurrence of dry periods during the growing season was considered to be important. Comparison of mean precipitation values for May to September for the years 1970 to 1986 with the year of outbreak of the disorder, however, did not show a relationship between a shortage of precipitation and an increased appearence of affected trees. Moreover, in 1987, a year with a particular wet summer, many new cases of dying ash have been observed. Drought periods as a direct cause of the disorder, therefore, can probably be rejected. The precipitation rate, however, surely acts upon shoot growth, as is clearly visible in Table 4.1.

The influence of other climatic aspects (e.g. extreme cold winters) has not yet been studied.

## Management practices

Attention was given to site preparation, plantation type (monoculture, mixed stand, roadside trees), provenance of the affected trees, weed control after planting (chemical, mechanical or not at all), pruning and thinning practices. The results of the inquiry seem to indicate that none of these factors bears a direct relation with the onset of the disorder. Affected trees are reported in all plantation types, independent of former management practices.

As far as a possible relation with the provenance of affected trees is concerned, no conclusion can be reached as in most plantations the exact provenance is unknown.

## Pathogenic organisms

As the disorder appears under very different conditions, the involvement of a pathogenic organism would appear to be probable. This possibility gains support by the fact that the symptoms are similar to those of some well known fungal wilt diseases such as Dutch elm disease, oak wilt and *Verticillium* wilt (caused by *Ophiostoma ulmi, Ceratocystis fagacearum* and *Verticillium sp.* resp.).

The results of the wood anatomical investigations can also be explained, at least partially, by the involvement of a pathogenic organism as tyloses are very common with fungal wilt diseases.

Culture of samples taken from affected trees has led to the isolation of some fungi. The *Phoma-* and *Fusarium sp.* isolated seem to be unlikely as causal factors. They are very commonly associated with dead and decaying wood and they could only be isolated from the discoloured parts of some stems. The fungus which has been isolated consistently from the wood of small branches and twigs of affected ash trees on the other hand, could be of much more importance.

Nevertheless it is pointless to make further predictions until further identification and inoculation experiments have been carried out.

## Dying of ash in other countries

In Great Britain and in the United States of America a very similar disorder is known.

In Great Britain the disorder called 'ash dieback', has been known to affect common ash (*F. excelsior L.*) since the 1950's. Several suggestions have been made regarding its causes, including moisture stress caused by adverse site and climatic conditions, pollution, scale insect attack and virus infection. Until now however, no certainty as to the cause exists. A first study of the problem showed a strong, but variable, positive correlation between incidence and severity of ash dieback and the intensity of arable farming in the area, but no specific causal factor was determined (Pawsey, 1983; 1984).

In the USA white ash (*F. pennsylvanica Marsch.*) have been affected by a mysterious disorder called 'ash-dieback' or 'ash decline' for more than half a century. Research into this disorder has been carried out since the 1950's, even so the problem is not yet fully understood (Holmes, 1986). Part of the problem can be explained by the involvement of fungi like *Cytophoma pruinosa* (Silver-

borg & Brandt, 1957), of fungi in combination with drought periods (Ross, 1964; Tobiessen & Buchsbaum, 1976), of virusses (Hibben & Silverborg, 1978; and of mycoplasma-like organisms (Matteoni & Sinclair, 1985). Air pollution, particularly ozone, has also been suggested as a possible factor involved (Hibben & Silverborg, 1978).

One of the main problems in clarifying the results of the preliminary investigations and in solving the 'essensterven' problem is the fact that the composition of and the interaction between the components of the forest ecosystem concerned are to a large extent still obscure (see also Oldeman, this volume), e.g. the nematode population in forests and in ash forests in particular. A preliminary investigation of the nematode populations in forests showed a high density of plant parasitic nematodes in some affected ash plantations (Bongers, 1985). In 1987 this was confirmed at the site of some recently affected ash trees. The meaning of this fact, however, is not yet apparent. Research of nematode populations in forests can perhaps clarify these observations.

*Conclusion*

Summarizing, there are many gaps in our results. Important questions to answer in solving the 'essensterven'-problem concern:
- The nature and the role of the isolated fungi.
- The influence of different factors that affect the trees' internal water balance, such as drought periods and of water supply in general.
- The condition and the functioning of the root system.
- The cause and meaning of the tyloses, found in the vessels of some severely affected ash trees.

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# 5 Evaluation of a ten year thinning experiment in Douglas fir

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## Summary

In connection with the discussions on the necessity of thinnings in young Douglas fir (*Pseudotsuga menziesii*) stands in The Netherlands, the demonstration plot het Grevenhout (established 1947; initial spacing 1 x 1 m; low thinning, high thinning, no-thinning in two replications), the results of treatments applied and the quality and possibilities of the not-thinned plot were analysed.

Differences in $h_{100}$ values in the plot indicated possible differences in site quality and differences in stem wood volume removed indicated variations in thinning intensities. The low thinning applied proved to be a low thinning indeed. In the not-thinned plots, enough dominant and co-dominant trees with long crowns and good growth potential remained after 40 year of no-thinning to select the 100-150 final crops trees as advised in forest practice. However, the h/d ratio, a measure of the stability of the tree, is high, indicating problems when final crop trees are released too quickly.

## 5.1 Introduction

In The Netherlands governmental plans exist to expand the area of Douglas fir plantations from 16000 ha to 54000 ha in the next decades (Anon., 1984). It seems likely that a considerable area of these future Douglas fir stands will be located on relatively poor sites, formerly occupied by first generation Scots pine. Under those circumstances an important management objective is to seek ways to minimize costs for thinning and other silvicultural practices.

The following considerations formed the basis for the present study:
1. In order to obtain a sustained yield it is questionable whether in all situations thinning is necessary in Douglas fir silviculture in western Europe.
2. From the viewpoint of stand stability there does not seem to be an absolute 'must' for thinning either. On the contrary: there is growing evidence that non-thinned stands are very stable (Savill, 1983).
3. No-thinning systems have the advantage that on the most valuable lower part of the stem the branches remain thin and that the annual rings will be relatively narrow and regular. If for good wood quality pruning is required, even in a non-thinned stand a limited number of crop trees can be selected to be pruned.

Unfortunately very few experiments exist to analyse the consequences of a no-thinning regime versus various thinning regimes that are or have been common praxis in Douglas fir silviculture.

In 1975 a thinning demonstration plot was established in a 28 year old, previously unthinned Douglas fir stand (1x1 m initial spacing), in 'het Grevenhout, vak 93 m', near Apeldoorn (Fig. 5.1). Three different treatments were applied with two replications each: two high thinning plots, in which only (dominant
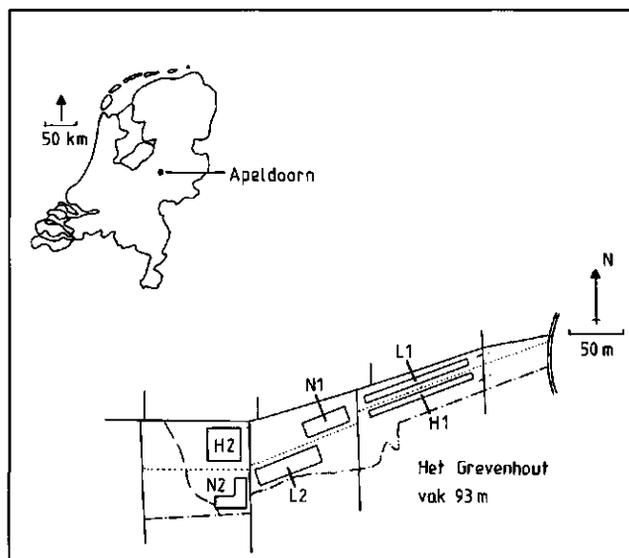
Fig. 5.1. Location of the sample plots in 'Het Grevenhout, vak 93 m'.

and codominant) trees from the higher strata were removed if they were competing with potential crop trees; two low thinning plots, in which only (intermediate and suppressed) trees were thinned from below; and two no-thinning plots. As far as we know the Grevenhout demonstration plot is the only experiment in The Netherlands in which different thinning methods in Douglas fir are compared. There exist other Douglas fir thinning plots (Tol, 1986), but these were established to study different thinning intensities of one particular high thinning method, which includes the selection of final crop trees.

## 5.2 Objectives

The main objectives of this study were:
1. to evaluate the Grevenhout experiment on its reliability and on the comparability of the three different treatments, given the fact that it was a demonstration plot rather than a carefully designed experimental plot;
2. to evaluate the development of the non-thinned plots so far, and to analyse the opportunities and consequences of more extensified silvicultural systems for Douglas fir.

### 5.3 Methods

To realize both objectives a number of hypotheses have been formulated and tested:
1. between the six plots there are no differences in site quality, as indicated by $h_{100}$;
2. the different thinning methods have been applied correctly over the past ten years;
3. the thinning intensities have been about the same for the high thinnings as for the low thinnings, i.e. the amount of stem volume removed by thinnings was approximately the same;
4. the number of dominant and codominant trees in the non-thinned plots is such that sufficient potential crop trees can be selected;
5. the quality and growth potential of potential crop trees in the non- thinned plots, as indicated by d.b.h., h/d-ratio, crown length, crown width and basal area increment is more or less similar to that of potential crop trees in the other treatments.

In the early spring of 1985 six sample plots were established within the demonstration plots (Fig. 5.1). In each sample plot trees were tagged and mapped on a stem map. Of all trees in a 5 m wide belt transect, d.b.h., height, crown base and crown radius in four directions were measured, and an increment core from the south side of each tree was taken. With these data the mean height of 100 largest trees regularly spaced over a hectare ($h_{100}$) was calculated. Vertical diagrams were constructed, including a map of the vertical crown projection area, to analyse differences in stand structure and within stand competition between the plots. On the diagrams all trees were classified according to social position. These diagrams provide an excellent means to check such a classification in a verifiable way (Kuiper & Dijk, 1987). Data of the situation before the demonstration plots were established, were compared with data of the remaining stands and the number and amount of trees removed by the thinnings in 1976, 1980 and 1985. Various distributions were analysed, including those for dbh, h/d-ratio, relative crown length and the number of stems over the social classes.

### 5.4 Results

Table 5.1 gives the results of inventories in 1975, 1980 and 1985. The stands were analysed in 1975 and in 1980 by means of small circular sample plots (0.01-0.02 ha), which make these inventory data not very representative for the stands as a whole. The inventory in 1985, by which 10-20% of the area was sampled in each thinning plot (Table 5.2), is more representative. The data on the number of stems and total volume removed by the thinnings are accurate and reliable. This is the reason that e.g. the number of trees in 1985 added to the total number of trees removed by the thinnings in 1980 and 1976 is not the same as indicated by the 1975 data. The discrepancy is the result of different

Table 5.1. Stand data of the Grevenhout experiment in 1975, 1980 and 1985 before thinning, and thinnings in 1976, 1980 and 1985, all converted to 1 ha-values (Schoenmakers, 1987)

| * | 1975 stand | | 1980 stand | | 1985 stand | | $h_{100}$ | 1976 removed | | 1980 removed | | 1985 removed | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | V | N | V | N | V | | N | V | N | V | N | V |
| H1 | 2905 | 202 | 1500 | 208 | 1600 | 282 | 20.9 | 802 | 76 | 150 | 11 | 340 | 48 |
| H2 | 1980 | 192 | 865 | 190 | 1000 | 222 | 21.3 | 355 | 52 | 45 | 6 | 211 | 46 |
| L1 | 3030 | 139 | 2100 | 204 | 1400 | 323 | 19.2 | 1649 | 44 | 650 | 37 | 400 | 37 |
| L2 | 3190 | 186 | 1190 | 233 | 1260 | 351 | 21.8 | 1911 | 59 | 350 | 37 | 167 | 24 |
| N1 | 3280 | 178 | 2190 | 247 | 1360 | 255 | 22.3 | | | | | | |
| N2 | 2560 | 200 | 1500 | 267 | 1475 | 312 | 21.6 | | | | | | |

* N = number of living trees/ha; V = total volume in $m^3$/ha; $h_{100}$ = the mean height (m) of the 100 largest trees/ha, regularly spaced over the area. H1 and H2 are high thinning plots; L1 and L2 are low thinning plots; N1 and N2 are no-thinning plots.

Table 5.2. plot size and sample plot size of the 1985 inventory.

| plot | size (ha) | sample plot size (ha) |
|---|---|---|
| H1 | 0.47 | 0.05 |
| H2 | 0.44 | 0.09 |
| L1 | 0.19 | 0.05 |
| L2 | 0.31 | 0.09 |
| N1 | 0.33 | 0.06 |
| N2 | 0.41 | 0.06 |

inventory methods.

From Table 5.1 can be derived that the $h_{100}$ values of e.g. plot H1, L1 and N1 are different. The differences correspond with more than one site class, according to the classification of La Bastide & Faber (1971). This would mean that hypothesis 1 is rejected. However, Dik (1987) could not find any significant differences in site quality between the plots. Some uncertainty remains about this point.

In Table 5.1 can also be seen that the thinning intensities, as indicated by the total volume removed, have been different for the high thinning plots compared with the low thinning plots. Thus hypothesis 3 is rejected.

Regarding an evaluation of a correct and consistent application of high and low thinning methods, the ratio of Delveaux (1968) is used, which classifies a thinning by comparison of the mean volume of the thinned trees with the mean volume of all trees before thinning. Values of this ratio smaller than 0.6 indicate an extreme low thinning; values larger than 1.2 indicate an extreme high thin-

Table 5.3. Values of the Delveaux-ratio for the thinnings in 1976, 1980 and 1985 (Schoenmakers, 1987).

|    | 1976 | 1980 | 1985 |
|----|------|------|------|
| H1 | 1.58 | 0.52 | 0.80 |
| H2 | 1.69 | 0.56 | 0.98 |
| L1 | 0.39 | 0.59 | 0.39 |
| L2 | 0.31 | 0.53 | 0.52 |
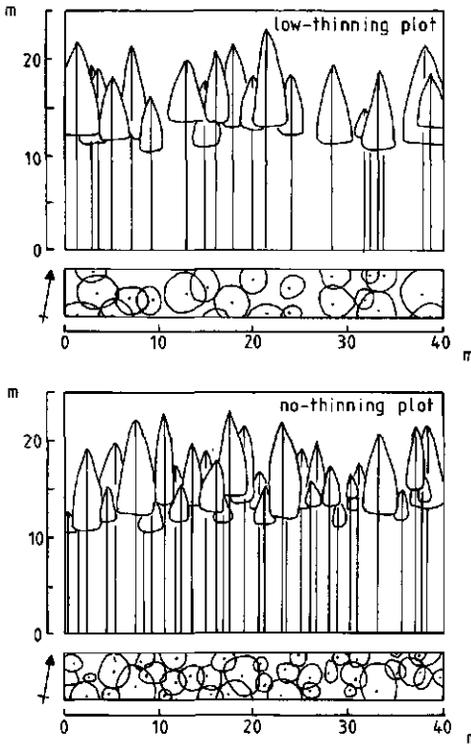


Fig. 5.2. Vertical diagrams of the structure of the low thinning plot L2 and of the no-thinning plot N1. In the non-thinned plot there are many intermediate and suppressed trees. In spite of the narrow spacing there seem to be as many well developed dominants as in the low thinning plot.

ning; values around 1.0 indicate a neutral thinning. Table 5.3 gives the results. In both low thinning plots the thinnings have been applied consistently. They are classified as extreme low thinnings, almost resembling self-thinning. The high thinnings on the other hand have not been applied correctly: in 1976 an

extreme high thinning was carried out; in 1980 the thinning resembled more a low thinning, whereas the 1985 thinning should be classified as neutral. On the basis of these results hypothesis 2 is rejected.

Figure 5.2 gives an impression of the forest structure in the low thinned plot L2 and in the non-thinned plot N1, which lie close to each other and which are almost equal in site class. The non-thinned plot is much denser, with a lot of small, suppressed trees. Standing dead trees are not indicated on the diagrams, but in plot N1 over 3000 dead trees/ha were found (versus 1360 living trees).

Figure 5.3 gives the distribution of the number of stems over the social classes,
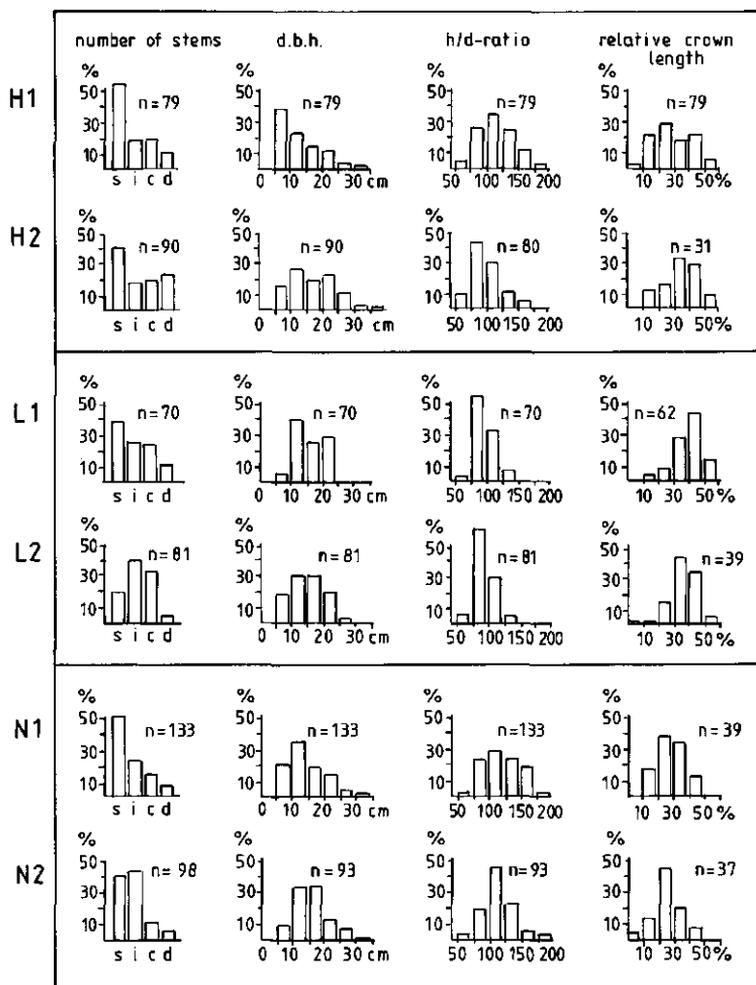


Fig. 5.3. Distributions of the number of stems over the social classes; of diameter at breast height; of h/d-ratio and of relative crown length for the six sample plots.

diameter distribution, distribution of h/d-ratio and of relative crown lengths for the 6 plots.

The total number of dominant and codominant trees/ha in the non-thinned plot N1 is 244 and 285 trees, respectively. In plot N2 there are 103 dominant and 211 codominant trees/ha, respectively. Schuetz & Tol (1982) advise to select no more than 100-150 Douglas fir crop trees per ha. This means that after 40 years of non-thinning there are still plenty of trees to make a selection of final crop trees from: hypothesis 4 approved. A complicating factor in the Greven-hout experiment is, that too many crop trees have been assigned at the beginning of the experiment: about 380 crop trees/ha. This is one of the reasons that the thinnings have not always been carried out correctly. Many crop trees have been spared that would otherwise have been thinned out if the thinning was applied irrespective of the presence of (too many) crop trees.

The number of dominant and codominant trees over 20 cm in diameter in the non-thinned plots is not much different from that in the other plots: on the average there are 350 trees/ha over 20 cm in diameter in the non-thinned plots; 375 trees/ha in the low thinning plots and 390 trees/ha in the high thinning plots. Both in the high thinning plots and in the no-thinning plots there are a few trees over 30 cm in diameter. In the low thinned plots such large trees are absent.

In the non-thinned plots only 43 trees/ha have an h/d-ratio smaller than 75. In the low thinning plots there are 79 such trees/ha and in the high thinning plots on the average there are 100 trees/ha with an h/d-ratio smaller than 75. Mind the risk of releasing crop trees! There are many trees with an h/d-ratio over 125 in both the high thinning plots and in the no-thinning plots.

Relative crown lengths longer than 35% of topheight amount to 130 trees/ha on the average in the non-thinned plots; 670 trees/ha in the low thinned plots and 460 trees/ha in the high thinned plots. Thus there are appreciable differences between the three treatments. The number of 130 trees/ha with relative crown lengths longer than 35% in the non-thinned plots, however, seems to be large enough to select candidates for crop trees.

Mean values of dbh, height, h/d-ratio, relative crown length and current annual basal area increment for dominant trees are given in Table 5.4. Analysis of variance indicated that there are no significant differences in these parameters between the plots.

To summarize, in the non-thinned plots there are sufficient large trees with relatively long crowns and a relatively good growth potential to provide a source for the selection of crop trees. Only the number of trees with an h/d-ratio lower than 75 is rather critical. Hypothesis 5 thus is (partly) approved.

## 5.5 Discussion

The Grevenhout demonstration plot has a number of serious disadvantages over a carefully designed experimental plot:

Table 5.4. Mean values with standard deviation (s) of various tree parameters for dominant trees in the six sample plots.

| * | dbh | h | h/d | rcl | $g_i$ | n |
|---|---|---|---|---|---|---|
| H1 mean | 25.4 | 20.2 | 81 | 48 | 35.1 | 12 |
| s | 4.3 | 1.3 | 10 | 4 | 11.2 | |
| H2 mean | 24.7 | 19.8 | 81 | 47 | 29.9 | 8 |
| s | 2.6 | 1.1 | 7 | 7 | 14.8 | |
| L1 mean | 22.8 | 18.4 | 81 | 47 | 26.8 | 12 |
| s | 1.1 | 0.6 | 5 | 4 | 6.1 | |
| L2 mean | 25.8 | 21.3 | 83 | 44 | 29.6 | 12 |
| s | 2.7 | 1.1 | 10 | 5 | 9.1 | |
| N1 mean | 25.6 | 21.3 | 84 | 40 | 21.1 | 8 |
| s | 3.9 | 1.8 | 8 | 4 | 6.4 | |
| N2 mean | 23.8 | 21.3 | 91 | 36 | 19.4 | 10 |
| s | 4.0 | 1.5 | 12 | 6 | 5.8 | |

* dbh in cm; h in m; rcl = relative crown length in % of topheight; $g_i$ = current annual basal area increment in $cm^2$; n = number of dominant trees sampled.

- the initial situation has not been documented thoroughly enough;
- there seem to be differences in site quality between the plots;
- the different thinning methods have not always been applied correctly;
- the thinning intensity has been different between the treatments;
- too many crop trees have been selected.

Thus it is concluded that this demonstration plot is not suitable for the purpose of studying the effect of different thinning methods on forest structure and on growth and yield (Schoenmakers, 1987; Dik, 1987).

On the other hand the non-thinned plots offer an unique opportunity for baseline studies. Especially the non-thinned plot N1 is very interesting, perhaps in combination with the low thinned plot L2. Therefore it is suggested not to continue the Grevenhout experiment in its present form, but to focus more specifically and in more detail on plots N1 and L2. The other plots than could be managed as a buffer zone. All trees in plots N1 and L2 should be tagged and mapped, so that reliable tree by tree data become available for future analyses.

An evaluation of the development of the non-thinned plots so far has made out some good cases in favour of more extensified silvicultural systems for Douglas fir on relatively poor sites. In spite of the narrow initial spacing of 1x1 m and consequently heavy competition, after 40 year of non-thinning apparently there are:

- sufficient trees with large diameters;
- sufficient trees with relatively long crowns;
- sufficient trees with a high basal area increment;

- many trees with a good wood quality and very thin branches, as judged subjectively;
- not sufficient trees with a low h/d-ratio.

Because the plots cannot be compared in a reliable way, no judgement can be made about total wood production. A thorough analysis of costs and yield can reveal whether or not under these site conditions the scale will deflect in favour of non-thinning. From a silvicultural point of view only the high h/d-values seem critical. The effect on all other parameters studied can be judged as positive. This suggests that silvicultural systems for Douglas fir based on less human interference deserve more attention in research and in forestry praxis.

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# 6 Stem and crown parameters related to structural root systems of Douglas fir

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## Summary

To analyse the relationship between crown, stem and root system of Douglas fir (*Pseudotsuga menziesii*) in relation to social position and to identify a simple above ground parameter to estimate the size of the root system, up to ten trees dispersed over all social classes in 28 stands on dry sandy soils in the Netherlands were pulled over and various above ground and subterranean parameters were assessed.

Size and shape of the crown projected area proved to be no good parameters to estimate root system size. The same holds true for d.b.h. and available growing space as estimators for root system diameter. However, the correlations between d.b.h. or basal area and root system size as indicated by root cross sectional area are high.

Social position has no appreciable influence on this relationship. This means that d.b.h. can be used as a diagnostic tool to evaluate the impact of various silvicultural treatments on root development.

## 6.1 Introduction

In silviculture most thinning strategies are based on observations of the aboveground parts of a tree. Information about the subterranean parts is often restricted to root system morphology (Groth, 1927; Hengst, 1958; Koestler & al., 1968; Eis, 1974; Sutton, 1980). Recently more attention has been paid to tree stability in relation to root system architecture (Sommerville, 1979; Coutts, 1983 a, 1983 b and 1986; Deans & Ford, 1983; Kuiper & Schooten, 1985; Nielsen, 1982 and 1986). To silviculturists it would be of some help if a simple parameter could be identified by which the size of the root system can be estimated throughout the life cycle of a tree. With such a parameter current silvicultural practices could be adjusted to optimize root development.

In literature there are some contradictions about the extension of Douglas fir root systems: according to Smith (1964) root spread can be estimated by crown width. Mc Minn (1963) states that Douglas fir root systems in general are smaller than the crown periphery, whereas Hengst (1958) indicates that Douglas fir roots protrude somewhat outside the crown radius. Figure 6.1 shows an example of a Douglas fir tree at the side of a 10 year old windthrow gap in The Netherlands, with an extremely long and thick root. Such roots, however, are rare in Douglas fir.

Kuiper & Schooten (1985) found a positive linear relationship between the mechanical anchorage of the root system and stem volume for 30-65 year old Douglas fir trees. Their observations were based on 25 trees only. They suggested a study of the relationship between the aboveground and subterranean parts

Fig. 6.1. *Root system of a 40 year old Douglas fir tree bordering a 10 year old windthrow-gap in a forest near Kootwijk. Note the exceptional development of the lateral root, as a result of lack of competition for water and nutrients in the gap (photograph: L.C. Kuiper, 1984).*

of Douglas fir trees in more detail (see also Bakker & Dijk, 1987), which is the main objective of the work presented here.

## 6.2 Objectives

1. To analyse the relationship between crown, stem and structural root system of Douglas fir for a large number of trees;
2. To measure possible effects of social position, available growing space and tree age on the root-shoot relationship;
3. To identify a simple stem or crown parameter to estimate the size of the structural root system.

### 6.3 Materials and methods

Twenty-eight plots were established throughout the Douglas fir area in The Netherlands, in which a total of 200 trees were selected to be pulled over by a handwinch. In order not to exceed the safety limits of the winch, the trees had to be limited in size (Kuiper & Schooten, 1985). Thus only stands younger than 40 years old were included. The study has focussed on Douglas fir trees in stands on relatively poor sites, characterized by dry sandy soils and an annual precipitation of 700-800 mm. Water stress is a commmon feature on many of these sites (Mohren, 1987). A few sites with no water stress (high groundwater table) were included. Usually 10 trees per plot were pulled over, which were mostly confined to the social classes of dominant, codominant and intermediate trees. Tree selection was based on a rough diameter distribution, which was constructed by measuring the d.b.h. of approximately 50 trees in each stand randomly. The trees to be pulled over formed a representative sample of this diameter distribution.

Fieldwork was done in winter and early spring 1986. With a crew of three men about 15 trees could be handled per day. By pulling over trees with a winch at least half the root system becomes quickly available for direct observation. On the sandy soils to which Douglas fir was largely restricted in this study, only small roots and rootlets with a diameter smaller than 0.5 cm stayed behind in the soil. The rest of the root system remained largely intact.

The following parameters were measured and calculated: d.b.h., basal area, tree height, stem volume (according to Dik, 1984), crown surface area (according to Assmann, 1961) and available growing space (according to Hamilton, 1975). From the subterranean parts root system diameter was calculated as two times the mean value of the three longest lateral roots down to a root diameter of 0.5 cm, regularly distributed over the root system. Root plate volume was calcu-
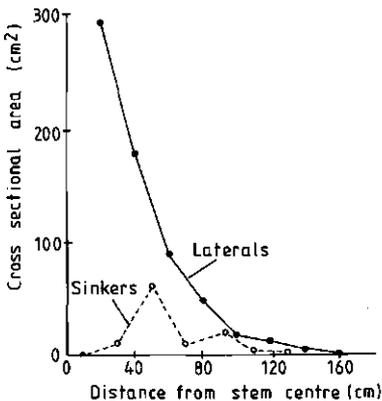


Fig. 6.2. Total cross sectional area of lateral roots (solid line) and sinker roots (broken line) of *Picea sitchensis*, measured at different distances from the anatomical stem centre (Coutts, 1983b): the total c.s.a. of the lateral roots decreases exponentially with distance from the stem base.

lated with the mean value of the radius of the root plate in three directions and the mean depth of the root plate. Cross sectional area (c.s.a.) of the roots was taken as a parameter for root volume. The root-c.s.a. is the sum of the basal areas of all roots at a certain distance from the anatomical stem centre. It is essential to choose this distance not too close to the stem centre due to buttresses, but also not too far away from the stem centre, because of pronounced root taper (Fig. 6.2). A distance of 40 cm seems to have become an international standard for root-c.s.a. (Coutts, 1983a and 1983b; Nielsen, 1982 and 1986). A non- linear relationship between above-ground and subterranean parts was established. The relationship that showed the highest correlation was used in further analysis to check possible effects of social position, growing space and age.

### 6.4 Results

The following hypotheses were tested:
1. D.b.h., basal area, stem volume and crown surface area are all highly correlated with c.s.a. of the roots, but stem volume will show the highest correlation (as expected from Kuiper, 1986).
2. Social position, growing space and tree age have no significant effect on this relationschip.

Figure 6.3 shows the plot locations; in Figure 6.4 the plots are represented according to site class. Table 6.1 gives additional plot information.

From 102 sample trees that were used to check the notion that tree roots extend as far as the crown periphery (Smith, 1964), 51 trees had roots that did not extend as far as the crown perihery; 14 trees had roots as long as the crown radius and 37 trees had roots that were longer than the crown radius. Typically the majority of the roots (to a diameter of 5 mm or less) were confined to an area close to the stem within a radius of 1-1.5 m: the usual root plate size. A
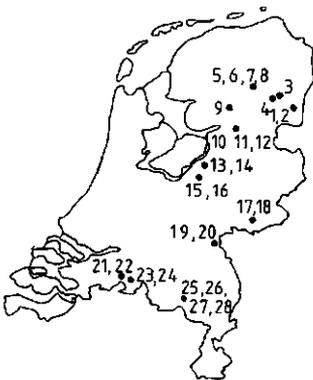
Fig. 6.3. Plot locations (numbers refer to Table 6.1).

Table 6.1. Additional plot information.

| nr | location and section | age | initial spacing (m) | initial number of stems | present number of stems | ground water class* | soil type ** |
|---|---|---|---|---|---|---|---|
| 1 | Emmen, 122 A | 37 | 1.5x1.5 | 4444 | 1360 | VI | hp |
| 2 | Emmen, 124 | 37 | 1.5x1.5 | 4444 | 1270 | VII | hp |
| 3 | Borger, 44 A | 37 | 2.0x1.5 | 3333 | 1620 | VII | gp |
| 4 | Schoonloo, 52 A | 32 | 1.5x1.5 | 4444 | 1010 | VII | gp+hp |
| 5 | Smilde, 52 A | 22 | 2.0x1.5 | 3333 | 1430 | VII | gp |
| 6 | Smilde, 108 | 8 | 2.0x1.5 | 3333 | 3333 | VII | gp |
| 7 | Smilde, 111 | 10 | 2.5x1.5 | 2667 | 2667 | VI | gp |
| 8 | Smilde, 113 | 13 | 2.5x1.5 | 2667 | 2667 | VII | gp+hp |
| 9 | Woldberg, 102 J | 41 | 1.2x1.3 | 6410 | 1112 | VII | gp |
| 10 | Staphorst, 49 E | 17 | 1.2x2.0 | 4000 | 2500 | VI | gp+hp |
| 11 | Staphorst, 49 E | 28 | 1.2x1.5 | 5333 | 1620 | VI | gp+hp |
| 12 | Staphorst, 49 | 11 | natural regeneration | | | | |
| 13 | Nunspeet, 42 A | 22 | 1.5x1.5 | 4444 | 1854 | VII | hp |
| 14 | Nunspeet, 42 A | 30 | 1.5x1.5 | 4444 | 1854 | VII | hp |
| 15 | Speulderbos, 202 E | 23 | 1.2x1.5 | 5333 | 1935 | VII | bps |
| 16 | Speulderbos, 202 G | 23 | 1.2x1.5 | 5333 | 2719 | VII | bps |
| 17 | Slangenburg, 8 C | 23 | 1.2x1.2 | 6400 | 992 | V | bps |
| 18 | Slangenburg, 30 J | 13 | 2.5x3.0 | 1333 | 1292 | VI | gp |
| 19 | Groesbeek, 51 B | 25 | 1.7x1.5 | 3810 | 2136 | VII | bps |
| 20 | Groesbeek, 51 B | 14 | 1.7x1.5 | 3810 | 3810 | VII | bps |
| 21 | Mastbos, 15 F | 11 | 2.0x2.0 | 2500 | 1860 | VI | gp |
| 22 | Mastbos, 14 K | 27 | 1.0x1.5 | 6667 | 2056 | VI | gp |
| 23 | Chaem, 49 A | 25 | 2.0x1.5 | 3333 | 1615 | V | gp |
| 24 | Chaem, 52 D | 35 | 2.0x1.5 | 3333 | 524 | V | gp |
| 25 | Leende, 6 D | 42 | 1.2x1.2 | 6944 | 718 | VI | gp |
| 26 | Leende, 8 A | 56 | 2.0x2.0 | 2500 | 530 | VI | gp |
| 27 | Leende, 54 A | 50 | 1.2x1.3 | 6410 | 475 | V | gp |
| 28 | Leende, 54 A | 10 | natural regeneration | | | V | gp |

* ground water classes (STIBOKA classification, 1964):

| mean highest level | | mean lowest level |
|---|---|---|
| V | < 40 cm | > 120 cm |
| VI | 40-80 cm | > 120 cm |
| VII | > 80 cm | > 160 cm |

** soil types: gp = gley-podzol
      hp = humuspodzol
      bps = brown podzolic soil

limited number of lateral roots exended as far as the crown radius, and only very few roots extended 1-1.5 m beyond the crown periphery, not necessarily linked up with assymmetric parts of the crown projection area. This rooting pattern was confirmed by data from excavations of Douglas fir root systems by the Dorschkamp Research Institute in Wageningen (Burg, unpublished data). A linear relationschip was calculated between mean crown diameter and mean root system diameter of 95 trees, but only a poor correlation was found (Table 6.2). Thus, size and shape of the crown projection area do not seem to be good
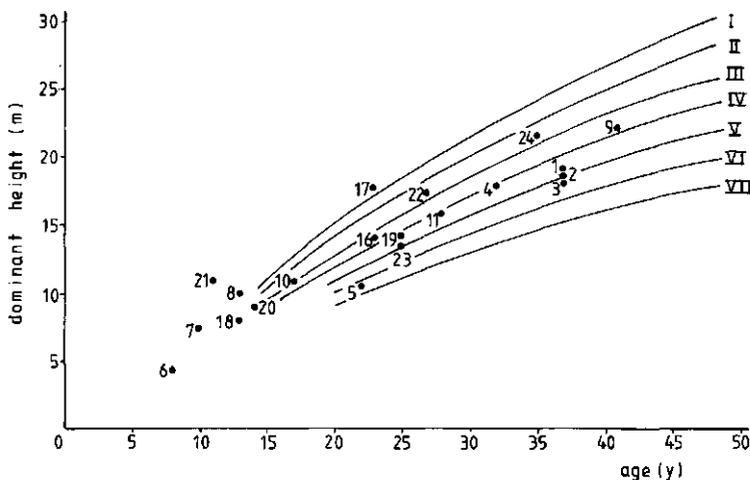
Fig. 6.4. Representation of the plots according to site class (site classes according to La Bastide & Faber, 1971). Plot numbers refer to Table 6.1.

Table 6.2. Relationship between crown diameter and root system diameter; between d.b.h. and root system diameter; and between growing space and root system diameter.

root system diameter = 0.54 (crown diameter) + 1.15 ($r = 0.50$; $n = 95$)

root system diameter = 0.83 $(d.b.h.)^{0.51}$ ($r = 0.53$; $n = 94$)

root system diameter = 2.78 $(growing\ space)^{0.1}$ ($r = 0.17$; $n = 91$)

root system diameter in m; crown diameter in m; d.b.h. in cm and growing space in $m^2$.

parameters to estimate the size of the structural root system of Douglas fir.

Relationship between diameter at breast height and root system diameter, and between available growing space and root system diameter also showed very poor correlation (Table 6.2).

Although the results of earlier tree pulling experiments with Douglas fir (Kuiper, 1986) suggested that stem volume would be best correlated with root-c.s.a., the results of the present study indicated that both diameter at breast height and basal area showed the highest correlation for all trees (Table 6.3). D.b.h. has the practical advantage over basal area that it is directly measurable. Its relationship with root-c.s.a. is presented in Figure 6.5.

When stratified according to social position it appeared that there were no appreciable differences between the regression lines of the d.b.h.- c.s.a. relationship for the different social classes. Dominant trees, when considered as a single group, had the highest correlation coefficient ($r = 0.95$; Table 6.3). Because root-c.s.a. usually decreases exponentially with distance within the zone of rapid taper near the stem (Fig. 6.2), this could account for the higher correlation coefficient

62

Table 6.3. Regression and correlation coefficients of various relationships studied, with the general equation $y = a x^b$

| x | y | n | a | b | r |
|---|---|---|---|---|---|
| dbh | csa | 199 | 0.26 | 2.54 | 0.92 |
| basal area | csa | 199 | 0.33 | 1.28 | 0.92 |
| stem volume | csa | 199 | 2.93 | 0.93 | 0.84 |
| crown surface area | csa | 199 | 0.19 | 1.80 | 0.85 |
| dbh dominants | csa | 70 | 0.22 | 2.60 | 0.95 |
| dbh codominants | csa | 45 | 0.44 | 2.37 | 0.85 |
| dbh intermediates | csa | 55 | 0.17 | 2.65 | 0.84 |
| dbh suppressed | csa | 29 | 0.65 | 2.11 | 0.79 |
| growing space | ba | 40 | 29.8 | 1.17 | 0.89 |
| growing space | csa | 40 | 28.3 | 1.52 | 0.86 |
| age | ba | 60 | 3.13 | 1.42 | 0.89 |
| age | csa | 60 | 1.30 | 1.89 | 0.88 |
| root plate volume | csa | 35 | 1.00 | 0.80 | 0.74 |

csa = total cross sectional area of the roots in $cm^2$; ba = basal area in $cm^2$; stem volume in $dm^3$; crown surface area in $m^2$; growing space in $m^2$; root plate volume in $dm^3$.
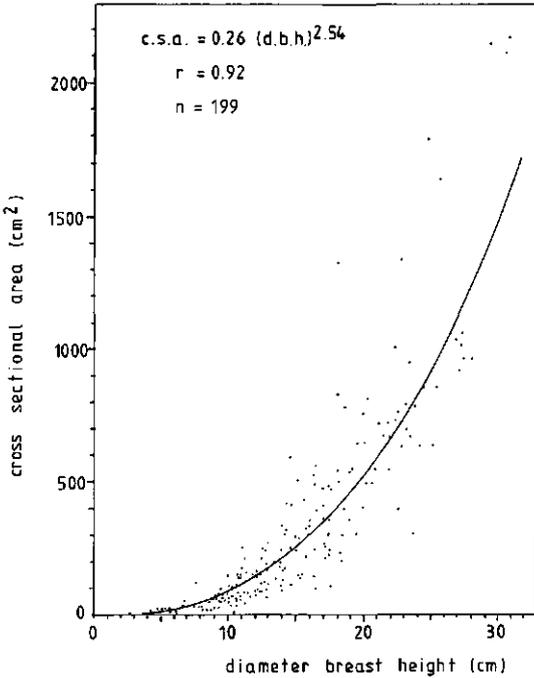


Fig. 6.5. Relationship between diameter at breast height and root-cross sectional area for all trees.

values for dominant trees, compared with trees of other social classes.

As has been demonstrated by Coutts (1983) for 20 year old Sitka spruce only a limited number of lateral roots contribute significantly to the total root-c.s.a. This could be confirmed for 15-25 y old Douglas fir in the present study: for dominant trees 80% of total root-c.s.a. on the average was determined by 6 prominent lateral roots.

Figure 6.6 shows that higher values for growing space of individual trees corresponded with much higher values for root-c.s.a. compared with values for stem basal area. Similar trends could be observed for increasing age, which of course, is closely linked to increasing growing space (Fig. 6.7).

The relationship between root-c.s.a. and root plate volume is given in Table 6.3.
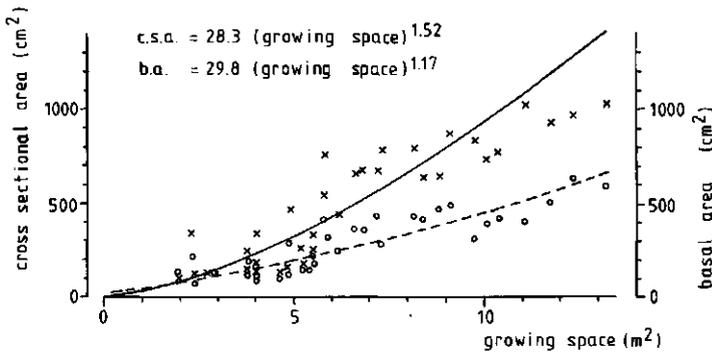


Fig. 6.6. Relationship between growing space and root-cross sectional area (solid line) and between growing space and basal area (broken line) for dominant Douglas fir trees (n = 34).
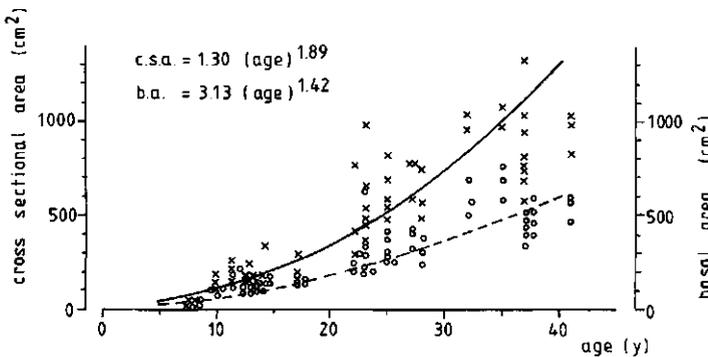


Fig. 6.7. Relationship between age and root-c.s.a. (solid line) and between age and basal area (broken line) for dominant Douglas fir trees (n = 55).

## 6.5 Discussion

In Figure 6.4 and Table 6.3 it was shown that diameter at breast height is a good parameter to estimate the size of the root system, as indicated by root-c.s.a. We now have a diagnostic tool at our disposal in the form of the diameter at breast height, to evaluate different silvicultural treatments with respect to their impact on the size of the structural root system. This can be useful in forestry praxis: e.g. measures that influence diameter increment also will have a strong influence on root system development, i.e. on the development of large structural roots.

Roots-c.s.a. is highly correlated with root volume (Nielsen, 1986), but the present study suggests that it seems to be only moderately correlated with root plate weight. Its significance as a parameter for tree stability comes from the close relationship with prominent lateral roots. Figure 6.5 showed that more growing space gives a large root-c.s.a. This implies that at wider spacings lateral roots will be thicker further from the tree. According to Coutts (1986) the resistance of roots under tension on the windward perimeter contributes most to the total anchorage. When windward roots are thicker, this anchorage component of tree stability will be greater. On the other hand, the good correlation between root-c.s.a. and crown surface area shown by this study, suggests that wider spacings might also produce high wind loading on a large crown and actually decrease tree stability. The exact magnitude of the various components of stability and their combined effects is an area that needs more study.

The results of the present study can help us to design silvicultural systems that aim at increasing root development. Such systems could include wider initial spacings and stronger precommercial thinnings than commonly used (Savill, 1983; Cremer & al., 1982). It is still a question whether the penalties of such systems in terms of decreased timber quality (wider growthrings, heavier branching) are acceptable. Grading rules which have been established for Dutch grown Douglas fir construction timber recently (N.N.I., 1986) suggest that most of the timber produced in such a system will be of B- and C-quality.

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# 7 Use of increment cores to evaluate wood quality of Douglas fir

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## Summary

Research on wood quality of Douglas fir formed a part of the project 'Growth, Yield and Wood Quality' of the three forestry departments of the Agricultural University Wageningen. The aim of the research on wood quality was to determine on the standing tree to what extent the timber produced can be used for construction.

Because of the need for more information about the strength properties of construction timber it was necessary that many physico-mechanical proporties were tested. The results were used in other research work and also in prepairing a standard for Douglas fir lumber in the Netherlands. With the physico-mechanical data and the understanding of the variables on which strength depends, we tried to assess strength by use of some increment core variables. Coefficients of correlation between estimates based on proportion of late wood and basic density, and real strength, proved best for fibre stress at maximum load and maximum crushing strength. With the knowledge of the correlations and also the dimensions of, for instance, ring width in relation to different qualities, the core can give information about wood quality of sawn timber as a function of the annual ring.

## 7.1 Introduction

At a time that everyone is talking about the limits to the earth's resources, it is of interest to know that one of these, wood, is renewable.

Interest in wood is growing not only because of its special characteristics, but also because its renewability strongly depends on sensible management of the world's wood resources. The world demand for timber is increasing and its quality is deteriorating with economic changes and with poor management. The forestry situation in the European Community has the European Commission's attention since the end of the 1970's. At the beginning of the 1980's a research subprogramme was proposed on 'Wood as a renewable raw material'as a subdivision of the raw materials Research and Development programmes.

The subprogramme was aimed at research proposals with the following objectives.
- to increase the physical and economic availability of wood and wood products
- to reduce the costs of growing, harvesting and processing wood
- to upgrade the quality and value of products
- to promote a more complete utilization of wood and wood waste.

The motivation was that the European Community depends on external sources for more than half of its demand for wood and wood products. The Wageningen University's forestry departments participated in the subprogramme through a research project called 'Growth, Yield and Wood Quality of Douglas fir in the Netherlands'. Part of the research on quality was of physical

and mechanical behaviour. Tests done earlier in the Netherlands (Wisse, 1968 and others) had showed promising results. On the basis of supplementary data (e.g. Hapla 1980; Polman 1988) it was possible to develop a Dutch timber standard for European Douglas fir. In this research the conventional method (ASTM – part 16, 1964) was followed to obtain the mechanical data, which implies working with clear specimens, i.e. without any defects. This destructive method has certain limitations in the number of samples, variation of the properties, time on preliminary operation and costs (handling and material). These limitations have contributed to the development of 'non-destructive' research methods through which larger number of samples can easily be tested. One of these methods is the use of increment cores. In forestry research, cores have a major role, but their use to determine wood properties and predict timber quality has only recently been introduced and seems to be promising.

## 7.2 Objective of this research

The objective of this research is to develop a method for the use of an increment core as estimator for the wood quality of Douglas fir.

## 7.3 Increment core analysis

### 7.3.1 Introduction
Traditionally the mechanical-strength tests have an important part in determining wood quality. The selected tree is felled and sawn into test pieces, which undergo various kinds of strength tests. Compared to this the use of increment cores has several advantages. The method is non-destructive and more samples can be taken at the same time and at the same costs. As Mitchell (1958) already noticed, this makes increment cores 'useful in studying the influence of environmental factors or silvicultural treatments on wood quality'.

Timber quality is influenced for a great deal by the composition of the annual ring. Important factors for any special use are uniformity of growth and the relative proportions of early and late wood in the rings. When Douglas fir is to be used for veneer the width of the annual rings should not exceed 3 mm according to Löffler (1966). The home grown Douglas fir, however, will normally exceed this limit over a longer period. Therefore the aim of management under Dutch circumstances will mainly be good quality timber for construction.

The formation of the annual ring depends on many factors such as climate, soil, and silvicultural treatment. The influences of certain silvicultural measures on wood quality of Douglas fir in Germany has been researched by Hapla & al. (1980, 1985) but hardly any results are available about Dutch grown trees. Figures on these influences may improve the decisions of foresters about their cultures in order to attain quality timber. From this point of view it is of interest and importance to obtain information on this subject for the Dutch situation,

and to compare the results to those from other European countries.

### 7.3.2 Material and data collection

Three Douglas fir stands in Schovenhorst, Speulder- and Sprielderbos and 't Loo were selected, all lying in the main forest area in the Netherlands. They will be referred to as respectively SCH, SP4 and LOO.

From the selected trees two increment cores (diameter of 5 mm) were extracted at breast height till the centre of the tree in perpendicular directions and if possible contained the pith. The cores were put into plastic tubes and kept under water till analysis to preserve the green condition. In addition information was gathered about height, dbh, crown length, and crown projections not only of the selected trees but also of the ones immediately surrounding them. Distances from the test trees to the surrounding ones were included in the measurements (see Creemers, 1987).

### Processing of the cores included:

A Measuring width of annual growth rings in the green condition, using the 'Dorschkamp' equipment (Beek & Maessen, 1981). Determination of the absolute width of late wood and calculating the late wood percentage.

B Crossdating the cores, i.e. assigning an exact date to each ring in order to be able to construct mean curves for the trees and stands. In a few cases available discs had to be used to verify the conclusions.

C Determination of density (based on oven-dry weight and green volume). Green volume was obtained by means of the waterdisplacement method. Then the pieces were dried at 103 °C for 24 hours to get the oven-dry weight.

## 7.4 Results

### 7.4.1 Annual rings

After crossdating all the cores the two corresponding cores from each tree were combined into one tree ring width series. Only those years were used that had been measured in both cores. Absolute width of late wood and late wood percentage were treated in the same way. Averages based on these tree ring series are displayed in Table 7.1. The number of years on which the value was based is added between parentheses.

Apart from a single exception the mean ring width is the largest in the 'Loo' stand. As the ring width frequency histograms (Fig. 7.1) indicate this can be attributed to a conspicuously large proportion of rings between 4 and 5 mm wide, which cannot be accounted for by age difference.

To eliminate individual variation as much as possible, ring width series per stand were obtained from the tree ring series by averaging each annual ring width for all trees in that stand. Each annual average is based on at least three ring widths. From these ring width curves pro stand (Fig. 7.2) it becomes clear that the deviating frequency distribution of the 'Loo' stand is caused by a dis-

Table 7.1. Average of annual ring width and proportion of latewood.

| Stand | Age | Tree | Mean ring width | Range | Mean late-wood proportion | Range |
|---|---|---|---|---|---|---|
| | years | | mm | mm | % | % |
| Sch | 63 | 401 | 3.01 (46) | 0.42-6.91 | 48.8 (44) | 36.1-64.0 |
| | | 402 | 2.56 (44) | 0.87-7.41 | 49.9 (44) | 28.7-65.9 |
| | | 403 | 3.35 (50) | 0.00-8.60 | 47.5 (45) | 26.6-58.1 |
| | | 404 | 3.23 (48) | 0.52-6.31 | 52.5 (48) | 38.4-67.8 |
| | | 405 | 2.98 (35) | 0.41-4.88 | 55.5 (33) | 23.9-68.1 |
| | | 406 | 2.24 (44) | 0.66-5.61 | 55.3 (44) | 39.3-69.1 |
| | | 407 | 2.53 (49) | 0.00-7.24 | 54.5 (45) | 38.4-72.1 |
| | | 408 | 2.55 (45) | 1.03-4.47 | 51.7 (45) | 38.5-63.0 |
| | | 409 | 2.26 (43) | 0.66-4.66 | 54.4 (41) | 38.6-68.9 |
| | | 410 | 3.12 (41) | 0.97-6.17 | 53.1 (41) | 42.0-67.8 |
| SP4 | 56 | 098 | 4.12 (42) | 1.89-7.18 | 52.9 (42) | 39.5-67.3 |
| | | 153 | 2.30 (42) | 0.72-6.22 | 49.5 (41) | 34.6-64.6 |
| | | 185 | 3.22 (47) | 1.13-6.20 | 53.5 (47) | 34.5-69.9 |
| LOO | 54 | 411 | 3.95 (41) | 2.34-5.34 | 49.5 (41) | 39.7-59.5 |
| | | 412 | 3.98 (21) | 2.17-5.59 | 49.9 (21) | 35.8-61.0 |
| | | 413 | 3.88 (39) | 1.83-6.36 | 51.3 (39) | 38.7-63.4 |
| | | 414 | 4.92 (34) | 3.49-6.26 | 47.9 (34) | 42.8-54.0 |
| | | 415 | 4.78 (40) | 2.81-6.45 | 47.4 (39) | 35.7-60.9 |
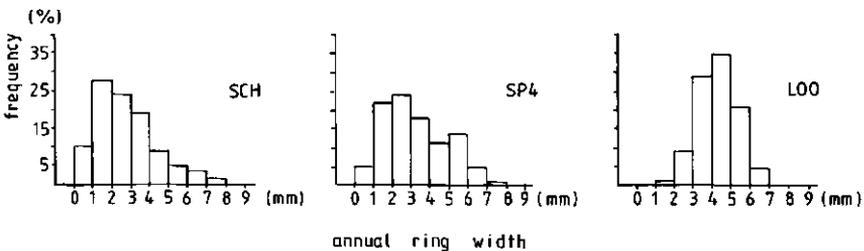


Fig. 7.1. Frequency of the annual ring width into classes from different stands.

tinctly different stand development. The very broad rings Douglas fir typically produces in its youth are absent, as well as the reduction of ring width normally associated with increasing age.

## 7.4.2 Density

The mass density is the main physical characteristic and many properties are related to it, e.g. strength, pulp yield and heat transmission. One of these expressions, called basic density (oven-dry weight divided by wet volume) can easily be determined from an increment core and has a predictive value for different wood properties, including strength.
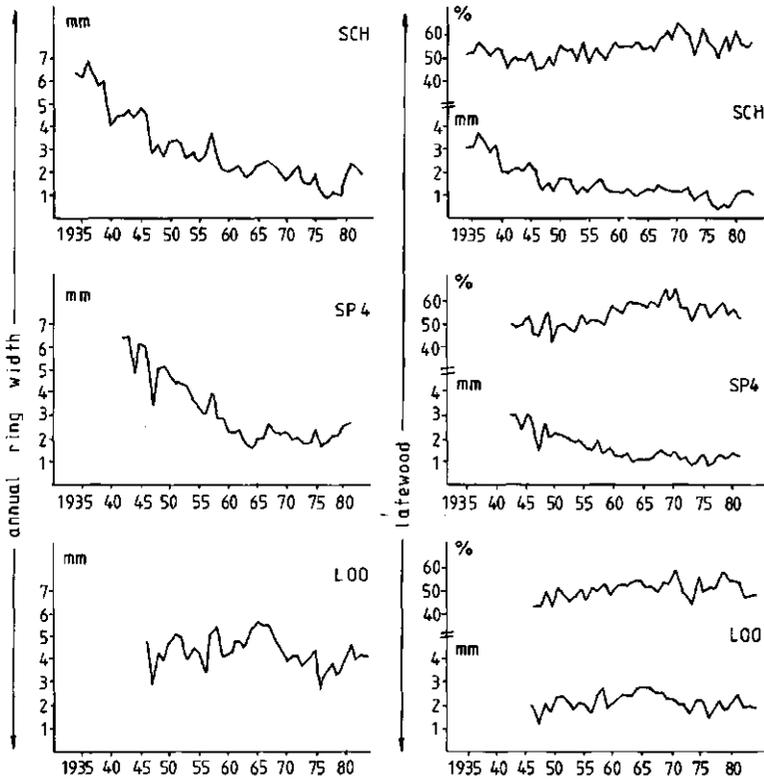
Fig. 7.2. Average annual ring width, proportion of late wood and width of late wood at Schoven-horst, Speulder- and Sprielderbos and 't Loo.

Table 7.2 gives the average basic densities of the cores and trees. To obtain information about the change in density from the inside of the tree to the outside, some of the cores were divided into smaller pieces (in principle five annual rings). Some of the results are shown in Figure 7.3. The small arrows left of the Y axis give the average per tree or stand. Figure 7.3 shows that slow juvenile growth and even annual ring width at 't Loo resulted in a shallower slope of basic density than in other stands.

From the basic density, density at different moisture contents was calculated. Table 7.3 gives the different corresponding values for different trees. These data allow comparison with other research (e.g. Creemers, 1987; Knigge, 1958; Wisse, 1968). The conversion equations can be found in appendix 6 of Creemers 1987.

Table 7.2. Average basic densities of cores and trees.

| stand | tree no. | direction | basic density (g/cm$^3$) | |
|---|---|---|---|---|
| | | | core | tree |
| SCH | 400 | W | 0.44 | 0.44 |
| | | S | 0.44 | |
| | 401 | SW | 0.44 | 0.44 |
| | | NW | 0.44 | |
| | 402 | SW | 0.44 | 0.46 |
| | | W | 0.47 | |
| | 403 | SW | 0.38 | 0.38 |
| | | S | 0.38 | |
| | 404 | SW | 0.46 | 0.45 |
| | | NW | 0.45 | |
| | 405 | SW | 0.49 | 0.49 |
| | | SE | 0.48 | |
| | 406 | SW | 0.48 | 0.48 |
| | | NW | 0.47 | |
| | 407 | SW | 0.45 | 0.45 |
| | | NW | 0.45 | |
| | 408 | SW | 0.45 | 0.46 |
| | | NW | 0.47 | |
| | 409 | SW | 0.47 | 0.46 |
| | | W | 0.46 | |
| | 410 | SW | 0.45 | 0.47 |
| | | SE | 0.48 | |
| SP4 | 098 | SW | 0.45 | 0.45 |
| | | NW | 0.46 | |
| | 153 | SW | 0.42 | 0.43 |
| | | NW | 0.45 | |
| | 185 | SW | 0.47 | 0.47 |
| | | NW | 0.48 | |
| LOO | 411 | N | 0.47 | 0.48 |
| | | E | 0.48 | |
| | 412 | N | 0.44 | 0.46 |
| | | E | 0.49 | |
| | 413 | N | 0.46 | 0.46 |
| | | E | 0.46 | |
| | 414 | N | 0.42 | 0.42 |
| | | E | 0.43 | |
| | 415 | N | 0.42 | 0.43 |
| | | E | 0.45 | |

Table 7.3. Average basic density per tree and – calculated – corresponding values for density at 0% mc and at 15% moisture content.

| stand | tree no. | basic density g/cm$^3$ | corresponding values | |
| --- | --- | --- | --- | --- |
| | | | density (0%) g/cm$^3$ | density (15%) g/cm$^3$ |
| Sch | 400 | 0.44 | 0.50 | 0.54 |
| | 401 | 0.44 | 0.50 | 0.54 |
| | 402 | 0.46 | 0.52 | 0.56 |
| | 403 | 0.38 | 0.43 | 0.46 |
| | 404 | 0.45 | 0.51 | 0.55 |
| | 405 | 0.49 | 0.56 | 0.60 |
| | 406 | 0.48 | 0.55 | 0.59 |
| | 407 | 0.45 | 0.51 | 0.55 |
| | 408 | 0.46 | 0.52 | 0.56 |
| | 409 | 0.46 | 0.52 | 0.56 |
| | 410 | 0.47 | 0.53 | 0.57 |
| SP4 | 098 | 0.45 | 0.51 | 0.55 |
| | 153 | 0.43 | 0.49 | 0.52 |
| | 185 | 0.47 | 0.53 | 0.57 |
| LOO | 411 | 0.48 | 0.55 | 0.59 |
| | 412 | 0.46 | 0.52 | 0.56 |
| | 413 | 0.46 | 0.52 | 0.56 |
| | 414 | 0.42 | 0.48 | 0.51 |
| | 415 | 0.43 | 0.49 | 0.52 |
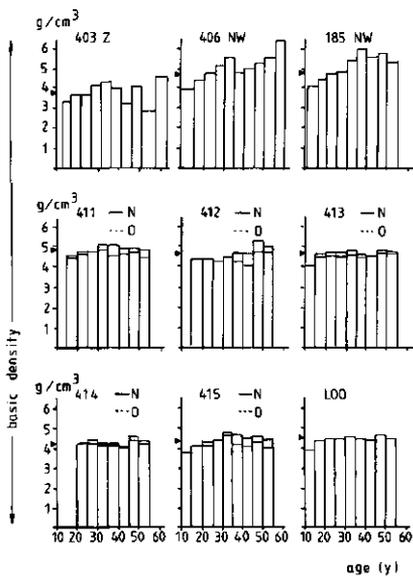


Fig. 7.3. Variation in basic density at different ages.

Table 7.4. Some physical-mechanical data of the different test samples at moisture content 15%.

| stand | tree no | bending density kg/m³ | bending modulus of elasticity N/mm² | bending modulus of rupture N/mm² | compression basic density g/cm³ | compression density g/cm³ | compression strength N/mm² | impact bending density tang g/cm³ | impact bending density rad g/cm³ | impact bending strength tang kgm/dm³ | impact bending strength rad kgm/dm³ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| SP4 | 98 | 580.7 | 12487.5 | 79.6 | 0.478 | 0.597 | 42.18 | 0.558 | 0.557 | 58.20 | 35.23 |
| | 153 | 525.3 | 7984.6 | 62.5 | 0.440 | 0.537 | 42.42 | 0.536 | 0.521 | 49.10 | 32.74 |
| | 185 | 596.6 | 11741.6 | 90.0 | 0.496 | 0.617 | 47.77 | 0.591 | 0.604 | 58.19 | 47.95 |
| | 400 | 560.6 | 11735.8 | 81.2 | 0.482 | 0.570 | 41.16 | 0.558 | 0.569 | 31.35 | 50.51 |
| | 401 | 570.4 | 12833.0 | 75.3 | 0.469 | 0.574 | 45.51 | 0.571 | 0.577 | 57.02 | 29.82 |
| | 402 | 559.8 | 12281.5 | 84.6 | 0.470 | 0.566 | 45.44 | 0.582 | 0.574 | 42.97 | 28.76 |
| | 403 | 488.6 | 7932.5 | 58.2 | 0.414 | 0.477 | 33.81 | 0.475 | 0.488 | 36.95 | 24.93 |
| | 404 | 565.5 | 12312.2 | 80.7 | 0.456 | 0.561 | 43.04 | 0.570 | 0.564 | 60.54 | 35.61 |
| | 405 | 586.9 | 11010.0 | 83.2 | 0.487 | 0.596 | 46.32 | 0.582 | 0.591 | 42.00 | 25.07 |
| | 406 | 598.5 | 11505.1 | 82.4 | 0.496 | 0.661 | 48.82 | 0.597 | 0.621 | 43.79 | 35.18 |
| | 407 | 594.3 | 12303.7 | 93.1 | 0.484 | 0.621 | 48.54 | 0.588 | 0.590 | 50.78 | 38.46 |
| | 408 | 590.1 | 11679.4 | 88.3 | 0.491 | 0.591 | 45.67 | 0.585 | 0.584 | 38.64 | 28.75 |
| | 409 | 601.2 | 12148.1 | 77.9 | 0.500 | 0.601 | 48.15 | 0.585 | 0.591 | 50.51 | 32.37 |
| | 410 | 602.7 | 12885.2 | 93.6 | 0.510 | 0.614 | 51.37 | 0.628 | 0.626 | 48.31 | 33.83 |
| | 411 | 582.5 | 12302.7 | 78.5 | 0.455 | 0.579 | 42.17 | 0.588 | 0.594 | 42.39 | 36.35 |
| | 412 | 558.7 | 10953.2 | 73.3 | 0.455 | 0.530 | 40.54 | 0.539 | 0.525 | 39.78 | 28.90 |
| | 413 | 689.2 | 13887.5 | 81.7 | 0.462 | 0.575 | 41.49 | 0.528 | 0.528 | 54.06 | 37.64 |
| | 414 | 527.8 | 12501.3 | 72.8 | 0.421 | 0.525 | 43.02 | 0.514 | 0.514 | 56.21 | 38.42 |
| | 415 | 537.7 | 11933.9 | 75.0 | 0.429 | 0.528 | 41.52 | 0.508 | 0.505 | 50.97 | 35.73 |

## 7.5 Relationships

### 7.5.1 Introduction

The first part of this paragraph will show the results of the mechanical tests. It will form the basis for the second part concerning the relationships between the core variables and mechanical properties. It was not the intension to find any relationship between variables and strength properties of the core itself. The relation of three core variables (annual ring-width, proportion of late wood and density) to the average strength of the same material (first two metres from the trunk) was investigated.

### 7.5.2 Strength properties

Section 5.2 of the final report of the EEC project 'Growth, Yield and Quality of Douglas fir' (Polman, 1988) gives an extensive report on the samples tested. Only the average data for the mechanical strength properties (EMOD, MOR, compression and impact bending) are presented here. (Table 7.4).

### 7.5.3 Relations between core variables and mechanical properties

To evaluate the relationships between the three core variables (annual ring width, proportion of late wood and basic density) and the average mechanical properties (modulus of rupture, modulus of elasticity, compression strength and impact bending) regression analysis was used. Table 7.5 gives the correlation between the different core variables and strength properties. The simple linear regression coefficients can be found in Appendix 8 of Creemers (1987). The best correlations were between proportion of late wood and basic density on the one hand and modulus of rupture and compression strength on the other.

Table 7.5. Correlations between core variables and strength properties.

| core variable | strength properties | | | | |
|---|---|---|---|---|---|
| | modulus of rupture | modulus of elasticity | compression strength | impact bending strength rad | tang |
| annual ring width | −0.315 | 0.170 | −0.584** | 0.240 | 0.109 |
| proportion of latewood | 0.650** | 0.249 | 0.713** | 0.177 | 0.110 |
| basic density | 0.706** | 0.474* | 0.687** | 0.080 | 0.015 |

** = significant to 0.01 level (0.575)
* = significant at 0.05 level (0.456)

## 7.6 Discussion

The possible use of cores to estimate quality of construction timber in standing trees has clear advantages but also limitations. The method is non-destructive. It is not necessary to cut many trees for test-material. The variables of the core can give correct answers about the strength properties. The amount of the test material can easily be increased, which increases the statistical reliability of conclusions.

The development of strength properties in stands based on wood characteristics and not on defects can be obtained by the samples taken and if there is enough knowledge about stand development, determining properties can be controlled. Inaccuracy is found partly in the measurement of variables and the use of increment cores representing the whole tree and partly in the correlation between core variables and strength properties. With the limited results, gathered up till now, only trends can be given.

An other disadvantage pointed out in literature (Schöpfer, 1962) is the damage to trees caused by taking increment cores, especially if the end-uses are veneer and high-quality sawn timber. This disadvantage can be limited for example by putting wax into the holes, the choice of stands and other measures. According to publications from other countries, the use of cores to evaluate wood quality, however, seems useful. For The Netherlands, complementary research is needed before its use can be established. By further developing this method it can be a valuable instrument for forestry research and for commercial forestry.

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# 8 Mycocoenology of marshy forests and scrubs. I. Host range of wood-decomposing Aphyllophorales and Heterobasidiomycetes

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## Summary

The ecology of wood-inhabiting Aphyllophorales and Heterobasidiomycetes was studied in 43 permanent plots from 500 to 1000 m$^2$ in the province of Drenthe during the autumns of 1981 and 1982. The plots were situated in plant communities dominated by *Alnus glutinosa*, *Salix cinerea*, *S. aurita*, *S. repens* or/and *Myrica gale*, growing on moist to wet, mineral and peaty soils. In all 2094 notations were made on the microhabitat of 147 species of wood-inhabiting Aphyllophorales and Heterobasidiomycetes, including notations on the host. The terms host specifity and host preference are discussed. The numbers of observations of all fungal species on all host plants are listed. The frequency of a fungal species on a certain host is calculated as the percentage of the observations of that species on all hosts. It is concluded that neither the number of observations, nor the frequency are good measures of host preference. The relative preference of a species is defined as the proportional frequency on a certain host, divided by the number of observations of all species on that host. It is demonstrated that the results of such calculations are only valid within the studied plant communities and within a restricted area. Examples of species with a distinct relative preference are given. The affinity between the floras of Aphyllophorales and Heterobasidiomycetes on various hosts was studied by means of a cluster analysis. It is concluded that differences in structure of the vegetation and habitat are more important than taxonomic affinity of the hosts.

## 8.1 Introduction

This study forms part of a series of mycocoenological investigations, carried out since 1965, aimed at the description of communities of larger fungi in the Drenthian phytogeographical district in the North-East Netherlands (Weeda, 1983). The results are related to characteristics of substrate, plant community and soil factors in order to interpret the data in an ecological context (Barkman, 1987).

Mycocoenological studies in marshy forests and scrubs were carried out by the second author from 1981 until 1985. The first author was involved in this project as a student of biology by investigating the field ecology of wood-inhabiting Aphyllophorales and Heterobasidiomycetes in 1981 and 1982. The aims of this study were (1) to compare the floristic composition of this group of fungi in the investigated plant communities; (2) to establish the relative importance of the various species; (3) to explain species diversity in terms of host range and (4) microhabitat differentiation. This paper deals mainly with the problem, mentioned sub (3). In following papers the other aspects will be treated. The

results have been published before in an internal report (Keizer, 1985).

## 8.2 Materials and methods

This research was carried out in 43 permanent plots, ranging from 500 to 1000 m², situated in the province of Drenthe in an area of approximately 50 x 50 km. This area is a flat to slightly undulating landscape with a few low ridges of pushed-up preglacial sands, situated between 0 and 20 metres above sea level. The soils are mainly mineralogically poor, acid, pleistocene cover sands, slightly richer pleistocene boulder clay and various mesotrophic and oligotrophic holocene peat soils (Wee, 1972; Stiboka, 1977, 1978). The climate is temperate-subatlantic with an average annual precipitation of $\pm$ 770 mm, an average daily maximum temperature of 21.5°C in August and an average daily minimum temperature of –1.5°C in January (Koninklijk Nederlands Metereologisch Instituut, 1972).

The plots were selected on the basis of representativity for the concerned vegetation types, undisturbed surface and degree of homogeneity. They were distributed over the following plant communities, mainly according to Westhoff & Den Held (1969):

1. *Myricetum gale*: 6 plots. Dense scrubs up to 2.5 metres tall, dominated by *Myrica gale*, on very wet to moist, acid peat.
2. *Salicion arenariae*: 5 plots. Dense to open scrubs up to 1.2 (-2.3) metres tall, dominated by *Salix repens*, in sandy depressions in heathlands with strongly fluctuating groundwater table.
3. *Frangulo-Salicetum auritae*: 9 plots. Scrubs up to 4 (-6) metres tall, dominated by *Salix aurita* or *Salix x multinervis*, often with an open tree layer of *Betula pubescens*, on permanently wet to periodically rather dry, oligotrophic, sandy and peaty soils.
4. *Alno-Salicetum cinereae*: 4 plots. Scrubs up to 6 (-8) metres tall, dominated by *Salix cinerea* or *Salix x multinervis*, often with scattered *Betula pubescens* or *Alnus glutinosa*, on wet to moist, mesotrophic peat.
5. Community of *Salix cinerea* and *Urtica dioica*: 1 plot. Scrubs up to 5 metres tall, dominated by *Salix cinerea*, planted on rather dry, eutrophic, disturbed, humus-rich sand.
6. *Sambuco-Salicion capreae*: 2 plots. Rather open forests up to 12 metres tall, dominated by *Salix caprea*, with grassy herb layer, on mesic to rather dry, loamy, eutrophic soils.
7. *Carici elongatae-Alnetum*: 5 plots. Forests up to 15 metres tall, usually former coppice woods, dominated by *Alnus glutinosa*, on wet, mesotrophic to eutrophic peat.
8. *Alno-Padion*: 8 plots. Forests up to 18 metres tall, often former coppice woods, dominated by *Alnus* and/or *Betula, Quercus robur, Fraxinus*, on moist, mesotrophic to eutrophic, loamy soils.
9. Community of *Alnus* and *Urtica*: 3 plots. Planted forests, up to 12 metres

78

tall, dominated by *Alnus* and *Urtica*, on mesic soils.

Consequently 6 plots are dominated by *Myrica gale*, 5 by *Salix repens*, 9 by *S. aurita*, 5 by *S. cinerea*, 2 by *S. caprea* and 16 by *Alnus glutinosa*. Data on stand composition, soil profile, soil chemistry and hydrology will be published shortly.

Mycocoenological research was carried out according to the methods described by Barkman (1976), Arnolds (1981) and Winterhoff (1984). Data on wood-decomposing Aphyllophorales and Heterobasidiomycetes were collected in 1981 and 1982. The Aphyllophorales considered here comprise polypores, corticioid fungi and a few clavarioid fungi (Arnolds, 1984). Terrestrial polypores, hydnaceous fungi and the majority of clavarioid fungi are not included in this study. Four taxa of corticioid fungi were exclusively found on herbaceous litter, each of them only once. These data are also included in the results. Nomenclature of fungi is mainly after Arnolds (1984), for the rest after Jülich & Stalpers (1980).

Each plot was visited one to three times during the mentioned period. For each observation details on the substrate were noted: species of woody plant, size of the substrate, degree of decomposition, height above the soil, inclination of the substrate and position of basidiomata on the substrate (bark or wood; upper side, underside etc.). For all species, identified in the field, at least one of such notations was made in each plot. The total number of observations was limited by the time spent in each plot, usually 2-3 hours per visit. Many species could not be identified in the field; these had to be identified in the laboratory. One or more collections of all species are preserved in the herbarium of the Biological Station. It was impossible to note all observations of the most abundant species, therefore the frequency of these species is underestimated (see 8.3.3).

## 8.3 Results

### 8.3.1 Number of species of Aphyllophorales and Heterobasidiomycetes

All species of wood-decomposing Aphyllophorales and Heterobasidiomycetes observed during this study are listed in Table 8.1 in decreasing order of their number of observations. The total number of ecological field notations amounts to 2094. The number of observations on each of the more important species of woody plants (number of observations > 40), further indicated as hosts, is mentioned as well. The total number of species amounts to 147, distributed over the hosts as follows: *Alnus glutinosa* 84 species, *Salix aurita* 78, *S. cinerea* 73, *Betula spp.* 48, *Fraxinus excelsior* 41, *Corylus avellana* 29, *Quercus robur* 23, *Salix caprea* 22, *Salix repens* 19, *Myrica gale* 15 species. Part of the observations were made on the hybrid between *Salix aurita* and *S. cinerea* (*S. x multinervis*) and on wood that could not be identified as belonging to one of these species. These observations (9% of the total number on the two species) were equally assigned to either *S. aurita* or *S. cinerea*.

Table 8.1. Number of observations on Aphyllophorales and Heterobasidiomycetes on various host plant species in marshy forests

Abbreviations of host plant species: Al gl = Alnus glutinosa, Sa au = Salix aurita, Sa ci = Salix cinerea, Be sp. = Betula spp., Fr ex = Fraxinus excelsior, Sa ca = Salix caprea, Sa re = Salix repens, Qu ro = Quercus robur, Co av = Corylus avellana My ga = Myrica gale, Ot sp = other species, Tot = Total number of observations, Nr sp = Number of plant species.

| Host plant species | Al gl | Sa au | Sa ci | Be sp | Fr ex | Sa ca | Sa re | Qu ro | Co av | My ga | Ot sp | Tot | Nr sp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total number of observations | 661 | 515 | 415 | 113 | 75 | 55 | 53 | 49 | 47 | 44 | 67 | 2094 | |
| Cerocorticium confluens | 34 | 50 | 40 | 3 | 3 | 1 | 2 | 5 | 5 | 3 | 5 | 151 | 13 |
| Hyphoderma praetermissum | 21 | 41 | 21 | 2 | 2 | 14 | 6 | 2 | 1 | 3 | 2 | 115 | 13 |
| Trechispora mutabilis | 15 | 42 | 30 | 1 | 1 | 2 | | 4 | | | 2 | 97 | 8 |
| Schizopora paradoxa | 34 | 9 | 8 | 2 | 1 | | | 3 | 1 | 6 | 2 | 66 | 10 |
| Trechispora farinacea | 13 | 23 | 16 | 2 | 2 | | 1 | 1 | 2 | 3 | 1 | 64 | 10 |
| Peniophora cinerea | 18 | 24 | 8 | 1 | 1 | 4 | 1 | | 4 | | | 61 | 8 |
| Hyphoderma sambuci | 15 | 14 | 14 | | 1 | 2 | | | | | 10 | 56 | 9 |
| Hyphoderma puberum | 31 | 5 | 6 | 6 | 1 | | | 2 | 1 | | 1 | 53 | 8 |
| Hyphoderma setigerum | 27 | 8 | 7 | 5 | | 3 | | | 2 | | | 52 | 6 |
| Athelia epiphylla | 18 | 10 | 9 | 1 | 1 | | 10 | | 1 | | | 50 | 7 |
| Scopuloides hydnoides | 8 | 14 | 12 | 1 | 4 | | 5 | | 3 | | 2 | 49 | 8 |
| Hypochnicium eichleri ss. lat. | 18 | 8 | 5 | 9 | 1 | | | | 1 | 3 | 4 | 49 | 9 |
| Daedaleopsis confragosa | 17 | 15 | 11 | 4 | | 1 | | | | | | 48 | 5 |
| Inonotus radiatus | 44 | | 1 | 2 | | | | | | | | 47 | 3 |
| Bulbillomyces farinosus | 13 | 14 | 13 | 1 | 2 | | | 2 | | | | 45 | 6 |
| Sistotrema brinkmannii | 17 | 12 | 6 | 4 | | 2 | | | 1 | | 2 | 44 | 7 |
| Antrodia semipileata | 11 | 12 | 11 | 2 | | | | 1 | 1 | | 1 | 39 | 7 |
| Dacrymyces stillatus ss. lat. | 7 | 14 | 14 | | 2 | | | | 1 | | 1 | 39 | 6 |
| Hymenochaete tabacina | 1 | 19 | 15 | | | | | 1 | 1 | | 2 | 39 | 6 |
| Stereum rugosum | 22 | 8 | 1 | 3 | | | 1 | | 2 | 1 | | 38 | 7 |
| Hypochnicium bombycinum | 3 | 13 | 17 | 1 | | 1 | | | | | 2 | 37 | 6 |
| Macrotyphula fistulosa | 27 | 2 | | 4 | | | | | | | | 33 | 3 |
| Trechispora cohaerens | 12 | 11 | 7 | 1 | | | | 1 | 1 | | 1 | 34 | 7 |
| Vuilleminia comedens | 27 | 1 | 1 | 1 | | | | 2 | | | | 32 | 5 |
| Mycoacia uda | 6 | 5 | 10 | | 8 | | 1 | | | | | 30 | 5 |
| Phlebia radiata | 16 | | 1 | 3 | 1 | | | 6 | 1 | | 1 | 29 | 7 |
| Peniophora incarnata | 9 | 5 | 2 | 2 | 1 | 2 | 2 | | 1 | | 3 | 27 | 10 |
| Ceraceomyces serpens | 7 | 2 | 10 | | 1 | | | 3 | 1 | | 2 | 26 | 8 |
| Steccherinum robustius | 21 | 2 | 1 | 1 | | | | | | | 1 | 26 | 5 |
| Calocera cornea | 8 | 3 | 4 | 5 | 3 | | 1 | | 1 | | | 25 | 7 |
| Rigidoporus sanguinolentus | 11 | 5 | 2 | 2 | | | | 2 | | | 1 | 23 | 6 |
| Kneiffiella crustosa | 1 | 7 | 14 | | | | | | | | | 22 | 3 |
| Meruliopsis corium | | 8 | 8 | 2 | | 1 | | | | | | 19 | 4 |
| Phanerochaete velutina | 1 | 8 | | 1 | 1 | | 1 | | 3 | 4 | | 19 | 7 |
| Trametes hoehnelii | 18 | | 1 | | | | | | | | | 19 | 2 |
| Tyromyces caesius ss. str. | 1 | 1 | 14 | 1 | 1 | | | | | | | 18 | 5 |
| Platygloea peniophorae | 1 | 8 | 3 | | 1 | 3 | | | | | | 16 | 5 |
| Tomentella ellisii | 6 | 5 | 1 | | | 4 | | | | | | 16 | 4 |
| Stereum hirsutum | 7 | 2 | | 2 | | | | 1 | 1 | 1 | 1 | 15 | 7 |
| Ceriporia reticulata | 1 | 6 | 2 | | 3 | | | | 2 | | | 14 | 5 |
| Chondrostereum purpureum | 4 | | 1 | 9 | | | | | 1 | | | 15 | 4 |
| Gloeocystidiellum porosum | 1 | 3 | 3 | | | 6 | | | | | | 13 | 4 |
| Hymenochaete corrugata | 4 | | 1 | | | | | | 5 | | 3 | 13 | 6 |
| Botryobasidium subcoronatum | | 1 | | | | | | | | 10 | 1 | 12 | 3 |
| Cylindrobasidium evolvens | 5 | 3 | | | | 1 | | | | 1 | 2 | 12 | 5 |
| Peniophora cinctula | | 7 | 1 | | | 1 | 3 | | | | | 12 | 4 |
| Tulasnella lactea | 4 | 3 | 5 | | | | | | | | | 12 | 3 |
| Saccoblastia farinacea | | 8 | 3 | | | | | | | | | 11 | 2 |
| Sebacinella citrispora | | 2 | | | | | 5 | | | 4 | | 11 | 3 |
| Paullicorticium niveocremeum | 3 | 1 | 4 | 1 | 1 | | | | | | | 10 | 5 |
| Stereum subtomentosum | 9 | | | | 1 | | | | | | | 10 | 2 |
| Trametes versicolor | 2 | 1 | | 1 | 3 | | | | 1 | 1 | | 9 | 6 |
| Tyromyces subcaesius | 1 | | 6 | | 2 | | | | | | | 9 | 3 |

Table 8.1 continued

| Species | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Coniophora puteana | 4 | 1 | | 1 | | 2 | | | | 8 | 4 |
| Kneiffiella arguta | 2 | 5 | 1 | | | | | | | 8 | 3 |
| Tulasnella pruinosa | 4 | 1 | 1 | 1 | 1 | | | | | 8 | 5 |
| Bjerkandera adusta | 3 | | | | | | 3 | | 1 | 7 | 3 |
| Polyporus varius | | 1 | 4 | | 2 | | | | | 7 | 3 |
| Tomentella sublilacina | 4 | 2 | 1 | | | | | | | 7 | 3 |
| Thelephora terrestris f. resupinata | 3 | 1 | 1 | 1 | | | | | 1 | 7 | 5 |
| Tyromyces chioneus | 1 | | 1 | 5 | | | | | | 7 | 3 |
| Hapalopilus nidulans | 1 | 1 | 4 | | | | | | | 6 | 3 |
| Tremella mesenterica | | 2 | 3 | | 1 | | | | | 6 | 3 |
| Xenasma pseudotsugae | 2 | 1 | 1 | | | | | 2 | | 6 | 4 |
| Hypochnicium sphaerosporum | 3 | | | | 3 | | | | | 6 | 2 |
| Oxyporus populinus | | 1 | 4 | | | | | | | 5 | 2 |
| Piptoporus betulinus | | | | 5 | | | | | | 5 | 1 |
| Polyporus brumalis | 1 | | | 2 | 1 | | 1 | | | 5 | 4 |
| Steccherinum fimbriatum | | | | 4 | 1 | | | | | 5 | 2 |
| Tomentella fuscoferruginosa | 1 | 3 | | | | | | | 1 | 5 | 3 |
| Tomentellopsis submollis | | 4 | 1 | | | | | | | 5 | 2 |
| Basidioradulum radula | | 2 | | 2 | | | | | | 4 | 2 |
| Ganoderma applanatum | 4 | | | | | | | | | 4 | 1 |
| Gloeocystidiellum leucoxanthum | | 2 | 2 | | | | | | | 4 | 2 |
| Hyphodontiella multiseptata | | | | | | 4 | | | | 4 | 1 |
| Kneiffiella subalutacea | | | 2 | 1 | 1 | | | | | 4 | 3 |
| Merulius tremellosus | 1 | | 3 | | | | | | | 4 | 2 |
| Peniophora lycii | | | | 4 | | | | | | 4 | 1 |
| Peniophora quercina | | | | | | | 4 | | | 4 | 1 |
| Phanerochaete sordida | | 1 | | 1 | 1 | | | 1 | | 4 | 4 |
| Phellinus ferreus | | 4 | | | | | | | | 4 | 1 |
| Basidiodendron deminutum | 1 | 1 | 1 | 1 | | | | | | 4 | 4 |
| Tomentella neobourdotii | | 2 | | | | 2 | | | | 4 | 2 |
| Tomentella spec. A. | | | | | | 4 | | | | 4 | 1 |
| Trechispora mollusca | 1 | 1 | | 1 | | | | 1 | | 4 | 4 |
| Tulasnella violea | 1 | | 2 | | | | | 1 | | 4 | 3 |
| Athelia arachnoidea | 3 | | | | | | | | | 3 | 1 |
| Hypochnicium geogenium | | | 3 | | | | | | | 3 | 1 |
| Legarobasidium detriticum | 1 | 2 | | | | | | | | 3 | 2 |
| ncrustoporia nivea | 1 | | | 1 | 1 | | | | | 3 | 3 |
| Rigidoporus vitreus | 2 | 1 | | | | | | | | 3 | 2 |
| Sebacina podlachica | 1 | | | 1 | | | 1 | | | 3 | 2 |
| Stereum ochraceo-flavum | | 2 | 1 | | | | | | | 3 | 2 |
| Tomentella ramosissima | 2 | | 1 | | | | | | | 3 | 2 |
| Tulasnella albida | 1 | | 2 | | | | | | | 3 | 2 |
| Tyromyces lacteus | | | | 1 | 2 | | | | | 3 | 2 |

Remaining species, found only once or twice:
Aleurodiscus delicatus 1 × (Carex rostrata). – Antrodia albida 2 × (Salix cinerea, S. caprea). – Antrodia lindbladii 1 × (Fraxinus). – Athelia binucleospora 1 × (Salix repens). – Athelia spec. 1 × (Alnus). – Athelopsis lacerata 2 × (Salix aurita, Dryopteris). – Basidiodendron caesiocinereum 1 × (Quercus). – Botryobasidium candicans 2 × (Alnus, Salix cinerea). – Botryobasidium conspersum 1 × (Alnus). – Botryobasidium danicum 2 × (Myrica, Salix aurita). – Ceriporia excelsa 1 × (Betula). – Ceriporia viridans 1 × (Quercus). – Christiansenia pallida 1 × (Fraxinus). – Coronicium alboglaucum 1 × (Salix aurita). – Cristinia helvetica 1 × (Sorbus aucuparia). – Dacrymyces lacrymalis 1 × (Salix cinerea). – Dendrothele acerina 2 × (Salix × multinervis, S. cinerea). – Epithele typhae 1 × (Carex acutiformis). – Exidia truncata 1 × (Alnus). – Haplotrichum capitatum 2 × (Alnus). – Hyphoderma pallidum 1 × (Salix cinerea). – Hyphoderma roseocremeum 1 × (Salix cinerea). – Hyphoderma corrugata 1 × (Salix cinerea). – Leucogyrophana olivascens 1 × (Salix cinerea). – Mycoacia aurea 1 × (Alnus). – Oliveonia pauxilla 1 × (Typha). – Peniophora imitata 2 × (Fraxinus). – Peniophora nuda 1 × (Frangula alnus).– Peniophora pseudoversicolor 1 × (Salix aurita). – Phellinus ferruginosus 1 × (Salix aurita). – Phellinus igniarius 1 × (Salix aurita). – Phellinus pomaceus 1 × (Prunus spinosa). – Phlebia rufa 1 × (Betula). – Phlebiopsis roumeguerii 2 × (Alnus). – Polyporus badius 1 × (Corylus). – Polyporus ciliatus 1 × (Salix cinerea). – Ramaricium alboochraceum 1 × (Salix caprea). – Sistotrema diademiferum 1 × (Salix aurita). – Sistotrema estonicum 1 × (Alnus, on leave). – Sistotrema subpyriforme 1 × (Alnus). – Stereum gausapatum 2 × (Quercus). – Thelephora penicillata 1 × (litter of Salix repens). – Thelephora terrestris f. terrestris 1 × (Salix repens). – Trametes zonatella 1 × (Alnus). – Trechispora vaga 1 × (Myrica). – Trichaptum abietinum 1 × (Alnus). – Tulasnella calospora 1 × (Alnus). – Uthatobasidium fusisporum 1 × (Salix aurita). – Vararia gallica 1 × (Salix caprea). – Xenasmatella allantospora 2 × (Salix aurita, S. spec.).

These figures are not appropriate to demonstrate whether some hosts accomodate more species of Aphyllophorales and Heterobasidiomycetes than others since the latter numbers are positively correlated with the numbers of observations on each host. The numbers of observations on their turn depend on the abundance of the hosts in the plots. For instance, the numbers of species on *Quercus* and *Betula* may easily equal or surpass those on *Alnus* and *Salix* when the numbers of observations were comparable and in particular if all species occurring in the entire ecological range of the first named trees would be considered.

On the other hand, it is to be expected that the number of species on *Myrica* and *Salix repens* remains in reality relatively low compared to other hosts since the variety of microhabitats offered by these shrubs is much smaller, for instance by the lack of thick branches and trunks.

### 8.3.2 Numbers of observations on species of Aphyllophorales and Heterobasidiomycetes.

The number of observations of each fungal species can be regarded as a reasonable estimation of its relative abundance in the complete set of studied forest communities. Due to the applied methods it cannot be used to estimate or determine the absolute abundance (Vries, this vol.). Two groups of species are certainly underestimated: (1) the striking, abundant species by purpose since notations on those species were restricted within each plot, (2) the very unconspicuous, thin species on easily overlooked substrates, such as the underside of twigs.
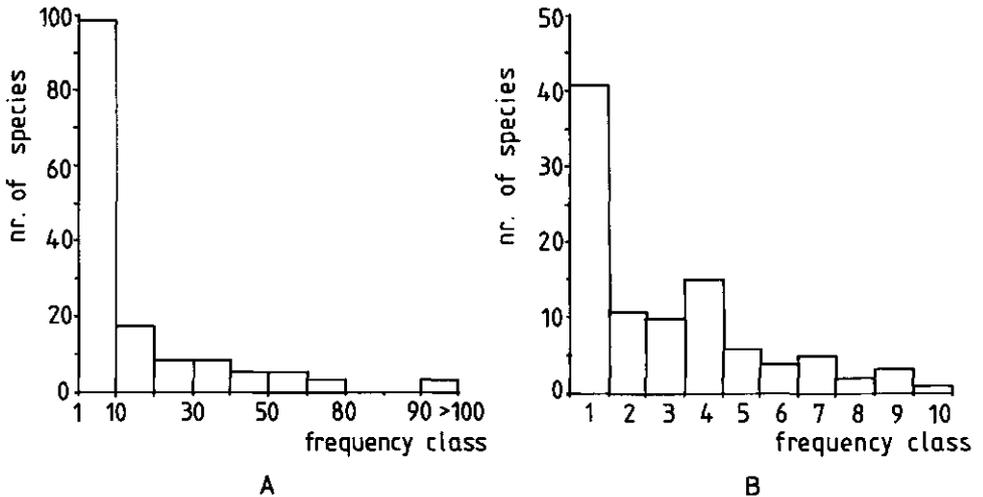


Fig. 8.1. Distribution of numbers of species of Aphyllophorales and Heterobasidiomycetes over classes of the total number of observations.
(a) classes with intervals of 10 observations
(b) subclasses with intervals of one observation for the class 1-10 observations only.

Table 8.2. Proportional frequency of Aphyllophorales and Heterobasidiomycetes on various host plant species in marshy forests.

Only species observed more than nine time are included.
For abbreviations of host species, see Table 8.1
Percentages > 75, indicating specialized species, are printed in italics (see text).

| Host plant species | Al gl | Sa au | Sa ci | Be sp | Fr ex | Qu ro | Sa ca | Sa re | My ga | Co av | Ot sp | Tot |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cerocorticium confluens | 23 | 33 | 26 | 2 | 2 | 3 | 1 | 1 | 2 | 3 | 3 | 151 |
| Hyphoderma praetermissum | 18 | 36 | 18 | 2 | 2 | 2 | 12 | 5 | 3 | 1 | 2 | 115 |
| Trechispora mutabilis | 15 | 43 | 31 | 1 | 1 | 4 | 2 | | | | 2 | 97 |
| Schizopora paradoxa | 52 | 14 | 12 | 3 | 2 | 5 | | | 9 | 2 | 3 | 66 |
| Trechispora farinacea | 20 | 36 | 25 | 3 | 3 | 2 | | 2 | 5 | 3 | 2 | 64 |
| Peniophora cinerea | 30 | 39 | 13 | 2 | 2 | | 7 | 2 | | 7 | | 61 |
| Hyphoderma sambuci | 28 | 25 | 25 | | | | 4 | | | | 18 | 56 |
| Hyphoderma puberum | 58 | 9 | 11 | 11 | 2 | 4 | | | | 2 | 2 | 53 |
| Hyphoderma setigerum | 52 | 15 | 13 | 10 | | | 6 | | | 4 | | 52 |
| Athelia epiphylla | 36 | 20 | 18 | 2 | 2 | | | 20 | | 2 | | 50 |
| Scopuloides hydnoides | 16 | 29 | 25 | 2 | 8 | | | 10 | | 6 | 4 | 49 |
| Hypochnicium eichleri ss. lat. | 37 | 16 | 10 | 18 | 2 | | | | 6 | 2 | 8 | 49 |
| Daedaleopsis confragosa | 35 | 31 | 23 | 8 | | | 2 | | | | | 48 |
| Inonotus radiatus | *94* | | 2 | 4 | | | | | | | | 47 |
| Bulbillomyces farinosus | 29 | 31 | 29 | 2 | 4 | 4 | | | | | | 45 |
| Sistotrema brinkmannii | 39 | 27 | 14 | 9 | | | 5 | | | 2 | 5 | 44 |
| Antrodia semipileata | 28 | 31 | 28 | 5 | | 3 | | | | 3 | 3 | 39 |
| Dacrymyces stillatus ss. lat. | 18 | 36 | 36 | | 5 | | | | | 2 | 2 | 39 |
| Hymenochaete tabacina | 3 | 49 | 38 | | | 3 | | | | 3 | 5 | 39 |
| Stereum rugosum | 58 | 21 | 3 | 8 | | | | 3 | 3 | 5 | | 38 |
| Hypochnicium bombycinum | 8 | 35 | 46 | 3 | | | 3 | | | | 5 | 37 |
| Macrotyphula fistulosa | *82* | 6 | 12 | | | | | | | | | 33 |
| Trechispora cohaerens | 35 | 32 | 21 | 3 | | 3 | | | | 3 | 3 | 34 |
| Vuilleminia comedens | *84* | 3 | 3 | 3 | | 6 | | | | | | 32 |
| Mycoacia uda | 20 | 17 | 33 | | 27 | | | | | | | 30 |
| Phlebia radiata | 55 | | 3 | 10 | 3 | 21 | | | | 3 | 3 | 29 |
| Peniophora incarnata | 33 | 19 | 7 | 7 | 4 | | 7 | 7 | | 4 | 10 | 27 |
| Ceraceomyces serpens | 27 | 8 | 38 | | 4 | 12 | | | | 4 | 8 | 26 |
| Steccherinum robustius | *81* | 8 | 4 | 4 | | | | | | | 4 | 26 |
| Calocera cornea | 32 | 12 | 16 | 20 | 12 | | | 4 | | 4 | | 25 |
| Rigidoporus sanguinolentus | 48 | 22 | 9 | 9 | | 9 | | | | | 4 | 23 |
| Kneiffiella crustosa | 4 | 32 | 64 | | | | | | | | | 22 |
| Meruliopsis corium | | 42 | 42 | 11 | | | 5 | | | | | 19 |
| Phanerochaete velutina | 5 | 42 | | 5 | 5 | | | 5 | 21 | 16 | | 19 |
| Trametes hoehnelii | *95* | | 5 | | | | | | | | | 19 |
| Tyromyces caesius ss. str. | 6 | 6 | *78* | 6 | 6 | | | | | | | 18 |
| Platygloea peniophorae | 6 | 50 | 19 | | 6 | | 19 | | | | | 16 |
| Tomentella ellisii | 37 | 31 | 6 | | 25 | | | | | | | 16 |
| Stereum hirsutum | 47 | 13 | | 13 | | 7 | | | 7 | 7 | | 15 |
| Chondrostereum purpureum | 27 | | 7 | 60 | | | | | | 7 | | 15 |
| Ceriporia reticulata | 7 | 42 | 14 | | 21 | | | | | 14 | | 14 |
| Gloeocystidiellum porosum | 8 | 27 | 19 | | | | 46 | | | | | 13 |
| Hymenochaete corrugata | 31 | | 8 | | | | | | | 38 | 23 | 13 |
| Botryobasidium subcoronatum | | 8 | | | | | | | *83* | | 8 | 12 |
| Cylindrobasidium evolvens | 42 | 25 | | | | | 8 | | 8 | | 17 | 12 |

Table 8.2 continued

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Peniophora cinctula | | 58 | 8 | | | 8 | 25 | | 12 |
| Tulasnella lactea | 33 | 17 | 50 | | | | | | 12 |
| Saccoblastia farinacea | | 73 | 27 | | | | | | 11 |
| Sebacinella citrispora | | 18 | | | | | 45 | 36 | 11 |
| Paullicorticium niveocremeum | 30 | 10 | 40 | 10 | 10 | | | | 10 |
| Stereum subtomentosum | 90 | | | | 10 | | | | 10 |

Figure 8.1A and B show the distribution of species numbers over classes of numbers of observations with equal intervals. It appears that only 15 species (10%) account for half of the number of observations. In reality their share is even higher due to the applied methods. No less than 40 species (27%) have been found only once.

At present no satisfactory explanation can be given for the high species diversity of wood-inhabiting fungi and the apparently high share of locally rare species. Species which were rarely observed are only exceptionally found on other than the dominant plant species in the forest communities. Their microhabitat seems in most cases not deviating from that of more common species (Arnolds & Keizer, in prep.).

*8.3.3 Host specificity and host preference of Aphyllophorales and Heterobasidiomycetes.*

The number of woody hosts on which each fungal species occurs within the studied forests is indicated in Table 8.1. It is striking that among the 51 more widespread species (total number of observations $\geq$ 10) not a single fungus is restricted to one host and that only three species are restricted to two hosts, viz. *Trametes hoehnelii, Saccoblastia farinacea* and *Stereum subtomentosum.* When the related *Salix aurita* and *S. cinerea* are regarded as a single host, *Saccoblastia farinacea* is the only widespread fungus exclusive on one host. In addition some species with low frequency exclusively occur on e.g. *Betula* (e.g. *Piptoporus betulinus*) and *Quercus* (e.g. *Peniophora quercina*). These observations agree with data in literature (e.g. Ryvarden, 1976-1978; Jahn, 1979). However, their total frequencies are too low to draw such conclusions on the basis of the present material only.

However, a large number of fungi were observed considerably more often on a certain host than on others. This is more manifest when the frequencies for all species are calculated, viz. the proportional number of observations on a certain host (Table 8.2). A fungus may be called specialized, if a large proportion of its observations is made on a single host. Specialized species – here arbitrarily defined as having at least 75% of its observations on one host – in the studied forests are on *Alnus: Inonotus radiatus, Trametes hoehnelii, Stereum subtomentosum, Vuilleminia comedens, Macrotyphula fistulosa* and *Steccherinum robustius*; on *Salix cinerea: Tyromyces caesius*; on *Salix aurita* and *S. cinerea*

together: *Hymenochaete tabacina, Hypochnicium bombycinum, Kneiffiella crustosa, Meruliopsis corium* and *Saccoblastia farinacea*; on *Myrica: Botryobasidium subcoronatum.*

When discussing the proportional frequency, the term preference has conciously been omitted since in our opinion preference also depends on the importance of the hosts, expressed in the total number of observations for each host. The figures for relative preference, indicated in Table 8.3, are corrected by dividing the percentages in Table 8.2 by the number of observations of all species on that host. In formula:

$$P \text{ rel.} = \frac{n_s \cdot 100}{n_t} \cdot \frac{100}{n_h}$$

P rel. = relative preference.
$n_s$ = frequency (number of observations) of a fungal species (s) on one host (h)
$n_t$ = total frequency (t) of that species on all hosts
$n_h$ = total frequency of all fungal species on host h.

The values of relative preference are only useful when a high number of observations ($n \geq 15$) is available. In other cases the relative preference is estimated too high for hosts with a low number of observations. It should be stressed that the value is necessarily restricted to the defined area and investigated plant communities (see conclusions and discussion).

From Table 8.3 it appears that the relative preference is often different from the degree of specialization, as defined earlier in this paper. Fungal species with a relative preference for a certain host are arbitrarily defined here as having a highest value of relative preference, which is at least twice as high as the next highest value. These species are on *Alnus: Ionotus radiatus, Steccherinum robustius* and *Trametes hoehnelii;* on *Salix cinerea: Kneiffiella crustosa* and *Tyromyces caesius ss. str.;* on *Betula: Chondrostereum purpureum;* on *Fraxinus: Mycoacia uda;* on *Quercus: Phlebia radiata, Ceraceomyces serpens* and *Rigidoporus sanguinolentus; on Salix caprea: Hyphoderma praetermissum, Platygloea peniophorae* and *Tomentella ellisii;* on *Salix repens: Athelia epiphylla;* on *Myrica: Schizopora paradoxa.*

### 8.3.4 Abundance of Aphyllophorales and Heterobasidiomycetes on various hosts.

A high degree of specialization or a high relative preference of a fungus on a certain host does not necessarily imply that this fungus is frequent on wood of that host. The relative abundance is expressed as the percentage that such a fungus takes of all fungal observations on that host. Diagrams of the relative abundance of the eight most frequent fungi on the four most common hosts are given in Fig. 8.2. The diagrams for the two species of *Salix* show much resemblance, whereas the diagrams for *Alnus* and *Betula* are very different from *Salix* and from each other.

The abundance of a fungal species is not necessarily representative of its

Table 8.3. Relative preference of Aphyllophorales and Heterobasidiomycetes on various woody plant species in marshy forests.

Only species observed over 14 times are included.
For abbreviations of host species, see Table 8.1
Figures indicating distinct preferences for one host (relative preference at least twice next highest value) are printed in italics (see text for explanation of figures).

| Host plant species | Al gl | Sa au | Sa ci | Be sp | Fr ex | Qu ro | Sa ca | Sa re | My ga | Co av | Ot sp | Tot |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cerocorticium confluens | 3.4 | 6.4 | 6.4 | 1.8 | 2.6 | 6.7 | 1.2 | 2.5 | 4.5 | 7.0 | 5.0 | 151 |
| Hyphoderma praetermissum | 2.8 | 6.9 | 4.4 | 1.5 | 2.3 | 3.5 | *22.1* | 10.0 | 5.9 | 1.9 | 2.6 | 115 |
| Trechispora mutabilis | 2.3 | 8.4 | 7.4 | 0.9 | 1.4 | 8.4 | 3.7 | | | | 3.1 | 97 |
| Schizopora paradoxa | 7.8 | 3.3 | 2.9 | 2.7 | 2.0 | 9.3 | | | *20.7* | 4.1 | 4.6 | 66 |
| Trechispora farinacea | 3.1 | 7.0 | 6.0 | 2.8 | 4.0 | 3.2 | | 3.0 | 10.7 | 6.6 | 2.4 | 64 |
| Peniophora cinerea | 4.5 | 7.6 | 3.1 | 1.5 | 2.2 | | 11.9 | 3.2 | | *14.0* | | 61 |
| Hyphoderma sambuci | 4.0 | 4.8 | 6.0 | | 2.7 | | 6.5 | | | | *27.1* | 56 |
| Hyphoderma puberum | 8.8 | 1.8 | 2.7 | 10.0 | 2.4 | 7.7 | | | | 4.0 | 2.9 | 53 |
| Hyphoderma setigerum | 7.8 | 3.0 | 3.2 | 8.5 | | | 10.5 | | | 8.1 | | 52 |
| Athelia epiphylla | 5.4 | 3.9 | 4.3 | 1.7 | 2.5 | | | *38.5* | | 3.7 | | 50 |
| Scopuloides hydnoides | 2.5 | 5.5 | 5.9 | 1.8 | 10.9 | | | *19.6* | | 13.0 | 6.2 | 49 |
| Hypochnicium eichleri ss. lat. | 5.5 | 3.2 | 2.4 | *16.3* | 2.7 | | | | 13.9 | 4.3 | 12.4 | 49 |
| Daedaleopsis confragosa | 5.3 | 6.0 | 5.5 | 7.3 | | | 3.8 | | | | | 48 |
| Inonotus radiatus | *14.1* | | 0.5 | 3.8 | | | | | | | | 47 |
| Bulbillomyces farinosus | 4.3 | 6.0 | 6.9 | 2.0 | 5.9 | 9.1 | | | | | | 45 |
| Sistotrema brinkmannii | 5.8 | 5.3 | 3.3 | 8.0 | | | 8.3 | | | 4.8 | 6.9 | 44 |
| Antrodia semipileata | 4.3 | 6.0 | 6.8 | 4.5 | | 5.2 | | | | 5.5 | 3.9 | 39 |
| Dacrymyces stillatus ss. lat. | 2.7 | 6.9 | 8.6 | | 6.8 | | | | | 5.5 | 3.9 | 39 |
| Hymenochaete tabacina | 0.4 | 9.4 | 9.2 | | | 5.2 | | | | 5.5 | 7.7 | 39 |
| Stereum rugosum | 8.7 | 4.1 | 0.6 | 7.0 | | | | 5.0 | 6.0 | 11.2 | | 38 |
| Hypochnicium bombycinum | 1.2 | 6.8 | 11.0 | 2.4 | | | 4.9 | | | | 8.2 | 37 |
| Macrotyphula fistulosa | 12.4 | 1.2 | | 10.7 | | | | | | | | 33 |
| Trechispora cohaerens | 5.3 | 6.2 | 5.0 | 2.7 | | 6.2 | | | | | | 34 |
| Vuilleminia comedens | 12.7 | 0.6 | 0.7 | 2.8 | | 12.8 | | | | 6.4 | 4.6 | 32 |

Table 8.3 continued

| Host plant species | Al gl | Sa au | Sa ci | Be sp | Fr ex | Qu ro | Sa ca | Sa re | My ga | Co av | Ot sp | Tot |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mycoacia uda | 3.0 | 3.2 | 8.0 | | 35.6 | | | | | | | 30 |
| Phlebia radiata | 8.3 | | 0.8 | 9.2 | 4.5 | 42.2 | | | | 7.3 | 5.2 | 29 |
| Peniophora incarnata | 5.0 | 3.6 | 1.7 | 6.6 | 4.9 | | 13.4 | 14.2 | | 7.9 | 16.8 | 27 |
| Ceraceomyces serpens | 4.1 | 1.5 | 9.2 | | 5.1 | 23.5 | | | | 8.2 | 11.7 | 26 |
| Steccherinum robustius | 12.2 | 1.5 | 0.9 | 3.4 | | | | | | | 5.8 | 26 |
| Calocera cornea | 4.8 | 2.3 | 3.8 | 17.7 | 16.0 | | | 7.7 | | 8.5 | | 25 |
| Rigidoporus sanguinolentus | 7.2 | 4.2 | 2.1 | 7.6 | | 17.8 | | | | 6.5 | | 23 |
| Kneiffiella crustosa | 0.7 | 6.2 | 15.2 | | | | | | | | | 22 |
| Meruliopsis corium | | 8.1 | 10.1 | 9.3 | | | 9.6 | | | | | 19 |
| Phanerochaete velutina | 0.8 | 8.1 | | 4.6 | 7.0 | | | 10.1 | 47.8 | 33.6 | | 19 |
| Trametes hoehnelii | 14.3 | | 1.3 | | | | | | | | | 19 |
| Tyromyces caesius ss. str. | 0.8 | 1.1 | 18.7 | 4.9 | 7.4 | | | | | | | 18 |
| Platygloea peniophorae | 0.9 | 9.6 | 4.5 | | 8.3 | | 34.1 | | | | | 16 |
| Tomentella ellisii | 5.7 | 6.0 | 2.3 | | | | 45.5 | | | | | 16 |
| Stereum hirsutum | 7.1 | 2.6 | | 11.8 | | 13.6 | | | 15.1 | 14.2 | 10.1 | 15 |
| Chondrostereum purpureum | 4.0 | | 1.6 | 53.0 | | | | | | 14.1 | | 15 |

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INONOTUS RADIATUS

SCHIZOPORA PARADOXA

CEROCORTICIUM CONFLUENS

HYPHODERMA PUBERUM

MACROTYPHULA FISTULOSA

VUILLEMINIA COMEDENS

HYPHODERMA SETIGERUM

STEREUM RUGOSUM
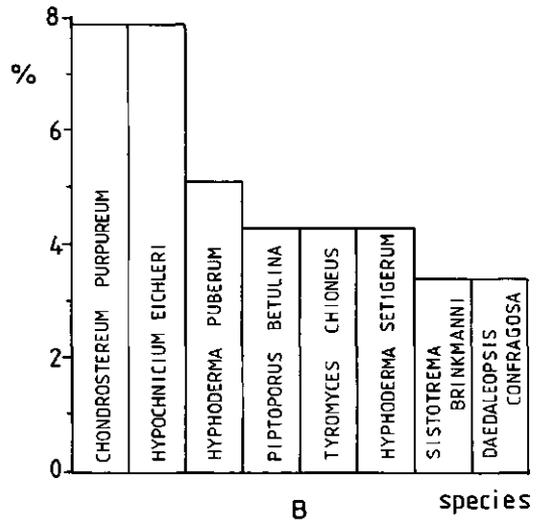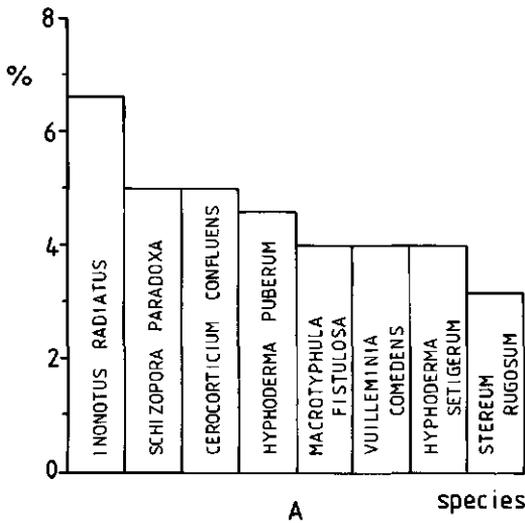
species

Alnus glutinosa (remaining species 63%)

**B**

8 %

6

4

2

0

CHONDROSTEREUM PURPUREUM

HYPOCHNICIUM EICHLERI

HYPHODERMA PUBERUM

PIPTOPORUS BETULINA

TYROMYCES CHIONEUS

HYPHODERMA SETIGERUM

SISTOTREMA BRINKMANNI

DAEDALEOPSIS CONFRAGOSA

species

Betula spp. (remaining species 60%)

**C**

10 %

8

6

4

2

0

CEROCORTICIUM CONFLUENS

TRECHISPORA MUTABILIS

HYPHODERMA PRAETERMISSUM

TRECHISPORA FARINACEA

PENIOPHORA CINEREA

HYMENOCHAETE TABACINA

DAEDALEOPSIS CONFRAGOSA

BULBILLOMYCES FARINOSUS
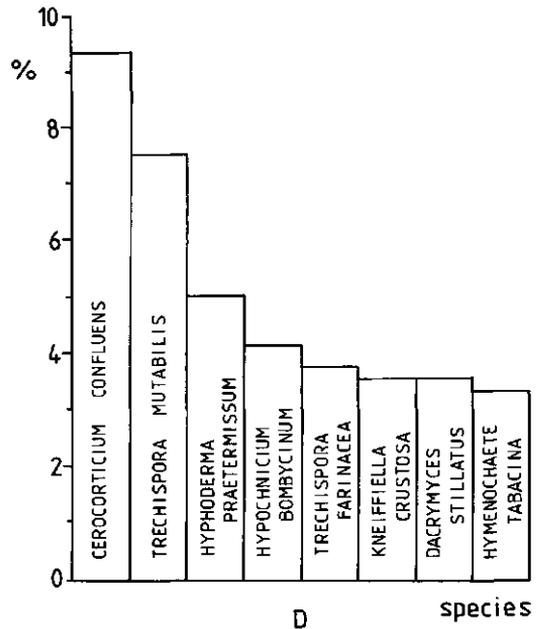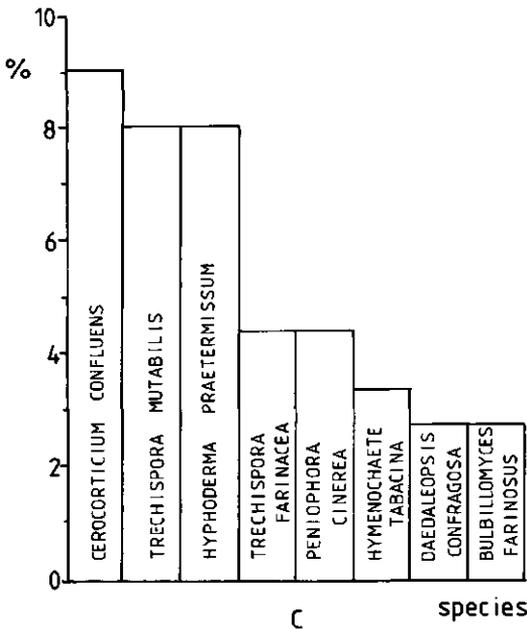
species

Salix aurita (remaining species 57%)

**D**

10 %

8

6

4

2

0

CEROCORTICIUM CONFLUENS

TRECHISPORA MUTABILIS

HYPHODERMA PRAETERMISSUM

HYPOCHNICIUM BOMBYCINUM

TRECHISPORA FARINACEA

KNEIFFIELLA CRUSTOSA

DACRYMYCES STILLATUS

HYMENOCHAETE TABACINA

species

Salix cinerea (remaining species 59%)

Fig. 8.2. Diagrams of the proportional frequency of the more important Aphyllophorales and Heterobasidiomycetes on *Alnus glutinosa* (A), *Betula spp.* (B), *Salix aurita* (C) and *Salix cinerea* (D).

importance in wood decay. This quality also depends on e.g. fastness of growing, deepness of penetration in the wood and volume occupied by a single mycelium. It is not possible to quantify these factors at present, but it is to be expected
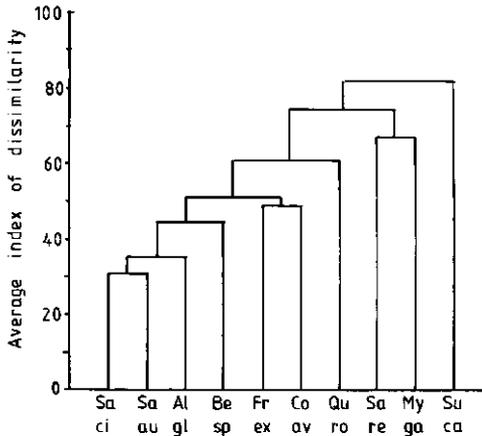
Fig. 8.3. Dendrogram, representing the affinity of the flora of Aphyllophorales and Heterobasidio-
mycetes on the more important host plant species. For abbreviations of host plants, see Table 8.1.
For explanation of the methods, see text.

that for example the vigorously growing *Daedaleopsis confragosa* is a more
important wood decomposer on *Salix aurita* than the more abundant *Trechi-
spora mutabilis*.

### 8.3.5 Affinity between the flora of Aphyllophorales and Heterobasidiomycetes on various hosts.

The affinity between the hosts as a substrate of Aphyllophorales and Hetero-
basidiomycetes was calculated using the index of similarity by Sørensen
(Mueller-Dombois & Ellenberg, 1974). This calculation was made on the basis
of presence or absence of fungal species only, because this qualitative criterion
was considered as having more biological significance than the ratio between
frequencies. On the basis of the similarity matrix a cluster analysis was carried
out, using the method of weighed reciprocal averaging described by Mueller-
Dombois & Ellenberg (1974) (Fig. 8.3). Instead of calculating the averages based
on the abundances in the original samples, the averages of the similarities have
been computed.

It appears that the flora of Aphyllophorales and Heterobasidiomycetes is
most similar between *Salix aurita* and *S. cinerea*. A high similarity was also
found with regard to the most important fungal species (8.3.4). It is striking
that the flora on the other two *Salix* species is widely different. Apparently in
this case the differences in structure of the vegetation and habitat between *Salix*
communities (see 8.2) are more important than taxonomic affinity. In this res-
pect it is also striking that a cluster is formed by *Corylus* and *Fraxinus*, both
of them characteristic of *Alno-Padion* on rich soils, and another cluster by *Salix
repens* and *Myrica gale*, both of them forming low, open scrubs (see 8.2).

## 8.4 Conclusions and discussion

Marshy forests and scrubs seem to constitute a very good habitat for wood inhabiting Aphyllophorales, both in quantitative sense (high abundance) and in qualitative sense (high species diversity). It is striking that many species were observed only once or twice. Part of the species are characteristic of these forest types and a considerable proportion is regarded as rare in western Europe (Arnolds, 1984; Ryvarden, 1976-1978; Eriksson & al., 1973-1984). During this investigation at least 31 species were recorded as new for the Netherlands (Keizer, 1985). This high number is also indicative of the very incomplete knowledge of this group of fungi in the Netherlands. The high species diversity and the occurrence of many rare species is not well understood on the basis of variation in green plants and microhabitats within these plant communities. Decomposition of wood is essential for carbon, nitrogen and mineral cycles in forest ecosystems (Frankland & al., 1982). The high diversity and local occurrence of organisms involved in this process hampers the simple modelling of this process.

The great species diversity in moist forests was demonstrated before by Grosse-Brauckmann & Grosse-Brauckmann (1983), who recorded 154 species of lignicolous Aphyllophorales in a large alluvial forest along the Rhine in Germany, and by Strid (1975), who observed 153 species in forests of *Alnus incana* in Central Norway.

Qualitative data on host range and host preference of wood-inhabiting fungi are included in many text books (e.g. Jahn, 1979; Eriksson, & al., 1973-1984; Ryvarden, 1976-1978). These authors did not indicate what is understood as preference: absolute frequency or relative preference as applied in this paper. Moreover it is usually unclear to which extent these data include literature accounts or original observations, and from which area and variety of habitats they originate. In the scope of this paper it is impossible to compare all our results with data on host preference in literature.

Quantitative data on host preference are scarce and always based on local studies (e.g. Grosse-Brauckmann & Grosse-Brauckmann, 1983). More similar data from many areas are necessary in order to obtain a reliable idea of host preference and frequency in a larger area. Such data are essential for the understanding of decomposition processes in various forest ecosystems, for the evaluation of the biological importance of forests (e.g. selection as nature reserves) and for the possible protection of rare fungal species.

The interpretation of frequency in terms of host preferences is enhanced with many problems:
1. Restriction of studies to certain habitats and a certain area may suggest false optima since only part of the potential hosts are present. A few examples are mentioned below. In this study *Tyromyces caesius* has a relative preference for *Salix cinerea*, but on the basis of own observations and literature it is most likely that its true optimum is on coniferous wood (e.g. Jahn, 1979). In the studied forests *Stereum hirsutum* is most frequent on *Alnus*, but it is

90

more abundant on *Quercus* wood in drier forests (e.g. Jahn, 1979). *Trichaptum abietinum* has been observed once on *Alnus*, but it is an abundant species on coniferous wood (Ryvarden, 1976-1978). In the studied plots *Mycoacia uda* has a relative preference for *Fraxinus*, whereas in Scandinavia it has a distinct optimum on *Alnus* (Eriksson & al., 1973-1984).

2. A reliable estimation of the relative frequency of Aphyllophorales and Heterobasidiomycetes is difficult, even within a restricted area, since the chance of observation varies for different species. This is especially true for the large number of species growing at the underside of fallen wood (Vries, this vol.).

3. The frequency of a certain fungus on a certain host is not necessarily indicative for host preference since some hosts are much more frequent than others. Calculation of the relative preference (see 8.3.3) is a better method, which corrects to a certain extent for this factor. However, the result is influenced by (a) the ratio of numbers of observations on different hosts (see 8.3.3); (b) the total number of fungal species that potentially are able to grow on a certain host; (c) the importance of the investigated group in wood decomposition, in this case Aphyllophorales and Heterobasidiomycetes. For example, in the studied plant communities these fungi were relatively scarce on *Myrica* wood and the potential species number on that host is much smaller than, for instance, the number on *Alnus*.

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# 9 On the quantitative analysis of wood-decomposing macrofungi in forests. I

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## Summary

The relation between plot size and number of species of wood-inhabiting macrofungi was studied in an even aged monoculture of *Picea abies*, planted in 1935, in Drenthe, the Netherlands. Four adjacent plots were studied of 0.5, 1, 2, 4, 8 and 16 m². In addition single nesting plots were studied of 32, 64, 125, 250, 500 and 1000 m². Fungi on all dead woody substrates were sampled and identified. In plots from 64 m² onward the sampling procedure was necessarily slightly less accurate.

The number of species of wood-inhabiting macrofungi increases continuously with increasing plot size. Consequently, no minimum area was established. On 1048 m² 60 species were found, the majority (75%) belonging to fungi with inconspicuous, tiny or thin carpophores and to crustose fungi growing at the underside of woody substrates. These groups of mainly hypoxylous fungi are usually neglected in mycocoenological studies, but contribute 44 % to the species diversity of all macrofungi (including terrestrial species) in this plot. The differences in species composition between the quadruplicate plots were considerable. Consequently, sampling of a few small plots is not an adequate method to study species diversity in wood-inhabiting macrofungi.

## 9.1 Introduction

The qualitative and quantitative composition of the mycoflora in ecosystems is usually described with mycocoenological methods (e.g. Arnolds, 1981; Winterhoff, 1984; Barkman, 1987). These methods have their limitations. Observations are restricted to macrofungi, a completely artificial group, arbitrarily defined by Arnolds (1984) as fungi with individual carpophores visible to the naked eye, that is larger than about 1 mm. The practical application differs from author to author. Some include small ascomycetes (e.g. Helotiales), others do not.

However, also among the unambiguous macrofungi as defined above, some groups are usually underestimated or neglected in forest ecosystems, viz. fungi with carpophores buried in the soil (hypogeous fungi: truffles and false truffles) and fungi fruiting at the underside of trunks, branches, twigs and other woody plant remains, subsequently indicated as hypoxylous fungi. Fungi on lateral and upper sides of wood are named epixylous fungi. Mycocoenological research in forests is usually carried out in permanent plots of ± 500-5000 m², studied repeatedly during several successive years. In practice it is impossible to dig up the entire area in search of hypogeous fungi or to turn all wood on the soil for hypoxylous fungi. A fundamental objection is the destructive character of such research because the numerous fungi fruiting in later periods cannot be observed

in this way. This is especially true for Agaricales with ephemeral basidiocarps.

Specialized studies on wood-decomposing Aphyllophorales have demonstrated that the majority belong to the hypoxylous fungi (Strid, 1975; Tortic, 1985). Quantitative data are lacking, however.

The present author attempts to develop methods for the quantitative analysis of wood-inhabiting macrofungi. Two approaches have been followed: determination of the relation between investigated surface and the observed species number ('minimum area') and accurate sampling of microplots of 1 m² in various forest communities. This paper treats the first aspect. Nomenclature of fungi is mainly according to Arnolds (1984); for species not mentioned in that list according to Jülich & Stalpers (1980) and Vries (1987).

## 9.2 Materials and methods

The species number of green plants in a homogeneous plant community increases when the studied surface is extended. Theoretically the increase will be zero when a certain surface is reached in which practically all plants of the stand are present. This surface is called the minimum area (Braun-Blanquet, 1964).

In a first attempt to determine the minimum area of wood-inhabiting fungi a very simple forest ecosystem was selected, viz. an even aged monoculture of *Picea abies,* planted in 1935. The plot was situated in the state forest near Dwingeloo, Drenthe (lot nr. 105). For some data on geography, pedology and climate of the area, see Keizer & Arnolds (this vol.). The herb layer in the plot covers less than 1%. The coverage of the moss layer is 70%, the more important species being *Campylopus flexuosus, Dicranum scoparium, Hypnum cupressiforme, Lophocolea heterophylla, Orthodontium lineare* and *Pohlia nutans.* The soil is a dry, sandy vague soil, mainly consisting of quartz sand poor in humus and loam, with a humus-rich top soil of 3-5 cm. The pH-H$_2$O in the top soil is 3.3-3.5, the C/N ratio $\pm$ 34.

The study started with the analysis of a plot of 0.5 m². The surface was doubled each time according to the principle of nesting plots (Braun-Blanquet, 1964), so that each larger plot includes all smaller plots studied before. Consequently the investigated surfaces were 0.5, 1, 2, 4, 8, 16, 32, 64, 125, 250, 500 and 1000 m², respectively. For practical reasons (see next paragraph) the surface was extended each time in only one direction (Fig. 9.1), whereas nesting plots are usually extended in all directions (Braun-Blanquet, 1964). This difference is not fundamental.

In addition three other plots of 0.5, 1, 2, 4, 8, and 16 m² were sampled, situated around the starting point of research (Fig. 9.1). These plots did not overlap each other in order to get an idea of variation in species number in the smaller plots. It was impossible to extend the quadruplication to the larger plots in the available time. Consequently the total investigated surface is 1048 m².

Within the plots up to 64 m² all visible (and sometimes hardly visible) fungi

94                                              *Wageningen Agric. Univ. Papers 90-6 (1990)*
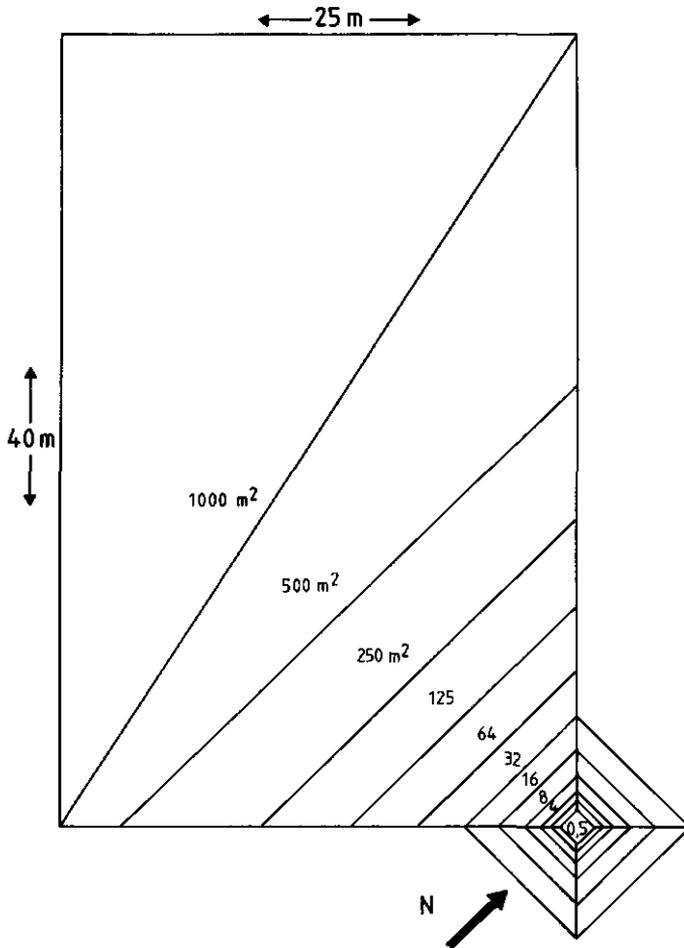
Fig. 9.1. Situation of nesting plots for determination of the relation between species number of wood-inhabiting macrofungi and plot surface.

on woody substrates were carefully collected in bags with parts of their substrate during October 1983. All collected pieces of wood were dried at ± 40°C and the fungi were identified afterwards in the laboratory. In the larger plots (>64 m²) complete sampling of all woody substrate became a practical impossibility. Fungi were collected here in a more selective way, although still very accurately compared to current mycocoenological research.

The identification of all fungi on the collected substrates was very laborious. In all 1634 identifications were made, which lasted several weeks. Within each enlarged partial plot a single species was not identified more than 100 times. In practice this means an underestimation of only one species, *Xenasma pseudotsugae*, in plots from 64 m² onwards (Table 9.1).

## 9.3 Results

On the entire surface of 1048 m² 60 taxa of wood-inhabiting fungi were observed, comprising 4 agarics, 6 polypores, 34 resupinate basidiomycetes, 8 heterobasidiomycetes, 1 gasteromycete and 7 ascomycetes. All taxa are listed in Table 9.1 with the number of identifications made with each doubling of the surface, expressed in a sixpartite scale. These figures are representative of the abundance of the respective taxa.

The fungi are divided into three groups according to their morphology and their position on the substrate:
1. fungi with prominent, often more or less pileate basidiocarps or ascocarps, e.g. all Agaricales, *Stereum* spp. and polypores.
2. resupinate fungi forming more or less thick, distinctly visible crusts, e.g. *Amphinema, Hyphoderma, Xenasma*.
3. resupinate fungi with thinner, pruinose or waxy basidiocarps and very small, easily overlooked ascomycetes, e.g. *Hyaloscypha, Basidiodendron, Tulasnella, Tubulicrinis.*

These groups are subsequently indicated for convenience sake as pileate fungi, crustose fungi and inconspicuous fungi, respectively. This grouping is arbitrary and the groups are not clearly delimitated. Some species may be assigned to two groups, because for instance thin and thicker basidiocarps are growing together. The division is based on the local conditions in the plot. Crustose and inconspicuous fungi together are mainly hypoxylous, the pileate fungi epixylous.

Only the first group is normally involved in mycocoenological research, although comprising only 15 species (25% of the total number) and 210 identifications (13%). The crustose fungi comprise 24 species (40%) and the bulk of observations, viz. 1254 (77%). The inconspicuous fungi comprise 21 species (35%) and 120 observations (7%). The importance of the latter group is certainly underestimated in spite of the special attention paid to them.

The average number of identifications per added square meter amounts in the plots going from 0.5, 1...1000 m² to 5, 13, 20, 7, 6, 5, 8, 6, 3, 1.4, 1 and 0.6. This number depends on the quantity of dead wood, especially variable in the smallest plots, and on the sampling intensity. The systematically decreasing numbers from the surface of 125 m² onwards reflect the less intensive sampling procedure in large plots.

The relation between species number and studied surface is given in Fig. 9.2, which is also subdivided for the three morphological groups distinguished above. The curve shows a weak sigmoid shape, but not a distinct flattening as would be expected when the minimum area is reached. The weak flattening in plots larger than 64 m² is probably an artefact due to the less accurate sampling method. Consequently the minimum area for wood-inhabiting fungi is not reached on a surface of 1000 m², in spite of the extreme homogeneity of structure and species composition of the investigated plant community.

The variability in species diversity between the four plots up to 16 m² is considerable. The number of taxa ranges from 1 to 4 in plots of 0.5 m², 1 to 14 in
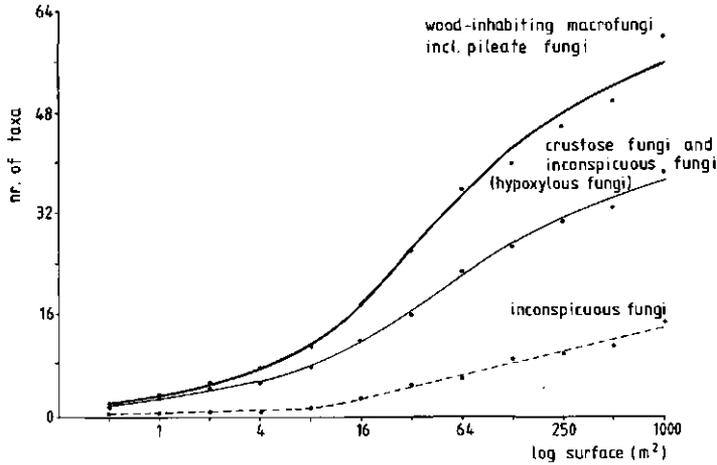
Fig. 9.2. The relation between species number of wood-inhabiting macrofungi and plot surface. The figures for plots up to 16 m² relate to average species numbers in four plots; for larger plots to the species number in one plot only.

plots of 4 m² and from 9 to 21 in plots of 16 m² (Table 9.1). The similarity in floristic composition is low (Table 9.2): at a surface of 0.5 m² not a single species of wood-decomposing macrofungi is common to all four plots of that size; at 4 m² only one species and at 16 m² five species. In plots of 16 m² still 14 species (42%) are only present in one plot. These data indicate that spatial variation in wood-decomposers in a forest is large. In methodological respect it implies that accurate study of few small plots cannot give a reliable impression of lignicolous fungi in forests.

## 9.4 Conclusions and discussion

The determination of a (theoretical) minimum area for fungal communities is complicated by the short duration of many carpophores, strong periodicity and strong annual fluctuations of carpophore formation. This phenomenon is well-documented for agarics (e.g. Arnolds, 1985; Thoen, 1976), but it is without doubt also important for many Aphyllophorales, especially species with thin, ephemeral basidiocarps. The incompleteness of sampling can be demonstrated in this case for agarics with generally more ephemeral basidiocarps because traditional mycocoenological research was carried out in the plot of 1000 m² during the years 1981-1984. In these years 12 species of wood-inhabiting agarics were observed against 4 during the study of the minimum area. Consequently the number of species is in fact considerably higher than established during a single sampling. However, repeated sampling is impossible in this case since it is neces-

Tabel 9.1: Frequency of lignicolous fungi in plots of different size in a Picea plantation near Dwingeloo (Netherlands). The frequency of each species in each subplot is indicated in a sixpartite scale: 1 = 1 carpophore, 2 = 2-3 carp., 4 = 10-29 carp., 5 = 30-99 carp., 6 = more than 99 carpophores. Frequencies are not accumulative and relate to carpophore numbers, added with the doubling to a certain surface.

The table gives, for the regions NORTH, EAST, SOUTH and WEST (each divided over surfaces of .5, 1, 2, 4, 8 and 16 m²) and over cumulative plot sizes (16, 32, 64, 125, 250, 500, 1000), the frequency of each species, together with the total number of observations.

'Pileate' fungi — Number of species, accumulative

| Species | Number of observ. |
|---|---|
| Dacrymyces stillatus | 61 |
| Mycena galericulata | 25 |
| Galerina camerina | 37 |
| Tyromyces rennyi | 20 |
| Tyromyces caesius | 10 |
| Tyromyces sericeomollis | 6 |
| Heterobasidion annosum | 3 |
| Stereum sanguinolentum | 3 |
| Calocera viscosa | 2 |
| Hypholoma fasciculare | 39 |
| Ascocoryne spp. | 1 |
| Hypholoma capnoides | 1 |
| Sphaerobolus stellatus | 3 |
| Trichaptum abietinum | 1 |
| Tyromyces stipticus | 1 |

'Crustose' fungi — Number of species, accumulative

| Species | Number of observ. |
|---|---|
| Xenasma filicinum | 730 |
| Kneiffiella breviseta | 87 |
| Botryobasidium subcoronatum | 98 |
| Hyphoderma praeterrissum | 46 |
| Trechispora farinacea f.farinacea | 45 |
| Coniophora arida | 113 |
| Resinicium bicolor | 31 |
| Amphinema byssoides | 11 |
| Paullicorticium niveocremeum | 6 |
| Trechispora vaga | 26 |
| Asterostroma laxum | 5 |
| Hyphoderma pallidum (tsugae) | 7 |
| Achroomyces peniophorae | 4 |
| Ceracorticium hiemale | 3 |
| Phanerochaete sanguinea | 10 |
| Thelephora terrestris f.resupinata | 7 |
| Coniophora puteana | 2 |
| Hyphoderma puberum | 3 |
| Tomentella spec. | 12 |
| Ceraceomyces sublaevis | 1 |
| Hyphoderma spec. | 1 |
| Kneiffiella alutaria | 1 |
| Trechispora farinacea f.elevata | 1 |
| Tylospora asterophora | 1 |

| | NORTH | | | | | | EAST | | | | | | SOUTH | | | | | | WEST | | | | | | | | | | | Number of observ. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Surface in m² | .5 | 1 | 2 | 4 | 8 | 16 | .5 | 1 | 2 | 4 | 8 | 16 | .5 | 1 | 2 | 4 | 8 | 16 | 1 | 2 | 4 | 8 | 16 | 32 | 64 | 125 | 250 | 500 | 1000 | |
| Cover of visible dead wood % | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | <1 | 1 | 2 | 1 | 1 | 60 |
| Total species number accumulative | <1 | 1 | 1 | 1 | 4 | 9 | 4 | 4 | 4 | 8 | 13 | 21 | 2 | 5 | 9 | 14 | 17 | 19 | 4 | 7 | 8 | 12 | 21 | 26 | 36 | 40 | 46 | 50 | 60 | |
| 'Inconspicuous' fungi | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Number of species, accumulative | 0 | 0 | 0 | 0 | 2 | 3 | 0 | 0 | 0 | 2 | 3 | 7 | 1 | 1 | 1 | 5 | 5 | 6 | 2 | 2 | 2 | 2 | 6 | 8 | 13 | 13 | 15 | 17 | 21 | 46 |
| Orbilia cf berberidis | | | | 1 | 1 | 1 | | | | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 3 | 2 | 17 |
| Tubulicrinis accedens | | | | | | | | | 1 | | | | | | | | | | | | 1 | | | 1 | 1 | 2 | | 2 | 1 | 11 |
| Ascocorticium anomalum | | | | | | 1 | | 1 | | | | 1 | | | 2 | 1 | | | | | | 1 | 1 | 1 | 2 | 1 | 1 | | 1 | 8 |
| Basidiodendron deminutum | | | | | | 1 | | | | | | | | | | | | | | | | | 1 | 1 | 2 | | 1 | | 1 | 8 |
| Tubulicrinis juniperinus | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | | | 2 | | | 7 |
| Basidiodendron cinereum | | | | | | | | | | | | | | | | 1 | | | | | | | 2 | | | | | | | 4 |
| Tubulicrinis regificus | | | | | | | | | | | | 1 | | | 1 | | | | | | | | | 1 | 1 | 1 | 1 | 1 | 1 | 2 |
| Hyaloscypha leuconica | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | | 3 |
| Mollisia species div. | | | | | | | | | | | | | 1 | | | | 1 | 1 | | | | | | | 1 | | | | | 2 |
| Sebacinella nodosa | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 2 |
| Tulasnella allantospora | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | 1 |
| Basidiodendron caesiocinereum | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | 1 |
| Ceratobasidium cornigerum | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | 1 |
| Dasyscyphus virgineus | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | 1 |
| Hyaloscypha hyalina | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 |
| Paullicorticium pearsonii | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | 1 |
| Repetobasidium americanum | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | | | | | | 1 |
| Sistotrema brinkmannii | | | | 1 | | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 |
| Sistotrema commune | | | 1 | 1 | | | | | | | | | | | | | | | | | | | 1 | | | | | | 1 | 1 |
| Sistotrema coroniferum | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 | 1 |
| Sistotrema efibulatum | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | 1 | 1 |

Table 9.2. Number of taxa of wood-decomposing macrofungi (n) in different numbers of plots of a particular size. Four plots of each size were investigated.

| Surface of plot m$^2$ | 0.5 | 1 | 2 | 4 | 8 | 16 |
|---|---|---|---|---|---|---|
| Total nr. of taxa (in 4 plots) | 5 | 8 | 13 | 16 | 25 | 33 |
| n in 1 plot | 3 | 4 | 7 | 7 | 13 | 14 |
| n in 2 plots | 1 | 3 | 5 | 4 | 5 | 6 |
| n in 3 plots | 1 | – | – | 4 | 5 | 8 |
| n in 4 plots | – | 1 | 1 | 1 | 2 | 5 |

sary to remove a considerable part of woody substrates and therefore the method is partially destructive.

It is remarkable that a single accurate sampling in this plot furnishes 60 species, of which 45 are not found with traditional mycocoenological methods. For comparison: during 4 years 58 species of macrofungi were found in this plot, comprising 19 ectomycorrhizal species, 24 terrestrial saprophytes and 25 lignicolous fungi. As a consequence hypoxylous species contribute no less than 44% to the species diversity of macrofungi.

The minimum area for wood-inhabiting fungi is not reached at a surface of 1000 m$^2$. It is questionable whether a methodological minimum area does exist in reality. According to most recent authors it cannot be demonstrated in green plant communities as well (e.g. Barkman, 1984). From an ecological point of view it is astonishing that so many species of macrofungi can grow together on one type of substrate (wood of *Picea*) in an extremely homogeneous environment. It is true that several microhabitats can be distinguished, e.g. on the basis of the size and degree of decomposition of the wood, but our knowledge cannot explain at present the great species diversity. Hypoxylous fungi are also important in quantitative respect (84% of all observations on lignicolous fungi) and therefore without doubt play an important role in the decomposition process of wood (Barkman & al., 1985).

Mycocoenological studies have strongly underestimated or neglected hypoxylous fungi so far. The sampling method described above is extremely laborious and therefore only appropriate in order to get fundamental information on this problem. It is important to develop methods to sample hypoxylous fungi in a practical way. Two possibilities can be mentioned:
1. Selective sampling of all available types of woody substrates in a plot. This method can give a reasonable, although necessarily incomplete, semi-quantitative picture of the species composition (e.g. Keizer & Arnolds, this vol.). No exact comparable data are available, but on empirical grounds it seems reasonable to estimate that in this way ± 75% of the wood-decomposing fungi present in a plot of ± 1000 m$^2$ will be observed in reality.
2. Accurate sampling of one or a few small partial plots (e.g. 1 m$^2$) within a large plot. This method can give a reasonable picture of the quantitative importance of the more abundant species, but many species may occur only outside these small plots (Vries, in prep.).

A combination of these two methods will probably give optimal results (Vries, in prep.).

## Acknowledgements

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# 10 Effects of fertilization on the mycoflora of a pine forest

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## Summary

A 25-year old pine forest on sand was subjected to a series of fertilization experiments. Three types of fertilization experiments were executed, viz. a factorial experiment with mineral nutrients (K, P, Ca, Mg), a liming experiment, and an experiment with liquid manure. The number of ectomycorrhizal species were significantly decreased after application of P and Ca in the first experiment, after liming, and after application of liquid manure. Litter decomposing fungi also significantly decreased after application of Ca and P in the first experiment and after liming, whereas application of liquid manure lead to an non-significant decrease. This decline is correlated with a (slight) increase in litter thickness. Except for *Pluteus atricapillus*, wood decomposing fungi are not yet affected by the fertilization treatments.

## 10.1 Introduction

The decrease of vitality of trees in large parts of Europe and industrialized countries abroad has caught the attention by both sylviculturalists and forest ecologists. Concomitant with this decrease in tree vitality, drastic changes in the macromycete flora have been noted (Arnolds, 1988). It seems very likely that these latter changes have large impacts on the functioning of forest ecosystems too.

There is much discussion about the causes of such a dramatic decrease in tree vitality. Frequently, a clear correlation with patterns of air pollution ('acid rain') has been demonstrated, although an unequivocal demonstration of a direct causal effect turned out to be far more difficult.

In the Netherlands both acidifying substances and nitrogenous compounds such as ammonia have been held responsible for this decline, which locally resulted in complete stand die-back. Especially nitrogenous compounds are considered to be very important, because (coniferous) trees have evolved under conditions of nitrogen shortage and most coniferous forests in the Netherlands are planted on nutrient-poor, nitrogen-poor, acid soils. Under such circumstances large additional amounts of ammonia-nitrogen can be expected to have strong destabilizing effects on forest ecosystems.

The natural nitrogen enrichment for Dutch forest ecosystems amounts to about 10-20 kg N/ha.yr, whereas an average additional deposition of 50 kg N/ha.yr has been measured. This latter figure shows large regional variation. In

the southeastern part of the Netherlands (De Peel) data in excess of 500 kg N/ha.yr have been measured.

Although much research remains to be done on the exact causes of stand die-back in various parts of the Netherlands, the paramount influence of nitrogenous compounds seems reasonable as a working hypothesis.

Equally important for the time being seems research that is aimed towards mitigating the effects of air pollution on forests. Although there seems to be consensus about the desirability of drastically reducing emission of both sulphur- and nitrogen-containing compounds, such measures are only slowly being accepted by national parliaments. Mainly for that reason short-term measures to bring forest decline to a stand-still are urgently needed.

Forest fertilization has been assumed to be such a measure, although its usefulness to increase wood-production is being mentioned as well. The main rationale for forest fertilization is to be found in the observation that concentrations of other essential elements such as K, P, Mg, and Ca are usually too low in situations where an excess of N is present. Calculations indicate, however, that such a corrective fertilization is only feasible when the N-deposition is less than 130 kg/ha.yr.

Research on the effects of forest fertilization has usually been directed towards assessment of the effects on tree growth or wood increment. Knowledge of the effects on other ecosystem components is, however, urgently needed before such a corrective fertilization can be applied on a large scale.

Not much is known about the effects of fertilization on the ectomycorrhiza-forming and saprotrophic macrofungi. Negative effects of N-fertilization on both groups have been noted in different countries, e.g. Poland (Heinrich & Wojewoda, 1976), German Democratic Republic (Ritter & Tölle, 1978), Federal Republic of Germany (Meyer, 1984), Finland (Ohenoja, 1978), and United States of America (Menge & al., 1977). The effects described by these authors resemble the effects that are now noted in heavily polluted regions such as the Netherlands (Arnolds, 1988). Much less work has been done on the effects of other types of fertilization on the mycoflora.

Fiedler & Hunger (1963) studied the effect of liming on the mycoflora of a Norway spruce forest (*Picea abies*). Nine years after the application of lime or dolomite these authors noted a clear decrease in productivity and diversity of mycorrhiza-forming fungi. On the other hand, litter decomposing fungi increased in both diversity and productivity. A pH-effect was considered to be largely responsible for these changes in species composition and productivity. Despite of the decrease in ectomycorrhiza-forming fungi, the increment of *Picea abies* was not inhibited. Hora (1959) noted a tremendous decrease of fruit-bodies of the mycorrhiza-forming *Lactarius rufus* (Scop.: Fr.) Fr. after liming a Scots pine forest (*Pinus sylvestris*).

Mycological research is often restricted to a study of the above-ground sporocarps of macrofungi. Fortunately, measures of above-ground species diversity, density and/or productivity are also good estimators of below-ground diversity and density (Agerer, 1985; Jansen & Nie, 1988).

In this paper some preliminary results after two years of observing sporocarps are reported. Independent work on the diversity and density of ectomycorrhiza, and on a quantification of mycelial activity are also executed.


## 10.2 Materials and Methods

**Description of study site**: the study site is located in the municipal forest of the municipality Harderwijk, prov. Gelderland, the Netherlands (km-sq. 26-47-54). It consists of a plantation of *Pinus sylvestris* of about 25 years old. The soil is sandy and has a pH (KCl) of about 4.0 in the uppermost 25 cm. Within this site 72 plots, each 22 m x 25 m = 550 m² have been laid down, and these plots have been subjected to different fertilization schemes (see below). In order to eliminate edge effects, the mycocoenological relevés have been made in subplots, each 12 m x 15 m = 180 m².

**Description of fertilization treatments**: Three different experiments have been carried out simultaneously. The first experiment should give an answer to the question whether the excess of N-compounds can be more effectively used when K, Ca, Mg, and P are applied. Each element is applied separately and also in all possible combinations, resulting in 16 different treatments (inclusive of a control).

The used quantities and the time of application of the fertilizers are indicated in Table 10.1.

The second experiment is a liming experiment. In September 1986 CaCO₃ in quantities of resp. 3, 6, 9, and 18 t/ha (the latter was applied in two equal doses in the autumn of 1986 and spring of 1987) was applied. These plots were fertilized simultaneously with K, Mg, and P in quantities as in the first experiment.

Finally an experiment with liquid manure was carried out. Manure of both calves (KM) and ducks (EM) was applied, supplemented with P, K, Mg, and Ca to the same level of fertilization as in the first experiment (see Table 10.2).

Each experiment is carried out in three replicates. A map showing the different plots with their respective treatments is given in Fig. 10.1.

**Mycocoenological methods**: The plots were visited in September, October, and November 1986, and in July, September, and October 1987. Unfortunately, both years were rather poor from a mycofloristic point of view.

The separate mycocoenological relevés have been combined into one synthetic relevé. Density of mycorrhizal species has been counted exactly, whereas density of litter-inhabiting and wood-inhabiting saprophytes has been estimated according to the scale as suggested by Barkman (1976). In the synthetic relevé the maximum number of carpophores per year (mACy, see Arnolds, 1981), transformed according to that same scale, are indicated.

Table 10.1. Quantity and time of application of different fertilizers in the factorial experiment.

| nutrient | quantity (kg/ha) | time of application |
|---|---|---|
| P | 104 kg $P_2O_5$ | autumn 1985 |
| K | 120 kg $K_2O$ | spring 1986, 1987, 1988 |
| Mg | 166 kg MgO | spring 1986, 1987, 1988 |
| Ca | 1680 kg CaO | autumn 1985 |

Table 10.2. Quantities of nutrients (kg/ha) in the liquid manure experiment.

| object | t/ha | N | $P_2O_5$ | $K_2O$ | CaO | MgO |
|---|---|---|---|---|---|---|
| KM1 | 20 | 60 | 58 | 120 | 10 | 6 |
| KM2 | 20 | 60 | 114 | 120 | 120 | 166 |
| EM2 | 11 | 71 | 114 | 120 | 120 | 166 |

Staircase plots (top):

| 72 EM 2 | | | |
|---|---|---|---|
| 71 O | 70 KM 1 | | |
| 69 KM 1 | 68 KM 2 | | |
| 67 O | 66 EM 2 | 65 KM 2 | |
| 64 EM 2 | 63 KM 2 | 62 O | 61 KM 1 |

Lower grid plots:

| 60 PKCa | 59 K | 58 PKMg | 57 Ca | 56 PKCaMg | 55 KMg | 54 PCa | 53 O | 52 3ton k | 51 18ton k |
|---|---|---|---|---|---|---|---|---|---|
| 50 P | 49 PCaMg | 48 KCaMg | 47 Mg | 46 CaMg | 45 PK | 44 PMg | 43 KCa | 42 6ton k | 41 9ton k |
| 40 PMg | 39 KCa | 38 PKCaMg | 37 KMg | 36 KCaMg | 35 Mg | 34 PCaMg | 33 PKMg | 32 9 ton k | 31 3 ton k |
| 30 PCa | 29 CaMg | 28 O | 27 PK | 26 Ca | 25 K | 24 PKCa | 23 P | 22 6ton k | 21 18ton k |
| 20 PK | 19 O | 18 CaMg | 17 KCa | 16 Mg | 15 PKMg | 14 P | 13 K | 12 9 ton k | 11 3ton k |
| 10 PKCaMg | 9 PCa | 8 KMg | 7 PMg | 6 KCaMg | 5 Ca | 4 PCaMg | 3 PKCa | 2 18ton k | 1 6ton k |

Fig. 10.1. The different plots with their respective treatments. k = lime; KM1 = manure of calves without addition; KM2 = manure of calves with nutrients added; EM2 = manure of ducks with nutrients added (see text for further explanation).

Table 10.3. Fungi found in the pine plantation of Harderwijk with their maximal numbers of present carpophores.
scale: 0 = present, not counted. 1 = 1-2, 2 = 3-5, 3 = 6-9, 4 = 10-30, 5 = 30-100, 6 = > 100 carpophores
P. = presence in number of plots.

| P. | plotnumbers: | UNTREATED 1 2 5 6 6 7 / 9 8 3 2 7 1 | K 1 2 5 / 3 5 9 | Mg 1 3 4 / 6 5 7 | P 1 2 5 / 4 3 0 | K Mg 0 3 5 / 8 7 5 | K P 2 2 4 / 0 7 5 | Mg P 0 4 4 / 7 0 4 | K Mg P 1 3 5 / 5 3 8 | Ca 0 2 5 / 5 6 7 | Ca P 0 3 5 / 9 0 4 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Mycorrhiza forming species** | | | | | | | | | | |
| 46 | Lactarius hepaticus | 2 1 1   3 1 | 2 3 4 | 1 2 2 | 1 1 1 | 1 3 3 | 3 4 | 1 1 | 1 1 1 | 1 | 1 |
| 23 | Paxillus involutus | 1   3 1 1 | | | 1 | 1 | | | | 2 | |
| 16 | Laccaria bicolor | 3   4 2 | | | 4 | 2 2 | 2 | 1 | 1 1 | | |
| 11 | Xerocomus badius | 1 | | 1 1 | 1 | 1 | 1 1 | | | | |
| 6 | Amanita gemmata | | | 1 | 1 | | | | | | |
| 6 | Russula ochroleuca | | | 1 | 1 1 | 1 | 1 | | | | |
| 5 | Hygrophorus hypothejus | | 1 | | 1 | | | 1 | 1 | | |
| 5 | Laccaria proxima | 2 | 2 | | | 4 | | | | 1 | |
| 4 | Inocybe lacera | | | | | | 2 1 | | | | |
| 1 | Amanita rubescens | | | | | | | 1 | | | |
| 1 | Laccaria spec. | | | | | | | 1 | | | |
| 1 | Lactarius rufus | | | | | | 1 | | | | |
| 1 | Russula emetica | | | | | 2 | | | | | |
| 1 | Tricholoma albobrunneum | 1 | | | | | | | | | |
| | **Litter decomposing species** | | | | | | | | | | |
| 70 | Marasmius androsaceus | 5 6 4 4 5 4 | 4 4 4 | 6 4 4 | 4 4 4 | 4 3 4 | 4 4 4 | 4 4 4 | 5 4 4 | 4 2 4 | 4 4 2 |
| 51 | Clitocybe vibecina | 4 5 4 4 4 4 | 4 4 6 | 5 4 4 | 4 4 4 | 4 5 4 | 4 5 4 | 2 5 4 | 4 4 4 | 2 2 | 1 2 |
| 50 | Hygrophoropsis aurantiaca | 2   1 1 4 4 | 2 | 1 | 4 2 | 4 | 2 2 4 | 2 1 4 | | 2 2 4 | 2 |
| 47 | Clitocybe metachroa | 2 1 | 1 | | 2 | | | 1 1 | 4 | 4 4 4 | 2 5 4 |
| 45 | Clitocybe ditopa | 1 1 2 | 1 | 1 | 1 | 1 1 | 1 | 1 1 | | 4 4 4 | 4 2 4 |
| 40 | Mycena sanguinolenta | 2 2 2 2 1 | 2 4 | 4 2 4 | 1 1 | 4 5 2 | 4 | 2 | 1 2 | 2 1 2 | |
| 38 | Cystoderma jasonis + amianth. | 1 2 2 2 4 2 | 1 1 4 | 2 1 1 | 1 2 | 2 2 1 | 1 1 2 | 1 1 | 1 1 2 | 2 | 1 |
| 38 | Galerina atkinsoniana | 4 4   2 2 2 | 2 2 2 | 4 1 4 | 4 4 4 | 1 4 2 | 4 4 | 2 1 1 | 4 2 2 | 1 1 | 1 |
| 32 | Entoloma cetratum | 2 2 2 1 2 2 | 4 2 1 | 1 2 2 | 2 2 1 | 2 2 1 | 2 4 1 | 2 1 1 | 2 1 1 | | |
| 30 | Mycena galopus | 1   1 1 | | 2 | 1 4 | | 1 2 | 1 | 2 | | 1 4 |
| 29 | Galerina hypnorum sl | 2 4 4   2 2 | 2 5 2 | 4 4 4 | 2 2 2 | 2 2 2 | 2 5 2 | 2 2 | 2 1 1 | | |
| 27 | Mycena speirea | | | | | | | | | 1 2 1 | 2 2 |
| 21 | Mycena epipterygia | 2 | 1 2 | 1 1 1 | 1   1 | 4 | 1 | 1 1 | 2 1 | | |
| 13 | Galerina calyptrata | 5 4 2 | 4 2 2 | 1 4 | 2 | 1 | | 1   2 | | 2 | |
| 9 | Entoloma turbidum | 1 | | | 1 | | 2 1 | | | | |
| 8 | Mycena metata | 1 | | | | | | 1 | | 2 | 4 2 |
| 6 | Mycena cinerella | 4 | | 2 | 1 | 4 | | | | | 1 |
| 4 | Galerina allospora | | 1 1 | | | 1 1 | | | | | |
| 4 | Galerina mniophila | 1 | | 2 | | 2 1 | | | | | |
| 2 | Galerina pumila | 2 | | | | | | | | | |
| 2 | Galerina stylifera | | | | | | | 2 | | | 1 |
| 2 | Lepista sordida + nuda | | | | | | | | | 2 | 2 |
| 2 | Myxomphalina maura | | | | | | | | | | |
| 2 | Panaeolus olivaceus | | | | | | | | | | |
| | **Wood decomposing species** | | | | | | | | | | |
| 69 | Trichaptum abietinum | 0   0 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 |
| 71 | Panellus mitis | 4 4 4 5 4 4 | 2 4 4 | 4 4 4 | 4 4 4 | 4 5 5 | 4 4 2 | 4 4 4 | 4 4 4 | 4 4 4 | 4 4 4 |
| 56 | Hypholoma capnoides | 4 1 1   1 | 1 4 2 | 1 1 2 | 1   5 | 5 2 2 | 4 1 | 5 2 | 4 1 1 | 4 4 2 | 4 4 |
| 61 | Skeletocutis amorpha | 0 0 0 0 0 0 | 0 | 0 0 | 0 0 0 | 0 0 | 0 0 0 | 0 0 0 | 0 0 | 0 0 0 | 0 0 0 |
| 66 | Stereum sanguinolentum | 0   0 0 0 | | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0   0 | 0 0 0 | 0 0 0 | 0 0 0 |
| 55 | Baeospora myosura | 2 1   1 1 1 | 1 1 | 2   1 | 1 2 1 | 1   1 | 1 1 1 | 1 2 1 | 1 1 | 1 1 | 1 1 |
| 58 | Dacrymyces stillatus | 0 0 0   0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 | 0 | 0 0 0 | 0 0 0 | 0 0 0 |
| 43 | Tricholomopsis rutilans | 1 1 2 1 1 1 | 1 | 1 1 | 1 1 | 2 | 1 1 | 1 1 | 1   1 | 1   1 | |
| 44 | Gymnopilus penetrans | 4   1 4 | 2 4 2 | 2 | 1   4 | 1 2 2 | 2 | 1 2 | 1   4 | 2 4 | |
| 39 | Hypholoma fasciculare | 1 2 | 4 4 | 5 1 | 2   4 | 5   4 | 2 2 2 | 4 2 | 2 | 4 4 1 | 5 4 4 |
| 36 | Tyromyces caesius | 0 0 | | 0 0 | 0 0 | 0 0 0 | 0 | 0 0 | | 0 0 0 | 0 0 0 |
| 36 | Calocera furcata | 0   0 0   0 | | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 0 0 0 | 0 0 |
| 31 | Pluteus atricapillus | | | | | | | | | 1 1 | 1 1 |
| 44 | Tremella encephala | 0   0 0 | 0 0 | 0 0 0 | 0 0 | 0   0 | 0 0 | 0   0 | 0 0 | 0 0 | 0 0 |
| 16 | Mycena galericulata | 1 | | | | 1 1 | 1 | 1 | | 1   1 | |
| 14 | Galerina camerina | 2 | | 2 | 1 | 4 4 1 | 2 | 1 | | | 1 |
| 3 | Schizopora paradoxa | | | | | | | | | | 0   0 |
| 3 | Sphaerobolus stellatus | | | | | | | | | | |
| 2 | Calocera viscosa | | | | | | | | | | |
| 3 | Heterobasidion annosum | | | 0 | | | | | | | 0 |
| 4 | Antrodia lindbladii | | | | | | | 0 | | | |
| 3 | Ascocoryne spec. | | | | | | 0 | | | | |

The saprophytic species below were found once in plotnumbers:
Ascocorticium anomalum : 33, Collybia maculata : 63, Collybia cirrhata : 64, Conocybe magnicapitata : 38, Ischnoderma benzoinum : 38, Mycena tenerrima : 6, Panaeolus acuminatus : 39, Peziza badia : 27, Peziza vesiculosa : 2, Pholiota astragalina : 61, Pluteus semibulbosus : 5, Polyporus ciliatus : 11, Tephrocybe ambusta : 47, Trichophaea abundans : 32, Tyromyces leucomallellus : 27.

| CaK | CaMg | CaMg | CaK P | CaMgK | CaMgKP | LIME3 | LIME6 | LIME9 | LIME18 | CALF2 | DUCK2 | CALF1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 3 4 | 1 2 4 | 0 3 4 | 0 2 6 | 0 3 4 | 1 3 5 | 1 3 5 | 0 2 4 | 1 3 4 | 0 2 5 | 6 6 6 | 6 6 7 | 6 6 7 |
| 7 9 3 | 8 9 6 | 4 4 9 | 3 4 0 | 6 6 8 | 0 8 6 | 1 1 2 | 1 2 2 | 2 2 1 | 2 1 1 | 3 5 8 | 4 6 2 | 1 9 0 |

First block:

|  | 3 1 | 2 2 3 |  | 1 | 1 2 1 | 1 2 |  | 3 4 |  | 2 |  | 3 |  | 1 | 2 1 | 3 1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  | 1 2 1 |  |  | 2 |  |  |  | 1 | 2 |  | 1 | 4 | 3 | 3 | 3 4 4 | 2 4 |
|  |  | 4 |  |  |  |  |  |  |  |  |  |  |  | 1 3 4 | 1 1 |
|  | 1 | 1 |  |  |  |  |  |  |  | 1 | 1 |  |  |  |  |
|  |  | 1 |  |  |  | 1 |  |  |  | 1 |  | 1 |  |  |  | 1 |
|  |  | 1 1 |  |  |  |  |  |  |  |  |  |  |  | 1 |  |
| 1 |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |

Second block:

| 4 4 2 | 4 2 2 | 4 2 4 | 2 2 4 | 4 2 2 | 4 4 2 | 2 2 4 | 1 1 1 | 1 2 1 |  | 2 | 2 2 2 | 4 2 4 | 6 4 5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 4 |  | 4 | 2 2 2 | 1 4 | 2 2 | 1 2 | 2 | 2 1 | 2 |  | 1 | 2 4 | 2 4 |
| 1 1 4 | 1 2 | 2 4 | 2 | 4 2 | 2 1 | 2 | 2 2 4 | 1 4 2 | 2 4 | 2 4 4 | 2 4 5 | 4 4 4 |
| 4 5 2 | 6 4 | 4 2 4 | 4 5 6 | 5 2 4 | 4 2 | 5 4 5 | 4 4 | 1 1 | 2 2 | 6 6 5 | 5 4 4 | 4 2 4 |
| 4 2 2 | 2 2 | 5 2 4 | 4 5 2 | 5 4 4 | 2 5 4 | 4 4 2 | 2 |  |  | 4 5 2 | 2 1 4 |
| 1 | 1 1 | 2 1 2 | 2 1 | 4 1 | 1 | 1 1 1 | 2 |  | 1 1 |  |  | 1 |
| 1 1 | 1 | 1 |  |  |  |  |  |  | 1 | 1 2 1 | 1 | 2 2 2 |
| 1 1 |  |  |  |  | 1 |  |  |  |  | 1 4 1 | 1 1 | 2 1 |
| 1 |  |  |  |  |  |  |  |  |  | 1 1 | 1 | 1 |
|  | 1 2 1 |  | 2 2 4 |  | 2 2 |  | 2 |  |  | 2 2 2 | 2 1 | 1 2 1 |
|  |  |  |  |  |  |  | 2 |  |  |  | 1 | 2 |
| 1 1 1 | 1 2 2 | 2 1 | 1 2 | 2 2 1 | 1 1 | 2 | 1 1 | 1 | 2 1 1 |  |  |  |
|  | 1 |  | 1 | 2 1 | 1 |  |  |  |  |  |  | 1 2 |
|  | 1 |  | 1 |  |  |  | 1 | 1 |  |  |  |
|  | 1 |  |  |  |  | 1 | 1 |  |  |  | 1 |
|  |  |  |  |  |  |  |  |  |  | 1 |  |
|  |  |  |  |  |  |  |  |  |  | 1 |  | 1 |

Third block:

| 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 | 0 0 0 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 4 4 4 | 4 4 4 | 4 2 4 | 4 4 4 | 2 4 4 | 4 4 4 | 4 4 4 | 4 4 4 | 4 2 | 2 4 4 | 4 4 4 | 6 4 4 | 4 4 4 |
| 1 2 | 2 5 4 | 2 4 | 2 5 2 | 6 2 | 5 1 2 | 2 2 2 | 6 2 4 | 4 2 | 4 1 | 2 | 1 4 | 2 |
| 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 | 0 0 0 | 0 | 0 0 | 0 0 |
| 0 0 0 | 0 0 0 | 0 0 | 0 0 0 | 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 |
| 1 1 |  | 1 | 1 2 2 | 4 1 1 | 2 1 2 | 1 1 | 2 2 | 2 1 | 1 1 1 | 1 2 1 | 2 2 |
| 0 0 | 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 0 | 0 0 | 0 0 0 | 0 0 | 0 0 | 0 | 0 0 | 0 0 |
| 2 1 1 | 1 | 1 2 2 | 1 | 2 1 1 | 1 1 | 1 | 1 2 | 1 | 1 | 2 4 1 |
| 1 2 | 2 4 | 1 2 | 4 5 1 | 2 1 | 1 | 1 4 2 | 2 | 1 2 | 2 1 1 | 1 2 | 2 1 4 |
| 1 | 4 2 | 4 4 | 4 4 2 | 2 2 | 4 | 5 2 | 4 |  | 4 |
| 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 | 0 0 | 0 | 0 | 0 | 0 |
| 0 0 0 | 0 0 | 0 0 | 0 0 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1 | 1 2 | 1 1 1 | 1 1 2 | 2 1 1 | 2 1 1 | 1 1 2 | 1 1 | 1 | 1 1 | 1 1 | 1 1 |
| 0 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 2 | 0 0 0 | 0 0 | 0 0 0 | 0 | 0 0 |
| 1 1 | 1 1 | 2 | 2 | 1 | 2 | 1 | 2 |
|  | 0 |  | 2 2 |
| 0 |  | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 |
|  | 0 | 0 | 0 | 0 | 0 0 |

Tabel 10.4. Diversity of ectomycorrhizal and litter-saprotrophic macrofungi in the different treatments (average number of species/treatment).

|  | ectomycorrhiza | saprophytes |
|---|---|---|
| control (n = 3) | 1.6 ± 0.6 | 11.0 ± 1.0 |
| + Mg  (n = 24) | 1.9 ± 1.7 | 8.3 ± 2.2 |
| − Mg  (n = 24) | 1.6 ± 1.1 | 9.0 ± 2.1 |
| + K    (n = 24) | 1.8 ± 1.4 | 8.2 ± 1.9 |
| − K    (n = 24) | 1.7 ± 1.5 | 9.0 ± 2.4 |
| + P    (n = 24) | 1.3 ± 1.3** | 8.0 ± 2.0* |
| − P    (n = 24) | 2.3 ± 1.4 | 9.2 ± 2.2 |
| + Ca  (n = 24) | 1.2 ± 1.3** | 7.3 ± 1.7*** |
| − Ca  (n = 24) | 2.3 ± 1.3 | 9.9 ± 1.8 |
| lime   (n = 12) | 1.0 ± 0.9 | 4.8 ± 1.6*** |
| control (n = 3) | 3.7 ± 0.6 | 9.3 ± 1.2 |
| manure (n = 9) | 2.1 ± 0.8*** | 7.9 ± 1.5 |

*: significant at $p < 0.05$; **: significant at $p < 0.01$; *** significant at $p < 0.005$.

Table 10.5. Effect of applying calcium on ectomycorrhizal fungi.

|  | with Ca<br>(n = 36) | without Ca<br>(n = 27) |
|---|---|---|
| Laccaria bicolor (+ proxima) | 6% | 48%** |
| Lactarius hepaticus | 47% | 89% |
| Xerocomus badius | 11% | 26% |
| Paxillus involutus | 25% | 26% |

*: significant at $p < 0.05$; **: significant at $p < 0.01$.

## 10.3  Results and Discussion

The results of the mycocoenological investigations are presented in Table 10.3.

In 1986 53 species were found, in 1987 55 species were found; 34 species were found in both years. It is clear from these data that the number of species found hitherto are rather small. This may partly be explained by unfavourable weather conditions during both years. However, the possibility that the forest is rather species-poor should not be excluded. Species densities are also very low and follow the same pattern.

Despite these restricted diversities and densities some general patterns can be noted.

Mycorrhizal species (Table 10.4) are not affected by fertilization with either

108

Table 10.6. Effect of applying calcium on saprotrophic fungi.

|  | with Ca (n = 36) | without Ca (n = 27) |
|---|---|---|
| Entoloma cetratum | 3% | 100%*** |
| Galerina atkinsoniana | 17% | 93%*** |
| G. hypnorum (+ calyptrata) | 8% | 100%*** |
| Cystoderma jasonis | 19% | 89%*** |
| Clitocybe vibecina | 58% | 100% |
| Clitocybe ditopa | 75% | 44% |
| Clitocybe metachroa | 86% | 26%** |
| Mycena speirea | 75% | 0%*** |
| Pluteus atricapillus | 75% | 0%*** |

**: significant at $p < 0.01$; ***: significant at $p < 0.001$.

K or Mg, whereas fertilization with P and Ca show a significantly negative effect ($p < 0.01$). The liming experiment also resulted in a negative effect and the lowest species diversity was observed here. The application of manure also had a strongly negative effect in comparison with the control plots ($p < 0.005$). However, the plots of the third experiment showed higher species diversity than those of the first and second experiment. *Betula verrucosa* is also more common in these plots (61 to 72), and this may provide a partial explanation of the higher diversity in the plots of the third experiment.

Most ectomycorrhiza-forming species were sensitive to the application of lime (Table 10.5). Only *Paxillus involutus* (Batsch: Fr.) Fr. was unaffected by lime. This species is also common in the manured plots. Laiho (1970) noted that a fertilisation with N lead to a distinct increase of that species which is able to utilise both ammonium and nitrate. Chemical analysis indicated an increased availability of nitrate after liming and manuring and therefore supports this explanation.

Saprotrophic fungi (Table 10.4) also show a decrease in species diversity after application of P and Ca in the first experiment ($p < 0.05$ and $p < 0.005$ respectively). This decrease is far more dramatic in the second liming experiment ($p < 0.001$). The application of liquid manure had a non-significant effect on species diversity in comparison with the control ($0.05 < p < 0.10$).

Several saprotrophic species turned out to be sensitive to calcium, but a few species were mainly restricted to these limed plots (Table 10.6). We also noted the presence of several grassland fungi such as *Conocybe magnicapitata* P.D. Orton, *Panaeolus acuminatus* (Schaeff.) Quél., and *P. olivaceus* F.H. Moell. after the application of lime or manure. Although their occurrence leads to an increase in total species diversity, it is not self-evident that such an increase should be valued unambiguously positive.

Concomitant with this decrease in species diversity, an increase in thickness of the litter layer has been observed (Hekstra, pers. comm.). This pattern was somewhat more marked in the relatively dry year 1986 than in the moist year

1987. Except for the manured plots differences in thickness of the litter layer are not statistically significant.

Although it is as yet difficult to attach statistical significance to the correlation between decrease in species diversity and increase in litter thickness, this correlation might well be of biological significance and it is therefore in need of a tentative explanation.

It has almost been axiomatic in decomposition ecology that the rate of decomposition at initial stages is limited by the nitrogen-content of the substrate, and that the C/N-ratio has to be lower than about 25 (i.e. a nitrogen content of about 2.3%) before effective decomposition takes place (cf Swift & al., 1979). This theory predicts that fertilization with either liquid manure or lime leads to increased pH, increased nitrogen availability, and hence higher decomposition rates. However, observations after two years seem to suggest a distinct retardation in decomposition rate, thereby falsifying the above theory.

Recent studies on decomposition indicate that the above concept only holds for substrates rich in (holo)cellulose and poor in lignin. For lignin-rich substrates on the other hand a negative effect of various nitrogen sources on ligninolytic activity was found by Kirk & Fenn (1982). A slowing down of decomposition is hence to be expected when nitrogen availability in lignin-rich litter is increased.

Besides such direct enzyme repression, this negative effect may also be caused by chemical reactions between amino-acids and phenolic groups in partly degraded lignin, where recalcitrant intermediates are formed (Stevenson, 1982).

Recent studies indicate that forest fertilization may increase the lignin level in needle and needle litter (Berg, 1986) and this combination of litter with high amounts of nitrogen and lignin may exert a negative effect on decomposition. If this phenomenon is of a more general nature, forest fertilization (even if aimed at correction of an unbalanced nutrient availability) might well have unexpected adverse effects.

Both liming and manuring lead to an increase in pH of the litter layer of about two units (from 4.0 to 6.0). This pH change probably shifts the competitive equilibrium between fungi and bacteria. Although nitrogen is released by bacterial activity, a very recalcitrant fraction will remain. If this is true, it also explains why this effect has not been noted before in other experiments, because the nitrogen-enrichment is peculiar to the Dutch situation. In other countries, no adverse effects on litter decomposition because of liming practices have been recorded.

Wood-decomposing fungi seem as yet hardly affected by the various treatments. Only *Pluteus atricapillus* (Batsch) Fayod is restricted to the lime and manure treatments (Table 10.3; $p < 0.001$). Apparently substrate quality is not yet affected by the fertilization, because these trunks are lying above the litter layer and therefore are outside the direct influence of improved nutrient supplies.

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