Simulation of growth and competition in mixed stands of Douglas-fir and beech

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Simulation of growth and competition in mixed stands of Douglas-fir and beech

H.H. Bartelink

Proefschrift
ter verkrijging van de graad van doctor
op gezag van de rector magnificus,
dr. C.M. Karssen,
in het openbaar te verdedigen
op vrijdag 13 maart 1998
des namiddags te 4 uur in de Aula.

Bartelink, H.H.

Simulation of growth and competition in mixed stands of Douglas-fir and beech.
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Thesis Landbouwuniversiteit Wageningen - With summary in Dutch -

ISBN: 90-5485-834-6

Voor mijn ouders

Voor Els en onze kinderen

Abstract

For a long time, the emphasis in silviculture in Western Europe was solely on even-aged, monospecific stands; many empirical stand-level growth models were developed and successfully used for managing such stands. In contrast, no generally accepted growth and yield approach has emerged so far for mixed forests. Moreover, the inexhaustible number of species combinations, management regimes, and site-dependent interactions make an empirical approach less suitable.

In the present study, a mechanistic model was developed that simulates growth and yield in mixed forest stands. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and beech (*Fagus sylvatica* L.) were used in this research. In the model, tree growth is dependent on radiation availability. Stand development is largely driven by competition for radiation. A spatial module was developed to investigate the effects of tree and stand characteristics on radiation interception. The study showed that in heterogeneous stands a spatial approach is needed to account for competition between trees.

Growth of the trees was estimated using the radiation-use efficiency concept (RUE). Results revealed that detailed process models can be used to estimate RUE and that it is a suitable tool for (mixed) forest modelling.

To describe the distribution of the dry matter growth, a separate module was developed using functional relationships between tree components: the dry matter distribution is driven by the aim to maintain structural balances within the tree. The study showed that this approach is able to reproduce the development of an individual forest tree. The approach was thus considered very suitable for modelling the effects of between-tree competition for resources on growth and development of mixed forest stands.

The overall growth model, COMMIX, was applied to investigate the effects of stand composition on mixed stand productivity, using a replacement series. Analysis showed that the productivity of mixed forest stands is generally somewhere in between the yield levels of the monocultures of the less productive and the most productive species. It will only be possible to achieve higher yields in mixed stands if these stands have a relatively small proportion of the sub-dominant species. In the case of Douglas-fir and beech, the maintenance of a mixed stand appeared to conflict with the maximization of the wood production.

Insufficient data are available on mixed stands to directly support decision taking in forest management. New research tools capable of providing forest managers with information on possible management scenarios and on the consequences of certain management regimes are therefore urgently required. The present modelling approach is part of an ongoing development of models for mixed stands. The infinite variety of possible species mixtures coupled with the range of environmental conditions under which mixtures might be grown, necessitates a mechanistic approach and emphasises the potential use of such models.

Keywords: allometry, allocation, beech, biomass, competition, Douglas-fir, functional relationship, light extinction, mechanistic model, mixed forest, partitioning, pipe-model, radiation use efficiency, root-shoot balance, sapwood, simulation, spatial model, structural balance, thinning.

Preface

Above all, many thanks are due to Frits Mohren (IBN-DLO): this thesis was realized, probably only because he suggested it, and strongly encouraged me to do it. His enthusiasm, as well as his serious support in my research over the past 8 years, were very motivating and ensured that I finally was able to finish this study. His straightforward supervision (best characterized by the words 'Wat een onzin!') was very motivating, and made this research project a challenging experience.

As a result of several discussions on forests and simulation modelling, the idea established to investigate growth and competition in mixed species stands with the help of a mechanistic simulation model. Once the idea was born, promoters had to be looked for. Because of the production-ecological aspects of the proposed study, links were established with the (former) department of Theoretical Production Ecology (TPE): I owe many thanks to Prof Rudy Rabbinge, who made it possible to carry out my study within the C.T. de Wit Research School of Production Ecology, and who remained very engaged during the project. Prof Jan Goudriaan (TPE) agreed to become the principal promoter: he surprised me several times with refreshing ideas and view-points on the research, which definitely resulted in much more interesting papers. His support throughout the years is greatly acknowledged. Prof Aad van Maaren from the (former) department of Forestry also agreed to act as a promoter, for which I am very grateful. His critical remarks and supporting comments during the final stage of the PhD work were of great help in sharpening the thesis. Many thanks are due to 'good old' Hans Jansen (Forestry dept.), my 'retaining pillar' and statistical back-up, who on several occasions provided me with statistical solutions and anecdotes.

At the department of Forestry, Pieter Schmidt gave me the opportunity to do the research, and, in the second half of the project, gave me several weeks off for writing papers. Prof Marius Wessel and Frans Bongers strongly encouraged me and kept me moving by asking (at the end almost daily) about the state-of-the-art of the work. I also owe a lot of thanks to Jan den Ouden, who has been a great help and supported my work through discussion and reviewing (I still owe him a beer or two). Leo Goudzwaard assisted me in the biomass study, and provided me with many growth and yield data from field plots: the best memories, however, are about pancakes.

I probably should have started these acknowledgements with my colleagues from the IBN-DLO, since they provided me during all these years with a very friendly and productive working atmosphere and with useful critical remarks, and supported me on several occasions. They greatly contributed in making this research project a nice and challenging effort. Irma Jorritsma is greatly acknowledged, for her contribution to discussions as well as for her support in many other ways. Ad van Hees taught me how to take a view, and, especially, how not to change one's point of view: the discussions and professional quarrels we had strongly motivated me, and made other people close their doors. I also owe thanks to Koen Kramer: his fundamental interest in biological processes and simulation models guaranteed that he significantly contributed to many discussions about the research. Finally, thanks are due to Ad Olsthoorn, who drew my attention to the below-ground world of roots.

But there are much more people who, one way or another, made this work possible. I would like to thank my colleagues from the department of Forestry of the WAU for their general support and discussions, and for creating a nice working climate: despite several stormy developments at the university, I have experienced 'Hinkeloord' as a pleasant working environment. In particular, I would like to thank the (ex-) PhD-boys Jan den Ouden, Toon Rijkers, Frank Sterck, Patrick Jansen, and Sander Wijdeven for their deep-digging discussions, especially at lunch time. Ellen Wilderink and Willem Scholten assisted in biomass analysis and providing material and suitable working conditions. I got much support from the administrative staff as well; especially Joke Jansen-Klijn, Kathinca Huisman, Inge Lamers-Bink, Annelies Leijdeckers and Michael Hegeman were of great help. Several MSc-students contributed to my research the past years: thanks are due especially to Toine Tünnissen, Baldwin de Kruyf, and Jeroen van de Bilt. Sure, my volleyball-mates: I don't know what would have happened when I would not have had the opportunity of some physical performances, after the exhausting brain-storming. Dik, Anton, Jan, Rob, Gerben, Hans, Juul, and Dick (in random order) are greatly acknowledged for the nice passes, set-ups, and the 'third half'.

Last but not least, I owe a lot to my family:
Mijn ouders, die zowel financieel als sociaal tot grote steun zijn geweest, en die altijd een grote betrokkenheid hebben getoond. Mede aan hen is dit proefschrift dan ook opgedragen. Maar mijn vrouw en kinderen hebben het meest te verduren gehad van mijn promotie-driften. De laatste jaren zijn voor Els niet de gemakkelijkste geweest; desondanks bleef zij geïnteresseerd in mijn werk, en vond de energie om mij daarin te blijven motiveren. Bovendien maakten haar opmerkingen en vragen het mij mogelijk bij tijd en wijle afstand te nemen, en het een en ander in de juiste proporties te blijven zien. Onze kinderen, tenslotte, zijn onze rijkdom: zij waren en zijn voor mij een bron van energie.

Oosterbeek,
December 1997,

Hank Bartelink.

Contents

Account

Chapters of this thesis have been based on the following publications:

Chapter 2:

Bartelink, H.H., 1996.
Allometric relationships on biomass and needle area of Douglas-fir. Forest Ecology and Management 86:193-203.

Bartelink, H.H., 1997.
Allometric relationships for biomass and leaf area of beech
(Fagus sylvatica L.).
Annales des Sciences Forestieres 54:39-50.

Chapter 3:

Bartelink, H.H., 1997.
Radiation interception by forest trees: a simulation approach.
Ecological Modelling 105(2-3):213-225.

Chapter 4:

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

Bartelink, H.H., 1998.
A model of dry matter partitioning in trees.
Tree Physiology 18:91-101.

Chapter 5:

Bartelink, H.H., 1998.
Growth and yield of monospecific and mixed Douglas-fir/ beech stands: a simulation study.
Ecological Modelling (submitted).

Stellingen

1. Het handhaven van een menging staat op gespannen voet met de maximalisatie van de houtproductie (dit proefschrift).

2. De in Nederland gangbare opbrengsttabellen en dan met name die voor beuk (*Fagus sylvatica* L.), zijn nauwelijks bruikbaar voor de bosbouwpraktijk als gevolg van het tekort aan groeigegevens en van de veranderingen die de afgelopen decennia in de groeiplaatsomstandigheden zijn opgetreden (dit proefschrift).

3. De stralings-conversie-efficiëntie vormt een bruikbaar concept voor de simulatie van boom- en bosgroei (dit proefschrift).

4. Gewasgroeimodellen waarbij gebruik gemaakt wordt van beschrijvende assimilaten- of drogestofverdeelsleutels kunnen onder gelijkblijvende groeiomstandigheden resulteren in betrouwbare primaire productie-schattingen: voor bomen groeiend in een opstand zullen deze omstandigheden echter variëren, zodat het noodzakelijk is de relatie tussen de beschikbaarheid van licht, water en nutriënten en de allocatie expliciet te kwantificeren (dit proefschrift).

5. De toename van het areaal gemengd bos en de veranderende eisen gesteld aan het beheer van bos maken de beschikbaarheid van modellen om groeivoorspellingen te kunnen doen en beheersalternatieven te kunnen doorrekenen, dringend noodzakelijk.

6. De traditionele opzet van opbrengstonderzoek gecombineerd met de kleinschaligheid van het Nederlandse bos (dat beter gekarakteriseerd zou kunnen worden als een verzameling bosranden) beperkt de bruikbaarheid van de uit dergelijk onderzoek afgeleide opbrengsttabellen.

7. De traagheid van de ambtelijke procedures en de gevraagde financiële en mentale offers van de aanstaande adoptie-ouders, staan in schril contrast met de schreeuwende behoefte aan adoptie-ouders en de wervende campagnes die daar mede vanuit de overheid voor worden gevoerd.

8. De meeste jagers in Nederland jagen voor hun plezier, maar verschuilen deze behoefte achter (in wezen legitieme) argumenten als populatie-beheer en schade-preventie.

9. Het beschrijven van boom- en bostoestanden middels zogenaamde architectuur-tekeningen levert in veel gevallen weinig meer op dan aardige plaatjes.

10. Het bestaan van een onderzoeksprogramma als het Overlevingsplan Bos en Natuur (OBN) en de aandacht voor effect-gerichte maatregelen (EGM) daarin, is een duidelijk teken van de zwakke positie van de bosbouwsector ten opzichte van die van de landbouwsector.

11. Discussies over verondersteide verschillen tussen concepten als 'geïntegreerd bosbeheer' en 'Pro Silva' vertonen een hoog 'academisch' gehalte en dragen niet bij aan een vergroting van het inzicht in het functioneren van het bos of aan de verbetering van het bosbeheer.

12. Het schrijven van complete EG-onderzoeksvoorstellen is een enorme verspilling van tijd, geld en energie: de procedure zou aanzienlijk efficiënter zijn wanneer gewerkt zou worden met tenders, op basis waarvan slechts een deel van de geïnteresseerden uitgenodigd wordt een compleet voorstel in te dienen.

Stellingen behorende bij het proefschrift
'Simulation of growth and competition in mixed stands of Douglas-fir and beech' van H.H. Bartelink

Chapter 1: Introduction

1.1 Background

Without human interference, most of Western Europe would be covered by forest; in some areas a single tree species would dominate, e.g. Norway spruce in mountainous areas in central Europe and at the timber line, or willow in riverine areas. Most of the woodland, however, would consist of mixed-species forests (Rackam, 1992). For many centuries, however, man has been using the forest, thus strongly affecting its structure and composition as well as the area covered by forest. Initially, forest products were used without paying much attention to the forest itself, but from the end of the 18th century on, forest management plans were made (van Laar, 1994). During the 19th century and the first half of the 20th century, much woodland was converted into even-aged, monospecies stands, and former woodland (heathland) was reforested, in order to produce wood efficiently. As a result, a large part of the managed forest area in Western Europe consisted of even-aged, monospecies stands by the mid 20th century.

To date, however, the area of mixed-species stands is quickly increasing again. A mixed stand is defined here in accordance with the Dutch Forest Service: an even-aged or uneven-aged forest containing two or more tree species, with the basal area proportion of each species amounting at least 20%, the smallest species being no smaller than 2/3 of the average height of the trees of the dominant species, and with each species occupying a minimum area of 0.2 ha (CBS, 1985). In the Netherlands, 8% of the forest area consisted of mixed species stands in 1960, but this had increased to 18% in 1980 (CBS, 1971, 1985). In Germany, the area of pure stands had dropped to only 33% of the forest area by 1990 (Smaltschinski, 1990). This increase in the mixed forest area partly resulted from the man-induced establishment of mixed stands, either through planting or natural regeneration, and also from the spontaneous transformation of (even-aged) monospecies stands, by natural regeneration. In the Netherlands, for instance, many planted second-generation Scots-pine stands have gradually become uneven-aged, mixed-species stands through natural regeneration of broadleaved species (Fanta, 1982). The latter process parallels the natural succession, and is facilitated by pedogenesis (Fanta, 1982).

From the management point of view, it is efficient to grow even-aged, monospecies stands. Such stands are highly accessible for silvicultural treatments, it is relatively easy to make decisions about them, the products (stems) are very uniform, and the area-oriented harvest (clear-cut) and re-establishment can be done mechanically and on a large scale. Nevertheless, there are good reasons for increasing the area of mixed forest. Firstly, from a silvicultural point of view, mixed stands are believed to be more resistant to storms and less susceptible to insect attacks and diseases. They are also believed to more closely approximate natural forests than single-species stands, and this enables the forest manager to exploit spontaneous forest development more efficiently. In economic terms, mixed forests may imply a spread of financial risks, as fluctuations of the wood market can be accommodated in mixed forests much more easily than in the situation where only one species and a restricted number of assortments are available (Lu & Buongiorno, 1993). Moreover, making use of spontaneous processes like natural regeneration saves forest managers much money. Lastly, (and this is especially relevant for densely populated countries such as in Western Europe) mixed stands are preferred for reasons of amenity and biodiversity (Kellomäki, 1975; Savolainen & Kellomäki, 1981). Both the ideological framework (mixed stands thought to be closer to nature) and the financial aspects have strongly encouraged the development of the 'close-to-nature' forestry. About 20 years ago, for example, Pro-Silva movements, in which foresters and forest scientists meet and discuss forest management and silviculture, were established in many European countries (e.g. Zwart, 1992).

1.2 Description of the problem

General

In Western Europe, the emphasis in silviculture has a long time been exclusively on even-aged, monospecific stands, as single-species plantation forestry was common practice. As a consequence, one of the building blocks of forest management, the growth and yield research, focused on this stand type for decades. This resulted in empirical stand-level growth models being developed. The yield table is a well-known example; it is based on data from permanent research plots. The first attempts to develop such tables were as early as 1721, with the work of Reaumur (cf Pretzsch, 1992).

Though large parts of European forests were transformed into single-species plantations, some parts of Europe have been covered by mixed forests for centuries, and there is field experience with the management of mixed forests, especially in central-Europe (e.g. Leibundgut, 1946; Schütz, 1989). In contrast to monospecific stands, however, in mixed forests thorough and systematic research on stand dynamics is still lacking, and no generally accepted growth and yield approach has yet emerged (Pretzsch, 1992; Cannell et al., 1992; Burkhart & Tham, 1992). The increasing mixed forest area and the growing concern about managing mixed stands stress the need for tools to support the decision taking about the management of mixed forests.

Though empirical stand-level models have been used successfully to manage pure stands, this descriptive approach is less suitable for application to mixed forests, mainly because these are more complex and diverse in terms of their structure and composition (see also Pretzsch, 1992). There are some empirical stand-level models for mixed stands, however. Back in 1942, for example, Wiedemann produced a yield table for even-aged spruce-beech mixtures (Assmann, 1961). However, not many attempts have been made, due to the large variety of possible stand dynamics and (thus) the lack of data. Even when only a two-species mixture is considered, the number of possible stand compositions is huge: apart from the species involved, stands may differ in terms of the species contributions to the mixture, the stand origin (whether trees are planted and/or there is natural regeneration), the planting pattern, and the site conditions (affecting inter-specific relations), resulting in different types of interactions (see e.g. Assmann, 1961).

In mixed species stands, treatments like thinnings not only affect total stand growth but also inter-specific competitive relationships (Holmes & Reed, 1991; Larson, 1992). The different characteristics of the species and the spatial distribution of the remaining trees thus have a different and in most cases a much stronger impact on stand development than is the case in monospecies stands. Moreover, a description of a mixed stand in terms of average tree dimensions covers a wide range of potential stand compositions, which disables the estimation of e.g. wood quality and assortments, and hampers the prediction of future stand development. As a consequence, the emphasis in forestry decision-making has started to shift from the stand-level towards the tree or tree group (Holmes & Reed, 1991; Pretzsch, 1992).

Trends in modelling

Two different trajectories can be distinguished in the development of models for mixed species stands: new empirical growth and yield models, and mechanistic growth models. The latter are models that estimate growth based on growing conditions and species requirements (Jarvis & Leverenz, 1983; Landsberg, 1986), using causal relationships rather than empirical descriptions.

1. Empirical models

Various attempts have been made to adapt yield tables (Wiedemann, 1950) and to develop new empirical tools for mixed stands (Alimi & Barrett, 1977; Deusen & Biging, 1985) to meet the demands of changing forests and forestry. Many recently developed empirical growth and yield models are tree-level (i.e. based on the individual tree), describing growth in terms of diameter increment (Biging & Dobbertin, 1995). So-called competition indices are crucial in the growth predictions in many models (Holmes & Reed, 1991). Generally, crown characteristics are used either to estimate stem diameter increment (Leersnijder, 1992; Pretzsch, 1992) or to indicate a tree's competitiveness (Holmes & Reed, 1991). Tree growth is thus estimated using descriptive relationships. The major drawbacks of this approach are the large amount of data needed, and the restricted applicability of the tools due to the limited validity of the empirical relationships.

2. Mechanistic models

In the 1970s, mechanistic models to simulate crop growth based on species requirements and growing conditions began to be developed (de Wit & Goudriaan, 1978). In the 1980's, the first attempts were made to translate the concept for application to forest stands. For example, Mohren (1987) developed a stand-level model for even-aged Douglas-fir stands, Mäkelä & Hari (1986) and Nikinmaa (1992) applied a stand-level approach in Scots pine, Bossel & Krieger (1994) did likewise for Norway spruce, and Ludlow et al. (1990) for Sitka spruce. Only recently have attempts been made to apply the mechanistic stand approach in mixed crops and mixed forests. Kropff & van Laar

(1993) developed a general carbon-balance model for mixed crops. Kramer (1996) extended this approach to forest species in a study on the role of phenology in competition between tree species.

Wiedemann's empirical yield table (1950) and the mechanistic model of Kropff & van Laar (1993) form two extremes in a range of possible model types. It seems that the two paths (empirical versus mechanistic) still are only marginally 'merged': there are contrasts between biologically-based process models and management-oriented growth and yield models (Mohren et al., 1994).

Apart from the difference between empirical and mechanistic models, a distinction can be made between stand-level and tree-level approaches. In the stand-level approach, no individual trees are described and the canopy is represented by horizontally homogeneous leaf layers. Most mechanistic models are based on the stand-level, as are the yield tables. Some of the recently developed empirical growth and yield models, however, model individual trees (e.g. Pretzsch, 1992; Leersnijder, 1992). Stand-level models, whether empirical or mechanistic, are by their very nature unable to represent different planting patterns in mixtures, or to take account of spatially non-systematic thinning measures. Neither can they take crown dynamics into account: so, because crown dimension is crucial in radiation interception and thus in growth and competition (Landsberg, 1986; Cannell, 1989), stand-approaches are less suitable for simulating the dynamics of mixed-species stands.

One of the first modelling attempts aiming specifically at simulating mixed forest growth was the development of the 'gap-models', which started with the work of Botkin et al. (1972). Gap-models can be classified as a special category of distance-independent models of tree growth, as they distinguish individual trees competing and growing in a restricted area, the gap (Botkin et al., 1972; Shugart, 1984). Many gap-models have since been developed, for example for central Europe (FORECE: Kienast, 1987), to simulate old pine stands in Sweden (FORSKA: Leemans, 1991), to estimate effects of climate change (Fischlin et al., 1992), or to determine the effects of ungulates on spontaneous forest development (Jorritsma et al., 1997). Early gap-models generally described growth using a diameter-over-time function (Botkin et al., 1972; Shugart, 1984; Kienast, 1987). Recently, models have been developed following a more mechanistic approach, for instance by estimating tree growth on the basis of photosynthesis or dry matter production (Friend et al., 1993; Jorritsma et al., 1997). The gap-model approach is much more suitable than the stand-level approach for simulating the growth of mixed stands. However, gap-models can not take spatial differences in the horizontal plane into account either, because of the distance-independence within the gap. This precludes gap-models from simulating horizontal crown expansion and its effect on radiation competition.

Though gap models and empirical tree-level models are more flexible than the empirical stand-level models, they still rely heavily on descriptive relationships. On the other hand, though more mechanistic approaches like the stand model presented by Kramer (1996) do relate growth to growing conditions, these are too theoretical to be of much value for forest managers. Models that include biological processes and are suitable to support taking decisions about forest management taking would be a great advantage, but unfortunately are still scarce (Mohren et al., 1994). There is, however, a trend towards more process-based approaches, especially when complex systems have to be simulated. Furthermore, forest growth modelling is shifting from the stand-level towards the tree-level (Judson, 1994). Figure 1.1 presents an overview of the different model types and characteristics.

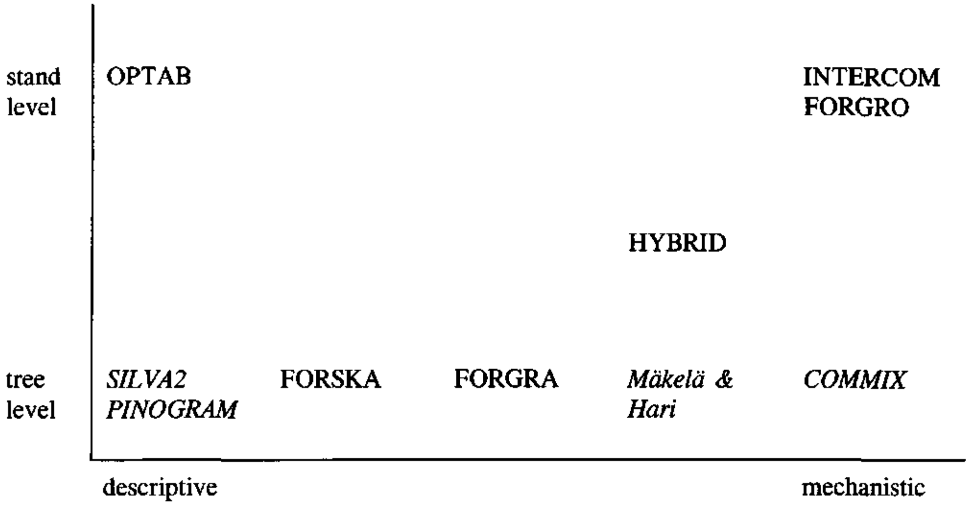


Figure 1.1: Differences between models developed to estimate growth, yield, and/or development of mixed species (forest) stands. Distance-dependent models are presented in italics. The authors of the models are Mäkelä & Hari (1986: name unknown), Leemans (1991: FORSKA), Pretzsch (1992: SILVA2), Leersnijder (1992: PINOGRAM), Friend et al. (1993: HYBRID), Kropff & van Laar (1993: INTERCOM), Jansen et al. (1996: OPTAB), Kramer (1996: FORGRO), and Jorritsma et al. (1997: FORGRA). The 'COMMIX' model represents the conceptual framework used in this thesis (see §1.3).

Though the need for tools to support mixed forest management and research is evident, no generally accepted growth and yield approach has yet evolved. Models are needed that can provide information to support the forest manager when taking decisions about mixed species stands, and that can contribute to the research on mixed forest dynamics.

1.3 Research aim and conceptual framework

Aim of the research

As noted above, both empirical and mechanistic models can be developed to estimate growth and yield of mixed forest stands. The major drawbacks of the empirical approach are the large amount of data needed, and the limited validity of the empirical relationships. The inexhaustible number of species combinations, management regimes, and site-dependent interactions in mixed stands, make a causal approach much more suitable (Lavigne, 1992; Burkhart & Tham, 1992; Pretzsch, 1995). A theoretical, process-oriented approach will probably be required for developing mechanistic models that can be used to estimate responses to hypothetical silvicultural treatments (Burkhart & Tham, 1992; Kelty & Cameron, 1994).

The aim of the present research was to analyse the effects of stand composition and forest management on growth and yield of mixed species forest stands, using a process-oriented model of forest growth. It was intended that the results would benefit the decision taking in mixed forest stands, and support research on mixed stand dynamics.

Conceptual framework

Both inter- and intra-specific competition are crucial in the stand dynamics in mixed-species forests; the responses of individual trees to resource availabilities and the impacts of tree growth on stand structure and composition are much more diverse than in the case of even-aged, monospecies stands. This implies that there is a need to shift forest growth modelling from the scale of the stand towards the individual tree, in accordance with observations in ecological research (Judson, 1994).

Analysing the growth and yield of mixed stands requires a modelling approach that relates the growth of individual trees to their resource availability. This is called a process-based or mechanistic approach. In a mechanistic model the impact of thinnings and other management activities on competition between trees and on forest growth and yield can be quantified. The within-stand competition is a key-factor in stand development. Generally, the effects of competition on growth are estimated from descriptive, statistical relationships, either at the stand level or the tree level, and may be either distance-dependent or distance-independent (Pretzsch, 1992; Holmes & Reed, 1991; Biging & Dobbertin, 1995).

In the research described here, competition between trees was quantified in terms of availability of radiation. A distance-dependent, tree-level model was developed and applied. Because growth of trees and forest is largely determined by the amount of absorbed radiation (Jarvis & Leverenz, 1983; Landsberg, 1986), much emphasis was put on estimating the radiation absorption of individual trees growing in a stand. Biomass data were collected to obtain information on tree structure and on biomass distribution.

The simulation model developed and applied in the present study is called COMMIX (COMpetition in MIXtures). It was developed on the basis of three main assumptions:

1. Radiation plays a key role in growth: the radiation absorbed by a tree will strongly determine its growth rate, and competition for radiation among stand members will determine stand development (Landsberg, 1986; Cannell, 1989).
2. The dry matter production of a tree is related to the radiation it absorbs, according to the radiation-use efficiency (RUE) concept (Monteith, 1977; Cannell, 1989).
3. The partitioning of the dry matter growth over the biomass components is dependent both on tree state and on growing conditions (e.g. site), and is largely determined by the efforts of a tree to maintain its structural balances (Mäkelä, 1986; Cannell & Dewar, 1994).

Figure 1.2 presents the dynamic structure of the modelling approach. The growth rates are integrated after each time-step (one year): in turn, the updated tree and forest structure will affect the radiation interception and hence the stand dynamics.

Research questions

The research addressed the following questions:

1. How is radiation interception by forest trees affected by a) crown size and dimension, and b) stand structure and composition?
2. Is there a relationship between the amount of intercepted radiation and the growth rate of a tree (in terms of dry matter), such that tree growth can be directly estimated from radiation interception?
3. How is growth (dry matter) distributed over the tree biomass components?
4. What are the effects of management treatments (e.g. thinning) on mixed stand growth and development?

The applied methodology is described and explained in the following chapters, each of them dealing with one or more of the research questions.

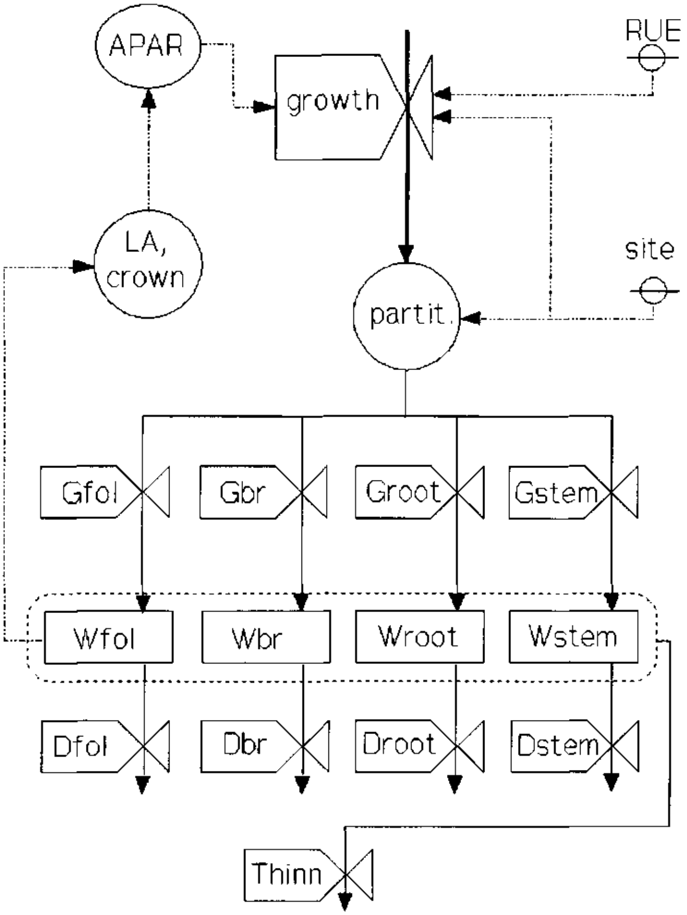


Figure 1.2: Structure of the COMMIX model. LA is leaf area, APAR is absorbed photosynthetically active radiation, RUE is radiation-use efficiency, 'partit' is partitioning, and 'site' represents site characteristics. A number of biomass components can be distinguished: G is growth rate, W is dry weight, and D is turn-over, of respectively the stem, branch (br), root, and foliage (fol) biomass. 'Thinn' is thinning; removing trees will affect both stand biomass and the canopy composition, and hence APAR.

1.4 Study sites and species

Two species were used in this research: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and beech (*Fagus sylvatica* L.). Beech is an indigious and commercially important species, in the Netherlands as well as in a large part of north-western Europe (Peters, 1992). Douglas-fir, introduced in the Netherlands at the end of the 19th century (Kuiper, 1994), is the most important commercial coniferous species after Scots pine (CBS, 1985). Though generally grown in large monospecies stands, Douglas-fir has occasionally been mixed, particularly with Japanese larch, Norway spruce, and beech.

Douglas-fir and beech were selected as the model species because of the data available on species biomass and on growth and yield data of monospecies stands and the mixtures. Furthermore, this two-species mixture is considered an interesting option in the Netherlands when the aim is to both grow mixed stands and to produce wood (Anonymous, 1993). Despite the latter argument, it is doubtful whether the area of Douglas-fir (whether in pure or in mixed stands) will increase much further in the near future; on the one hand this is due to forest policy, which strongly encourages the growing of indigious stand types, on the other hand climate change might form a serious constraint to the ecological spread of the species (Kramer, 1996). However, the methodological aspect is even more important than the species *per se*: by studying such a mixture it was hoped that the interactions between coniferous and broadleaved species when growing in mixed stands would be elucidated.

Because most mixed stands of Douglas-fir and beech in the Netherlands are even-aged (i.e. species differ in age by a maximum of three years), the present study focused on even-aged mixed stands. More information on the species is given in §2.1. Field observations were carried out in the central part of the Netherlands (Veluwe), resulting in tree and stand data on radiation interception, stand structure and composition, tree biomass, growth, and yield.

All stands investigated were growing on well-drained, acid brown podsolic soils on ice-pushed pre-glacial deposits with deep water tables (>4m below surface). According to the yield tables (Jansen et al., 1996), the sites were suitable or very suitable for both species, resulting in an estimated maximum mean annual stand volume increment (MMAI) of 14-16 m^3 ha^{-1} y^{-1} in case of Douglas-fir, and 10-12 m^3 ha^{-1} y^{-1} for beech. This soil type is among the best of the 'traditional' forest soils in the Netherlands and is thus suitable for commercially growing the relatively demanding (in terms of nutrients) beech and Douglas-fir.

Note that classifying the sites as 'relatively good' clearly reflects the forestry viewpoint: compared with agricultural sites and given the optimal growing conditions required by the species, there is definitely a lack of water and nutrients in the sites examined. The biomass and growth data of the species concerned thus include the effects of a non-optimal production situation. In this research, therefore, the growing conditions for the stands are considered as optimal *for these particular site conditions* only, i.e. well-drained, acid brown podsolic soils on ice-pushed preglacial deposits.

Not only traditional silvicultural parameters like stem diameter (usually measured at 1.30 meter above the forest floor, the so-called 'breast height') and tree height are of interest when investigating growth and yield of mixed stands. Tree characteristics like crown dimensions and leaf area play an important role in the competition process in (mixed) stands, but were until recently virtually ignored in forest growth and yield modelling. This was possible due to the relatively simple system (the even-aged monospecies stand) that had to be described. Nowadays, on the one hand there is an increased attention for tree-level data, on the other hand the system the forest manager has to deal with has become much more complex (Holmes & Reed, 1991; Pretzsch, 1992). When trying to explain both inter- and intra-specific competition between species, more information is needed than traditionally collected in forest inventories.

The first major studies on world-wide biomass data were carried out within the IBP framework (e.g. Cragg & Reichle, 1981; DeAngelis et al., 1981). Other early studies were carried out by Burger in Switzerland, amongst others on beech (Burger, 1950). Cannell (1982) summarized world-wide existing knowledge on tree and stand biomass: Figure 2.4 shows data of Douglas-fir and beech.

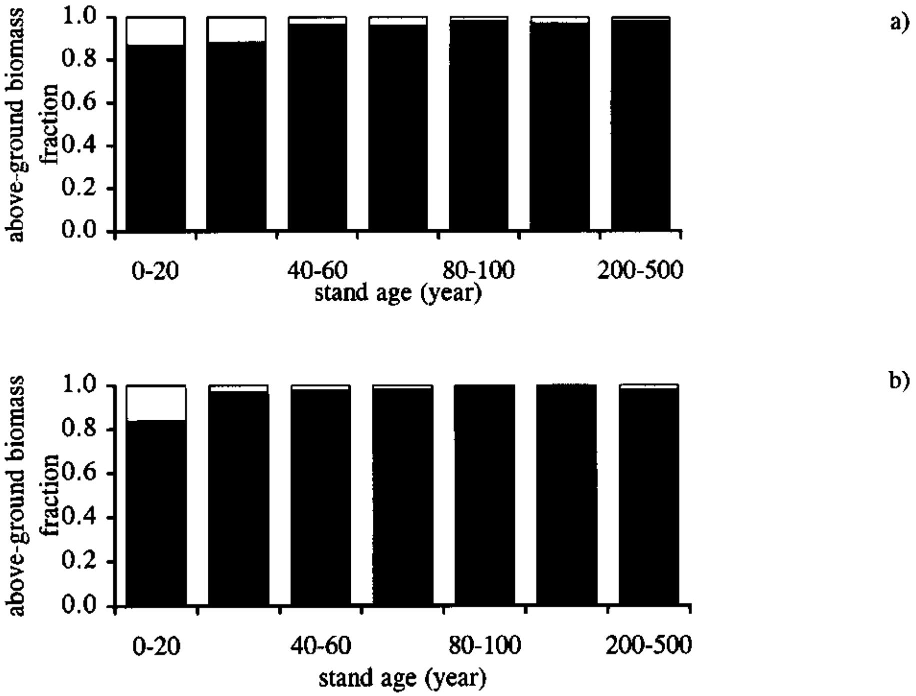


Figure 2.4: Average fractions of total above-ground biomass (dry weight) based on data from 25 Douglas-fir stands (a) and 22 beech stands (b), respectively: stems (black), branches (hatched), and foliage (open area). After Cannell (1982) and Bartelink (1997a).

Figure 2.4 shows that the largest part of the above-ground dry weight consists of stem biomass. In Douglas-fir the stem fraction increases with stand age, but in beech this is less obvious. Note, however, that the data presented in Figure 2.4 were collected from different sites and locations. This might also explain the relatively high variability in the total above-ground stand biomass. In Douglas-fir stands younger than 50 years, stand biomass varied between 30-500 ton/ha, and between 400-1000 ton/ha at older ages (up to 450 years old). In beech, above-ground biomass amounted 150-300 ton/ha in stands younger than 100 years, and 200-400 ton/ha in older stands (Cannell, 1982). This variability restricts the general applicability of such data-sets.

Monospecies versus mixed stands

Mixed stands have been established though row planting, individual planting, or group planting (Hekhuis & van Nierop, 1988). More recently, mixtures have been established using natural regeneration, sometimes in combination with planting: a nice example consists of the planting of beech saplings in gaps in mature Douglas-fir stands (Oosterbaan, 1996). This treatment, where natural regenerated Douglas-fir will form mixed stands with the planted beeches, is gaining increasing importance in Dutch forestry. It is also a suitable way to convert monospecies stands into mixtures (Sevenster, 1992; Oosterbaan, 1996).

Data on mixed species stands of Douglas-fir and beech, however, are still scarce. Available data at present consist of tree and stand data derived from a small number of research plots. The data from the permanent plots only cover a short time period. For that reason, a preliminary study was carried out using increment cores to estimate growth and yield over the past decade (Bartelink & Tünnissen, 1996). Figure 2.5 presents the temporal development of the stand basal area of 13 mixed Douglas-fir/ beech stands. The stands differed in species share and age, but were grown on comparable sites (acid brown podsolic soils in ice-pushed preglacial deposits with a water table lower than 4m below surface): age differences between the two species within stand amounted 3 years at maximum.

To allow comparison with monospecies stands, the basal area developments of the Dutch yield tables (Jansen et al., 1996) were added: only the curves for the site classes comparable with the site classes of the dominant species in the mixed stands (the Douglas-fir) were presented. From Figure 2.5 it appears that the total (stand) basal area of the mixed stand is generally somewhere in between the total basal areas of the monospecies stands derived from the yield tables (Jansen et al., 1996).

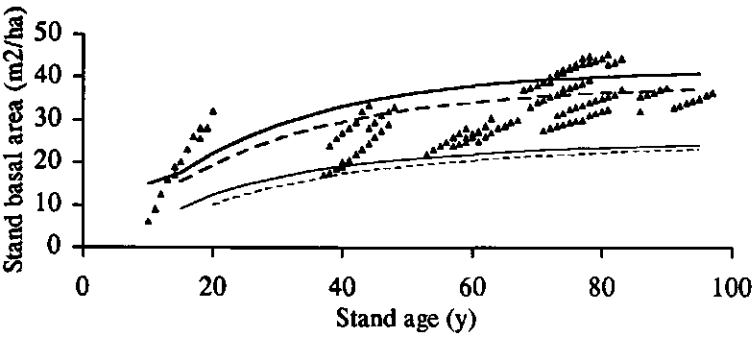


Figure 2.5: Comparison of the total stand basal area (BA: m^2 ha^{-1}) of the mixtures (symbols) with the BA of the monospecies stands (lines: Jansen et al., 1996). Site quality is expressed as the maximum mean annual volume increment (MMAI: m^3 ha^{-1} y^{-1}). Yield table data are shown for Douglas-fir, representing MMAI 14 (bold, solid line) and MMAI 10 (bold, dashed), and for beech, representing MMAI 8 (thin, solid) and 6 (thin, dashed), respectively. After Bartelink & Tünnissen (1996), modified.

Figure 2.6 presents the total stand basal area increment (BAI: m^2 ha^{-1} y^{-1}): on several occasions BAI's of mixed stands exceed those of the monospecies (yield table) stands.

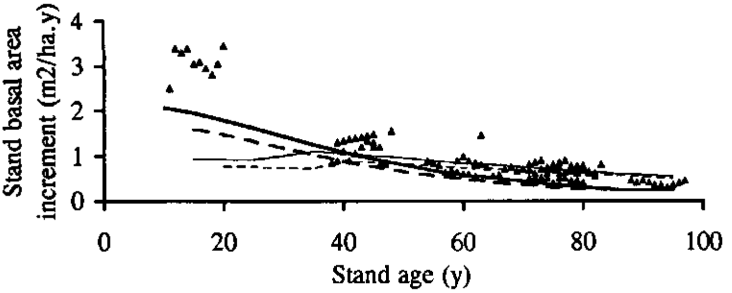


Figure 2.6: Comparison of the total stand basal area increment (BAI: m^2 ha^{-1} y^{-1}) of the mixtures (symbols) with the BAI of the monospecies stands (lines: Jansen et al., 1996). Site quality is expressed as the maximum mean annual volume increment (MMAI: m^3 ha^{-1} y^{-1}). Yield table data are shown for Douglas-fir, representing MMAI 14 (bold, solid line) and MMAI 10 (bold, dashed), and for beech, representing MMAI 8 (thin, solid) and 6 (thin, dashed), respectively. After Bartelink & Tünnissen (1996), modified.

It is generally believed that a mixed stand is able to use the site (resource availability) more effectively, i.e.: when a mixture would be defined as a combination of two monospecies stands, then the growth rate of the mixture would be higher than the sum of the growth rates of the contributing monospecies stands. To investigate this, Bartelink & Tünnissen (1996) used the approach of Rasul (1929). Equation 2.1 allows the calculation of a mixing percentage (R%), as well as the comparison of the growth rates of monospecies stands and artificial mixtures:

$$R\%_{dg} = \frac{Gmix_{dg}/Gmon_{dg}}{(Gmix_{dg}/Gmon_{dg}) + (Gmix_{be}/Gmon_{be})} \text{ x } 100\% \qquad (2.1)$$

With R% Mixing percentage
Gmix Field basal area of the species in a mixture (m^2 ha^{-1})
Gmon Yield table basal area of the monospecies stand (m^2 ha^{-1})

Using Equation 2.1, the basal area increment ratio (BAIR) was calculated (Eq.2.2):

$$BAIR = \frac{BAI_{mix}}{R\%_{dg}{*}BAI_{dg} + R\%_{be}{*}BAI_{be}} \text{ x } 100\% \qquad (2.2)$$

With BAI_{mix} basal area increment of the real mixed stand
BAI_{dg} basal area increment of the monospecies Douglas-fir stand
BAI_{be} basal area increment of the monospecies beech stand

Note that BAIR is highly comparable to the so-called Relative Yield Total (RYT) in the approach of de Wit (1960).
From Figure 2.7 it appears that BAIR is strongly dependent on the mixture composition: when more than 50% of the basal area consists of beech, the benefits of a mixture over a combination of monospecies stands will disappear.

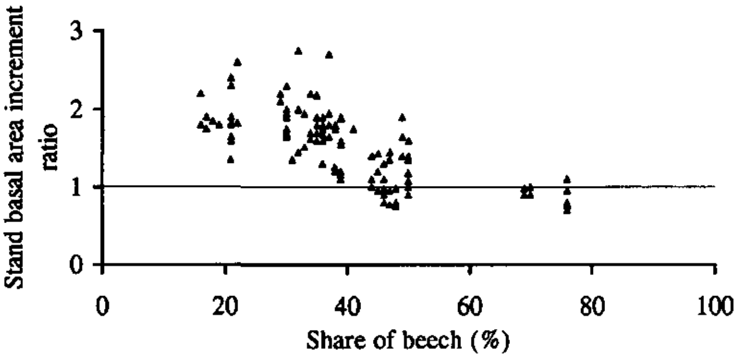


Figure 2.7: Effects of the proportion of beech (in terms of basal area) on the basal area increment ratio (BAIR) of the mixed stand: BAIR values higher than 1 (see horizontal line) imply that the mixture is more productive than the sum of the fractions of the contributing monospecies (yield table) stands. After Bartelink & Tünnissen (1996).

The data in Figures 2.5-2.7 indicate that mixed stands would be more productive than a combination of monospecies stands. However, an important drawback of the current yield tables was pointed out by Schoonderwoerd & Daamen (1995), who showed that in Douglas-fir stands older than 40 years, BAI is generally 0.5 m^2 ha^{-1} y^{-1} higher than indicated by the yield table of Jansen et al. (1996). Though this implies that the yield benefits of mixed stands are smaller than at present assumed, the growth rate of a mixed stand would still be higher than that of a beech stand, and at least be comparable with the performance of Douglas-fir stands (Bartelink & Tünnissen, 1996).

Mixtures of beech and Norway spruce and/or fir

The combination Douglas-fir beech, although occurring in e.g. Germany and France, is probably most typical for the Netherlands, which restricts the availability of comparing mixture performance. It is therefore worthwhile to look for mixtures that are comparable with Douglas-fir/beech. Most suitable appeared mixtures of beech with Norway spruce (Picea abies), and/or with fir (Abies alba), because Douglas-fir, Norway spruce, and fir share some typical characteristics: they are all shade-tolerant, fast growing, and heavy shading coniferous tree species. Mixtures of beech and Norway spruce occur mainly in Germany and Switzerland (Wiedemann, 1950; Zimmermann, 1988; Schütz, 1989). The availability of data, however, is very restricted: almost no data are found in literature.

Regarding Norway-spruce and beech, Wiedemann (1950) and Assmann (1961) distinguished two types of mixed spruce-beech stands. Stand differences consisted of different stand dynamics, caused by site differences:

a) relatively rich soils:
    beech tends to over-grow spruce, and the yield of the mixture is less than the yield of a monospecies spruce stand

b) relatively poor soils:
    beech remains in the lower part of the canopy (serving the spruce), and the yield of the mixture is larger than in a monospecies spruce stand (Assmann, 1961).

For each soil condition a separate yield-table was developed (Wiedemann, 1950). The combined use of existing tables for monospecies stands had appeared unsuitable; moreover, in mixed stands also the spatial distribution of the species in the stand had appeared to affect growth and yield (Assmann, 1961). Priesol & Hladik (in: Wenk et al., 1990) stated that the yield of mixed stands of fir and beech increased with increasing proportion of the fir, running from 10.5 m^3/ha in case of 30% fir to 13.2 m^3/ha when 70% of the trees are firs. However, because data on monospecies stands were not presented, a comparison between the performance of mixtures and monospecies stands could not be made. Both Kennel (1965) and Zimmermann (1988) showed that the growth rate of spruce trees in mixed stands of spruce and beech is superior to the growth of spruce in pure stands, but that beeches in mixture with spruces are inferior to beeches in pure stands. Spruce dominance was presumed on most of the sites involved, and beech dominance on some. Nusslein (1993) found that a mixture containing 20-40% beech is most profitable in terms of growth. Figure 2.8 gives an impression of the performance of mixed-species stands of Norway spruce and beech, compared with the growth and yield of the monospecies stand (after Wiedemann, 1950).

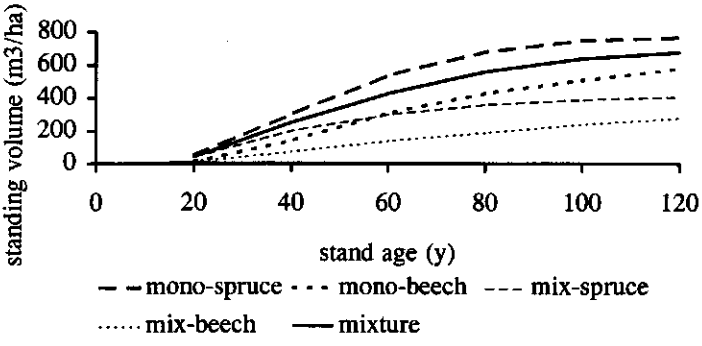


Figure 2.8: Performance of monospecies and mixed-species stands of Norway spruce and beech in Germany (after Wiedemann, 1950). Bold lines represent stand totals, thin lines indicate species fractions.

From Figure 2.8 it appears that the standing volume of the mixture is a somewhere in between that of the monospecies Norway spruce stand and that of the monospecies beech stand. Moreover, the share of beech in the standing volume of the mixture increase with stand age. Definitely, in most of the mixed stands of spruce and beech, management favours the beech in order to maintain the mixture (Wiedemann, 1950; Zimmermann, 1988).

Concluding remarks

Although some data on mixed Douglas-fir/ beech stands exist, it is far too few yet to directly support decision taking in forest management. The establishment of new long-term research plots in mixed stands, to collect growth and yield data, is definitely an important task: these data will be used to evaluate growth and yield prediction models. However, the data itself won't serve forest managers: on the one hand it takes too much time before 'yield tables for mixed stands' could be developed, on the other hand there are far more different growing conditions and stand compositions to be defined, which can impossibly be covered all by permanent research plots.

There is thus a need for new research tools, that should be able to provide forest managers with information on possible management scenarios and on the consequences of certain management regimes. The infinite variety of possible species mixtures, coupled with the range of environmental conditions under which mixtures might be grown, necessitates a mechanistic modelling approach.

2.2 Allometric relationships on biomass and needle area of Douglas-fir.

Introduction

Allometric relationships among tree parts originate from physical or physiological interrelations among stem dimensions, crown dimensions, foliage area, and biomass amounts. Of all tree parts, foliage plays a key role in forest growth as it is the main site of radiation interception, with intercepted radiation determined by total foliage area and foliage distribution, and affected by the spatial distribution of the branch biomass. The amount of foliage area is related to the water-conducting sapwood area, because a functional interrelationship exists (Shinozaki et al., 1964; Jarvis & Leverenz, 1983). The relationship differs between species, and is affected by site and climate conditions (Mencuccini & Grace, 1995). Foliage biomass and branch biomass together form the crown biomass, which has to be supported by the tree trunk: the relationship between stem diameter, tree height, and crown dimensions reflects the tree's attempt to maintain mechanical stability (McMahon & Kronauer, 1976; Niklas, 1992). Stem size is hence an important indicator of both the physiological and physical support of the trunk (Causton, 1985).

Such allometric relationships form important tools for building mechanistic models of forest growth (Causton, 1985; Jarvis & Leverenz, 1983). Relationships between stem dimensions and biomass amounts are useful to estimate dry weights of tree components, both to calculate initial stand conditions and to evaluate simulation results. Relations among tree components based on physical or physiological interdependencies can serve as guide-lines for dry matter allocation in growth models (Cannell & Dewar, 1994).

The present study focused on allometric relationships in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), as part of the development of a mechanistic model of forest growth. To build, initialize, and evaluate the model, data on tree biomass and foliage area are needed, and allometric relationships among tree parts have to be established. Many previous studies on Douglas-fir concentrated on empirical relationships with stem diameter at breast height (e.g. Snell & Brown, 1978; Causton, 1985; St.Clair, 1993), or on functional relationships between stem cross-sectional sapwood area and needle area (Brix & Mitchell, 1983; Espinosa Bancalari et al., 1987; St.Clair, 1993). Less attention has been paid to biomass and crown dimensions. The aims of the present study were 1) to establish allometric relationships among stem and crown dimensions, biomass amounts, and needle area, (2) to describe the above-ground dry matter distribution, (3) to quantify the relationship between sapwood area and needle area, and (4) to describe the vertical distribution of needle area and branch biomass in the crown. The role of the tree's dominance position and the effect of differences between stands on the allometric relationships and the biomass distributions was investigated.

Methods

Data collection

Twenty-three trees were selected from four even-aged monospecies stands of different ages, to ensure a range of tree sizes. The stands were located in the central part of the Netherlands (52°0'N, 5°4'E). The three oldest stands had been thinned at least once, in accordance with forest management practice. The stands were growing on acid brown podsolic soils in ice-pushed preglacial deposits with deep water tables (>4m below surface).

Sampling took place in the winter of 1990/91. In each stand the stem diameters of all trees in a sample plot (30-100 trees) were measured at breast height (at 1.30m above the forest floor); this diameter is further referred to as 'dbh'. Stand characteristics are presented in Table 2.2. The trees of the sample plot were distributed over 2 diameter classes, the lower class containing trees with a dbh smaller than the average dbh, the upper class containing trees with a dbh larger than the average. Out of each class three trees (in one case only 2 trees) were chosen randomly. Regarding the crown characteristics, the sample trees from the lower diameter class could be classified as suppressed trees, whereas the sample trees from the upper diameter class were (co-) dominant (Kraft, 1884). The sample trees were felled and pruned, height positions and dimensions of all branches (length and diameter at 1 cm from the branch base) were measured, and stem volume was estimated from diameter measurements along the stem. Crown projection area (vertical projection) was estimated from the length of the branches of the oldest living whorls. From each tree a stem disk was removed at breast height (1.30m above the forest floor). Sample branches were collected from each tree; to account for spatial heterogeneity within the crown, a branch was sampled from every whorl.

Table 2.2: Characteristics of the sample stands. N = tree number (ha^{-1}), G = basal area ($m^2.ha^{-1}$), H_{dom} = dominant stand height (m), d = average dbh (cm).

stand	age	N	G	H_{dom}	d
1	9	2133	9.0	6.7	6.9
2	19	1296	21.6	13.9	13.8
3	29	765	26.6	19.0	20.6
4	39	406	27.2	25.9	28.5

In the laboratory, of each branch all needle-bearing twigs were clipped and weighed, separating the different needle age-classes. A subsample was stripped, and weights of needles and twigs were determined. Projected needle area was determined using the

Delta-T Image Analyses System. The subsamples were oven-dried and weighed to determine dry weight percentages of needles (24hrs; 70°C), and twigs and branches (48hrs; 105°C). Stem dry weight was determined by multiplying stem volume with the basic density. Wood basic density was estimated to be 450 kg dry weight per m^3 fresh-volume, based on data for Douglas-fir in the Netherlands (van der Zwan & van der Zee, 1991). Crown volume, crown silhouette area (horizontal projection), and crown mantle area were calculated from the crown projection area and the length of the living crown (tree height minus crown base height), assuming that the crown can mathematically be described by a cone.

Data analysis

Multiple regression analysis was carried out using the GENSTAT statistical package. The presented regression estimates are significant at the 5% level. The calculated fraction of variance accounted for (R^2) includes adjustment for the number of degrees of freedom.

Branch level

First biomass and projected needle area per branch were estimated to enable the determination of the total crown biomass per tree. Bare branch dry weight (further referred to as 'branch dry weight'), needle dry weight per branch, and projected needle area per branch were correlated to branch size and position. Branch dry weight appeared to be strongly correlated to the product of branch basal area (including bark) and branch length, which is proportional to volume. Branch needle amounts were significantly correlated to branch diameter (over bark) and height of the branch in the crown. Table 2.3 presents the resulting regression equations. The intercept of the models was set to zero, which prevents estimates becoming negative. Total needle and branch dry weights and total projected needle area of each sample tree were calculated by applying the regression equations from Table 2.3 on the dimensions and heights of all the branches, as measured in the forest.

Table 2.3: Regression of bare branch dry weight (WB_b, in g), needle dry weight per branch (WN_b, g), and needle area per branch (NA_b, dm^2) on branch dimensions, being: b_d = branch diameter over bark (cm), b_l = branch length (cm), h_{rel} = relative height in the crown (= height above the base of the crown divided by the length of the crown).

Regression equation	R^2
$WB_b = 0.245*b_d^2*b_l$	0.948
$WN_b = 14.12*b_d^2 + 159.10*b_d^2*h_{rel}*(1-h_{rel})$	0.903
$NA_b = 10.07*b_d^2 + 78.10*b_d^2*h_{rel}*(1-h_{rel})$	0.904

Tree level

Next, relationships among stem and crown dimensions, biomass, and projected needle area were determined. Stem dimensions considered were diameter at breast height (dbh), dbh^2 (proportional to basal area), tree height (h), and the product term dbh^2*h. Crown dimensions involved were projection area, volume, mantle area, and length. Double-sided logarithmic transformations (natural logarithm) were applied when necessary, to account for the non-constant variance that exists in many biomass relationships (Causton, 1985).

Biomass distribution was described as a function of total above-ground biomass. In this approach, first the ratios of foliage to stem dry weight and branch to stem dry weight are calculated and, after a two-sided logarithmic transformation, related to the total biomass. The following relationships were analyzed (Eq.2.3):

$$\ln (WN/WS) = c_1 + c_2 * \ln (Wtot) \qquad (2.3a)$$

$$\ln (WB/WS) = c_3 + c_4 * \ln (Wtot) \qquad (2.3b)$$

With	WN	tree needle biomass (kg)
	WB	tree branch biomass (kg)
	WS	tree stem biomass (kg)
	Wtot	total tree biomass (kg)
	c_1-c_4	regression constants

From these equations, the mathematical descriptions of respectively WN/Wtot, WB/Wtot, and WS/Wtot as a function of Wtot, were solved.

Although several studies found strong relationships between Douglas-fir needle area and sapwood area at breast height (SA_{bh}) (Granier, 1981; Kaufmann & Troendle, 1981; Waring et al., 1982), sapwood area below the lowest living whorl (SA_{cb}) is functionally closer related to needle area (Shinozaki et al., 1964; Maguire & Hann, 1987). Here, both relationships were analyzed. From every tree a stem disk taken at breast height was available. From a subsample of 19 trees also the sapwood area just below the lowest living whorl (the crown base) was determined. Sapwood and heartwood area were distinguished within each stem disk, both by eye and by using ferric chloride (Kutscha & Sachs, 1962).

Vertical distributions of the needle area and the branch biomass were described using the 2-parameter Weibull-formula, where the x-value ranges from zero to infinity (Eq.2.4a).

$$y = 1 - e^{-(\frac{x}{p_1})^{p_2}} \qquad (2.4a)$$

where	y	Relative needle area distribution (dimensionless)
	x	Relative height in the crown (dimensionless)
	p_1,p_2	Regression constants (dimensionless)

To force the curve through zero (the crown base) and 1 (the tree top), the Weibull-formula was truncated, by dividing Equation 2.4a by the area between x=0 and x=1 (Eq.2.4b). Describing the change of the needle area density (m^2 foliage per m^3 crown volume) per unit height (m) results in a description of the relative needle area distribution, which is dimensionless.

$$y = \frac{1 - e^{-(\frac{x}{p_1})^{p_2}}}{1 - e^{-(\frac{1}{p_1})^{p_2}}} \tag{2.4b}$$

Projected needle area and branch dry weight of each whorl were determined applying the equations of Table 2.3. Whorl amounts were then divided by tree totals to obtain proportions of the total. The running sum of the relative whorl amounts was described by the integral of the Weibull-formula. Taking the derivative of the fitted integrals resulted in the distribution curves. The area below each curve equals 1, the total relative needle area or total relative branch biomass.

Results

Allometric relationships

Within each stand tree height and dbh were linearly correlated ($R^2=0.990$). The overall relationship between tree height and dbh was best described using a logarithmic transformation (natural logarithm) of both variables (Eq.2.5):

$$\ln(h) = 0.218 + 0.853*\ln(dbh) \quad (R^2=0.851) \tag{2.5}$$

With dbh tree diameter at breast height (cm)
h tree height (m)

The height of the base of the living crown was relatively constant within each stand. Crown length appeared to be linearly correlated with dbh (Eq.2.6). Linear relationships also appeared between dbh and crown radius, respectively between tree basal area (at breast height) and crown projection area (Eq.2.7). All crown relationships were independent of diameter class or stand characteristics.

$$Cl = 2.320 + 0.363*dbh \quad (R^2=0.892) \tag{2.6}$$

$$Cpa = 2.500 + 6.890*ba \quad (R^2=0.950) \tag{2.7}$$

With Cl length of the living crown (m)
Cpa crown projection area (m^2)
ba tree basal area at breast height (cm^2)

Tree biomass generally increased with increasing dbh. The relationship between stem biomass and dbh was stand-independent (Fig.2.9a) and best described by an exponential curve, derived from a two-sided log-transformation. Adding tree height as a predicting variable further improved the regression: the data fitted well with the common Dutch volume equation (see Table 2.4). Branch and needle biomass also increased with dbh, but the relationships clearly differed between the stands (Fig. 2.9b and 2.9c).
In addition, branch biomass differed significantly between suppressed and (co-) dominant trees. Differences were no longer significant when tree height was added as an independent variable. Both the relationships between stem dimensions and biomass amounts and the relationship between stem dimensions and needle area were best described using two-sided log-transformations; these accounted for at least 94% of the variance (Table 2.4).

Table 2.4: Regression of stem biomass (WS), branch biomass (WB), needle biomass (WN), crown biomass (WCr), total biomass (Wtot), and needle area (NA, in m^2) respectively, on dbh (d, in cm) and tree height (h, in m). Biomass amounts are in kg per tree.

Regression equation	R^2
ln WS[1] = -2.535 + 2.009*ln(d) + 0.709*ln(h)	0.998
ln WB = -2.675 + 4.420*ln(d) - 2.784*ln(h)	0.944
ln WN = -1.346 + 3.351*ln(d) - 2.201*ln(h)	0.941
ln WCr = -1.345 + 3.924*ln(d) - 2.514*ln(h)	0.945
ln Wtot[2] = -1.620 + 2.410*ln(d)	0.995
ln NA = 0.417 + 3.345*ln(d) - 2.206*ln(h)	0.941

[1] The equation on WS common in the Dutch yield table, multiplied with the wood basic density, reads as: -3.229 + 1.901*ln(d) + 0.807*ln(h)
Applying this formula resulted in an R^2 of 0.990.

[2] Tree height is not significant.

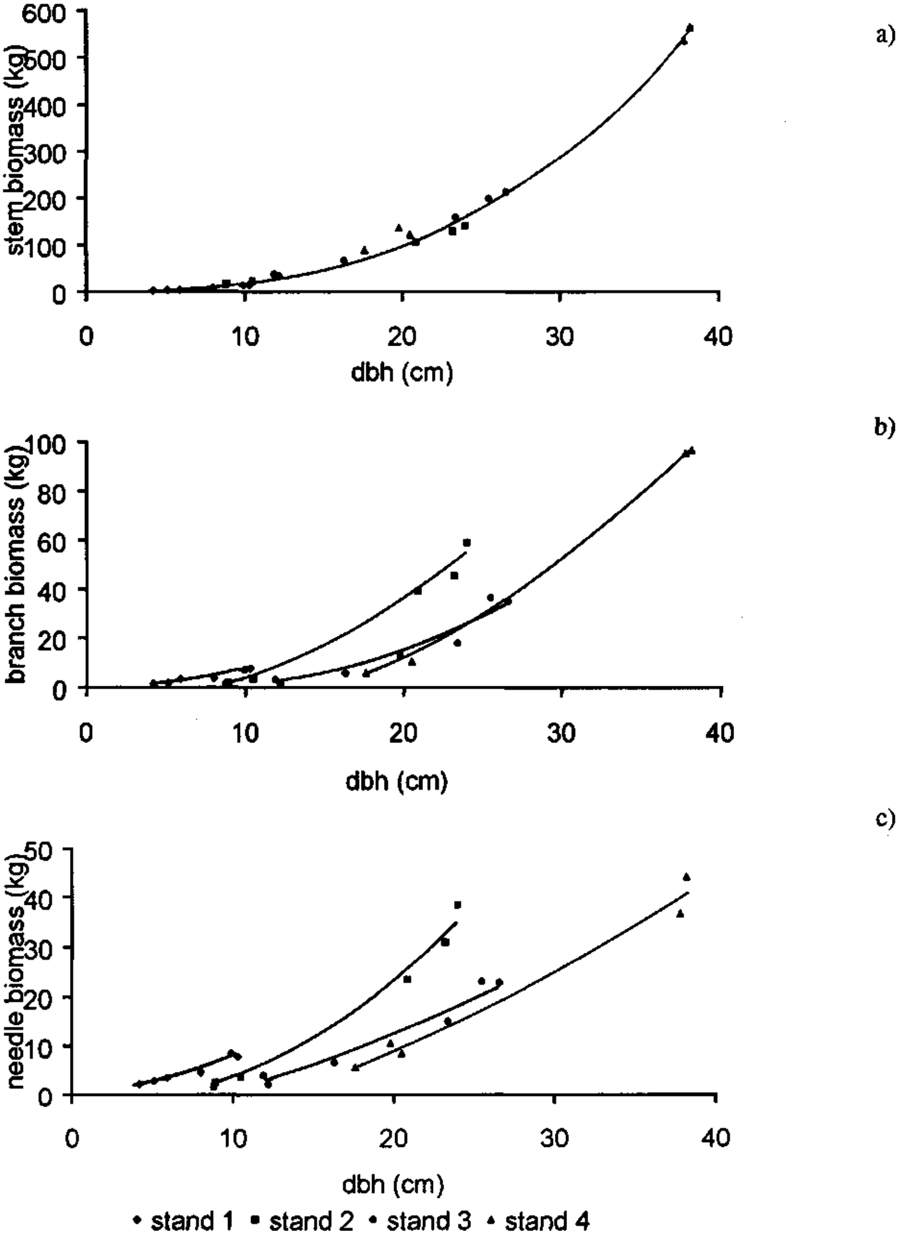


Figure 2.9: Relationships between dbh and biomass. Symbols represent the different stands, the curves show the main trends: a) stem biomass, b) branch biomass, and (c) needle biomass.

Needle biomass and projected needle area were strongly linearly interrelated (R^2=0.999): SLA amounted on average 56.2 $cm^2.g^{-1}$ (Fig.2.10).

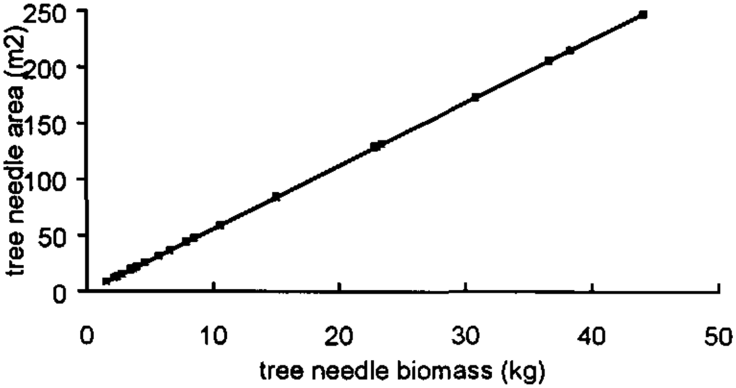


Figure 2.10: Relationship between needle biomass and needle area. The solid line represents the regression function.

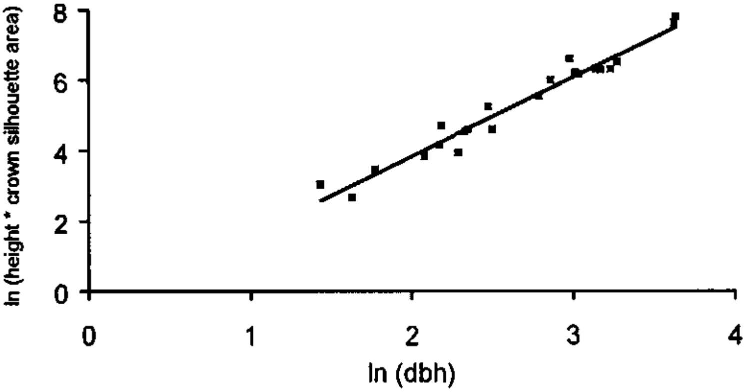


Figure 2.11: Relationship between the natural logarithm of dbh and the natural logarithm of the product of crown silhouette area and tree height. The solid line represents the regression function.

The mechanical relationship between dbh and crown size was analyzed following Niklas (1992). A strong linear relationship appeared (Fig.2.11, Eq.2.8) between the natural logarithm of dbh and the natural logarithm of the product of crown silhouette area (Csa) and tree height (h).

$$\ln(Csa*h) = -0.609 + 2.228*\ln(d) \quad (R^2=0.957) \qquad (2.8)$$

Dry matter distribution

Branch biomass stronger increased with increasing dbh than did needle biomass. As a result, the ratio between needle biomass and branch biomass decreased with increasing tree and crown dimensions or biomass (Fig.2.12).

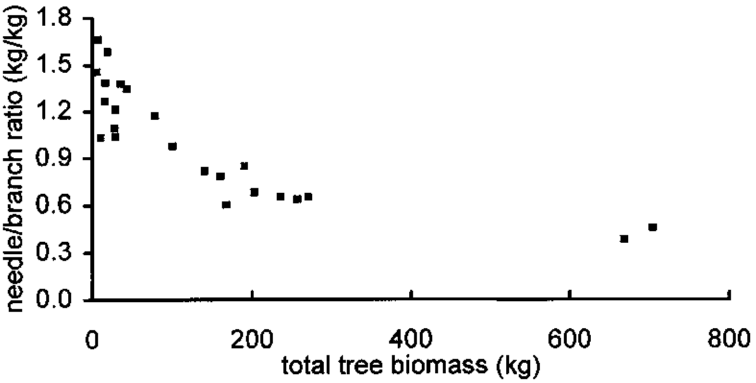


Figure 2.12: Relationship between the needle biomass / branch biomass ratio and total tree biomass.

Figure 2.13 shows the dry matter distribution as a function of total above-ground tree biomass. The distributions differed significantly between suppressed trees and (co-) dominant trees: suppressed individuals had much less crown biomass than dominating stand members.

SLA

Specific needle area (SLA) decreased with needle age and, within each needle age-class, it increased going down from tree top to crown base (Fig.2.14). Average SLA was estimated 56.3 $cm^2.g^{-1}$, calculated as the ratio of the sum of the projected needle areas of all trees and the sum of the needle biomass of all trees. Note that this weighted SLA does not differ from the previously calculated non-weighted tree average.

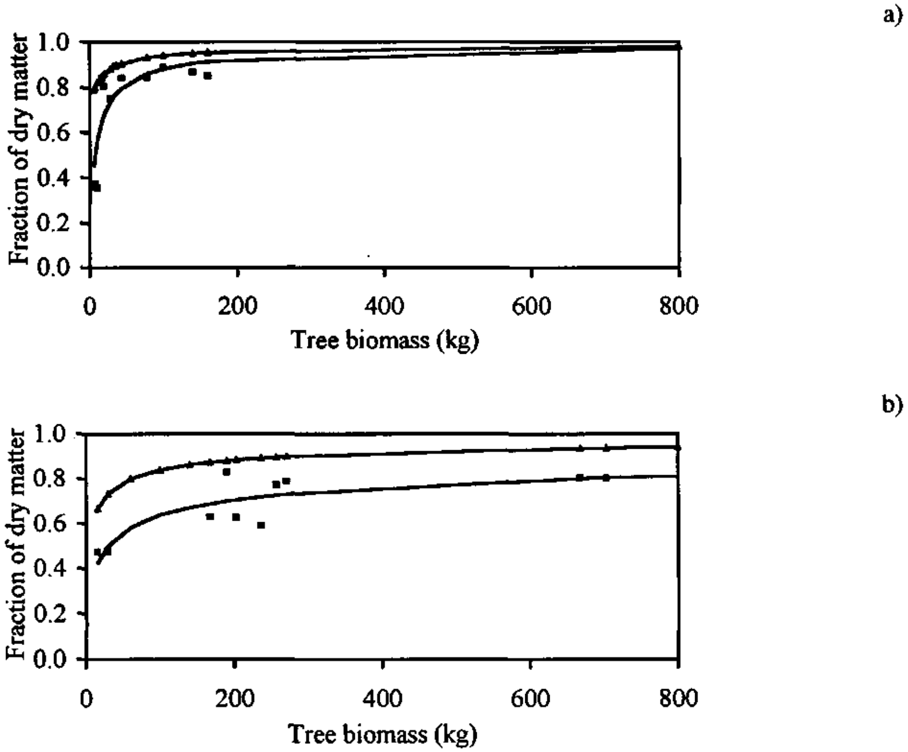


Figure 2.13: Above-ground dry matter distribution for trees from a) the smallest diameter class, and b) the largest diameter class. The squares represent relative stem amounts, the triangles represent sums of the relative branch and the relative stem amount. The two regression-curves divide each graph in three sections: the upper section is the relative amount of needle biomass, the middle part the relative branch biomass, and the lower part the relative stem biomass.

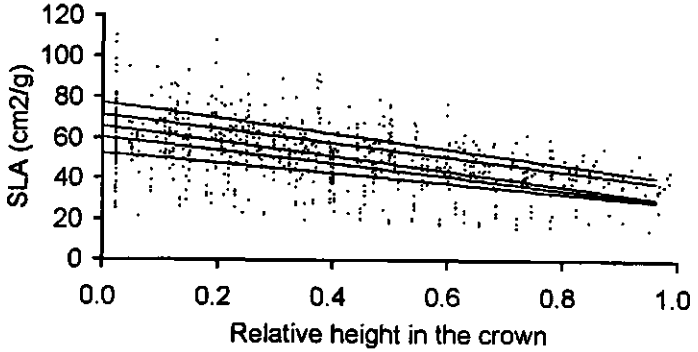


Figure 2.14: SLA in relation to height position in the crown (1 = tree top) and needle age-class. Symbols represent measured SLA-values. Differences in the SLA-height-relationship between needle age-class are indicated by lines: the upper line represents the fitted relationship when considering 1-year needles only, the line below represents the 2-year old needles, and so on down to the 5-year old needles.

Relationship between needle area and sapwood area

Linear regression of total projected needle area (NA) on sapwood area at breast height (SA_{bh}) explained 91.4% of the variance (the non-significant intercept was omitted). The resulting NA/SA_{bh}-ratio amounted 0.465 $m^2.cm^{-2}$ (Eq.2.9). However, clear between-stand differences appeared (Fig.2.15): the NA/SA_{bh}-ratios were comparable, but the intercept significantly differed among the stands. Between-stand differences disappeared and the fraction of explained variance increased when the height of the crown base was added as a co-variable (R^2=0.933): trees with a higher crown base had a lower amount of needle area (Eq.2.10).

$$NA = 0.465*SA_{bh} \tag{2.9}$$

$$NA = 0.518*SA_{bh} - 2.85*(h_{cb}-1.30) \tag{2.10}$$

With NA projected tree needle area (m^2)
SA_{bh} sapwood area at breast height (cm^2)
h_{cb} height of the crown base (m)
Note 1.30 = breast height

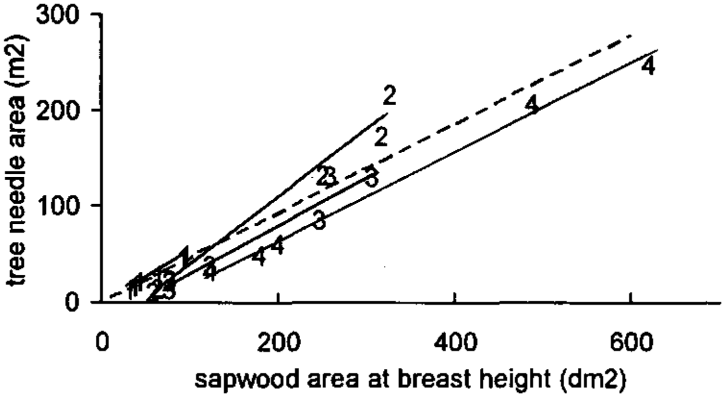


Figure 2.15: Relationship between sapwood area at breast height and tree needle area. Numbers represent the different stands. The solid lines represent regressions, the dashed line represents Equation 2.7.

Sapwood area at the crown base (SA_{cb}: subsample of 19 trees) accounted for 84.6% of the variation in needle area. This was slightly less than the percentage accounted for by SA_{bh} when the same subsample was used (85.6%).

Spatial distribution of needle area and branch biomass

The Weibull equation fitted well to both the branch biomass distribution (R^2=0.972) and the needle area distribution (R^2=0.985). Both amounts culminated in the lower part of the crown (towards the zero-value of the x-axes); the position of the maximum relative distribution was lower for the branch biomass than for the needle area. The distributions differed significantly between the stands (Fig.2.16). No significant differences occurred between trees from the lower and the higher diameter class. Table 2.5 gives the parameter estimates.

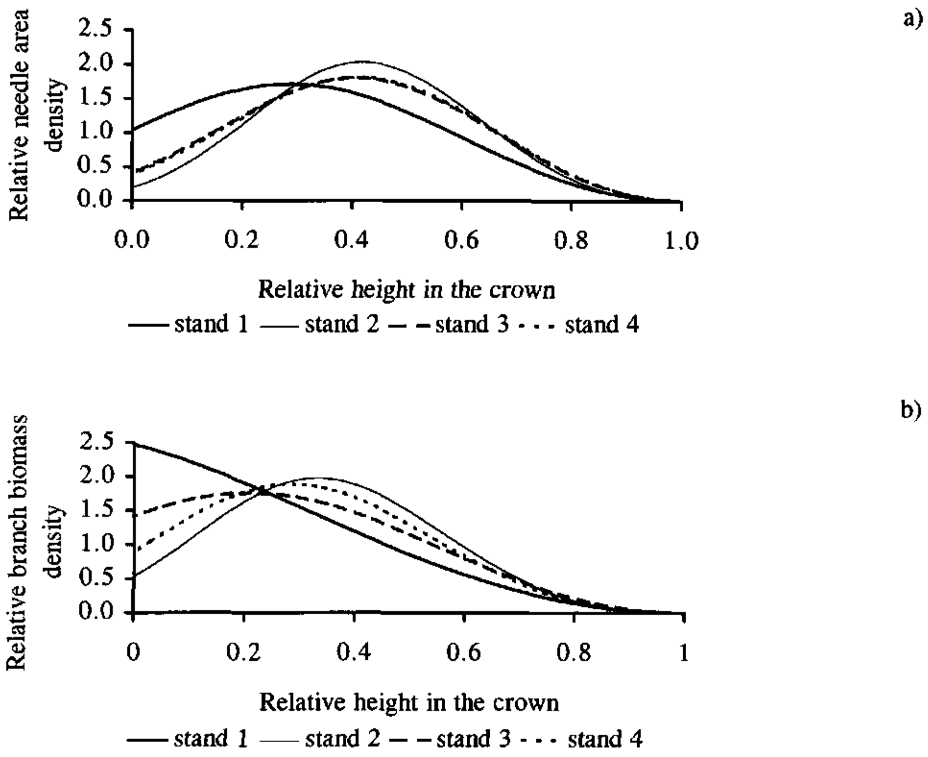


Figure 2.16: Average vertical distribution of (a) the relative tree needle area and (b) the relative tree branch biomass per stand.

Table 2.5: Parameter estimates of the Weibull-distribution equation applied to describe the relative vertical distributions of the needle area and the branch biomass respectively.

Stand	Needle area		Branch biomass	
no.	*p1*	*p2*	*p1*	*p2*
1	0.817	2.999	1.373	3.015
2	0.646	3.364	0.731	3.591
3	0.680	2.999	0.903	3.015
4	0.674	2.999	0.788	3.472

Stand amounts

In Table 2.6 total biomass and projected needle area of the sample stands are presented, calculated using the equations of Table 2.4. Above-ground stand biomass increased with stand age, amounting up to 143 tons per hectare. LAI reached a maximum value of 7.4 m^2m^{-2}. Comparing the four sample stands revealed that the ratio between needle biomass and branch biomass decreased with stand age.

Table 2.6: Estimated stand biomass (ton ha^{-1}), needle biomass / branch biomass ratio (WN/WB: dimensionless), and LAI (m^2m^{-2}).

stand	needle	branch	crown	stem	total	WN/WB	LAI
1	9.7	8.5	18.2	14.7	32.9	1.14	5.6
2	13.1	17.0	30.0	59.1	89.1	0.77	7.4
3	10.0	13.6	23.6	96.3	119.9	0.74	5.6
4	8.7	14.6	23.4	119.8	143.2	0.60	4.9

Discussion and conclusions

Allometric relationships

Dbh and basal area were strongly correlated with tree biomass and needle area, in agreement with results of others (Snell & Brown, 1978; St.Clair, 1993). The relationship between dbh and stem biomass was independent of stand characteristics, as both parameters are a result of culmination of stem growth. In contrast, the relationship between dbh and needle and branch biomass varied strongly between trees of different stands. Part of this variation can, in general, be attributed to the fact that dbh represents a culmination of growth history, whereas crown biomass, and especially foliage is determined by actual and/or recent growing conditions only. Nevertheless, clearly part of the variation should be addressed to differences in stand structure, as this affects crown size.

The relationship between dbh and tree height indicates the mechanical support function of the stem (McMahon & Kronauer, 1976). Niklas (1992) stated that in case wind stress is most important, dbh will be proportional to the 0.33-0.5 power of the product of crown silhouette area and the tree height, depending on how free the base of the tree is to move. Inverting the dependent and independent variables in Equation 2.8 reveals that, in the present data set, dbh is proportional to the 0.431 power of the product of crown silhouette area and tree height. This outcome supports the so-called constant-stress model: especially wind force will determine the relative growth rates of both tree diameter and height

(Niklas, 1992). Stem diameter growth and height growth are thus mechanically attuned to each other. Mechanical interrelationships within the trees also appeared from the strong correlations found between dbh and crown dimensions (Eq. 2.6 and 2.7). In even-aged mono-species stands, the height of the crown base will be largely determined by the radiation conditions inside the canopy. The relationship between crown length and dbh in Eq.2.6 thus indicates that within a stand, dbh and tree height are strongly correlated. At the same time, a certain tree diameter or basal area will be needed to physically support the crown. From Eq.2.7, where the crown is represented by its vertical projection area, it follows that in the present sample trees a rather fixed ratio between crown size and stem basal area exists. Growth of tree components is apparently influenced by the tree's attempts to maintain mechanical stability. These mechanically-based interrelationships hence form suitable tools when describing dry matter allocation in growth models.

Dry matter distribution

The decreasing ratio between needle biomass (WN) and branch biomass (WB) with increasing tree size (Fig.2.12) is a consequence of crown expansion. As the tree matures and crown size increases, both the branch and the needle biomass increase. However, as needles will be concentrated at the end of the branches in order to optimize radiation interception (Kellomäki et al., 1980), relatively more branch biomass will be needed to physically support a unit needle biomass. Smith & Long (1989), in a research on *Pinus contorta*, additionally pointed out that relatively more branches can be expected in vigorous, deep-crowned trees than in shallow-crowned trees, resulting in a higher WN/WB-ratio for the latter group. An important consequence is that the vigorous, dominant trees are not the most efficient in terms of stemwood production per unit foliage area, because of the lower ratio of assimilatory to respiratory tissue (Smith & Long, 1989). These functional dependencies form useful tools for the development of dry matter allocation keys in growth models.

Fig.2.13 clearly shows that the dry matter distribution is affected by dominance position. Suppressed trees have relatively much less crown biomass than dominant individuals. This can be attributed to a lower growth rate in combination with the cumulative character of stem growth. When a tree suffers from a lack of resources, less assimilates will be produced, and less dry matter will be allocated towards the crown. Due to turn-over of the foliage and the branches, the amount of crown biomass may even decrease. However, as the stem biomass can not decline (unless the tree dies) this will cause the fraction of crown biomass to decrease.

Dry matter distribution patterns derived from dominant trees can be regarded as target patterns; these can be applied to simulate allocation. Including a measure of the competitive power of the tree, like height/dbh-ratio, enables to account for effects of dominance position on dry matter allocation as well.

Needle area and sapwood area

The large spread in SLA-values, caused by differences in needle age and its spatial position, is in accordance with results from Del Rio & Berg (1979), Kellomäki et al. (1980), and Borghetti et al. (1986). However, despite the large variability within the trees, SLA hardly differed among the trees: needle biomass and projected needle area were strongly linearly correlated.

The calculated average ratio between the sapwood cross-sectional area at breast height (SA_{bh}) and the projected needle area (NA) in Douglas-fir (0.465 $m^2.cm^{-2}$) falls within the range of values found by Grier & Waring (1974), Snell & Brown (1978), Kaufmann & Troendle (1981), Waring et al. (1982), and St.Clair (1993). SA_{bh} appeared to be a better estimator than basal area, due to the fact that sapwood conducts water to the foliage (Grier & Waring, 1974; Long et al., 1981; Marshall & Waring, 1986). However, the NA/SA_{bh}-ratio differed remarkably between trees of the different stands. A similar result was found in *Pinus contorta* by Dean & Long (1986) and Dean et al. (1988). This could be due to differences in site quality (Brix & Mitchell, 1983; Espinosa Bancalari et al., 1987) or climate (Mencuccini & Grace, 1995), or to family differences (St.Clair, 1993), but in the present study such differences could be ignored. In *Pinus contorta*, Dean & Long (1986) found the relationship between SA_{bh} and NA to be curvilinear; they attributed this non-linearity to both sapwood area taper in the stem and variation in crown-free bole lengths within a stand. The latter seems to make sense in the present study as well. Fig.2.15 and Eq.2.9 and 2.10 indicate that ratio differences were caused by differences in crown base height. Some workers assumed the water conductivity of the sapwood below the crown base to remain constant, implying that the increasing stem basal area points to an increasing amount and proportion of heartwood (Kaufmann & Troendle, 1981; Long et al., 1981). However, sapwood area tapers not only in the crown, but in the branch-free bole as well (Dean & Long, 1986; van der Zee & Bartelink, in prep.). Differences in crown base height are therefore a probable cause of variability in the NA/SA_{bh}-ratio at breast height. This is in accordance with results of Maguire & Hann (1987). The NA/SA_{bh}-ratio will decline with increasing height of the crown base (Waring et al., 1982; Brix & Mitchell, 1983; Espinosa Bancalari et al., 1987; van der Zee & Bartelink, in prep.), and the sapwood conductivity is hence not constant throughout the stem cross-sectional area (Brix & Mitchell, 1983; van der Zee & Bartelink, in prep.). Additional tree-to-tree variability may exist due to sapwood area taper in the stem (Dean & Long, 1986). Although statistical evidence was presently lacking, SA_{cb} will thus be functionally closer related to NA than SA_{bh} will. Hence, when sapwood area at breast height is related to needle area, adding a variable accounting for the foliage-less "pipe-length" (the distance between breast height and crown base) will improve the relationship. Ignoring within-stand variation in the NA/SA_{bh}-relationship will substantially bias the estimate of tree leaf area and stand LAI (Dean et al., 1988).

Spatial distribution of needle area and branch biomass

Between stand 2, 3, and 4, differences in the relative vertical needle area and branch biomass distributions were small. The needle area and the branch biomass of stand 1, on the contrary, culminated close to respectively at the base of the living crown, which can be attributed to the non-closed canopy of this stand: radiation intensity at the crown base will be relatively high, enabling the survival of larger amounts of needles and branches in the lower part of the crown (Kellomäki et al., 1980). The relative branch biomass density concentrated lower in the crown than did the needle area, which can be attributed to the crown form; towards the crown base the distance from trunk to crown mantle increases, so more branch biomass will be needed to support the needle area. Crown length and canopy depth themselves are measures of stand structure (Smith & Long, 1989), and could thus serve as indicators for the spatial distribution. Smith & Long (1989) for example, stated that in *Pinus contorta* the length of the living crown affects not only the absolute amounts of foliage and branches but also the spatial distributions.

2.3 Allometric relationships for biomass and leaf area of beech.

Introduction

Allometric relationships among tree dimensions, biomass amounts, and foliage area form useful tools when developing mechanistic models of forest growth (see Jarvis & Leverenz, 1983; Causton, 1985). Leaf area is generally considered to play a key role as it is the main variable controlling radiation interception. The amount of leaf area is functionally related to the water-conducting sapwood area (Shinozaki et al., 1964; Jarvis & Leverenz, 1983), and to the branch biomass, which mechanically supports the foliage.
The stem provides the physiological and physical support of the crown. Sapwood area is related to the amount of water-transpiring foliage (Jarvis & Leverenz, 1983), stem diameter indicates the amount of biomass that is supported (Causton, 1985), whereas the relationship between stem diameter and tree height and/or crown dimensions will be determined by the need for mechanical stability (Niklas, 1992). Stem dimensions hence form important indicators of crown size.

Not enough data are available yet to build reliable mechanistic models (Cannell, 1989). The present study hence focused on tree dimensions, biomass, and leaf area interrelationships of beech (*Fagus sylvatica* L.), as part of the development of a mechanistic model of forest growth. Aims of the study were: 1) to establish allometric relationships among stem and crown dimensions, biomass amounts, and leaf area, 2) to describe the above-ground dry matter distribution, 3) to quantify the relationship between sapwood area and leaf area, 4) to determine the vertical gradient of the specific leaf area within the crown, and 5) to estimate above-ground stand biomass and leaf area index (LAI). The results of this study will be used to simulate growth and yield of forest stands.

Methods

<u>Data collection</u>

Thirty-eight trees were selected from six even-aged beech stands, located in a forest area in the centre of the Netherlands. To obtain a range of tree sizes, stands of different ages were chosen. All stands were growing on acid brown podsolic soils in ice-pushed preglacial deposits with deep water tables (>5m below surface). Stand characteristics were derived from measuring the diameter at breast height (dbh) of all trees in a certain sample area, and from the heights of the selected trees (Table 2.7). The sizes of the sample areas varied between 250 and 1000 m^2, including at least 36 trees: the largest sample consisted of 81 trees. Within the sample areas the trees were divided into two diameter classes ('small trees' versus 'large trees') of equal tree number: from each class 1-3 sample trees were chosen which had dbh's equal or close to the average dbh of that class.

According to the criteria of Kraft (1884), all small trees could be classified as suppressed individuals, whereas the large trees were classified as (co-) dominants.

Table 2.7: Characteristics of the sample stands. Cutting age (years), number of trees per hectare (N), basal area (G, $m^2.ha^{-1}$), average height of the three highest sample trees (Hdom, m), average diameter of the beeches (square root of average tree basal area: d, cm), year of harvest (Hy), and number of sample trees (Ns).

stand	cutting age	N	G	Hdom	d	Hy	Ns
1	8	7200	5.54	3.5	3.13	1990*	3
2	11	9920	2.88[a]	4.2	3.17	1993*	6
3	20	5200	31.42[b]	10.2	7.81	1990*	4
4	21/22	2920	19.69	9.5	9.27	1992*/1993	10
5	38/40/41	810	26.21	17.8	20.30	1990/1992*/1993	11
6	58/59	360	21.97	22.5	27.87	1992*/1993	4

[a] With 17% of G and 69% of N being douglas-fir and birch
[b] With 33% of G and 15% of N being oak
* Year of stand inventory

Sampling took place in the second half of July and the first half of August, in 1990, 1992 and 1993 (Table 2.7). Before felling, vertical crown projection area was determined. Horizontal crown extension was estimated visually from the ground in 8 different azimuthal directions: crown projection area was estimated from the average crown radius. After felling, tree length was measured. From a subsample of 20 trees, height of the crown base (height of the lowest living foliage, excluding epicormics) was measured as well. Random leaf samples were collected from each crown to determine average SLA (cm^2 fresh area per gram dry weight). The crowns of the 1993 sample trees were divided into 10 horizontal layers of approximately uniform depth, and at each boundary a subsample of 20-25 leaves was taken to determine height-related SLA differences. Next, all living branches and leaves were collected: of each tree the leaf-bearing branches were cut into smaller pieces (with a maximum length of 1.5m) and put into plastic bags, whereas the leaf-less branch parts were sawn into 4-m pieces. All biomass samples were taken to the laboratory. Stem volume followed from stem diameter measurements at regular distances along the stem. From each tree a stem disk was removed at breast height and taken to the laboratory.

In the laboratory, projected leaf areas of the fresh leaf samples were determined using the Delta-T Image Analyses System. The leaf-bearing branches were dried for 2 days at 22-25°C in a drying chamber (relative air humidity decreased to approximately 30%), to simplify the separation of foliage and woody parts. After the leaves had been removed physically, samples were oven-dried to determine dry weights of the leaf (24h; 70°C) and of the defoliated branches (48h; 105°C), and to estimate total dry weights. The leaf-less branch parts were chipped and weighed; dry weight was determined based on the ratio between fresh weight and oven-dry weight of a sample of chipped branch parts. Total branch dry weight followed from summing the dry weights of the defoliated branches and the leaf-less branch parts. Stem dry weight was determined by multiplying stem volume with a wood basic density of 550 kg dry weight per m^3 fresh volume (Burger, 1950).

As the boundary between sapwood and heartwood can be difficult to recognize in beech (Zimmermann, 1983; Hillis, 1987), the visual check was accompanied with the application of several chemical solutions which work on differences in chemical composition between sapwood and heartwood (Bamber & Fukazawa, 1985; Hillis, 1987): we applied Ferric Chloride, Floroglucinol, Fuchsine, Safranine, and Fastgreen, respectively. The cross-sectional area of each sapwood-ring was determined using a digital stem disk analysis system.

Data-analysis

Relationships between stem and crown dimensions, biomass amounts, and leaf area were analyzed. Crown silhouette area (horizontal projection) was derived from crown length and vertical projection area, assuming that the crown can be described by an ellipsoid. Apart from the total sapwood area at breast height (sa_{bh}), also the cumulative area of the most recent growth rings was determined. The area of only the most recent rings might be closer related to total leaf area because in general the contribution of a growth ring to the vertical water transport declines with ring-ageing (Zimmermann, 1983). To be able to include data from younger trees as well, only up to 6 growth rings were taken into account.

Biomass distribution was described as a function of total above-ground biomass. In this approach, first the ratios of foliage to stem dry weight and branch to stem dry weight are calculated and related to the total biomass, after a two-sided logarithmic transformation. The following relationships were analyzed:

$$\ln (w_l/w_s) = c_1 + c_2 * \ln (w_t)$$
$$\ln (w_b/w_s) = c_3 + c_4 * \ln (w_t)$$

With	w_l	tree leaf biomass (kg)
	w_b	tree branch biomass (kg)
	w_s	tree stem biomass (kg)
	w_t	total tree biomass (kg)
	c_1-c_4	regression constants

From these equations, the mathematical descriptions of respectively w_l/w_t, w_b/w_t, and w_s/w_t were solved as functions of w_t.

Regression analyses were carried out using the GENSTAT statistical package. All regression estimates presented were significant (at least) at the 5%-level. The fraction of variance accounted for (R^2) has been adjusted for the number of degrees of freedom.

Both linear and non-linear models were tested. In case of linear regression analysis the model was fitted by linear least squares. Linear regression analysis is commonly used in biomass research after carrying out a so-called two-sided log-transformation: a log-transformation (natural logarithm) of both the dependent and the independent variables (Causton, 1985). In case of non-linear regression analysis the model was fitted directly by non-linear least squares. The presentation of the fitted models is in accordance with the statistical approach applied. In case of linear regression after a log-log-transformation, the power-model derived from the log-model is presented as well to facilitate comparison with other models.

Results

Allometric relationships

Stem biomass, branch biomass, leaf biomass, crown biomass (branches and leaves), and leaf area were non-linearly related to dbh (Fig.2.17), which in all cases explained over 90% of the variance (Table 2.8). The relationships did not differ between trees from different size classes or different stands. Adding tree height as a predicting parameter resulted in a slight increase of the regression-coefficients R^2 (Table 2.9). Leaf area and leaf biomass were strongly linearly interrelated ($R^2=0.987$); the average ratio (SLA) amounted 172 $cm^2\ g^{-1}$.

Stem and crown dimensions generally increased with increasing dbh, but large variability occurred. The relationship between dbh and tree height was best described after a log-log transformation of both variables (Eq.2.11a):

$$\ln(h) = 0.549 + 0.769*\ln(dbh) \qquad R^2=0.934 \qquad (2.11a)$$

Transformed to a power function it reads as follows (Eq.2.11b):

$$h = 1.732 * dbh^{0.769} \qquad (2.11b)$$

With h tree height (m)
dbh stem diameter at breast height (cm)

Table 2.8: Non-linear models between tree biomass amounts or leaf area (Y: in kg or m^2) and dbh (in cm): the models are of the form $Y = c_0+c_1*dbh^{c2}$. Standard errors of the estimates are indicated (s.e.). The number of observations is 38.

Y	c_0	c_1	s.e.c_1	c_2	s.e.c_2	R^2
leaves	0.375	0.0024	0.0021	2.517	0.253	0.906
branches	1)	0.0020	0.0016	3.265	0.236	0.916
crown	1)	0.0031	0.0023	3.161	0.216	0.924
stem	1)	0.0762	0.0224	2.523	0.088	0.979
total	1)	0.0798	0.0191	2.601	0.072	0.988
leaf area	8.560	0.0286	0.0213	2.623	0.218	0.932

1) Intercept not significant.

Table 2.9: Non-linear models between tree biomass amounts or leaf area (Y: in kg or m^2) and dbh (in cm) and tree height (h: in m): the models are of the form $Y = c_1*dbh^{c2}*h^{c3}$. Standard errors of the estimates are indicated (s.e.). The number of observations is 38.

Y	c_1	s.e.c_1	c_2	s.e.c_2	c_3	s.e.c_3	R^2
leaves	0.0167	0.0097	2.951	0.283	-1.101	0.375	0.923
branches	0.0114	0.0117	3.682	0.373	-1.031	0.568	0.920
crown	0.0183	0.0164	3.614	0.339	-1.078	0.507	0.929
stem	0.0109	0.0028	1.951	0.060	1.262	0.117	0.996
total	0.0306	0.0119	2.347	0.096	0.590	0.183	0.991
leaf area	0.2410	0.1230	2.899	0.240	-0.984	0.322	0.942

Crown base height (subsample of 20 trees from 4 different stands) was rather constant within a stand, but differed significantly between the stands. Crown length appeared to be strongly correlated with stem basal area (Eq.2.12).

$$c_l = 2.897 + 1.432*ba \qquad R^2=0.888 \qquad (2.12)$$

With c_l crown length (m)
ba stem basal area at breast height (dm^2)

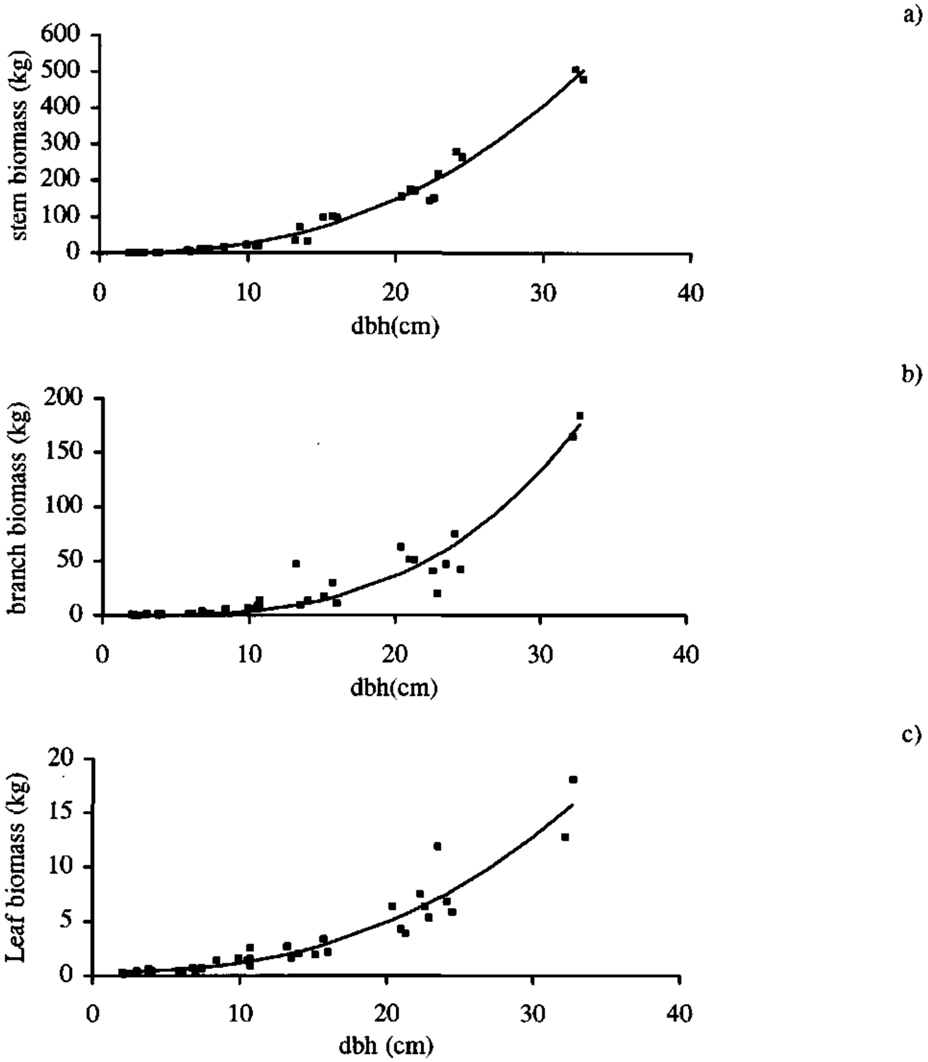


Figure 2.17: Stem, branch, and leaf biomass, respectively, related to dbh. Data are represented by symbols, the regression equations by solid lines. Parameter estimates of the regression equations can be found in Table 2.8.

Crown silhouette area and tree height were clearly correlated with dbh. Following Niklas (1992), the product of silhouette area and tree height was related to dbh, after a two-sided log-transformation (Eq.2.13a). Exchanging the dependent and independent variables revealed that dbh was proportional to the 0.50-power of the product of tree height and crown silhouette area.

$$\ln(h*c_{sa}) = 0.712 + 1.813*\ln(dbh) \qquad R^2=0.899 \qquad (2.13a)$$

Transformed to a power function it reads as follows (Eq.2.13b):

$$h*c_{sa} = 2.038 * dbh^{1.813} \qquad (2.13b)$$

With c_{sa} crown silhouette area (m^2)

Tree leaf area and crown biomass were both correlated with crown projection area (Fig.2.18). The relationships were best described by non-linear regression equations (Eq.2.14 & 2.15).

$$la = 3.38 * c_{pa}^{1.028} \qquad R^2=0.835 \qquad (2.14)$$

$$w_{cb} = 0.699 * c_{pa}^{1.351} \qquad R^2=0.919 \qquad (2.15)$$

With la tree leaf area (m^2)
c_{pa} crown projection area (m^2)
w_{cb} crown biomass (kg)

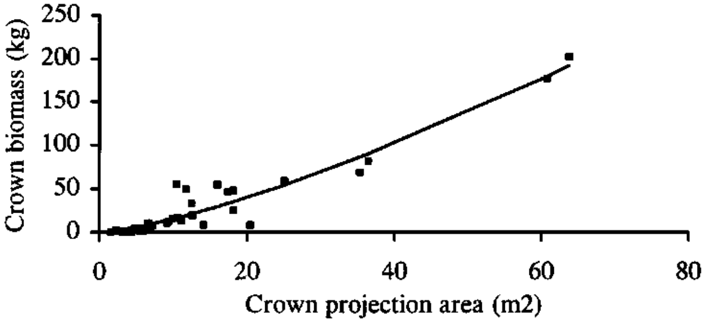


Figure 2.18: Relationships between crown projection area and crown biomass.

Biomass distribution

The biomass amounts of the tree components were expressed as fractions of the total above-ground tree biomass. One tree had many stem forks; because the boundary between 'stem' and 'branch' was difficult to define, this tree was excluded from the calculation of the distribution curves. In general, the fraction stem biomass increased with increasing tree size, whereas the fraction leaf biomass decreased. However, the regression-constants differed significantly between trees from different diameter classes. Fig.2.19 presents the relative biomass distributions for each diameter class separately. Larger trees in a stand appeared to have relatively more crown biomass than smaller trees.

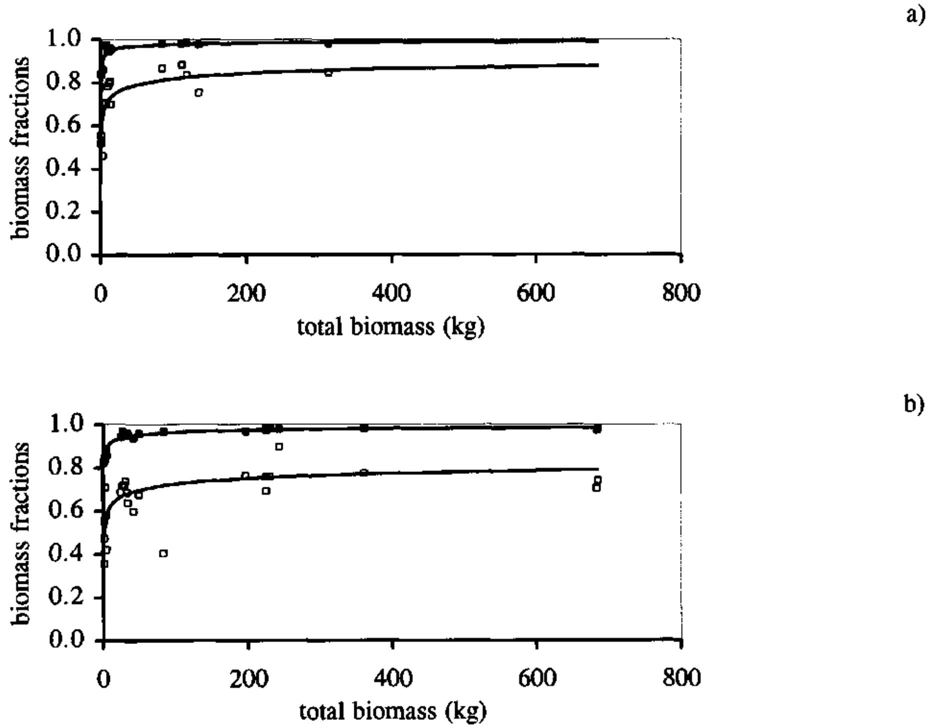


Figure 2.19: Relative above-ground biomass distribution. Symbols represent the fractions of stem biomass (open squares) and stem-plus-branch biomass (closed squares) of individual trees. The solid lines indicate how, according to the regression analysis, the relative amount of biomass is distributed over respectively the stem (lower part), branches (middle part), and leaves (upper part) in the trees. Results are presented for a) suppressed trees, and b) dominant trees.

The amount of leaf biomass decreased with increasing branch biomass; no significant difference between diameter classes occurred. The ratio between leaf biomass and branch biomass (L/B-ratio) decreased with increasing tree size. The most significant relationships appeared when the L/B-ratio was related to dbh, tree height or crown biomass (Fig.2.20).

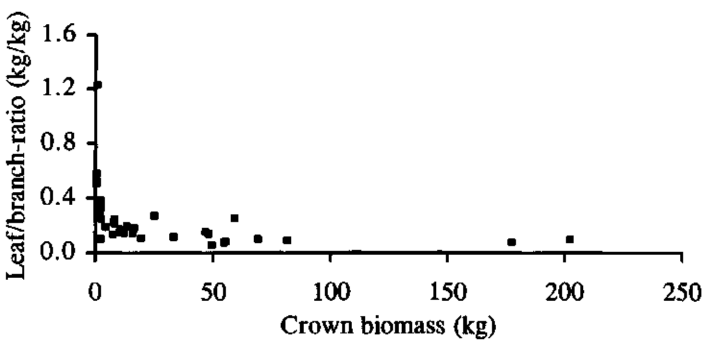


Figure 2.20: Leaf biomass/ branch biomass ratio as a function of crown biomass.

SLA

Strong variation in SLA was found. SLA of leaf samples varied between 80 and 340 cm^2 g^{-1}, but overall SLA was remarkably consistent among the trees (weighted average SLA amounted 172 cm^2 g^{-1}, with a standard deviation of 16 cm^2 g^{-1}). Figure 2.21 presents the pattern of change of average SLA within the crown, derived from data of the 1993 sample trees. In the tree top SLA amounted 80-120 cm^2 g^{-1}, increasing to 300-340 cm^2 g^{-1} at the crown base. The pattern was consistent among the stands, though in the youngest stand height-related differences were less pronounced. To investigate the role of canopy closure, in addition SLA-measurements were carried out on a small solitary tree (height=2m). In this tree SLA showed the same trend, but differences were less pronounced than in the forest-grown trees: SLA decreased from on average 180 cm^2 g^{-1} at the crown base to 100 cm^2 g^{-1} at the tree top.

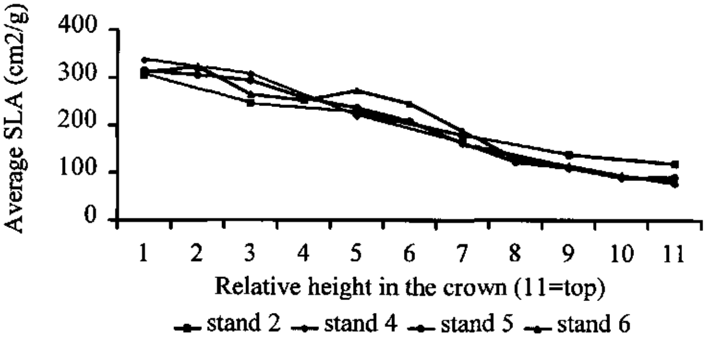


Figure 2.21: Mean SLA at different heights within the tree crowns. Heights are expressed as positions relative to the length of the living crown. Each SLA-value was based on 6 samples, except for stand 6 where only two samples per height position were available.

Sapwood - leaf area relationships

None of the chemical indicators applied indicated any presence of heartwood, hence sapwood area was considered to be equal to basal area (without bark) in all sample trees. Tree leaf area appeared to be strongly correlated with this sapwood area (sa_{bh}). Ignoring the non-significant intercept resulted in a leaf area - sapwood area ratio of 0.331 m^2cm^{-2} ($R^2=0.926$), but the relationship differed significantly between stands. Stand differences disappeared when crown dimensions, especially the height of the crown base, were used as co-variables. Crown length data were available for the subsample (20 trees). In this subsample sa_{bh} explained 96.2% of the variance in leaf area. This percentage was increased to 98.2 when the height of the crown base was applied as a co-variable. Equation 2.16 implies that in case of identical sa_{bh} amounts, trees having the lowest crown base will have the highest amount of leaf area.

$$la = 0.341*sa_{bh} - 1.674*h_{cb} \qquad R^2=0.982 \qquad (2.16)$$

where la tree leaf area (m^2)

sa_{bh} tree sapwood area at breast height (cm^2)

h_{cb} height of the crown base (m)

Total leaf area also appeared to be correlated with the area of the most recent growth rings. Best correlation was with the cross-sectional area of the three youngest rings ($R^2=83.6\%$).

Stand biomass and LAI

Stand biomass and LAI (Table 2.10) were derived by applying the equations from Table 2.8. In Fig.2.22 some stand totals are compared with data from literature, as collected by Cannell (1982): all data on beech are included here, covering different sites and management regimes. Present data showed an almost linear increase of the total above-ground stand biomass with stand age (Fig.2.22a). LAI in the closed-canopy stands generally varied between 5.5 and 7.2 (Fig.2.22b): the low value of stand 2 can be ascribed to the large contribution to the canopy of the birches.

Table 2.10: Biomass (ton.ha^{-1}) and LAI (m^{2}.m^{-2}) of the sample stands.

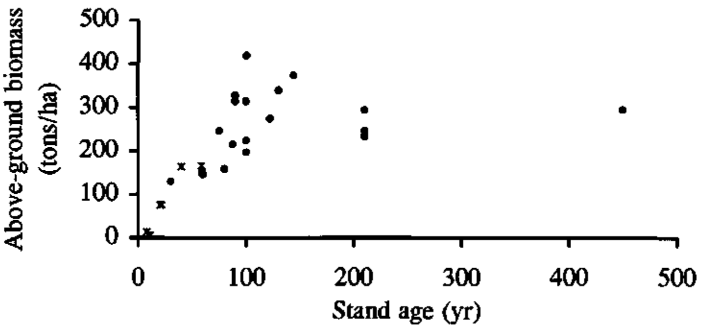
stand	leaf	branch	stem	total	L/T-ratio	LAI
1	3.01	0.64	9.96	13.61	4.70	6.58
2	1.28	0.29	4.37	5.94	1.57	2.79
3	3.61	8.45	63.10	75.16	0.43	6.71
4	3.08	9.54	63.90	76.52	0.32	5.53
5	4.22	33.38	126.90	164.5	0.13	7.18
6	3.93	39.49	123.30	166.72	0.10	6.79

Discussion and conclusions

Allometric relationships

The amounts of biomass presently found are comparable with data from Burger (1950) and Pellinen (1986). Dbh explained a large part of the variation in tree biomass, in accordance with results of others (Burger, 1950; Kakubari, 1983; Pellinen, 1986). The relationship between dbh and stem biomass was stand-independent, which can be expected as both are cumulative parameters. The relationship between dbh and leaf and branch biomass, in contrast, can be expected to differ between stands, as stand density will affect crown form and size (Burger, 1950). Adding parameters accounting for stand structure will reduce such variability, as was presently indicated by the increased R^2 when tree height was added to the allometric relationships. In the present data set, however, though some stand-effects were visible, the relationships between dbh and foliage respectively branch biomass did not significantly differ between stands.

a)



b)

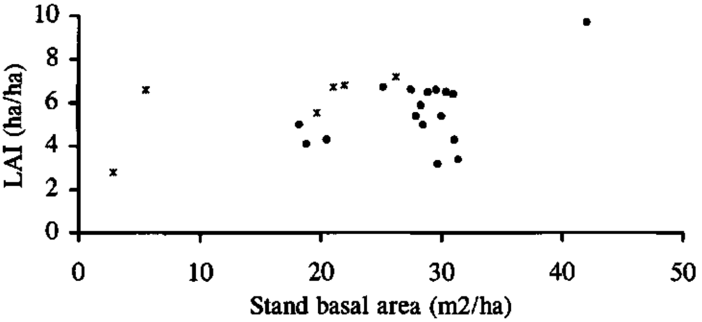


Figure 2.22: Stand data from present research (*) and from literature (dots), after Cannell (1982); a) Stand age versus above-ground biomass, b) Stand basal area versus LAI.

The presently established models fitted well. However, because the leaf and branch biomass of the two largest trees had a relatively strong effect on the parameter estimations, care should be taken when the models are used for extrapolation.

The well-known relationship between dbh and tree height was confirmed by the present data set (Eq.2.11). This relationship can be regarded indicative for the mechanical support function of the stem. According to Niklas (1992), dbh is expected to be proportional to the 1.5-2.0 power of tree height when primarily biomass (static loads) determines stem diameter. Inverting dependent and independent variables in Equation 2.11 results in an exponent of 1.22, which is clearly lower. An explanation for this might be that crown size is ignored. In case wind stress is most important, dbh will be proportional to the 0.33-0.50 power of the product of crown silhouette area and the tree height, depending on how free the base of the tree is to move (Niklas, 1992): the presently found exponent of 0.50 supports this so-called constant-stress model, implying that especially wind force will determine the relative increments in height and diameter.

Biomass distribution

The dry matter distribution pattern presented in Fig.2.19 is comparable with the general pattern found in many tree species (see data Cannell, 1982). Presently, relatively large stand members had a higher fraction of leaf and branch biomass than smaller neighbours. Regarding diameter-class as an indicator of dominance position, this means that dominance position affects the amount of crown biomass. Cannell (1989) concludes that in case of increased inter-tree competition, a lower fraction of the dry matter will be allocated towards the branches, and probably towards the foliage as well. This coincides with the presently found effect of dominance position. Dominant trees hence invest more in the canopy, and are thus able to maintain a relatively large crown. Including an indicator of a tree's dominance position would hence improve dry matter allocation keys.

Because foliage is concentrated at the end of the branches (the crown mantle) in order to optimize radiation interception (Kellomäki & Oker-Blom, 1981), relatively more branch biomass will be needed to physically support a unit leaf biomass when crown size increases. The decreasing L/B-ratio (Fig.2.20) can hence be ascribed to crown expansion. The ratio between leaf biomass and branch biomass was independent of diameter class. A certain amount of leaf biomass apparently needs a certain amount of supporting branch biomass, independent of a tree's dominance position, but dependent on its size.

SLA

SLA varied strongly, both in the vertical and in the horizontal plane (results not shown): values between 80 and 340 $cm^2 g^{-1}$ were found. SLA generally increased when going from the tree top downwards (Fig.2.21). Comparable results have been reported by Decei (1983), Pellinen (1986), and Gratani et al. (1987) in *Fagus sylvatica*, and by Tadaki (1970) in *Fagus crenata*. The variation in SLA is due to morphological differences between sun and shade leaves (Gratani et al., 1987), caused by differences in light conditions within the canopy (Kellomäki & Oker-Blom, 1981; Gratani et al., 1987). The presently found trend of SLA increasing towards the crown base can hence be explained by the decrease in radiation availability. This is supported by the fact that the rate of SLA-increase was lower in the youngest stand and far lowest in the solitary tree: the light extinction rates here will be less pronounced due to respectively the relative open canopy

(compare the basal areas in Table 2.7) and the absence of neighbouring trees. Hence, stand density affects the rate of change of SLA with depth in the canopy.
Part of the variability in SLA might also be attributed to seasonal effects, as data collection was spread over three years. However, despite the large variation in SLA, overall SLA at the tree level was consistent among the trees. Tree leaf biomass and tree leaf area were strongly interrelated ($R^2=0.987$), implying that at the tree level SLA is rather independent of stand density.

Sapwood - leaf area relationships

Presently, sapwood area explained 92.6% of the variance in leaf area (la). However, sapwood area (sa_{bh}) equalled basal area (without bark): no heartwood was found, which agrees with remarks from Hillis (1987) that in beech heartwood generally is formed only after 80-100 years. The la/sa_{bh}-ratio may hence as well point to the mechanical as to the functional support function of the stem. The significant role of the height of the crown base in the relationship between sa_{bh} and leaf area (Eq.2.16) is in agreement with the pipe-model theory (Shinozaki et al., 1964): when leaf area is related to total cross-sectional stem area (ba), the la/ba-ratio will decrease when going downward from the crown base to breast height, because transpiring tissue is lacking here. The length of the branch-free bole thus affects the la/sa_{bh}-ratio, as is predicted by Eq.2.16: the higher the crown base, the lower the leaf area per unit sapwood area measured at breast height. It also implies that the water-conductivity below the crown is not constant within the cross-sectional stem area. This can be explained by the fact that water-conductivity decreases with ring-ageing, in conifers, in ring-porous, as well as in diffuse-porous species like beech (Zimmermann, 1983; Bamber & Fukazawa, 1985). However, due to the smaller vessels in diffuse-porous species when compared with ring-porous species, more growth rings can be expected to contribute to the vertical water transport in beech than, for example only the recent 1-3 rings as in oak (Rogers & Hinckley, 1979).

Since in this study no water transport was measured, estimation of the number of contributing rings was based on the regression analysis. The area of the three most recent growth rings gave statistically the best result, but explained clearly less of the variation in leaf area than did total sapwood area. Another reason for the correlation between leaf area and area of the recent rings might be that this reflects a different mechanism, for example assimilate translocation. Nevertheless, regarding the ageing of growth rings, tree leaf area can be expected to be closer related to the area of a restricted number of growth rings than to the total basal area. Additional research on the contribution of separate growth rings to vertical water transport is necessary to determine whether a restricted number of (sapwood) growth rings contribute to the water transport, as has been found in some ring-porous species (Rogers & Hinckley, 1979).

Maximum LAI and natural thinning

The presently found biomass amounts are rather low, which is apparently due to the relative young age of the sample stands (Fig.2.22a). Biomass is hence expected to further increase with stand age. LAI, on the contrary, can be expected to reach a site-dependent maximum value (Fig.2.22b). According to the data in Fig.2.22b, it seems that for the present site-type a maximum LAI of 7 is reasonable, which is reached as soon as canopy-closure is complete. Note the large variability in LAI-values in the literature data (Cannell, 1982), which is probably due to site differences.

LAI depends on the tree number and the amount of leaf area per tree, and is expected to not exceed LAI_{max} (Jarvis & Leverenz, 1983; Landsberg, 1986). Hence the following relationship appears:

$$LAI_{max} = N_{max} * la_{av}/10000 \qquad (2.17)$$

With LAI_{max} site-specific maximum LAI (ha ha^{-1})
N_{max} maximum number of living trees (ha^{-1})
la_{av} average tree leaf area (m^{-2})

Referring to the presently found linear relationship between leaf area and basal area, Eq.2.17 can also be described as:

$$LAI_{max} = N_{max} * r*(\pi/4)*dbh^2/10000 \qquad (2.18)$$

With r equal to 0.331 m^2 leaf per cm^2 basal area

Assuming a maximum LAI implies that self-thinning among the stand-members will occur (see Harper, 1977; Landsberg, 1986). The actual tree number (N) is thus dependent on the maximum LAI that can be maintained. Replacing N_{max} by N and rewriting Eq.2.18 results in:

$$dbh = k * N^{-0.5} \qquad (2.19)$$

With $k = (40000*LAI_{max}/(\pi*r))^{0.5}$

When expressed in terms of stem biomass (see Table 2.8) this becomes:

$$w_s = k_2 * N^{-1.262} \qquad (2.20)$$

With $k_2 = 0.0762*k^{2.523}$

The power represents the slope of the self-thinning line. The value -1.262 is a little lower than the generally expected -1.5 (Harper, 1977; White, 1981), which probably is due to the fact that presently stem biomass instead of total plant weight was used. Another reason might be that in case of increasing competition, some trees initially show decreasing leaf amounts, so maximum LAI will be reached just before the onset of self-thinning.

Equation 2.19 states that as the trees grow (the average diameter increases), the number of trees will decline: the amount of biomass that can be maintained on a certain site depends on the site-specific maximum LAI. This dependency makes LAI a causal factor when simulating natural mortality in forest stands. A comparable theoretical analysis of the role of maximum LAI was carried out by Landsberg (1986).

Applying Eq.2.19 with the current parameter values also implies that stand basal area remains constant as long as LAI is at its maximum value. From $G=N*(\pi/40000)*dbh^2$ and Eq.2.19 it follows that:

$$G = (40000*LAI_{max}/(\pi*r))*dbh^{-2} * (\pi/40000)*dbh^2 = LAI_{max}/r \qquad (2.21)$$

Based on the present data and assuming $LAI_{max}=7$, G is estimated 21 m^2/ha from Eq.2.21.

Note, however, that although presently no heartwood was detected, leaf area can be expected to be proportional to the water-transporting cross-sectional area rather than to the basal area (Shinozaki et al., 1964; Cannell, 1989). As a result, the term dbh^{-2} in Eq.2.21 should actually be $(\text{water-transporting-area})^{-1}$: because this area is generally lower than the tree's basal area, G can be expected to gradually increase with average tree diameter i.e. with stand age.

Chapter 3: Radiation interception by forest trees: a simulation study on effects of stand density and foliage clustering on absorption and transmission.

Introduction

Radiation availability is one of the main driving forces behind tree and forest growth. The representation of the canopy and the simulation of the absorption of photosynthetically active radiation (PAR) thus play key roles when building mechanistic growth models (Landsberg, 1986; Grace et al., 1987). The most elementary canopy description applied in mechanistic models is the stand-oriented approach; the canopy is assumed horizontally continuous, and radiation absorption is calculated per hectare. The approach has proven to work out satisfactorily when simulating regularly built-up, mono-species stands with closed canopies (e.g. Mohren, 1987; Nikinmaa, 1992; Bossel & Krieger, 1994). However, statistical models describing horizontally homogeneous stands are not applicable in stands where the foliage is grouped into individual plant crowns (Oker-Blom, 1986). In systems with discontinuous canopies, a more detailed canopy description is necessary, since the diurnal variation in radiation availability and interception will be much larger than in closed forests (Palmer, 1977). Array models have been developed that account for horizontal differences (Palmer, 1977; Jackson & Palmer, 1979), but because individual crowns are not distinguished, their application is limited to canopies which can be defined in simple geometrical terms (Jackson & Palmer, 1979).

In case of complex forest structures like mixed species stands, a more detailed canopy description is needed to account for intra- and inter-specific competition for radiation. Some workers (Bossel & Krieger, 1994; Ludlow et al., 1990) developed models that estimate average absorbed PAR (APAR) per tree from radiation absorbed at the stand level, without taking into account the actual crown position. This method is unlikely to allow for a wide range of stand conditions to be simulated (West & Wells, 1992). When simulating mixed species stands, attention should be paid to individual crown dimensions, as these strongly determine the tree's ability to compete for radiation (Landsberg, 1986; Oker-Blom et al., 1988; West & Wells, 1992). Because growth rate is proportional to APAR (Monteith, 1977; Cannell et al., 1987; Grace et al., 1987), the amount of radiation absorbed by a tree crown is directly related to its competitive position in the forest canopy (Cannell, 1989).

Several models have been developed that estimate the radiation environment of individual tree crowns in a forest canopy. The most suitable appear those based on the approach of Norman & Welles (1983): here, the passage of a beam of radiation is described through an array of crowns (e.g. Nunez, 1985; Grace et al., 1987; Mordacq & Saugier, 1989; van Kraalingen et al., 1989; Wang & Jarvis, 1990; West & Wells, 1992). These studies have confirmed the general efficacy of the approach in various crop canopies (West & Wells, 1992). In the present study, a spatial model of radiation transmission is presented that estimates the amount of radiation absorbed by individual trees growing in a stand. The model will be used in growth and yield research of mono-species and mixed-species forests. The description of the canopy structure in the model is comparable with the approach of Norman & Welles (1983), however, an alternative approach is used to describe the radiation interception and absorption. The aim of the present study was to analyze the model's performance, to determine the role of crown characteristics on radiation transmission and absorption by individual trees, and to analyze the effects of stand density and foliage clustering on transmission.

Materials & methods

Model description

The model, called FORFLUX2, describes the path of a sun ray travelling through the canopy, keeping track of intersections with tree crowns. FORFLUX2 estimates both absorbed PAR (APAR) per tree and the remaining radiation intensity at the forest floor (transmission). Summing the tree amounts results in estimates of total absorption by the stand. Van Kraalingen (1989) presented a comparable model, that has successfully been used in oil palm plantations (van Kraalingen et al., 1989) and orchards (Wagenmakers, 1991). FORFLUX2 differs from this approach mainly with respect to the descriptions of the crown form and of the radiation attenuation within the canopy.

In FORFLUX2, rays move upward from the forest floor rather than come down, for reasons of calculation convenience; this, however, does not affect the estimations of radiation absorption and transmission (van Kraalingen, 1989). A grid is defined at the forest floor, rays start from the different grid points. Whether or not intersection occurs depends on:

- the location of the gridpoint (X- and Y-coordinates),
- the ray orientation, determined by its azimuthal direction (α) and inclination (β),
- the location of the tree trunk (X- and Y-coordinates),
- the size of the tree crown.

The tree crown is represented by a cone or an ellipsoid. Crowns are assumed to be symmetrical around the tree stem. The orientation of a ray is described by its inclination (β), the shortest angle between the path of the ray and the horizon, and by its azimuth (α), the angle with the north in the horizontal plane. When a ray enters the canopy it may cross one or more trees: it is assumed that only the crown intercepts radiation, stems and branches are 'invisible' for the sun beams.

Two different radiation conditions above the canopy are distinguished in the model. Direct radiation is geometrically described by the sun's azimuthal angle and inclination. Diffuse radiation conditions are described by the uniform overcast sky UOC (Goudriaan, 1977). The UOC consists of 9 inclination and 36 azimuthal directions, thus 324 rays (van Kraalingen, 1989). The model can calculate both relative and absolute interception and transmission, depending on the input data. To estimate absolute radiation amounts, information on daylength, sun position, and fraction diffuse PAR is necessary: several models are available to calculate these (e.g. Goudriaan, 1977; Spitters et al., 1986), which can easily be attached. For the present study relative amounts (fractions) of diffuse radiation were calculated.

The extinction rate of the flux will be determined by the orientation of the ray (α,β), the length of the distance covered inside crowns, the leaf area density (LAD: m^2/m^3), and the leaf angle distribution (spherical or horizontal). The extinction rate is determined by the projection area of the leaves when projected in the ray direction. Leaves are assumed to be black. Assuming a uniform distribution of the foliage, the relationship between radiation regime, leaf characteristics, and radiation extinction can be described by the Lambert-Beer equation (Eq.3.1):

$$I_l = I_0 \cdot e^{-\int_0^l O_\beta \cdot LAD \cdot dl} \tag{3.1}$$

With	I_l	Irradiance at depth l (along ray direction) in the canopy (J m^{-2} s^{-1})
	I_0	Irradiance outside the canopy (J m^{-2} s^{-1})
	O_β	Projection coefficient
	β	Ray inclination
	LAD	Leaf area density (m^2 m^{-3})
	l	Distance the ray covers inside the canopy (m)

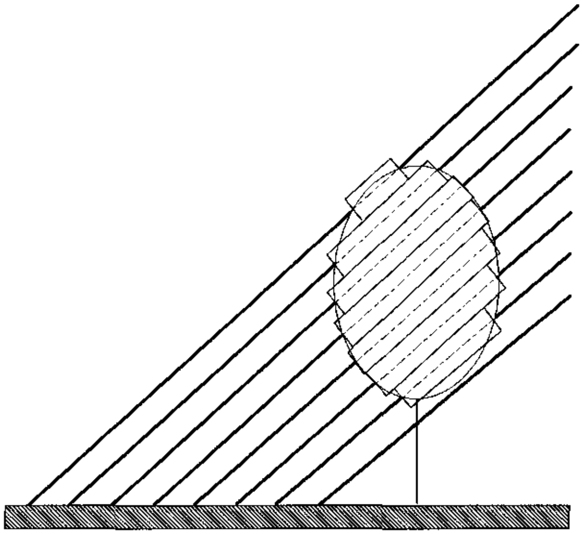


Figure 3.1: Crown form and cell width together determine the size of the beam-sections representing the crown volume (after Bartelink, 1996b).

To calculate absorption, the beam is assigned a width equal to the grid cell size. When the heart of the beam intersects a crown, the beam cross-sectional area perpendicular to the beam direction (ß) is determined. The distance covered in the crown determines the attenuation rate. The difference between irradiance input and irradiance output (in W m^{-2}), multiplied with the beam cross-sectional area, results in an estimate of the amount of radiation absorbed by that part of the crown (Fig.3.1). Summing the crown parts results in an estimate of the total amount of APAR per tree. A detailed description of the model structure and assumptions can be found in Bartelink (1996b).

Field measurements

To test a radiation model, estimates should be compared with field data on radiation transmission and absorption. Transmission is relatively easy to determine in the field. Absorption, however, is difficult to measure directly; radiation models are thus commonly evaluated based on transmission values (West & Wells, 1992; Cannell & Grace, 1993). In the present study, transmission data were used to check the model's performance. Field measurements on transmission at the forest floor were carried out in 4 stands, situated in the central part of the Veluwe area in the Netherlands (52°N, 5°E). The stands were selected based on differences in canopy closure, to analyze effects of stand density on the transmission (see Table 3.1). Stand 1 was a young, dense Douglas-fir stand, stand 2 an old, open Douglas-fir stand, stand 3 a closed beech stand, and 'stand' 4 a solitary oak tree. Douglas-fir and beech stands were used because local allometric relationships were available on these species (Bartelink, 1996a, 1997a). To estimate the leaf area of solitary trees, allometric relationships are less suitable, because most relationships are based on data from forest trees. For the solitary oak tree thus the LAI-2000 leaf area meter (LI-COR Inc.) was used to estimate leaf area density (LAD). Note that, since the LAI-2000 uses a radiation model comparable with FORFLUX2, differences between estimated and measured transmissions can be expected to be smaller than when using radiation-independent methods of estimating LAD.

*Table 3.1: Characteristics of the radiation measurements. Stand data derived from sample areas: stand age (y), area (m*m), number of trees (N: ha^{-1}), basal area (BA: m^2 ha^{-1}), average height (H: m), leaf area index (LAI: ha/ha). Length of the radiation measurement transects was 30m; the number of recording hours (Rec) varied between the stands.*

stand	code	spec	age	sample area	N	BA	H	LAI	Rec
1	109d	dg	25	40x50	1010	36.6	18.3	7.6	12
2	24k	dg	74	65x90	132	21.7	27.8	5.1	6
3	341	beech	62	50x70	357	23.4	23.0	7.4	6
4[1)]	GiH	oak	--	--	1	0.52	11.6	7.6[1)]	2

[1)] Solitary tree: LAI estimated from LAD, crown volume, and crown projection area.

Radiation measurements were carried out May 1996 in the Douglas-fir stands and July 1996 in the beech stand and the solitary oak. Measurements were carried out under completely overcast sky conditions (diffuse radiation). Within the selected stands, a 30m transect was marked in the field. Along the transect, each 2 meters a radiation sensor (LICOR SA-100) was placed horizontally on the top of a pole i.e. 1m above the forest floor, to minimize shadowing by herbs and shrubs. The 16 radiation sensors measured photosynthetically active radiation (PAR) in μmol m^{-2} s^{-1}. Two data-loggers (LICOR LI-1000) were used to store the data and to integrate the 16 instantaneous measurements to arrive at half-an-hour values (Table 3.1). Reference values, recorded at the same time as the field measurements, were derived from a separate sensor and data logger, put at a platform in the forest that arose above the forest canopy. The longest distance between a sample stand and the platform was about 500m.

The lowest inclination angle considered in the UOC was 5° above the horizon (Goudriaan, 1977). This implies, for a forest of 30m height, that even trees at 343 meter distance (30/tangent 5°) may affect the radiation transmitted to a certain gridpoint. As a consequence, a very large sample area should have been defined (about 12 hectare), in which all trees should have been measured, including their geographical position. To avoid this, location and dimensions of trees were only determined in a restricted sample area around the transects (see Table 3.1); the rest of the stand and/or the stands adjacent to the sample stand were described using their average tree dimensions, whereas the stem foot positions were derived from the stand densities.

Within the sample areas, data on crown sizes and location of the trees were collected: the size of the sample areas depended on stand density and tree height (Table 3.1). For the trees in the sample areas, stem foot position (X- and Y-coordinates in a local grid), stem diameter at breast height (1.30m above the forest floor: dbh), tree height, height of the crown base, and horizontal crown projection were determined. Average crown radius was calculated based on the estimation of the projected crown radius in 4 compass directions.

The leaf area density (LAD) of the solitary oak was measured using the LAI-2000 Plant Canopy Analyzer (LI-COR Inc.). Allometric relationships on Douglas-fir (Bartelink, 1996a) and beech (Bartelink, 1997a) were applied to estimate the foliage area of the individual trees in the forest stands. The measured and estimated tree data were input for the radiation model. Based on the tree data and the location of the sample points at the forest floor, transmission was simulated for each sample point, and compared with the radiation transmission measured in the field.

Uncertainty analysis

The transmission to the forest floor is strongly dependent on the leaf areas of the trees that build up the stand. The radiation model will thus be sensitive to uncertainties in the applied allometric relationships (Eq.3.2) and to the variability in the estimated leaf area density. To determine the model's sensitivity, tree leaf area LA (or leaf area density LAD) was increased and decreased, respectively, by two times the standard error of the observations (σ). The standard error, derived from the original data of Bartelink (1996a, 1997a), was $16.4m^2$ for beech, $12.6m^2$ for the old Douglas-fir, and $17.5m^2$ for the young Douglas-fir. Average LAD of the oak was $0.57\ m^2m^{-3}$, with σ being $0.05\ m^2m^{-3}$.

$$LA = c_0 * dbh^{c1} * h^{c2} + \sigma \underline{e} \tag{3.2}$$

With	LA	Tree leaf area (m2)
	dbh	Stem diameter at breast height (cm)
	h	Tree height (m)
	c_x	Regression coefficients
	σ	Standard error

The transmission in each gridpoint of the four 30m transects was re-estimated using the altered leaf areas. To analyze also the effect on the radiation absorption, a sub-sample of at least 20 trees was taken, and APAR per tree was compared for the three leaf area scenarios (default, $+2\sigma$, and -2σ).

Effect of stand density and clustering

In a forest stand, foliage is not distributed homogeneously over the canopy; instead, at least two levels of clustering can be distinguished. At the stand level, foliage is concentrated in tree crowns; next, at the tree level, foliage can be concentrated around shoots. The latter phenomenon especially occurs in coniferous species (Oker-Blom, 1986; Mohren, 1987). This so-called shoot-level clustering implies that the internal shading in a foliage cluster is larger than that for a random foliage distribution (Goudriaan, 1977).
In the present model, shoot-level clustering was accounted for by adjusting the projection coefficient (O_β), based on the ratio between the theoretical extinction-coefficient K (see Goudriaan & van Laar, 1984) and the apparent extinction-coefficient K_{app} (Goudriaan, 1977). In case of shoot-level clustering, K_{app} is about two-third the value of K, hence resulting in a much slower extinction rate than in case of a random foliage distribution (Goudriaan, 1977).

To investigate the role of stand density on transmission and absorption, simulations were carried out for a range of stand densities, of a Douglas-fir stand and a beech stand respectively. To simulate Douglas-fir stands, the data of the old Douglas-fir stand were used to calculate the size of an average tree: a range of stand densities was defined by varying the planting distance (Table 3.2). The artificial stands were built up by uniform Douglas-fir trees of height 30m, crown base height 18m, crown radius 4m, leaf area $350m^2$, and with a spherical leaf area distribution. The beech stands were simulated based on the average size of the trees in stand 3 (see Table 3.1): height of the trees was 23m, crown base height 12m, crown radius 4m, and leaf area $200m^2$, and a horizontal leaf area distribution was assumed. Here also a range of stand densities was defined (Table 3.3).
Scenarios consisted of different stand densities (N, ha^{-1}). For each scenario, both average transmission and average absorption were calculated. To estimate daily absorption, irradiance was assumed to be 5 MJ PAR $m^{-2}\ day^{-1}$.

Table 3.2: Estimated transmissions (fractions: T), extinction-coefficients (K_{sim}), and cluster-coefficients (CLUS), for the range of Douglas-fir stand densities (N: ha^{-1}).

scenario	N	LAI	T	K_{sim}	CLUS
1	1	0.04	0.994	0.17	4.2
2	21	0.72	0.844	0.23	3.1
3	51	1.79	0.640	0.25	2.9
4	100	3.50	0.419	0.25	2.9
5	156	5.47	0.208	0.29	2.5
6	204	7.14	0.098	0.33	2.2
7	278	9.72	0.039	0.33	2.2
average	-	-	-	0.26	2.8

Table 3.3: Estimated transmissions (fractions: T), extinction-coefficients (K_{sim}), and cluster-coefficients (CLUS), for the range of beech stand densities (N: ha^{-1}).

scenario	N	LAI	T	K_{sim}	CLUS
1	1	0.02	0.994	0.30	2.4
2	21	0.41	0.838	0.43	1.7
3	51	1.02	0.642	0.43	1.7
4	100	2.00	0.404	0.45	1.6
5	156	3.13	0.184	0.54	1.3
6	204	4.08	0.086	0.60	1.2
7	278	5.56	0.031	0.63	1.2
8	494	9.88	0.002	0.63	1.1
average	-	-	-	0.50	1.5

To determine the effect of clustering within the crowns on the transmission to the forest floor, simulations were carried out both with and without taking into account the clustering around shoots. To determine the effect of clustering of foliage into tree crowns, simulated transmissions were compared with estimates derived from applying Lambert-Beer's equation (Eq.3.3):

$$I_{sim}/I_0 = \exp(-K_{sim}*LAI) \tag{3.3}$$

With I_{sim} Simulated irradiance at the forest floor (J m^{-2} s^{-1})
I_0 Irradiance at the top of the canopy (J m^{-2} s^{-1})
K_{sim} Extinction-coefficient (-)
LAI Leaf area index (-)

K_{sim} was thus calculated by:

$$K_{sim} = -\ln(I_{sim}/I_0)/LAI \tag{3.4}$$

The theoretical value for a homogeneous canopy in case of diffuse radiation conditions (K_{LB}) was calculated according to Equation 3.5 (Goudriaan & van Laar, 1994):

$$K_{LB} = K_{black}*\sqrt{(1-\sigma)} \tag{3.5}$$

With K_{black} Extinction-coefficient for black leaves (-)
σ Scattering-coefficient of the leaves (-)

The average K for black leaves and a spherical leaf angle distribution amounts 0.8 (Goudriaan & van Laar, 1994). Assuming σ to be 0.2 for PAR (Goudriaan & van Laar, 1994) results in an estimate of K_{LB} of 0.72. Based on the former two equations, a cluster-coefficient (CLUS) was determined as (Eq.3.6):

$$CLUS = K_{LB}/K_{sim} \tag{3.6}$$

Clustering will cause a reduced interception so that K_{sim} will be smaller than the theoretical value K_{LB}.

Results

Transmission and uncertainty analysis

In Figure 3.2 field measurements are compared with model estimates: results are shown of the default simulation, the situation where the leaf area is increased with 2σ, and the 2σ-decrease scenario. The area between the two dotted lines represents the 95%-confidence-interval. Estimated transmissions along the transects at the forest floor appeared largely comparable with the field data, but the model slightly over-estimated the transmission. In the young, dense Douglas-fir stand, over-estimation could be attributed to the high stand density, implying that a lot of radiation will be intercepted by stems. Moreover, the stand had not been pruned: the dead branches also will take away a lot of the radiation. In the old Douglas-fir stand and in the beech stand, again the stems will be responsible for the small discrepancies between simulated and estimated transmissions.

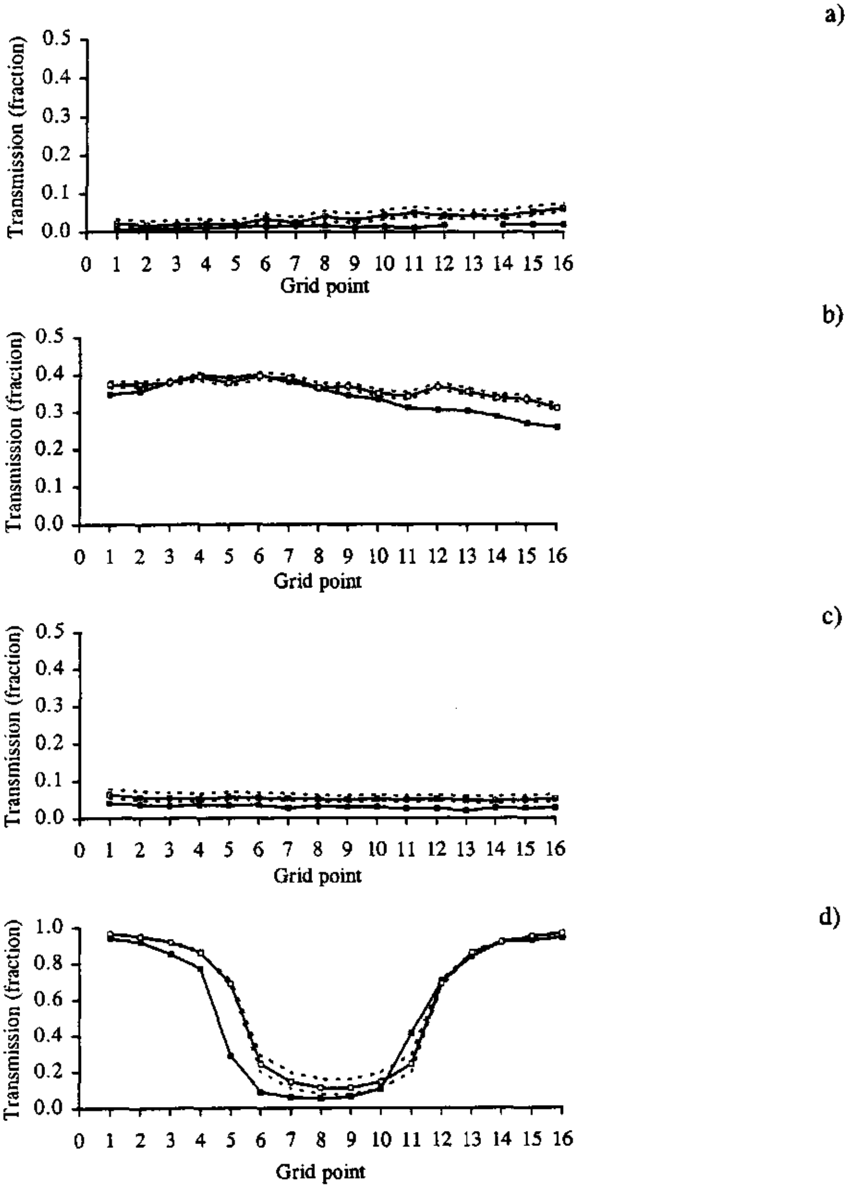


Figure 3.2: Comparison between measured radiation transmission in the field (closed symbols) and simulated values (open symbols): a) stand 1 (young Douglas-fir), b) stand 2 (old Douglas-fir), c) stand 3 (beech), d) the solitary oak.

In the open Douglas-fir stand (stand 2) and the solitary oak, both the simulated pattern along the transect and the transmission estimates at individual grid points were highly comparable with the field measurements. Note, however, that the good fit in case of the solitary oak can partly be attributed to the fact that the LAI-2000, to estimate leaf area density, uses a comparable radiation model as the one presented here. In the open Douglas-fir stand, an up to 4 meter high shrub-layer starting just beyond the end of the transect is likely to be responsible for the small over-estimated transmissions in the last grid points. The small deviations in the oak plot are due to the fact that the tree crown radius was not constant, whereas in the model an average radius is applied.

The fit at the level of the individual grid points was poorest in the two dense, closed stands; however, due to the low radiation levels at the forest floor (less than 5% of the flux density above the canopy), absolute flux differences are negligible. The deviations at the point level can be attributed to the fact that in dense stands transmission to a certain point at the forest floor is much less dependent on the location and dimensions of individual trees: total canopy leaf area and woody biomass are of greater importance. Within-canopy variability that is not taken into account in the model will cause such deviations. The lower fit of transmission at the single point level has commonly been observed, e.g. by Palmer (1977) and Wagenmakers (1991) when simulating transmission in hedgerow orchards, and by West & Wells (1992) in a eucalypt forest. Such deviations will occur since self-shading effects within each tree crown could be expected to produce a much more heterogeneous radiation environment than is the case with the homogeneous distribution of foliage assumed in the model crowns (West & Wells, 1992).

The present model, nevertheless, was able to reproduce the differences between the sample areas, and also to mimic the transmission trends within the stands, especially in the more open situations. Model performance was thus considered to be satisfying, and the model was assumed to be able to give reliable estimates of the amounts of radiation absorbed by individual trees.

Apart from transmissions, the model was used to estimate absorption by the sample trees in the sample stands. Comparing APAR with tree leaf area LA revealed that a clear relationship exists in relatively dense stands 1 and 3 (Fig.3.3). In the open Douglas-fir stand, however, this relationship was much weaker.

In Figure 3.4 the estimated amounts of APAR per sample tree in case of the default leaf areas are printed against the scenario with a 2σ-increase of the leaf area and a 2σ-decrease, respectively. The tree response, in terms of APAR, to the changed leaf area amounts appeared to depend on the amount of APAR intercepted under default conditions: in case of the $+2\sigma$-scenario, APAR had increased for trees that intercepted a relatively low amount of PAR, whereas APAR was lower in case of trees that intercepted relatively much PAR in the default situation. Opposite trends were observed in case of the -2σ-scenario. However, overall effects of changes in the tree leaf areas on APAR were marginal.

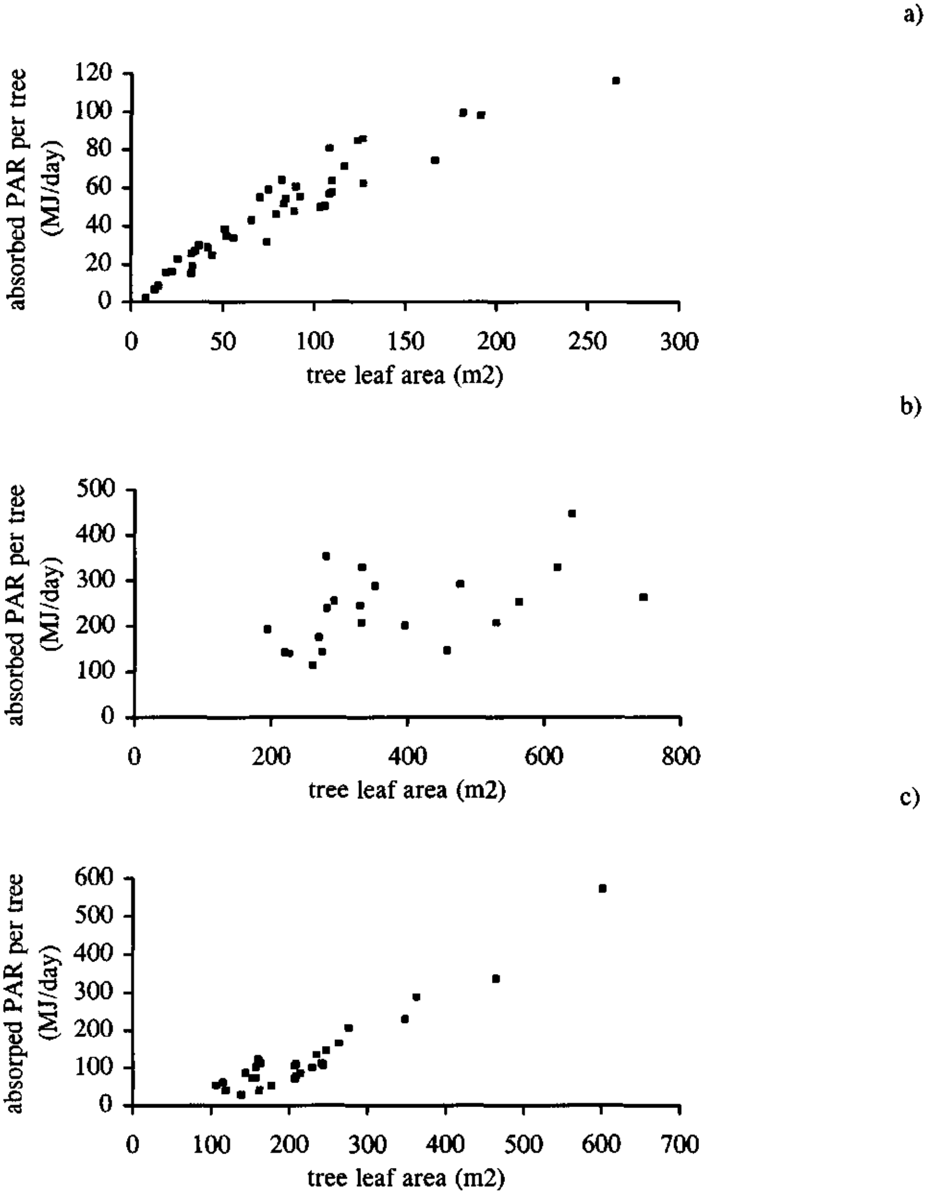


Figure 3.3: Relationship between estimated tree leaf area and simulated amount of absorbed radiation (APAR), for the sample trees in the sample stands. I_0 was assumed to be 5 MJ PAR m^{-2} day^{-1}: a) stand 1 (young Douglas-fir), b) stand 2 (old Douglas-fir), c) stand 3 (beech).

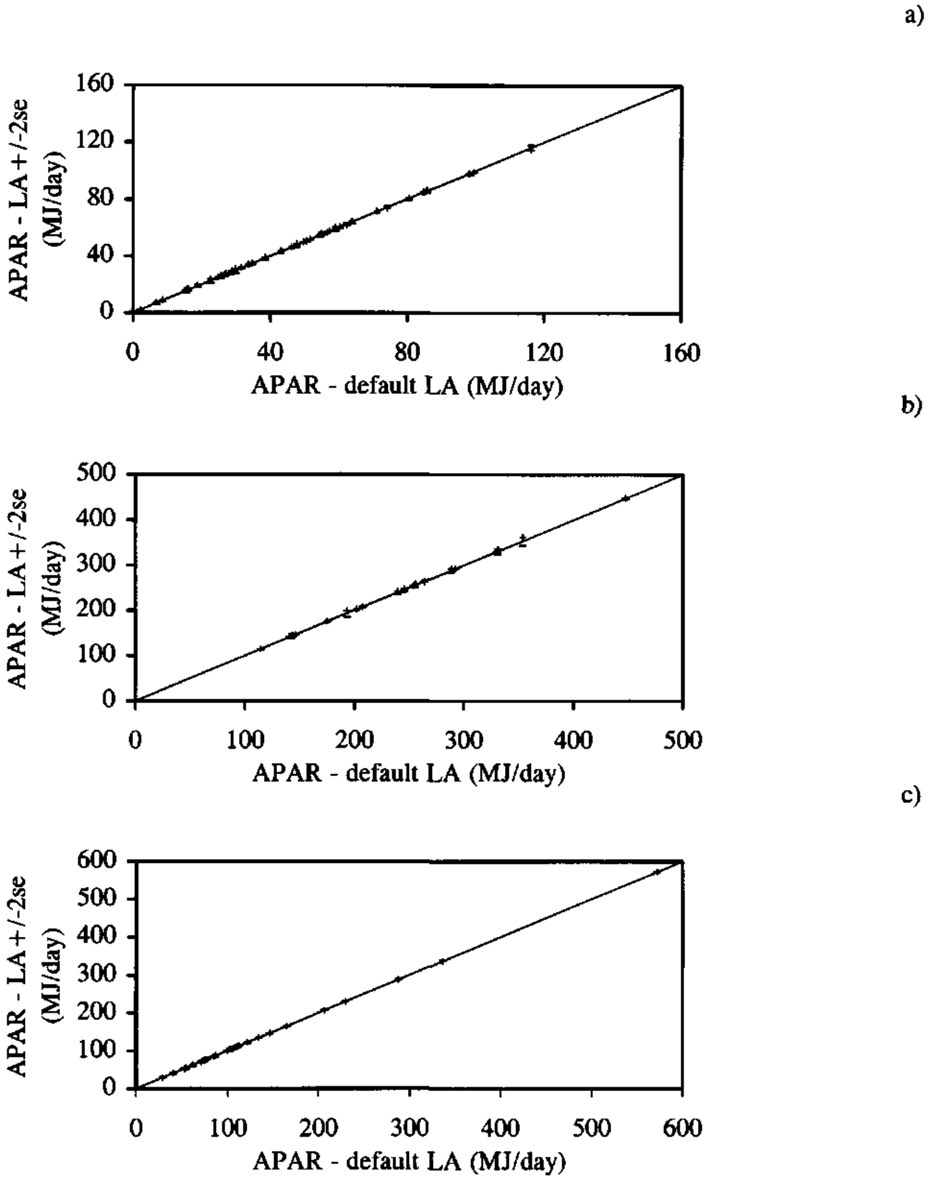


Figure 3.4: Effects of changed leaf areas on APAR per sample tree; results of simulations where the leaf area was increased (+) or decreased (-) with 2σ are printed against results of the scenario with default leaf areas: a) stand 1 (young Douglas-fir), b) stand 2 (old Douglas-fir), c) stand 3 (beech).

Effects of stand density and clustering

The estimated transmissions to the forest floor for the different stand densities are presented in Table 3.2, Table 3.3, and Figure 3.5. In Fig.3.5, transmission is printed against LAI, which follows from stand density since the stands were built up by uniform trees. To determine the effect of clustering on transmission, the transmissions estimated by the Lambert-Beer equation are presented as well. It appears from Fig.3.5 that relatively large discrepancies occur between estimates from the presently applied spatial model and from the Lambert-Beer stand-approach, especially in case of the Douglas-fir stands: Figure 3.5a indicates that the over-estimation of interception can amount up to 25% of PAR.

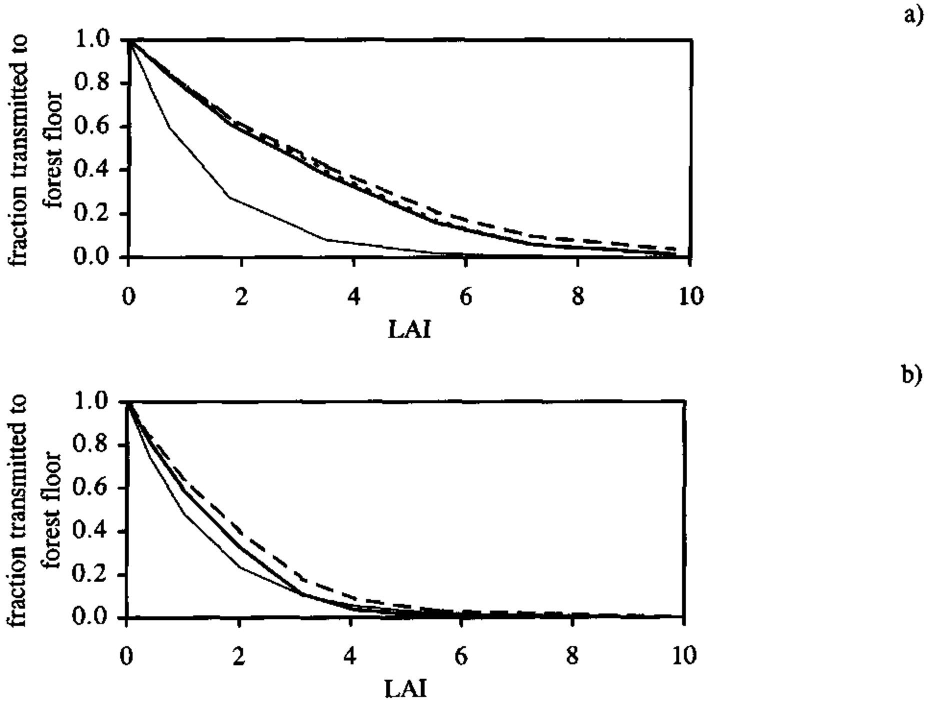


Figure 3.5: Impact of stand density (expressed as LAI) on the stand-level average transmitted fraction of radiation. Bold solid lines represent calculations without shoot-level clustering, bold dashed lines represent simulation results when shoot clustering is taken into account: a) Douglas-fir, b) beech. The dotted line in a) represents the same stand, but assuming a horizontal leaf angle distribution. Transmissions calculated using Lambert-Beer's law are presented as well (K_{LB}=0.72: thin solid line).

Taking into account the clustering of foliage inside crowns resulted in a clear increase of the transmission. To show the effect of the leaf angle distribution, Fig.3.5a additionally presents the transmission in a Douglas-fir stand when a horizontal leaf angle distribution is assumed. It appears that radiation extinction was clearly faster in case of the horizontal distribution. In case of beech, shoot-clustering also affected transmission. At higher stand densities (LAI larger than 3.5), ignoring shoot-clustering resulted in transmission estimates even lower than those calculated with Lambert-Beer's law.

Fig.3.6 presents the relationship between stand density, expressed as LAI, and the estimated extinction-coefficient K_{sim}. Table 3.2 and Table 3.3 present the extinction-coefficients (K_{sim}) and the cluster-coefficients. K_{sim} clearly increased with increasing stand density or LAI; K was largest in beech. CLUS decreased with increasing LAI, and was smaller in beech. Average K_{sim} appeared to be much lower than K_{LB} (0.72): K_{sim} was on average 0.26 in Douglas-fir (0.30 without shoot-clustering), and 0.50 (0.66) in beech. The cluster-coefficient amounted on average 2.8 (2.4) in Douglas-fir and 1.5 (1.1) in beech.

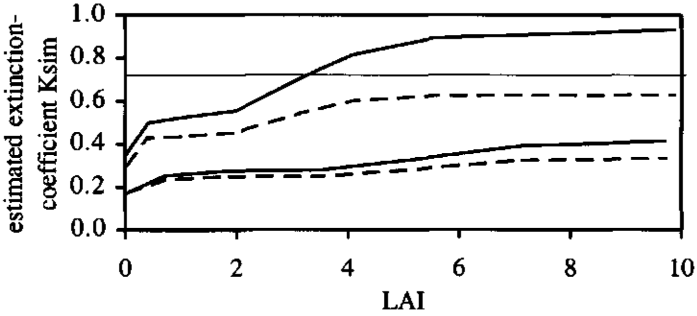


Figure 3.6: Relationship between the average estimated extinction-coefficient (K_{sim}) and the stand density (expressed as LAI). Solid lines represent estimates without shoot-level clustering, dashed lines represent simulation results when shoot clustering is taken into account. The two upper lines are for beech stands, the two lower ones are Douglas-fir. The straight line represents K_{LB}.

The relationship between stand density and the amount of absorbed radiation (APAR) is presented in Fig.3.7. Leaf area per tree was kept constant, only distance between the trees was changed. At the tree level, APAR decreased with increasing stand density (i.e. increasing LAI).The attenuation was much faster in case of beech (horizontal leaf angle distribution) when compared to Douglas-fir (spherical distribution). As a consequence, total absorption of the available radiation in the beech stand occurred earlier (in terms of LAI) than in the Douglas-fir stand (Fig.3.7), indicating that K_{sim} was larger in beech.

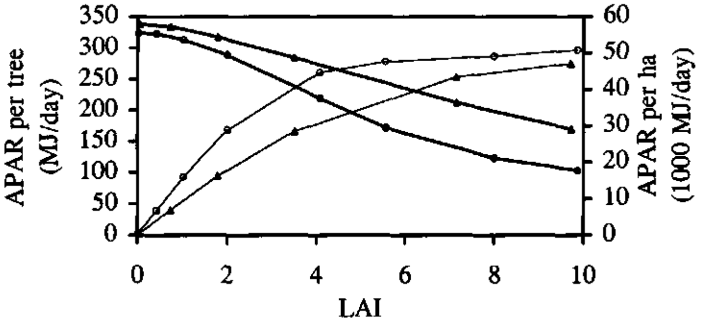


Figure 3.7: Effect of stand density on the amount of absorbed radiation per tree (bold line) and per stand (thin line), for Douglas-fir (triangles) and beech (circles). Leaf amounts per tree were kept constant. I_0 was assumed to be 5 MJ PAR m^{-2} day^{-1}.

Discussion and conclusions

Model uncertainty

Though some discrepancies occurred between field measurements and simulated transmissions, the general tendency within the transects was comparable, and deviations could be attributed to factors like interception by stems and (dead) branches, which were not part of the model. The small effects of altered leaf areas on transmission indicate that spatial information like crown size and location of the trees might be of much greater importance when focusing on transmission, than uncertainties in estimates of individual tree leaf areas might be.

Though radiation absorption also was hardly affected by the small changes in leaf area, different trends appeared among stand members in the closed forest stands, as a result of the changed radiation climate inside the stand. Trees that intercepted relatively low amounts of PAR in case of default leaf areas, were able to intercept more radiation when leaf areas were increased with 2σ, and, in accordance, showed lower APAR values when leaf areas were decreased with 2σ. Remarkably, the opposite appeared for trees that intercepted relatively much PAR in the default situation. This implies that these trees fully intercept the beams that reach their crowns, i.e. they are not able to use the extra leaf area to increase interception, but, on the contrary, will suffer more from competition since neighbouring trees were attributed larger leaf areas as well.

Effects of stand density and clustering

Figures 3.2a and 3.2c indicate that to estimate absorption by trees growing in a homogeneous stand, tree leaf area might be a strong indicator. This implies that a detailed spatial model could be replaced by a simple relationship between tree LA and APAR. However, results of the old Douglas-fir stand (Fig.3.3b) show that in case of a non-closed canopy, locations of the trees and dimensions of the crowns will strongly affect APAR, in accordance with remarks from Oker-Blom (1986) and West & Wells (1992). A spatial model like FORFLUX2 will thus be needed to account for spatial differences, or, when choosing a stand-oriented approach, a cluster-coefficient should be incorporated to adjust K_{LB}.

From Figure 3.5 it clearly appears that, due to clustering of foliage in individual crowns, large errors will arise when the Lambert-Beer stand-oriented approach is applied to heterogeneous (forest) canopies. It has been shown in other studies as well that the elementary Lambert-Beer model does not effectively account for radiation attenuation in a variety of stands (Smith, 1993). The attenuation of radiation is slower in case of clustering inside the tree crowns, in accordance with results of Oker-Blom (1986) and Smith (1993). Grouping of foliage into individual crowns results in a considerable decrease in the interception of radiation per unit leaf area as compared with a horizontally homogeneous stand: this is particularly evident for a stand with a low density (Oker-Blom, 1986).

The estimated average extinction-coefficient (K_{sim}) was lower than the theoretical value K_{LB}, resulting in a cluster-coefficient lying between 2.2-4.2 for Douglas-fir and 1.1-2.4 for beech, depending on the stand density (LAI). Smith (1993) also found K to be dependent on stand density, ranging approximately from 0.2 to 0.4. Pierce & Running (1988) stated that a single extinction-coefficient of 0.52 would be appropriate for a wide range of Douglas-fir stands. Results of Smith (1993), however, indicated that a single K-value using Lambert-Beer's model cannot be used effectively to predict radiation extinction in Douglas-fir stands. The present estimates (K_{sim}) in the closed Douglas-fir stands (LAI>4) fall nicely within Smith's (1993) range, but are a little lower than the range 0.4-0.6 for conifers mentioned by Jarvis & Leverenz (1983). The estimated K_{sim} in the closed beech stands (LAI>3) is in agreement with the range 0.5-0.8 found in broadleaves (Jarvis & Leverenz, 1983).

Clustering of foliage into individual crowns appeared to have a much larger effect on transmission than clustering of foliage around shoots (Fig.3.5). Radiation extinction appeared to be faster in case of a horizontal leaf angle distribution when compared with a spherical distribution (Fig.3.5a, Fig.3.7): this can be expected in case of UOC-conditions, since in forests most available radiation will come from the vertical inclination angles (Oker-Blom, 1986). In West-Europe, where most radiation comes from diffuse sky conditions, this implies that, when maximizing APAR, beech stands will need a lower LAI than Douglas-fir stands do. This agrees with many observations on LAI (e.g. Bartelink, 1996a, 1997a; Jarvis & Leverenz, 1983).

Model applications

An important application of theoretical models in general is to identify the structural characteristics that significantly affect the radiation regime within a stand (Oker-Blom, 1986). The present study shows that structural properties like the clustering into crowns and within crowns strongly affect the radiation regime and therefore should be considered when modelling stand structure.

The presented model can be applied both to estimate radiation conditions at the forest floor, e.g. to indicate conditions for natural regeneration, and to estimate growing opportunities for individuals. When simulating transmission in dense stands, however, it might be worthwhile to include a stem or branch area index (BAI) to account for the woody components, since FORFLUX2 does not take these into account. When simulating radiation absorption, on the contrary, woody components can be ignored, as inside the canopy these play a relatively unimportant role in the radiation interception (West & Wells, 1992).

A promising application of the presented model consists of the analysis of competition for radiation in mixed forests. Biomass growth rate is proportional to the amount of radiation absorbed by the stand (Cannell et al., 1987; Grace et al., 1987), and it might be true for individual trees as well (Oker-Blom et al., 1988; West & Wells, 1992). In a follow-up study, the radiation model will be used to simulate growth and development of mixed-species stands.

Chapter 4: Modelling growth and dry matter partitioning

4.1 Applicability of the radiation-use efficiency concept for simulating growth of forest stands.

Introduction

Based on results of many productivity studies, Monteith (1977) proposed the concept of radiation-use efficiency (RUE), stating that the ratio between the amount of absorbed photosynthetically active radiation (APAR: 400-700nm) and the amount of dry mass produced would be a conservative parameter. In many productivity studies, a linear relationship between APAR and crop growth has been found since, both in agricultural crops (e.g. Gallagher & Biscoe, 1978; Stockle & Kiniry, 1990), and in tree species (e.g. Jarvis & Leverenz, 1983; Cannell et al., 1988). Landsberg (1986) and Cannell et al. (1987) concluded that under non-limiting growing conditions (ample supply of water and nutrients) RUE may be constant for a single species: when RUE refers to total dry mass production it is likely to be a conservative value for C3-crops growing in similar temperature and radiation environments (Cannell et al., 1988).

In many situations, however, RUE will be lower than the theoretical maximum of about 3 g MJ^{-1} (Landsberg, 1986; Cannell, 1989). The reduction will either be temporary, as a result of unfavourable growing conditions during the growing season (low temperature, severe drought, nutrient stress) or permanent, because of non-optimal site-conditions. Despite the seasonal variability, RUE is expected to be stable on larger time scales, e.g. on an annual base (Cannell, 1989; Jarvis & Leverenz, 1983). Productivity differences between trees or forest stands growing on comparable sites would thus be primarily the result of differences in the amount of absorbed radiation (Monteith, 1977). Because site conditions strongly determine the leaf area index (LAI) and hence the amount of APAR, RUE may be different on sites with different nutrient or soil water availabilities (Linder, 1987; McMurtrie et al., 1994). The amount of APAR will also depend on the length of the growing season, therefore differences may occur between broadleaved and evergreen species (Jarvis & Leverenz, 1983).

In recent years, the concept of RUE has been mentioned as a promising tool for studies on forest productivity, especially because only few plant physiological data are required compared to complex carbon-balance models (Jarvis & Leverenz, 1983; Landsberg, 1986; Cannell, 1987, 1989; Landsberg & Wright, 1989). The use of RUE as a growth-concept in simulation models, however, is hampered because of the lack of data, especially for mature trees. Most estimations of RUE reported in literature refer to one-year experiments with seedlings and saplings (e.g. Cannell, 1987; Cannell et al., 1988; Dalla-Tea & Jokela, 1991; Philips & Riha, 1993). Studies on mature trees mostly consider above-ground biomass production only (e.g. Linder, 1987; Grace et al., 1987; Dalla-Tea & Jokela, 1991).

One method of estimating RUE involves the application of comprehensive, mechanistic carbon-balance models. Such models allow the calculation of growth efficiencies and the investigation of effects of growing conditions and canopy structure on RUE. A recent example is given by McMurtrie et al. (1994), who investigated the effect of climatic factors on RUE in pine stands by applying a carbon-balance model.

In this article we report the suitability of RUE as a growth-concept to be used in a simulation model of growth of mixed forest stands. In the model, growth will be calculated based on RUE and APAR. We used Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and beech (*Fagus sylvatica* L.) as examples representing an evergreen and a broadleaved species. Many physiological and biomass data are available for these species already. Both are frequently grown as even-aged, monospecific stands. Less frequently, they also occur in mixed stands, mainly in western Europe.

The aim of this study was to estimate RUE and to investigate its suitability as a tool for the simulation of growth of mixed forest stands. We applied the mechanistic forest growth model FORGRO (Mohren, 1987; Mohren et al., 1993) to investigate differences between RUE of broadleaves and evergreen conifers for a range of stand densities, and to analyze the effects of stand structure and stand composition on RUE in mixed species forests. Model estimates of the net primary production (NPP) were compared with data derived from the literature, to determine the legitimacy of applying FORGRO.

Methodology

The radiation-use efficiency as model output

The radiation-use efficiency RUE was calculated as the ratio between the net amount of produced dry mass (g) and the amount of absorbed photosynthetically active radiation (APAR: MJ). For the calculation of the radiation attenuation, a closed canopy was assumed. In the horizontal plane no differences in canopy structure or leaf area density (LAD: $m^2\ m^{-3}$) were assumed. LAD did vary in the vertical plane, following a parabolic distribution (Kropff & van Laar, 1993; Bartelink, 1996a). Tree height and crown base height of each species together determine the length of the living crowns and hence affect both LAD at a certain depth in the crown and cumulative LAI.

The weather data used consisted of daily averages of global radiation of the years 1980 through 1989, derived from time series from a local weather station (Wageningen: 5°40'E, 51°58'N). Using the stand structure data, the amount of APAR was calculated for each day, assuming 50% of the global radiation to be photosynthetically active. From APAR and the dry mass production, radiation-use efficiency was calculated daily according to Equation 4.1; assimilates, the products of the photosynthetic process, are indicated as CH_2O.

$$\epsilon = (P-R_m)\, R_g / I_a \tag{4.1}$$

With	ϵ	Radiation-use efficiency RUE (g [dry mass] MJ^{-1} [APAR])
	P	Photosynthetic rate (g [CH_2O] m^{-2} [ground] d^{-1})
	R_m	Maintenance respiration (g [CH_2O] m^{-2} [ground] d^{-1})
	R_g	Growth respiration coefficient (g [dry mass] g^{-1} [CH_2O])
	I_a	Absorbed radiation APAR (MJ [400-700 nm] m^{-2} [ground] d^{-1})

Annual RUE was derived by dividing annual NPP by annual APAR.

The model FORGRO

Radiation absorption, photosynthesis and dry mass production

The model FORGRO (Mohren et al., 1993) is a comprehensive carbon-balance model simulating growth and development of either monospecies or mixed-species forest stands. The principal time-step of FORGRO is one day. Radiation intensity is assumed to decrease exponentially with LAI (according to the Lambert-Beer law). Extinction-coefficients are calculated for diffuse and direct radiation separately, and depend on leaf reflection, leaf angle distribution, and foliage clustering within the canopy (Goudriaan, 1977). The photosynthetic rate is derived from the photosynthesis-light response curve, described by a negative exponential function (Equation 4.2). Parameters characterizing the curve are the initial light-use efficiency and the maximum photosynthetic rate (Table 4.1). The maximum photosynthetic rate is reduced in less than optimal conditions such as low temperature, or during foliage senescence (see Mohren et al., 1993).

$$A_h = A_m\, (1 - \exp(-\epsilon_0\, I_a/A_m)) \tag{4.2}$$

With	A_h	Photosynthetic rate (g [CO_2] m^{-2} [foliage] s^{-1})
	A_m	Photosynthetic rate at light saturation (g [CO_2] m^{-2} [foliage] s^{-1})
	ϵ_0	Initial radiation-use efficiency (g [CO_2] MJ [APAR])
	I_a	Absorbed PAR (MJ m^{-2} [foliage] s^{-1})

Daily (gross) canopy photosynthesis, i.e. the produced assimilates in g [CH_2O] m^{-2} [foliage] d^{-1}, without taking into account respiration, is calculated from instantaneous photosynthetic production using a Gaussian integration scheme (Goudriaan, 1986). Maintenance respiration is calculated based on the approach of Penning de Vries et al. (1989), assuming that the costs of maintenance depend on the biochemical composition (especially N) of the structural biomass.

Table 4.1: Values of the photosynthetic parameters for Douglas-fir and beech as used in the FORGRO model.

parameter	units	Douglas-fir	beech
Maximum photosynthetic rate	g [CO2] m^{-2} leaf s^{-1}	0.47	0.55
Initial light-use efficiency	g [CO2] MJ^{-1}	12.5	12.5
Specific leaf area	m^2 kg^{-1}	5.6	17.2
Maximum leaf area index[1)]	m^2 m^{-2}	7.0	7.0
Extinction coefficient of diffuse radiation	-	0.65	0.65
Budburst (day of the year)	-	130	121

[1)] Monospecific stand

Allocation of assimilates is modelled using fixed allocation proportions, except in the case of allocation to foliage and a reserve pool, for which saturation curves relative to predefined maximum amounts were used (Kramer, 1995) (Equation 4.3). Allocation of assimilates to the reserve pool has priority over all other organs once maximum LAI has been reached. The reserve pool provides the assimilates necessary for budburst and for maintenance respiration in case requirements exceed photosynthetic production. After subtraction of the assimilates allocated to reserves and foliage, the remaining assimilates are distributed towards branches, stems, and roots using fixed allocation proportions.

$$a_{re} = (R_{max}-R) / R_{max} \tag{4.3a}$$
$$a_l = (L_{max}-L) / L_{max} \tag{4.3b}$$

With	
a_{re}, a_l	Fraction of assimilates allocated to reserve pool and foliage
R, R_{max}	Reserve pool and maximum level of reserve pool (g [CH_2O] m^{-2} [ground])
L, L_{max}	Leaf area index (LAI) and site and species-specific maximum LAI (m^2 [foliage] m^{-2} [ground])

Competition for radiation

For the purpose here, it was assumed that species only compete for radiation: optimal water and nutrient supplies were assumed. The radiation-competition approach used in the model FORGRO is an extension of the concept presented in the model of Kropff & van Laar (1993). Species-specific values for total foliage, average tree height, and crown base height determine the LAD and cumulative LAI at different heights in the canopy. For each species, radiation absorption at a certain height depends on the net radiant flux, the species' local LAD, and the extinction-coefficient. To calculate the overall extinction-coefficient, the leaf areas of the contributing species are weighted by species-specific extinction-coefficients, following Kropff & van Laar (1993) (Equation 4.4).

$$I_h = (1\text{-}r)\ I_o \exp(-\Sigma k_j L_{h,j}) \tag{4.4}$$

With	I_h	net radiant flux at height h (MJ m^{-2} [ground] s^{-1})
	r	reflection coefficient of the canopy (-)
	I_o	net radiant flux density at top of the canopy (MJ m^{-2} [ground] s^{-1})
	k_j	extinction coefficient of species j
	$L_{h,j}$	cumulative leaf area index of species j above height h (m^2 [leaf] m^{-2} [ground]).

Both radiation regime and species characteristics affect the amount of APAR. Important species characteristics regarding competition for radiation are date of budburst, leaf properties (e.g. reflection), leaf inclination, leaf area, tree height, crown length, and vertical leaf area distribution.

Initializing the model

We used field data of monospecies Douglas-fir and beech stands to initialize FORGRO, allowing simulation of 1 to 10 year growth of initially 40-year old stands. Biomass amounts, stand structural data, and species characteristics of Douglas-fir were mainly derived from Mohren (1987) and Bartelink (1996a). Data for beech were obtained from Ellenberg et al. (1986), Schulze (1981), Kramer (1994, 1995), and Bartelink (1997a). Dates of leaf unfolding were fixed based on data from Mohren (1987) and Kramer (1994). Table 4.1 shows the photosynthesis, respiration, and extinction coefficients of each species, as used in the simulations. Table 4.2 presents the initial stand conditions. Cumulative amounts of net dry mass production (NPP) and APAR were calculated to investigate species-specific differences in RUE, both during the year and over a ten-year period.

We carried out a sensitivity analysis to determine the effect of several photosynthetic parameters on RUE. Relative sensitivity (S_{rel}) of the parameters was defined according to Equation 4.5. Generally, in a sensitivity analysis the relative change of the output is directly related to a relative change in the input value. Presently, in order to define the rate of change, S_{rel} was defined in a small interval between -5% and +5% of the input parameter value:

$$S_{rel} = (\epsilon_{+5\%}-\epsilon_{-5\%}) \;/\; (\epsilon_{def}*0.1) \tag{4.5}$$

With S_{rel} Relative sensitivity (-)
$\epsilon_{+5\%}$ RUE resulting from 5% increase of parameter value (g MJ^{-1})
$\epsilon_{-5\%}$ RUE resulting from 5% decrease of parameter value (g MJ^{-1})
ϵ_{def} RUE when using default parameter values (g MJ^{-1})
0.1 Interval length (1.05-0.95) of the parameter (-)

Thus, the relative sensitivity equals 1.0 when changes in a photosynthetic parameter have a proportional response in RUE.

Table 4.2: Initial stand conditions of Douglas-fir and beech as used in for simulation of growth of the monospecific stands.

Variable	units	Douglas-fir	beech
stand age	yr	40	40
tree height	m	23.5	17.0
stem biomass	Mg ha^{-1}	130.0	129.6
branch	Mg ha^{-1}	15.0	35.0
foliage	Mg ha^{-1}	12.0	0
coarse roots	Mg ha^{-1}	15.0	35.0
fine roots	Mg ha^{-1}	3.5	4.0

To estimate RUE in mixed-species stands we initialized FORGRO with biomass data from the monospecific stands. We defined a range of imaginary mixed stands, each consisting of different contributions of the two species. In the range of imaginary stands, the fraction of species 1 increased from 0% to 100%, whereas simultaneously the fraction of species 2 decreased from 100% to 0%: the two fractions hence always summed up to 100%. For each species the ratio between the basal area in a mixed stand and its basal area in the monospecific stand was used to calculate the biomass amounts of the species in the mixed stand (Equation 4.6).

$$W_{ij,x} = (G_{j,x}/G_{j,m})\ W_{ij,m} \tag{4.6}$$

With $W_{ij,x}$ mass of component i of species j in the mixed stand
$W_{ij,m}$ mass of component i of species j in the monoculture
$G_{j,x}$ basal area of species j in the mixed stand
$G_{j,m}$ basal area of species j in the monoculture

In distance-independent models like FORGRO, neither tree height nor crown length affects the amount of APAR in monospecific stands. In mixed stands, however, tree height may differ between the contributing species, thus affecting radiation availability: the competitive power of a species is then strongly determined by its tree height relative to the height of its competitor. To investigate the effect of height differences on RUE, the heights of the contributing species were fixed, resulting in three different height scenario's (Table 4.3). Crown length was 10 m for both species in all situations.

Table 4.3: Heights (m) of the species in the imaginary mixed stands in three different scenario's, used to analyze the effect of height position on RUE. Capitals in the abbreviation indicate the largest species. Crown length was fixed to 10m.

Scenario	Abbreviation	Douglas-fir	beech
Douglas-fir larger than beech	Db	25	20
Both species of equal height	DB	25	25
Beech larger than Douglas-fir	dB	20	25

Results

Comparing simulated NPP with data from literature

To determine the legitimacy of applying FORGRO to estimate RUE and effects of stand composition on RUE, we firstly compared estimates of NPP derived from calculations with FORGRO with estimates found in literature. Model calculations for the 40-year-old monospecific stands resulted in estimations of annual NPP of 20.9 and 21.7 Mg [dry mass] ha^{-1} yr^{-1}, for Douglas-fir and beech, respectively. The model estimates were compared with primary production data on Douglas-fir and beech from the literature (Table 4.4). The low NPP's of Ovington & Pearsall (1956) can be attributed to the fact that turn-over was not taken into account in their calculations. Differences in climate and site conditions probably explain the largest part of the variability in Table 4.4. Age, in contrast, seems to be of less importance.

The maximum measured NPP values found for Douglas-fir amounted to 18 Mg ha^{-1} yr^{-1}, a little lower than the NPP of 20.9 Mg under optimal growing conditions predicted using FORGRO. For beech, measured annual NPP reached 18 Mg ha^{-1}, as against 21.7 Mg estimated by FORGRO assuming optimal water and nutrients. In case of non-optimal conditions, NPP will be lower: the reduction of NPP and RUE will be dependent on the factor causing the stress, e.g. site quality (Wang et al., 1991), and the length of the impact period (Jarvis & Leverenz, 1983; Landsberg, 1986; Linder, 1987). However, since FORGRO estimates potential NPP, the present estimates seem to be reliable values for both species. Encouraged by this correspondence we used FORGRO to estimate RUE.

Table 4.4: Data on net annual primary production (in Mg ha^{-1}), derived from literature.

species	location	age	NPP	source
beech	south Sweden	78	17.8	Nihlgard 1972
beech	Solling, Germany	120	17.2[2]	Schulze 1981
beech	Solling, Germany	21	17	Schulze et al. 1989
beech	Solling, Germany	120	14	Schulze et al. 1989
beech	Ardennes, Belgium	144	12.2	Duvigneaud et al. 1977
Douglas-fir	England, Great-Britain	22	7.2-9.2[1]	Ovington & Pearsall 1956
Douglas-fir	England, Great-Britain	40-47	9.8[1]	Ovington & Pearsall 1956
Douglas-fir	Washington, USA	40	15.4-17.8	Keyes & Grier 1981

[1] Losses due to turn-over not included

[2] Assuming carbon content of dry mass to be 50%

Seasonal pattern and annual RUE

Beech attained its maximum LAI earlier than the evergreen Douglas-fir (Fig.4.1a). However, in both species LAI exceeded the value 6 soon after bud burst, implying that almost all radiation was intercepted by that time. The species differences in daily photosynthesis (Fig.4.1b) could thus be mainly attributed to differences in maximum photosynthetic rates (Table 4.1). Figure 4.1c shows that daily variability in RUE was high, amounting up to 2.3 g MJ^{-1} in case of Douglas-fir and to 2.7 g MJ^{-1} in beech. A large part of the variability was caused by fluctuations in temperature: up to about 10-15°C, RUE increased with temperature, whereas above 15 °C RUE decreased with increasing temperatures, because of increased maintenance costs (results not shown). In Table 4.5, monthly totals of APAR, photosynthetic rate, respiratory loss, turnover, and RUE are presented, showing the carbon gains and losses in different parts of the year. The table shows the large temporal variability of average RUE. For Douglas-fir RUE is low (and sometimes even negative) in the winter period, which can be attributed to maintenance costs (Table 4.5). Average RUE was 0.78 g MJ^{-1}, and 1.01 g MJ^{-1} when only months with positive NPP were considered. RUE of beech was zero in winter (actually undetermined due to the zero value of APAR); averaged over the foliage-bearing months RUE was 1.59 g MJ^{-1}.

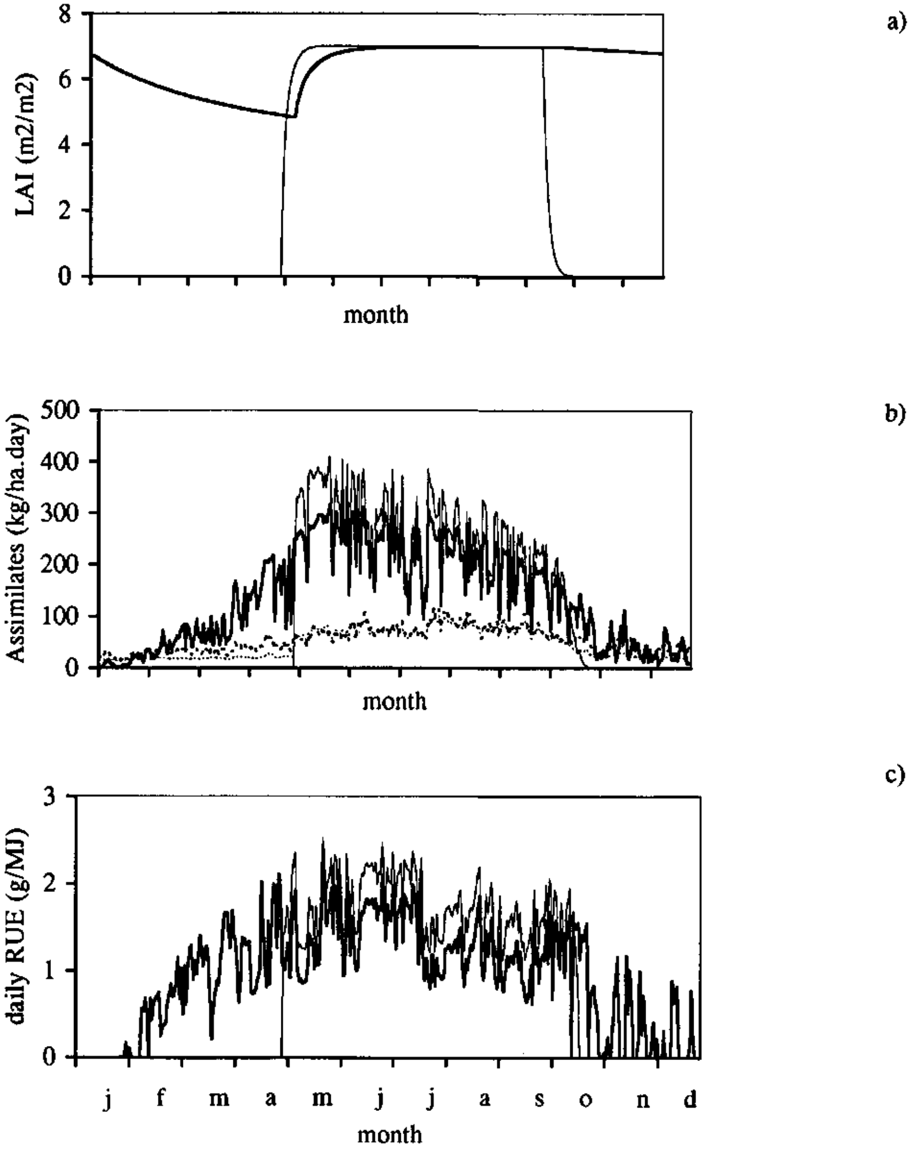


Figure 4.1: Simulation results of the monospecific stands of Douglas-fir (thick lines) and beech (thin lines): a) Seasonal pattern of LAI, b) Daily photosynthetic (solid lines) and respiration rates (dotted lines), c) Radiation-use efficiency on a daily basis.

Table 4.5: Monthly totals of APAR (1000 MJ ha^{-1} month^{-1}), photosynthetic rate (PHOT), total respiratory loss (MRt), respiratory loss of the foliage (MRfol), total turnover (D), turnover of the foliage (Dfol), and RUE. Mass is in kg C ha^{-1} month^{-1}, RUE is in g [dry mass] MJ^{-1}. Carbon content of dry mass is assumed to be 50%.

month	APAR	PHOT	MRt	MRfol	D	Dfol	RUE
Douglas-fir							
Jan	551	162	296	167	854	674	-0.40
Feb	687	559	361	180	557	404	0.48
Mar	1097	1042	421	176	474	315	0.94
Apr	2214	1962	536	182	368	223	1.07
May	3484	3344	774	277	324	178	1.23
Jun	2438	3049	920	385	282	139	1.46
Jul	2161	2695	994	434	270	121	1.31
Aug	2194	2665	1096	498	257	106	1.19
Sep	1975	2185	978	454	241	92	1.02
Oct	1170	1559	699	309	242	87	1.23
Nov	607	542	483	249	223	78	0.16
Dec	366	365	426	231	237	94	-0.28
beech							
Jan	0	0	191	0	414	0	-
Feb	0	0	205	0	351	0	-
Mar	0	0	234	0	365	0	-
Apr	0	0	257	0	332	0	-
May	3497	4221	853	98	329	0	1.61
Jun	2441	3591	890	126	314	0	1.84
Jul	2162	3135	918	140	321	0	1.71
Aug	2194	3116	1004	161	319	0	1.60
Sep	1975	2604	907	147	306	0	1.43
Oct	865	1288	587	56	2314	2004	1.35
Nov	0	0	308	0	293	9	-
Dec	0	0	270	0	277	0	-

Figure 4.2 shows the relationship between the cumulative daily amounts of the dry mass produced and the absorbed radiation for monospecific stands of beech and Douglas-fir. Because the evergreen Douglas-fir intercepts radiation even when NPP is zero or negative, the ratio between the two variables decreases and ultimately becomes negative at low PAR flux densities. Douglas-fir attained 1.07 g dry mass MJ^{-1}, equalling the average slope of the line of in Fig.4.2. For beech, after budburst the ratio was initially negative because the cumulative maintenance costs are higher than the photosynthetic rate (Table 4.5). The average ratio between NPP and APAR was 1.44 g MJ^{-1}. The annual RUE of the stands was rather constant over a 10-year period of growth (Fig.4.3).

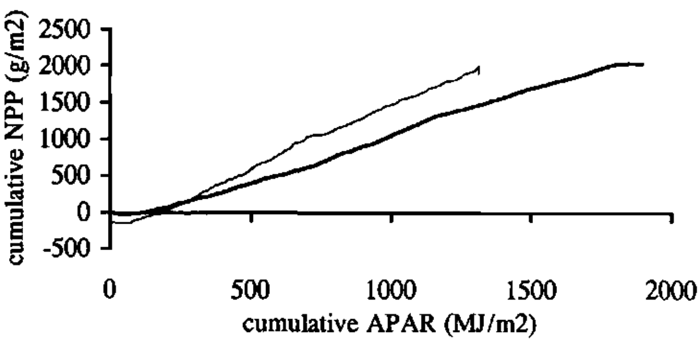


Figure 4.2: Relationship between the cumulative amount of produced dry mass (NPP) and the cumulative amount of absorbed radiation (APAR) in one year, for Douglas-fir (thick line), and beech (thin line).

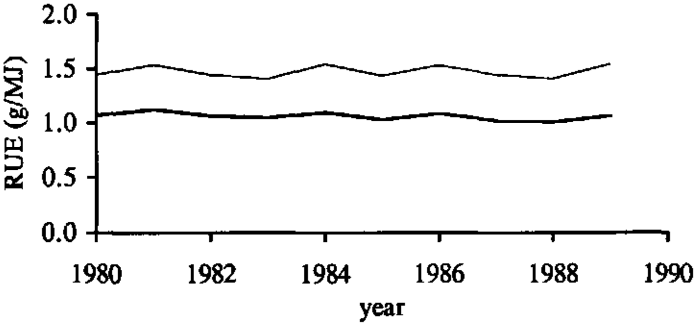


Figure 4.3: Simulated annual estimates of RUE in monospecific stands of respectively Douglas-fir (thick line) and beech (thin line) for a 10-year period.

Factors affecting RUE

Results from the sensitivity analysis are presented in Table 4.6. Values of the relative sensitivity (S_{rel}) are negative when a higher parameter value results in a lower RUE and vice-versa. Table 4.6 shows that for all model parameters considered, the absolute value of S_{rel} is lower than 1, indicating that the response in terms of RUE is less than the change in the value of the parameter. The largest responses were found for changes of temperature, APAR and ϵ_0, and to a lesser extent to changes in A_m and in the temperature effect on maintenance respiration (Q_{10}). Most parameters appeared to be less sensitive for beech than Douglas-fir.

Table 4.6: Results of the sensitivity analysis: relative sensitivity in terms of RUE to a 5% increase or decrease of the value of the photosynthetic parameters, respectively. The reference value of RUE was 1.07 g MJ^{-1} for Douglas-fir and 1.44 g MJ^{-1} for beech. Relative sensitivities in the table were calculated according to Equation 4.5. R/S represents the ratio of assimilates allocated to the roots and shoots, respectively. SLA is specific leaf area. T is average daily temperature (°C). The other parameters are explained in the text.

	relative sensitivity (S_{rel})	
parameter	Douglas-fir	beech
A_m	0.45	0.32
ϵ_0	0.70	0.73
K_{dif}	-0.22	-0.16
Q_{10}	0.51	0.26
R/S	-0.01	-0.01
SLA	0.04	0.05
L_{max}	0.05	-0.01
PAR	-0.81	-0.65
T¹⁾	-0.06	-0.03

1) Alternative approach: temperature was increased/decreased with 1 °C rather than increased/decreased with 5% of its value: S_{rel} was alternatively calculated as $(RUE_{+1°C}-RUE_{-1°C})/(RUE_{def})$.

Effect of mixing species on RUE

Simulating growth of mixed species stands revealed that APAR per species decreases non-linearly with decreasing proportion of the species in the mixed stand (the 0% and 100% values in Fig.4.4a). RUE of Douglas-fir and beech in the mixed stand was generally higher than in the monospecific stands (Fig.4.4b). Starting from a low contribution of either Douglas-fir or beech in a mixed stand, in both species RUE initially increased with an increase of the species' share, but decreased again at higher contributions (Fig.4.4b), probably due to an increase of maintenance costs. However, in absolute terms, the mixture effect was almost negligible. RUE in Douglas-fir was almost independent of the presence of beech. RUE of beech was slightly affected by tree height: consequences of the species contribution in the mixed stand were most obvious (in terms of RUE) when beech was less tall than Douglas-fir.

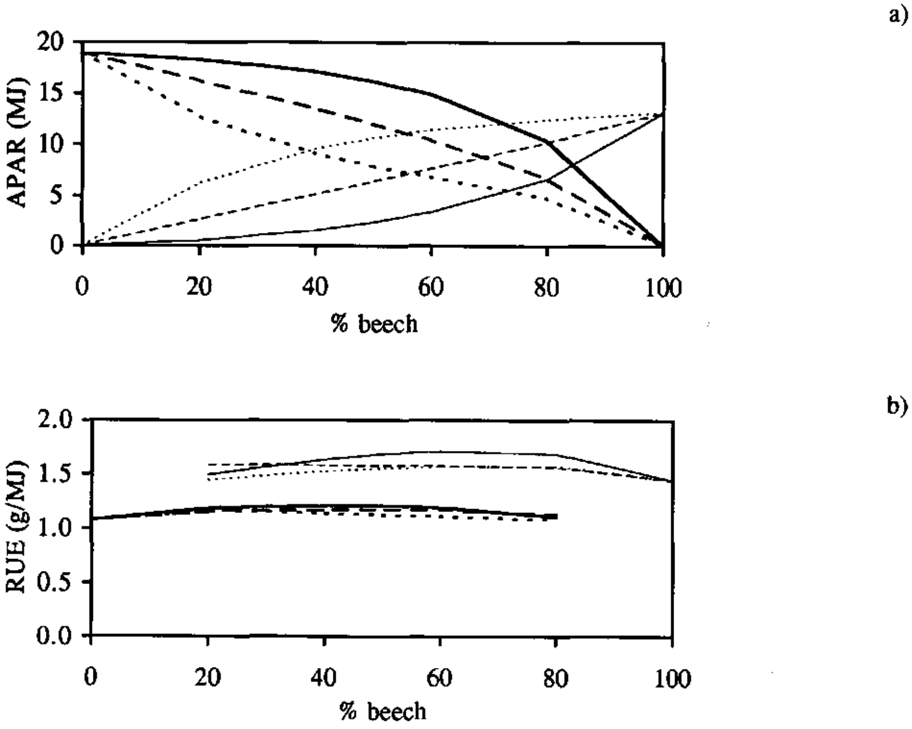


Figure 4.4: Absorbed radiation APAR (a) and radiation-use efficiency RUE (b) in mixed stands, with varying proportions of Douglas-fir (thick lines) and beech (thin lines), for the height scenario's Db (solid), DB (dashed), and dB (dotted lines), respectively (see Table 4.3).

Discussion

Seasonal pattern and annual RUE

The estimated daily values of RUE ranged from 0 - 2.7 g MJ^{-1}. Although RUE showed large day to day variability, RUE derived from cumulative APAR and NPP was virtually constant throughout the year. Estimated annual RUE values encompassed values found in literature (Table 4.7). The low value of Acacia is probably due to fertilizer stress or to a lower radiation absorption (Phillips & Riha, 1993).

Table 4.7: Estimates of RUE (g MJ^{-1}), based on annual amounts of APAR and produced above-ground dry mass (RUE_{ag}) or total dry mass (RUE_t), under non-limiting water and nutrient conditions. Data derived from literature.

species	location	RUE_{ag}	RUE_t	Source
Acacia auriculiformis	New York USA	0.11	-	Phillips & Riha, 1993
Pinus sylvestris	Sweden	-	1.80	Jarvis & Leverenz, 1983
Populus trichocarpa	Scotland, UK	1.98	3.00	Cannell et al., 1988
Salix viminalis	Scotland, UK	2.76	3.16	Cannell et al., 1988
Pinus taeda	Florida, USA	0.81	-	Dalla-Tea & Jokela, 1991
Pinus elliottii	Florida, USA	0.47	-	Dalla-Tea & Jokela, 1991
Pinus radiata	New Zealand	1.34	-	Grace et al., 1987
Picea sitchensis	Scotland, UK	1.98	-	Wang et al., 1991

Monthly averaged RUE of Douglas-fir was comparable with the annual estimate; in beech the latter value was slightly lower due to cumulated maintenance requirements. Annual RUE differed between Douglas-fir and beech. However, because of the evergreen character of Douglas-fir, RUE will be higher when only APAR absorbed and NPP produced during the growing season are considered (Linder, 1987; McMurtrie et al., 1994). To determine the effect of adjusting for the length of the growing season on RUE of Douglas-fir, the growing season was here defined as the period between budburst and the first day at the end of the year when NPP was negative. Considering only APAR and NPP during this growing season resulted in an RUE estimate of 1.26 g MJ^{-1} for Douglas-fir. This value is much closer to the 1.44 g MJ^{-1} presently found in beech. Assuming the carbon-content to be 50% of the structural dry mass results in estimates of 0.72 g C MJ^{-1} APAR for beech and 0.63 g C MJ^{-1} APAR for Douglas-fir during the growing season. These values are slightly lower than those found in species of pine: 0.87 g C MJ^{-1} APAR (McMurtrie et al., 1994). The difference is probably due to the fact that McMurtrie et al. (1994) did not take root maintenance respiration into account.

The clear effect of length of the growing season on RUE corresponds with findings of Linder (1987) and was also found in the study of McMurtrie et al. (1994) on different pine species growing in several parts of the temperate zones. Evergreen species, in contrast with deciduous species, have a permanent foliage cover which on the one hand, enables continuous interception of PAR throughout the year, but, on the other hand, incurs permanent maintenance costs. These costs are supplementary to the maintenance requirements of the woody skeleton, which occur both in evergreens and deciduous trees. Because of unfavourable temperatures and low PAR availability outside the growing season, maintenance requirements in evergreens might become larger than photosynthetic production, as happened with Douglas-fir in this study (Fig.4.1b), resulting in a negative RUE. Differences between evergreens and deciduous trees will thus be smaller when differences in foliage cover are taken into account. Hence, the current findings do not contradict the hypothesis of Cannell et al. (1988), that RUE is a conservative value for C3-crops growing in similar radiation environments.

The annual RUE of the monospecific stands was rather constant over a 10-year period of growth, in accordance with remarks from Jarvis & Leverenz (1983) and Cannell (1989). McMurtrie et al. (1994) concluded that primary production per unit growing season APAR will hardly vary among stands because quantum yield is a conservative parameter which varies little among C3-plants. This makes RUE a useful parameter to estimate growth.

Factors affecting RUE

The sensitivity analysis revealed that RUE is rather insensitive to changes in the tested photosynthetic parameters, as all relative sensitivities were less than 1. Impacts of specific leaf area (SLA) and maximum LAI (L_{max}) were negligible. Strongest responses were related to PAR availability, temperature, temperature effect on maintenance respiration (Q_{10}) and initial radiation-use efficiency (ϵ_0). Although simulated temperature increase resulted both in higher photosynthetic rates and maintenance costs, according to the simulation results increase of temperature will result in a lower dry mass production, as expressed by the negative value of S_{rel} (Table 4.6). The effect on RUE differed between Douglas-fir and beech. Species-specific responses to temperature can hence be expected to affect competitive interrelationships in case of climate change (Kramer, 1995).

Applicability of RUE in simulation models of mixed forest stands

Cannell (1989) stated that for building reliable comprehensive mechanistic models too few data are yet available, making summary approaches like the concept of radiation-use efficiency a more appropriate framework for analyzing forest growth. Examples of models using RUE to simulate growth, however, are still scarce. From the present study it appeared that RUE is a rather stable variable, both in monospecies and in mixed-species stands. The almost constant value of RUE in the 10-year simulation indicates that the RUE-concept can be a useful tool in simulation models. In mixed stands some variability in RUE can be expected in broadleaved species growing in the under storey. The larger RUE of beech in scenario I (beech lower than Douglas-fir) when compared with the monospecies beech stand can be attributed to the non-linear relationship between LAI and radiation absorption: under a open canopy of Douglas-fir (20% of normal density), APAR of beech was halved whereas its dry mass production was only reduced by 30%, thus resulting in a higher RUE. However, this variability in RUE is low when compared to the estimated absolute values of RUE.

Conclusions

Although RUE is very variable on a daily basis, it is constant when derived from cumulative amounts of NPP and APAR. Based on annual amounts, RUE is conservative for certain tree species growing at a certain site, both in monospecies and mixed-species forest stands. The conservative behaviour of RUE makes the concept suitable for application in simulation models of forest growth.

Applying the RUE-concept in modelling avoids the estimation of many yet unknown physiological parameters. In a follow-up study we will apply the concept of RUE in a model of mixed forests, where annual growth rates follow from APAR, RUE, and temperature. We will use the model to estimate growth and development of mixed stands, and to predict effects of climate change on inter-specific competition and forest development.

4.2 A model of dry matter partitioning in trees

Introduction

In mechanistic models of tree and forest growth, a key role is played by the description of assimilate allocation or dry matter partitioning (Valentine, 1985; Landsberg, 1986; Cannell, 1989). Allocation is generally defined as the apportion of assimilates among plant parts (Cannell & Dewar, 1994), whereas partitioning refers to the apportion of growth to certain tree or stand components (Cannell, 1985; Mäkelä, 1986; Mooney & Winner, 1991). Both allocation and partitioning are dynamic features, whereas distribution describes a tree or stand state in terms of the shares (dry weights) of the biomass components. Although there is much information on the distribution of dry matter in plants, there is little understanding of the mechanisms that govern allocation (Wardlaw, 1990). Much work on theoretical considerations has been carried out (e.g. Cannell, 1985; Thornley, 1991), the main concepts suitable for modelling purposes have been summarized (Cannell & Dewar, 1994). However, though theoretically sound, most of the concepts are unsuitable for forest modelling studies, because many of the included parameters are unknown. As a consequence, many forest growth models use descriptive keys, representing the proportions of the dry matter or carbohydrates that should go to a certain plant component (e.g. Mohren, 1987; Ludlow et al., 1990). This static approach may give satisfactory results when growing conditions and plant state do not change; however, a growth model that does not include feed-back of growing conditions and plant state on allocation or partitioning, is less suitable to estimate growth in dynamically changing growing situations (Cannell, 1985, 1989; Mäkelä, 1986; Landsberg, 1986).

In a mechanistic approach of dry matter partitioning, attention should be paid to the role of functional balances between tree components, and to the effects of growing conditions on these balances (Cannell & Dewar, 1994). Several studies on partitioning have used the maintenance of so-called structural balances for modelling growth dynamics (Valentine, 1985; Mäkelä, 1986). In this approach, relationships between biomass amounts or tree dimensions determine how growth is apportioned. However, only a few models contain a (partly) mechanistic allocation or partitioning module (e.g. Nikinmaa, 1992; Sievanen, 1992). The advantage of considering dry matter partitioning, rather that assimilate allocation, is that no data on maintenance respiration are needed. The calculation of respiratory costs is one of the major pitfalls of mechanistic models.

The aim of this study was to develop a model describing the dynamic partitioning of dry matter in individual trees, and to investigate the effects of growing conditions on the partitioning pattern on Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) and Common beech (Fagus sylvatica L.). Many data on biomass and allometric relationships are available for these species (e.g. Cannell, 1982; Pellinen, 1986; Kuiper & van Dijk, 1988; Olsthoorn, 1991; Hendriks & Bianchi, 1995; Bartelink, 1996a, 1997a). The final partitioning model will be used in a simulation model of mixed species forest stands.

Materials and methods

Model framework

Plant growth can conveniently be analyzed with a mass balance model that incorporates total tree growth rate G (kg dry matter per unit time), the biomass of the organs W_i (kg), their turn-over (loss rates) D_i (kg per unit time), and the partitioning coefficients f_i (dimensionless) for each biomass component i (Mäkelä, 1986). When adopting the concept of maintaining structural balances, functional interrelationships between tree parts have to be defined. Partitioning is then determined by physiological and/or mechanical interdependencies among tree parts (Mäkelä, 1986). A suitable procedure is first to divide the plant into parts that have clearly different functions, and to identify the phenomena that determine or constrain the allocation or partitioning of dry matter among them (Cannell & Dewar, 1994). Table 4.8 presents an overview of the tree components that are presently distinguished.

Table 4.8: Tree components distinguished in the partitioning model, and the initial values for an average tree on a relatively rich site (Scenario 1). Biomass amounts are dry weights. Tree diameter (dbh) is measured at breast height (1.30m above the forest floor).

tree characteristic	unit	name	Douglas	beech
tree age	y	-	10	10
foliage biomass	kg	W_s	3.1	0.2
branch biomass	kg	W_{br}	2.9	0.6
stem biomass	kg	W_s	2.9	0.9
fine-root biomass	kg	W_{fr}	1.1	0.4
coarse-root biomass	kg	W_{cr}	1.7	0.0
sapwood area	m^2	A_s	0.003	0.001[2)]
foliage area[1)]	m^2	A_f	17.5	3.4
stem diameter	cm	dbh	7.0	3.9
tree height	m	h	5.7	2.7
crown ratio	-	CR	0.9	0.9

[1)] One-sided, projected area.

[2)] Equals basal area inside bark, as heartwood is formed only after approximately 100 years (Hillis, 1987).

The partitioning coefficient, f_i, is defined as the fraction of the total growth apportioned to a certain biomass component W_i; the sum of the partitioning coefficients equals 1. The net growth rate of a biomass component at time t then equals the difference between the gross absolute growth rate and the loss due to turn-over of living biomass (Eq. 4.7):

$$dW_i/dt = f_i G - D_i \qquad (4.7)$$

During the growth process, the structural balance between the size of the different organs must be maintained. This requirement introduces a formal relationship between the time dependence of partitioning and distribution.

Implementation

Two concepts that have great potential in modelling partitioning are the pipe-model theory (Shinozaki et al., 1964; Jarvis & Leverenz, 1983), and the root-shoot balance (Brouwer, 1962; Reynolds & Thornley, 1982). Mäkelä (1986) and Valentine (1985) used both concepts to determine partitioning, and Nikinmaa (1992) and Sievanen (1992) used the concepts to build allocation sub-models. These concepts mainly interrelate fine roots, foliage, and sapwood area; to include other tree components in the partitioning model, additional relationships are needed. The criterion for applying a relationship in the present partitioning model was that it should have biological meaning, or could be explained by functional reasoning, based on either a physiological or a mechanical interdependency.

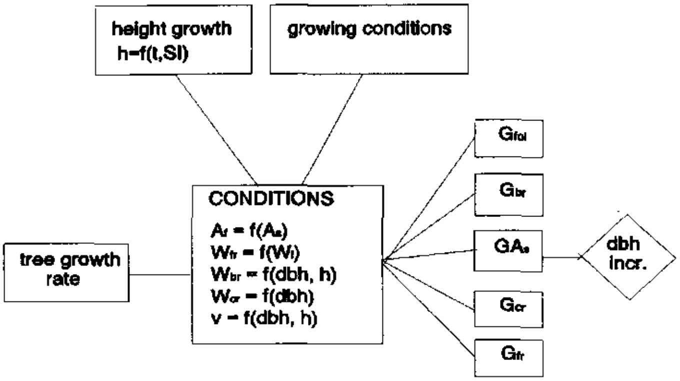


Figure 4.5: Structure of the partitioning model. Growth is subdivided into five growth rates, one for each tree component: foliage (G_{fol}), branches (G_{br}), sapwood area (GA_s), coarse roots (G_{cr}), and fine root (G_{fr}) growth. Conditions affecting the partitioning consist of functional and allometric relationships between the tree components. These conditions are dependent on the height growth pattern over time and the growing conditions (site). Based on the estimated growth rate of the sapwood cross-sectional area, the stem diameter (dbh) increment can be calculated. For explanations of the equations see text.

The following relationships were used (Fig.4.5):

1. *An empirical relationship describing height development over time.* Height growth, being primary growth, is mainly sensitive to resource availability. Height growth was considered to be a driving variable for partitioning, independent of dry matter growth rate (secondary growth). Height growth was estimated from site index Si (tree height at infinite age) and tree age (t), using the Chapman-Richards equation (Eq. 4.8). In this equation the site condition is expressed by the value of parameter Si; the values of the (other) regression constants are not affected by site conditions. The values of the equation parameters were derived from yield tables (Jansen et al., 1996).

$$h = Si * (1-e^{-c11*t})^{c12} \qquad (4.8)$$

In equation 4.7, c_{11} and c_{12} are constants. The estimates of these and the following constants in the relationships applied were derived from literature; Table 4.9 presents the parameter values and units, as well as the sources of the estimates.

2. *A linear relationship between stem cross-sectional sapwood area (A_s) and total foliage area (A_f), based on the pipe-model theory (Shinozaki et al., 1964; Long et al., 1981; Jarvis & Leverenz, 1983).* The cross-sectional sapwood area immediately below the lowest living whorl should be used, rather than the stem cross-sectional sapwood area at breast height (see Table 4.8) (Shinozaki et al., 1964; Jarvis & Leverenz, 1983; Maguire & Hann, 1987). The foliage/sapwood-ratio depends on climate conditions (Mencuccini & Grace, 1995) and may differ among families (St.Clair, 1993), but for a certain site and provenance, the ratio (c_{fs}) is assumed to vary only among species (Eq. 4.9a).

$$A_f = c_{fs} * A_s \qquad (4.9a)$$

When only data of sapwood area at breast height are available, the length of the branch free bole can be used to account for the foliage-less pipe-length below the living crown (Maguire & Hann, 1987; Bartelink, 1996a, 1997a).

$$A_f = c_{21} * A_{sbh} - c_{22} * (h_{cb}-c_{23}) \qquad (4.9b)$$

Constant c_{23} equals the reference height (generally being breast height). To calculate foliage area from foliage biomass, specific leaf areas (SLA) were used (see Table 4.9).

3. *A linear relationship between fine-root biomass and foliage biomass, based on the root-shoot balance hypothesis (Brouwer, 1962, 1983; Cannell & Dewar, 1994).* This relationship enables one to focus on biomass, rather than on the difficult-to-determine uptake area. According to Reynolds & Thornley (1982), the proportionality between fine-root biomass and foliage biomass can be understood in terms of a balanced carbon and nitrogen ratio in the tree, when other nutrients are non-limiting (Eq. 4.10a), but generally soil water availability also plays a role (Brouwer, 1962, 1983).

$$\sigma_{fr} * W_{fr} = c_s * \sigma_f * W_f \tag{4.10a}$$

With W_{fr} Fine root biomass (kg)
W_f Foliage biomass (kg)
σ_{fr} Specific root activity: nutrient uptake (kg^{-1} roots)
σ_f Specific foliage activity: carbon production (kg^{-1} foliage)
c_s species-specific parameter (dimensionless)

In case of constant radiation, nutrient, and soil water availabilities, Eq. 4.10a can be simplified to:

$$W_{fr}/W_f = c_3 \tag{4.10b}$$

4. *An allometric relationship between tree (stem) diameter at breast height (cm) and tree height (in m) on the one hand, and the amount of branch biomass on the other hand (Bartelink, 1996a, 1997a).* The stem diameter of a tree is mechanically related to branch biomass, because the stem provides the physical support (Causton, 1985). The relationship between diameter and amount of branch biomass, however, varies, because it is strongly affected by stand density. Taking tree height into account removes this density effect (Bartelink, 1996a, 1997a).

$$W_{br} = c_{41} * dbh^{c42} * h^{c43} \tag{4.11}$$

5. *An allometric relationship between tree diameter (dbh) and coarse root biomass.* Data and allometric relationships are scarce because they are difficult to obtain. Moreover, most data on roots are stand totals rather than individual tree estimates. Here, two different models were applied, presented by Kuiper & van Dijk (1988) and by Pellinen (1986), respectively:

$$W_{cr} = c_{52}*dbh^{c53} \quad \text{for Douglas-fir} \tag{4.12a}$$

$$W_{cr} = c_{52}*dbh + c_{54}*dbh^2 \quad \text{for beech} \tag{4.12b}$$

Equation 4.12c followed from combining the above two allometric relationships:

$$W_{cr} = c_{51} + c_{52}*dbh^{c53} + c_{54}*dbh^{c55} \tag{4.12c}$$

From the above equations, the partitioning coefficients f_i can be solved once total growth rate (G) and turn-over (D_i) are known. In the present model, turn-over of the biomass components was assumed to be proportional to the amount of biomass (Valentine, 1985; Mäkelä, 1986). The longevity of the sapwood was estimated to be 20 years for Douglas-fir (Mohren, 1987). Beech sapwood rings may live up to 100 years (Hillis, 1987). However, it is questionable whether all these rings contribute to vertical water transport

(Zimmermann, 1983). Because basal area without bark appeared to be strongly related to total leaf area (Bartelink, 1997a), longevity of beech sapwood rings was estimated to be 100 years (Hillis, 1987). Table 4.10 lists the applied loss rates.

Table 4.9: Values of the parameters used in the functional relationships of the partitioning model. Data are derived from the literature.

		Douglas-fir		beech	
constant	unit	value	source[1]	value	source[1]
c11	yr^{-1}	0.0337	JSF	0.0135	JSF
c12	-	1.4114	JSF	1.2600	JSF
c21	$m^2 m^{-2}$	5180	Ba	3410	Ba
c22	m	2.850	Ba	1.674	Ba
c23	m	1.30	Ba	0.0	Ba
c3	$kg\ kg^{-1}$	0.35	Ol, K&G	2.0	H&B
c41	#	0.069	Ba	0.011	Ba
c42	-	4.420	Ba	3.682	Ba
c43	-	-2.784	Ba	-1.031	Ba
c51	kg	-	-	-	-
c52	#	0.01	K&D	-0.863	Pe
c53	-	2.63	K&D	1.000	Pe
c54	#	-	-	0.150	Pe
c55	-	-	-	2.000	Pe
c61	-	1.901	JSF	1.861	SKS
c62	-	0.807	JSF	1.043	SKS
c63	-	-3.229	JSF	-3.053	SKS
SLA	$m^2 kg^{-1}$	5.63	Ba	17.20	Ba
BAD	$kg\ m^{-3}$	450	Z&Z	550	Bu

Compound unit

[1] Abbreviations for authors: Ba = Bartelink (1996a, 1997a), Bu = Burger (1950), JSF = Jansen et al. (1996), H&B = Hendriks & Bianchi (1995), K&D = Kuiper & van Dijk (1988), K&G = Keyes & Grier (1981), Ol = Olsthoorn (1991), Pe = Pellinen (1986), SKS = Schoonderwoerd et al. (1992), Z&Z = van der Zwan & van de Zee (1991)

Table 4.10: Loss rates (turn-over), expressed as fractions (biomass, area) per year, in case of an average tree on a relatively rich site (Scenario 1).

component	Douglas-fir	beech
foliage	0.4	1.0
branches	0.05	0.05
stem	0	0
coarse roots	0.05	0.05
fine roots	0.75	0.75
sapwood ring	0.05	0.01[1]

[1] Heartwood is formed only after approximately 100 years (Hillis, 1987).

The final outcome of the partitioning model consists of the absolute amounts of dry matter partitioned to the different tree components. Increases in the stem diameter follows the sapwood area increment (Eq. 4.13). Stem diameter growth and tree height increment determine the new stem volume, derived from the Shumacher-Hall tree volume equation (Eq. 4.14). Finally, stem biomass is estimated using the wood basic density (BAD: see Table 4.9).

$$dbh_{i+1} = 100 * ((dbh_i/100)^2 + 4/\pi * GA_s)^{0.5} \tag{4.13}$$

$$v = 0.001 * dbh^{c61} * h^{c62} * e^{c63} \tag{4.14}$$

With		
With	dbh_i	stem diameter at breast height (cm) at time i
	GA_s	sapwood area increment (m²/yr)
	v	tree volume (m³)
	h	tree height (m)
	e	base value of the natural logarithm

The structure of the developed partitioning model is presented in Figure 4.5: growth is partitioned over tree components (resulting in growth rates G), according to the current tree state (in terms of biomass amounts and stem dimensions), and to driving forces (height growth and growing conditions). The model uses time-steps of one year. Growth rates of the different tree components are derived from iterative calculations, based on the equations mentioned above.

<u>Initial states, growing conditions, and growth</u>

To test the model, the growth of a Douglas-fir and a beech tree was simulated, growing on acid brown podsolic soils in the Netherlands. Starting age was 10 years, and tree sizes corresponded with those of an average tree, i.e. a tree with a stem basal area corresponding to the stand average basal area. Initial tree conditions were derived from yield tables and allometric relationships. An overview of the initial biomass amounts and tree dimensions is presented in Table 4.8. Model simulations were carried out for a 50-year period. Initial growing conditions are described in Table 4.11.

Table 4.11: Initial growing conditions and descriptions of Scenario 1 (rich site) and 2 (poor site) for Douglas-fir and beech: a = average tree, b = suppressed tree (all resources equally lacking), c = suppressed tree (nutrients and water are most limiting), d = suppressed tree (radiation is most limiting). Subscript i indicates the initial condition, subscript f refers to the final situation. Absorbed radiation (APAR) is expressed as fraction of the tree average. Si stands for site index (m), R/S is the root/shoot-ratio (kg/kg), CR is the crown ratio (m/m), Df is turn-over of the fine roots.

Scenario	dbh_i	h_i	Si	R/S	CR_i	CR_f	RUE	Df	APAR
	cm	m	m	-	-	-	g/MJ	yr^{-1}	-
Douglas-fir									
1a	7.0	5.7	40.0	0.35	0.9	0.6	1.1	0.75	1.0
1b	5.0	4.8	38.0	0.35	0.8	0.5	1.1	0.75	0.5
1c	5.0	4.8	38.0	0.70	0.8	0.5	1.1	0.75	0.5
1d	5.0	4.8	38.0	0.20	0.8	0.5	1.1	0.75	0.5
2a	6.0	4.3	30.0	0.60	0.9	0.6	0.8	1.0	1.0
2b	4.0	4.0	28.0	0.60	0.8	0.5	0.8	1.0	0.5
2c	4.0	4.0	28.0	1.30	0.8	0.5	0.8	1.0	0.5
2d	4.0	4.0	28.0	0.35	0.8	0.5	0.8	1.0	0.5
beech									
1a	3.9	2.7	48.0	2.0	0.90	0.70	1.65	0.75	1.0
1b	2.8	2.5	45.0	2.0	0.80	0.60	1.65	0.75	0.5
1c	2.8	2.5	45.0	3.0	0.80	0.60	1.65	0.75	0.5
1d	2.8	2.5	45.0	1.5	0.80	0.60	1.65	0.75	0.5
2a	2.3	1.7	37.0	3.0	0.90	0.70	1.2	1.0	1.0
2b	1.9	1.3	34.0	3.0	0.80	0.60	1.2	1.0	0.5
2c	1.9	1.3	34.0	4.0	0.80	0.60	1.2	1.0	0.5
2d	1.9	1.3	34.0	2.0	0.80	0.60	1.2	1.0	0.5

Absolute total growth rate (kg dry matter per tree per year) was estimated from the amount of available radiation and the radiation-use efficiency (RUE). The radiation-use efficiency is defined as the ratio between the amount of absorbed photosynthetically active radiation (APAR) and the amount of dry matter produced (Landsberg, 1986).
Both species have a maximum leaf area index (LAI) of about 7 in closed mono-species stands (Bartelink, 1996a, 1997a), indicating that almost all radiation will be absorbed. For the Netherlands, the annual total incoming photosynthetically active radiation (PAR) is about $1.7*10^7$ MJ ha^{-1}. For beech, the length of the foliage-bearing period had to be taken into account: available PAR during the growing season of beech was estimated to be 73% of the annual available PAR (Bartelink et al., 1997). Assuming suitable growing conditions, the radiation-use efficiency was 1.1 and 1.65 g MJ^{-1} PAR for Douglas-fir and beech, respectively (Bartelink et al., 1997). The estimated annual growth rates thus amounted about 19 and 20 ton dry matter ha^{-1}. Dividing these amounts by the respective stand densities results in an estimate of the average annual tree growth rate. The stand densities from the yield tables of Jansen et al. (1996) were used to describe the (site dependent) continuous decrease of tree density with time.

Scenarios

When built into an overall growth model, the environment (growing conditions) and the initial tree state will be driving variables for a partitioning sub-model. When applying the present partitioning model independently, these conditions are defined as scenarios. For instance, changes in the root/shoot ratio will normally be a function of the environment, whereas in this study the root/shoot ratio was imposed, estimated from the site conditions.
In the present model, the interrelationship between growing conditions (available PAR, water and nutrient availability) and partitioning were represented by:

- the relationship between site condition and height growth (through Si),
- the dependence of root/shoot ratio (R/S) on absorbed PAR (APAR), soil water and nutrient availability: in case of a lowered nitrogen or soil water availability R/S will increase, whereas the opposite happens when radiation availability decreases (Reynolds & Thornley, 1982; Brouwer, 1983),
- the effects of soil water and nutrient availability on fine root turn-over: in case of poor site conditions, root turn-over will be higher than under more favourable conditions (Keyes & Grier, 1981; Santantonio & Hermann, 1985),

And indirectly by:

- the allometric relationship on branch biomass (through the changed height growth),
- the sapwood area (through the effect of absorbed PAR on self-pruning).

To demonstrate model behaviour, dry matter partitioning was calculated for several tree states and growing conditions. Partitioning was simulated on a relatively rich site and a relatively poor site, that differed with respect to:

- height growth rate (through the site index Si),
- root/shoot ratio, and
- fine root turn-over.

In addition, on the poor site absolute growth rate was reduced, through a reduction of the radiation-use efficiency (RUE) in case of lower water and nutrient availability.
At both sites, a distinction was made between growth of an average tree and growth of a suppressed tree, assuming that suppressed individuals:

- were smaller at the start of the simulation,
- had a lower height growth rate,
- intercepted less radiation,
- had a lower crown ratio.

The crown ratio (crown length divided by tree height) was assumed to differ between trees with different dominance positions, as the upward shift of the crown-base (the result of self-pruning) will be strongly dependent on radiation conditions inside the canopy. The root/shoot ratio might be different in suppressed individuals as well; however, as reductions in available radiation and in available water or nutrients affect the root/shoot ratio in opposite ways, the net effect of competition on the ratio is unpredictable. Thus, in case of a suppressed tree, both the effects of an increased and of a decreased root/shoot ratio were analyzed.

The scenarios are described in Table 4.11. In the default situation (Scenario 1a), growth of an average tree on a relatively rich site is simulated. Scenarios 1b, 1c, and 1d refer to the same site conditions, but describe the situations for a suppressed tree. Scenario 2 refers to the site with a lower nutrient and soil water availability. In addition to the default Scenario 1a, a situation was simulated where the stem number does not decrease gradually in time, but is decreased as a result of thinning. This Scenario 3 should show the effect of sudden changes in resource availability on partitioning and diameter growth.

Sensitivity analysis

A sensitivity analysis was carried out to determine the robustness of the model: this analysis determines whether the model is sensitive to certain parameters, and indicates whether high-accuracy estimates of the parameters are needed. The sensitivity analysis was applied on a number of key-parameters (see Table 4.12); relative sensitivity (RS) of the parameters was defined according to Equation 4.15. Tree dbh and living biomass at age 60 were used as criteria.

$$RS = (V_{+5\%}-V_{-5\%}) / (V_{def}*0.1) \tag{4.15}$$

With		
	RS	Relative sensitivity (dimensionless)
	$V_{+5\%}$	Resulting value of the critical parameter (dbh or living biomass) when the value of the parameter to be analyzed is increased by 5%
	$V_{-5\%}$	Resulting value of the critical parameter when the value of the parameter to be analyzed is decreased by 5%
	V_{def}	Resulting value of the critical parameter under default conditions
	0.1	Relative range (1.05-0.95) of the parameter to be analyzed (dimensionless)

Thus, the relative sensitivity equals unity when changes in a partitioning parameter have a proportional response on dbh or living biomass at age 60.

Because height growth is imposed (through a forcing function) in the present model, simulations were carried out for different values of the site index (Si). For the analysis of effects of Si on growth, again dbh and living biomass at age 60 were taken as references.

Special attention was paid to root/shoot ratio, because of the broad range of values presented in the literature (Olsthoorn, 1991; Hendriks & Bianchi, 1995). To estimate the impact on partitioning, simulations were carried out for different values of the root/shoot ratio, using dbh and living biomass at age 60 as references.

Table 4.12: Results of the sensitivity analysis, carried out for an average tree on the rich site (Scenario 1). The reference values at age 60 were 39.7 cm for Douglas-fir dbh and 589 kg living biomass, whereas for beech the values were 31.2 cm and 727 kg. The columns labelled 'dbh' and 'biom' contain the relative sensitivities (RS) calculated with respectively tree diameter and tree living biomass as criteria (see Equation 4.15).

	Douglas-fir			beech		
parameter	default	dbh	biom	default	dbh	biom
root/shoot-ratio	0.35	-0.086	-0.170	2.0	-0.103	-0.193
pipe-ratio	5180	-0.237	-0.441	3410	-0.176	-0.344
foliage turn-over	0.4 yr^{-1}	-0.124	-0.289	1.0 yr^{-1}	-0.064	-0.138
sapwood turn-over	0.05 yr^{-1}	0.134	0.255	0.01 yr^{-1}	0.026	0.055

Results

Dry matter partitioning

The predicted dry matter partitioning in the average tree is presented in Fig.4.6a and 4.6b, for Douglas-fir and beech, respectively: the graphs show the fractions of the annual current increment of total dry matter. It appears that the fractions gradually change with tree age and that the changes are relatively small, especially after age 20. The small fluctuations are the result of the iterative way of calculating apportioned fractions. Also differences between the two species occurred. Douglas-fir invested relatively more dry matter in its foliage, especially at the cost of the branch and stem components.

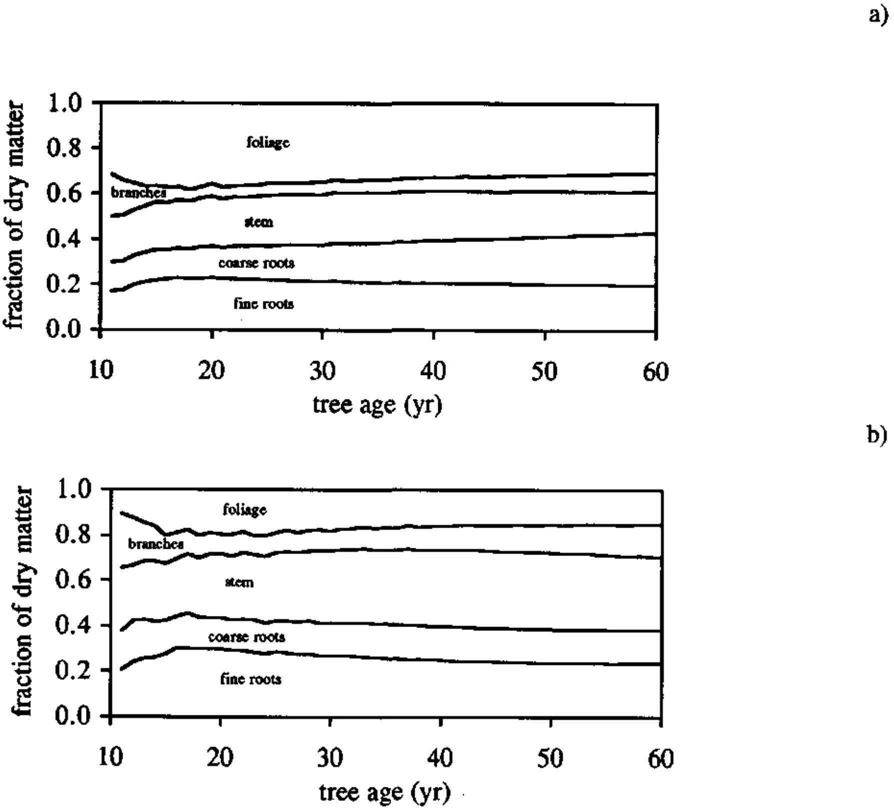


Figure 4.6: Dry matter partitioning in an average tree on a relatively rich site (Scenario 1). Fractions of the annual current increment of total dry matter: a) Douglas-fir, b) beech.

The partitioning patterns of the suppressed trees showed comparable trends, thus results were summarized by calculating the average partitioning over the last 40 years (see Table 4.13). The first 10 years were omitted here, because in young, suppressed beech, the low initial diameter resulted in negative estimates of the coarse root biomass, because of the structure of the allometric relationship (see Pellinen, 1986). Table 4.13 reveals that the average trees (Scenario 1a) invested relatively more dry matter in the branches and less in the stem than the suppressed tree (Scenario 1b), both in Douglas-fir and beech, provided that the root/shoot ratio did not differ between the average and the suppressed individuals.

Different partitioning patterns resulted when suppressed trees had a different root/shoot ratio (R/S) as well (scenarios 1c and 1d). A suppressed tree with a higher R/S (scenario 1c: radiation is less limiting than nutrients and water) apportioned a higher fraction towards the fine roots, and a lower fraction to the foliage, when compared with a suppressed tree with a lower R/S (scenario 1d: radiation is more limiting than nutrients and water are) (see Table 4.13).

Table 4.13: Partitioning percentages per tree component: values derived from averaging annual partitioning percentages over the last 40 years (age 21-60 years).

	rich site				poor site			
Scenario	1a	1b	1c	1d	2a	2b	2c	2d
Douglas								
foliage	33	33	27	37	28	26	18	32
branch	6	4	3	5	4	4	2	5
stem	21	23	20	25	15	18	15	20
coarse roots	19	18	15	20	13	14	10	16
fine roots	21	21	34	13	40	38	55	27
Beech								
foliage	17	17	15	18	16	16	14	20
branch	11	8	7	9	7	7	6	9
stem	32	36	32	37	21	19	17	21
coarse roots	15	14	13	16	10	9	8	11
fine roots	26	25	34	21	47	49	56	39

Diameter (dbh) development over time

Figure 4.7a and Figure 4.7b show that the simulated diameter increase over time generally fitted yield table data well. Only in case of an average Douglas-fir on a poor site, diameter development was under-estimated at higher ages. Because of the assumed lower absolute growth rate of suppressed trees (50% of the dry matter when compared with average trees), the diameter growth of the suppressed trees will be lower (Fig.4.7ab).

Effects on diameter development were different when the root/shoot ratio (R/S) of suppressed trees changed as well (scenarios 1c and 1d). A suppressed tree with a low R/S reached a higher dbh at age 60 than an average tree, both in Douglas-fir and beech (results not shown).

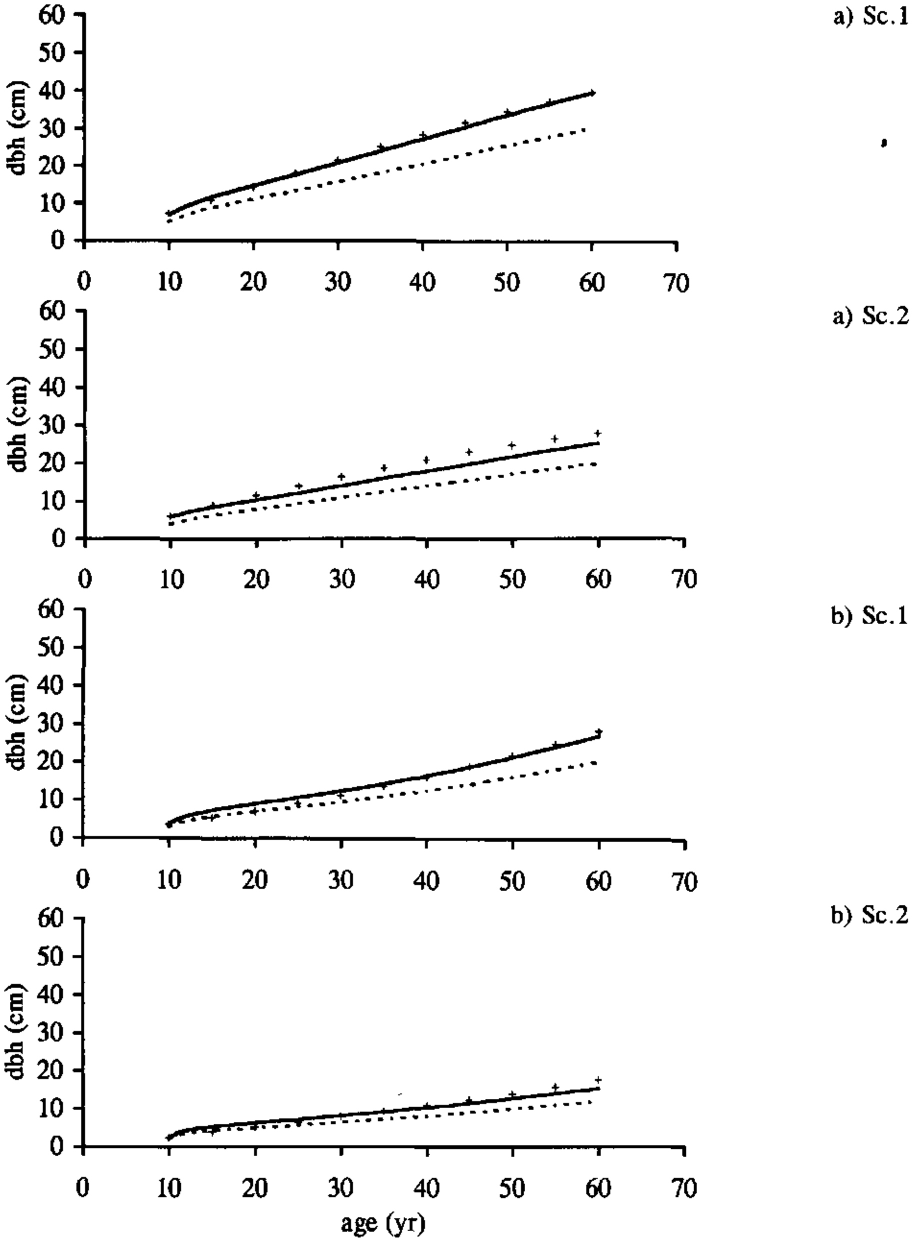


Figure 4.7: Tree diameter (dbh) against tree age; yield table data (symbols) compared with results of Scenario 1 (rich site) and 2 (poor site). Average trees (solid line) and suppressed trees (dotted lines), in case of a) Douglas-fir, b) beech.

Dry matter distribution

Figures 4.8a and 4.8b show the biomass distribution, i.e. the fraction of standing biomass in different tree parts, for average trees growing on the rich site. The graphs of the two species show the same trends, i.e. a gradual decline of the foliage and fine root fraction, and a gradual increase of the stem fraction. This can be attributed to different loss rates between components. Foliage and fine roots have a high turn-over, whereas other components have lower loss rates, or as in case of the stem it is zero (dry matter accumulation). In beech, there was relatively less foliage, as a result of the smaller pipe-model coefficient compared with Douglas-fir. The distribution patterns of the suppressed trees (not shown) were comparable to those of the average trees, though the size of the fractions differed between trees from different dominance classes.

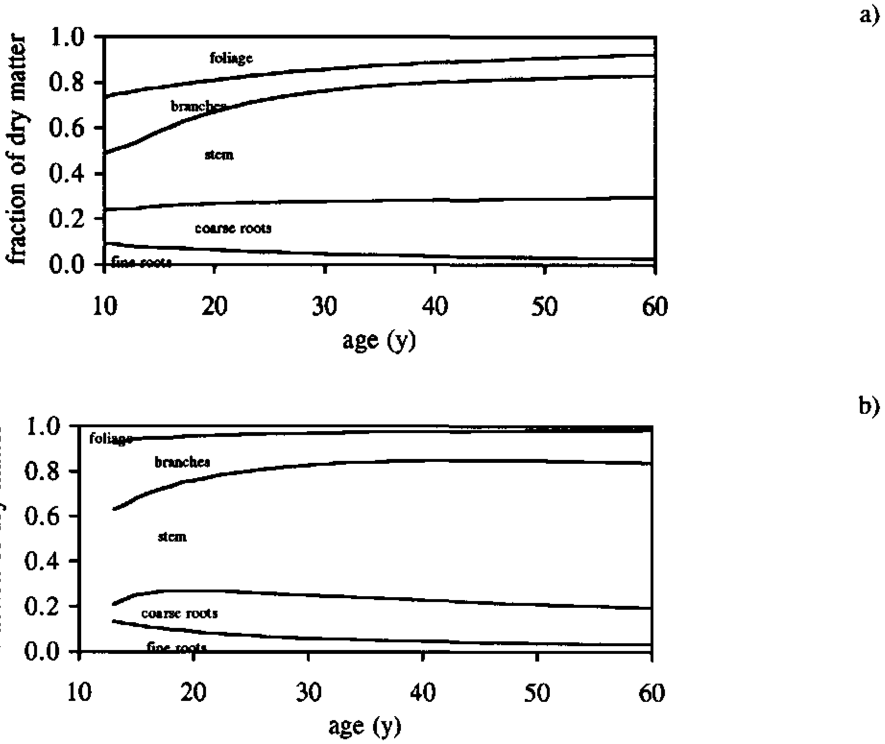


Figure 4.8: Fraction of standing biomass in different tree parts (dry matter distribution) in an average tree on a relatively rich site (Scenario 1): a) Douglas-fir, b) beech.

Site effects

The trees grew less in diameter on the poor site than on the rich site (Fig.4.7), simply owing to the lower absolute growth rate, resulting from the pre-defined lower radiation-use efficiency. However, diameter development was also affected by differences in relative partitioning to the stem. Table 4.13 reveals that on a relatively poor site, the fraction partitioned to the fine-roots is doubled, mainly at the expense of the stem and coarse roots. The biomass distribution patterns also differed among the sites. At the poor site, both Douglas-fir and beech had relatively more fine root biomass and less coarse root and stem biomass.

Effects of thinning

Figure 4.9 presents the results of running Scenario 3 (thinning). It appears that thinning, i.e., a discontinuous reduction of stem number, results in a slow decrease in partitioning to the stem (Fig.4.9a, see also Fig.4.6a). The direct response to thinning consists of a sharp decrease in partitioning to fine roots and foliage on one hand, and an extra investment in the branches on the other (Fig.4.9a). Diameter increment tends to decrease in time, but in the long term diameter growth is rather constant as a result of the thinnings (Fig.4.9b). As a consequence, diameter will increase almost linearly with time.

Sensitivity analysis, role of root/shoot ratio and site index

Values of the relative sensitivity (RS) are negative when a higher parameter value results in a lower value of the dbh or the biomass, and vice-versa. Table 4.12 shows that, for all model parameters considered, the absolute value of RS was lower than 1, indicating that the relative response (in terms of changes in dbh or biomass) is less than the relative change in the value of the parameter. This implies that the partitioning model is robust for all of the parameters tested. The highest responses were found for changes of the pipe-model ratio. The model also showed more response in biomass than in dbh, which can be attributed to the allometric relations. Most parameters were less sensitive for beech than for Douglas-fir.

Though the model was also relatively insensitive to changes in the root/shoot ratio, varying the root/shoot ratio strongly affected growth. Fig.4.10 shows that in both Douglas-fir and beech, dbh and living biomass at age 60 decreased with increasing root/shoot ratio. This effect was much stronger in Douglas-fir than in beech.

The effects of height growth rate, manipulated by varying the values of the site index (Si), differed between Douglas-fir and beech (Fig.4.11). In Douglas-fir, dbh at age 60 increased with increasing Si, mainly at Si values lower than 40. In beech, height growth rate only had a minor effect on dbh increment (Fig.4.11a). The effect on biomass at age 60 deviated from the response in dbh: in both species a linear to exponential increase in biomass at age 60 occurred with increasing Si (Fig.4.11b).

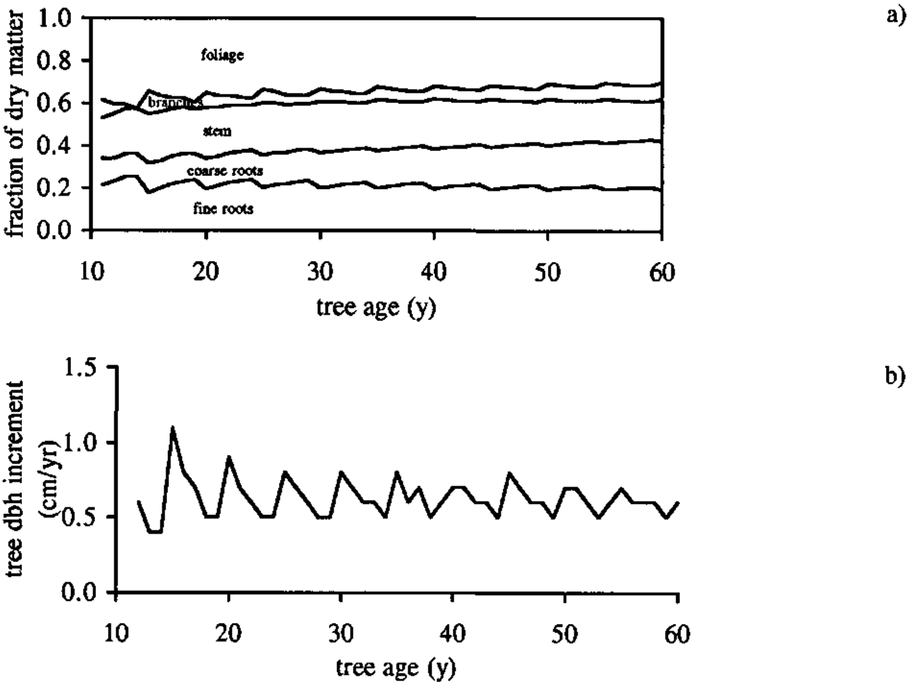


Figure 4.9: Effects of thinning on a) partitioning, and b) diameter increment, in case of an average Douglas-fir on a relatively rich site (Scenario 3).

Discussion

Plausibility of the partitioning model

Many attempts have been made regarding the simulation of allocation or partitioning, running from purely empirical to highly mechanistic models (see Ågren & Wikström, 1993; Cannell & Dewar, 1994). In the present study, the same concepts were used as in the mechanistic approaches of Valentine (1985) and Mäkelä (1986), but in addition allometric relationships were applied. This approach generally results in a loss of explanatory quality. Moreover, regression coefficients may be dependent on the internal and external conditions of a tree, although this kind of uncertainty also may exist in mechanistic models: the key assumption in Mäkelä's and Valentine's models, for example, is that sapwood and foliage biomass occur in constant ratios. Especially in case of trees differing in social position this does not hold (Bartelink, 1997a). Both when applying allometric and functional relationships it is worthwhile to investigate the effects of tree and site conditions on the parameter estimates.

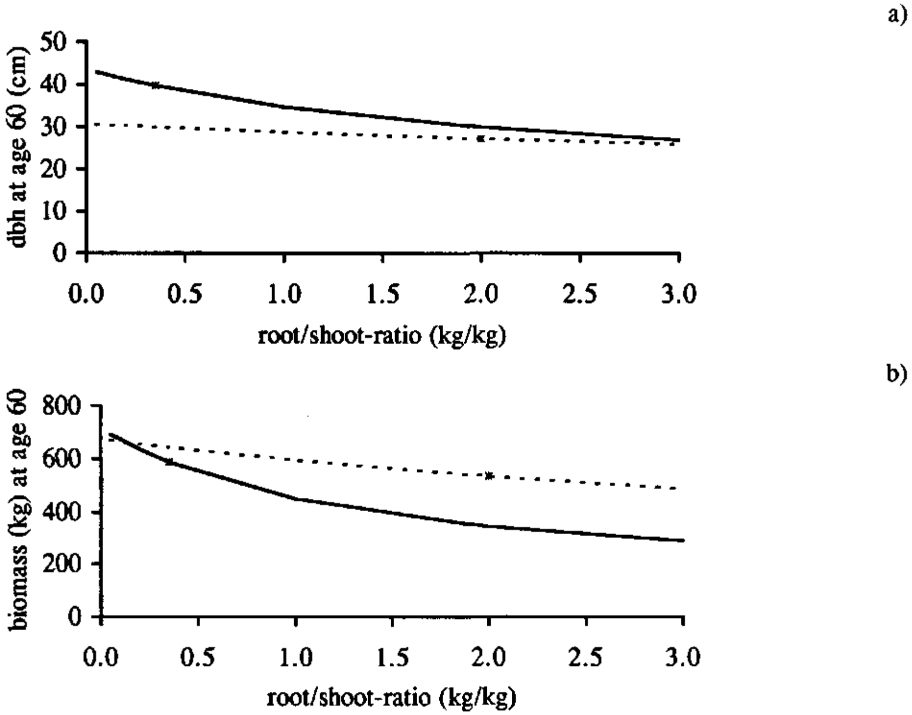


Figure 4.10: Effect of the root/shoot-ratio after a 50 year simulation period, on a) the tree diameter reached at age 60, and b) the tree biomass reached at age 60. Estimations are indicated by a solid line (Douglas-fir) and a dashed line (beech); the asterix represents the default value.

A point of concern in the present approach is that tree height growth follows a predescribed pattern, only dependent on species and site conditions. However, the significance of height growth for survival of a tree is probably not in its contribution to the internal balance of growth, but rather to the competitive ability for light and space (Mäkelä, 1986). The main problem here is the translation of 'site condition' into a quantitative parameter like site index.

Another critical point in the present model consists of the root/shoot ratio. Plant nutrient status is probably the most important factor associated with carbon allocation; this feedback should thus be included in allocation models (Ågren & Wikström, 1993). Present model calculations showed that the ratio has a strong impact on partitioning, so reliable data on roots and shoots are needed. Data on fine roots however, are scarce.

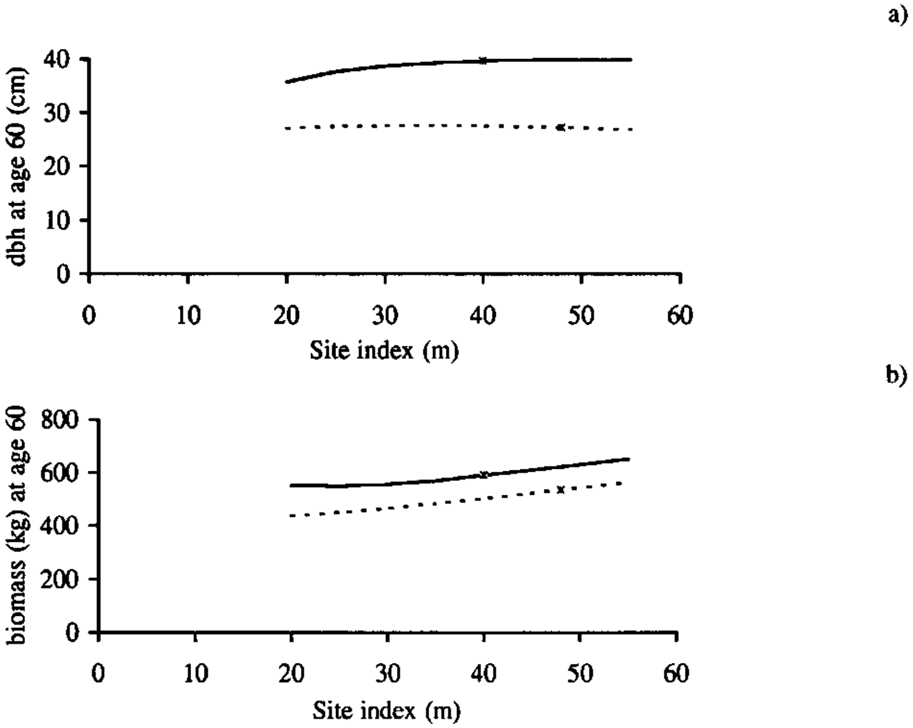


Figure 4.11: Effect of the site index after a 50 year simulation period, on a) the tree diameter reached at age 60, and b) the tree biomass reached at age 60. Estimations are indicated by a solid line (Douglas-fir) and a dashed line (beech); the asterix represents the default value.

The main advantage of the model is that it enables a dynamic partitioning to be simulated: internal and external conditions that affect partitioning can be taken into account, resulting in a tree level estimate of growth and development. The model is based on the maintenance of structural balances; although less attention has been paid to this aspect so far, the maintenance of the structural balance have strong implications to partitioning and allocation (Mäkelä, 1986; Cannell & Dewar, 1994). A second advantage is that for the present model no respiration data are needed: the calculation of respiratory costs is one of the major pitfalls of mechanistic models. A study on Scots pine, for example, showed that results appeared sensitive especially to the maintenance requirements of the living woody tissue (Mäkelä, 1986); this again indicates that reliable respiration estimates are needed to take advantage of detailed physiological allocation models.

In view of the criteria that should be satisfied by allocation models, to date there are no models that satisfy all requirements (Ågren & Wikström, 1993). Model suitability thus largely depends on the aims of the study. Though the present approach is less theoretical that the approach of e.g. Thornley (1991), and not as mechanistic as the models of Valentine (1985) and Mäkelä (1986), it did meet the requirements of this study rather well. The model appeared able to reproduce the known development of an individual tree, in terms of dbh and biomass. The simulated diameter (dbh) increment and time-pattern of Douglas-fir closely followed the yield table of Jansen et al. (1996). The resulting dry matter distributions of both Douglas-fir and beech are comparable with results of Cannell (1984), Pellinen (1986), and Bartelink (1996a, 1997a). The model thus produces realistic estimates of partitioning coefficients. Furthermore, because the sensitivity analysis showed that the model is robust, the partitioning approach is a suitable tool for estimating dry matter partitioning in individual trees.

In Douglas-fir, height growth affected partitioning (not shown) and dbh (Fig.4.10) only for less optimal site conditions (Si lower than 40): the approach thus has a minor effect on the partitioning coefficient estimates.

Effects of growing conditions on partitioning

Suppressed trees invested relatively less dry matter in the crown than average trees (Table 4.13). As a result, the share of crown biomass in the dry matter distribution is lower for suppressed individuals. These findings correspond with the results of biomass studies (Bartelink, 1996a, 1997a).
Scenario analysis revealed that on a poor site, because of the lower root/shoot-ratio, relatively more dry matter will be apportioned to the fine roots. This is in accordance with findings of Keyes & Grier (1981) and Santantonio & Hermann (1985). In general, site condition (availability of soil water and nutrients) can be expected to affect partitioning strongly, especially regarding the impact of the below-ground components. In relatively poor soils, fine-root turn-over will be high, and the root-shoot ratio will also be high (Keyes & Grier, 1981; Santantonio & Hermann, 1985). As a consequence, up to 80% of the available assimilates may go to the fine roots (Santantonio & Hermann, 1985). This stresses the necessity of taking into account the effects of site condition on allocation or partitioning when modelling forest growth.

Varying the root/shoot ratio resulted in eager changes in dbh at age 60, stressing the importance of accurate information on site conditions. Several studies on biomass have been presented in the literature, but data on (fine) roots are relatively scarce, and highly variable. Taking all roots smaller than 2mm into account, estimates for the root/shoot-ratio in Douglas-fir, for example, range from about 0.1 (Olsthoorn, 1991) and 0.2 (Keyes & Grier, 1981) up to 1.2 (estimated from Hendriks & Bianchi, 1995). Even on neighbouring sites, root/shoot ratio estimates range from 0.1 to 1.2 (Olsthoorn, 1991; Hendriks & Bianchi, 1995). For beech, on the same sites, estimated ratios varied between 2.5 and 3.30 (Hendriks & Bianchi, 1995: assuming LAI to be 7). Though the sensitivity analysis indicated that the partitioning model is not very sensitive to the accuracy of estimates of root/shoot-ratio, the effect on dbh is strong (Fig.4.10), indicating that estimates of growth in terms of wood production require a precise estimate of the root/shoot ratio.

Differences between species

Partitioning differences between Douglas-fir and beech can be largely attributed to general differences between coniferous species and broadleaves. Because beech drops its leaves at the end of each year, much dry matter has to be partitioned to foliage. However, from Fig.4.6ab it appears that the dry matter fraction that Douglas-fir apportions to its foliage is larger than for beech. This can be explained by the higher SLA (m^2 kg^{-1}) in broad-leaved trees. The SLA of beech is three times as large as the SLA of Douglas-fir, implying that much less foliage biomass is needed for a certain leaf area in beech.

Applications

Partitioning appeared more or less constant, especially after the juvenile phase (up to 10-20 years), provided that growing conditions do not change (Fig.4.6ab). The elementary approach of an annually fixed dry matter partitioning key, as has been applied in several crop growth and forest growth models (e.g., Mohren, 1987), thus might work quite well. However, to account for effects of changing growing conditions, a dynamic approach is needed. The presently developed partitioning model includes feed-back between growing conditions and plant state on partitioning. Dynamically changing growing conditions, e.g., changed resource availability as a result of thinning, can thus be taken into account. This partitioning approach will be used in a simulation model for mixed species forests. As part of ongoing research on growth and development of mixed species stands, a forest growth model has been developed that simulates growth of individual trees in a forest, based on resource availability and species characteristics. The present, more mechanistic approach of partitioning, is necessary to model effects of competition for resources on partitioning patterns, and hence on growth and development of forest trees.

Chapter 5: Growth and yield of monospecies and mixed Douglas-fir and beech stands: a simulation study

Introduction

Models estimating growth and yield of forest stands form important tools for forest management. Pure stands have been modelled extensively and rather successfully for decades, resulting in yield tables for different species on a range of sites (e.g. Jansen et al., 1996). In contrast, thorough and systematic research on the stand dynamics of mixed forests is lacking, and relatively few models for mixed-species stands have been developed. This makes the development of the mixed forest structure in many situations unpredictable (Pretzsch, 1992; Burkhart & Tham, 1992). One of the few attempts to model mixed stands involves the gap approach, a distance-independent tree-level approach, where forest development is simulated by summing the gap dynamics of a couple of regeneration patches (Botkin et al., 1972; Shugart, 1984). Gap models, however, are developed to study natural developments rather than growth and yield of managed stands (cf Burkhart & Tham, 1992). Restrictions in the spatial detail of the gap models also pose limitations on their applicability. A second approach consists of the use of competition indices (e.g. Holmes & Reed, 1991); these are empirical relationships between (tree) growth and tree and stand characteristics, applicable only to a limited range of growing conditions. The inexhaustible number of species combinations, management regimes, and site-dependent interactions in mixed stands, however, make a causal approach much more suitable (Lavigne, 1992; Burkhart & Tham, 1992).

In mixed species stands, treatments like thinnings not only affect total stand growth but also inter-specific competitive relationships (Holmes & Reed, 1991; Larson, 1992). The different characteristics of the species and the spatial distribution of the remaining trees thus have a different and in most cases a much stronger impact on stand development than in case of monospecies stands (Füldner & Von Gadow, 1994; Solomon & Leak, 1994). Moreover, a description of a mixed stand in terms of average tree dimensions covers a wide range of potential stand compositions, which hampers the estimation of e.g. wood quality and assortments, and the prediction of future stand development. As a consequence, the emphasis in forestry decision-making has started to shift from the stand-level towards the tree or tree-group level (Holmes & Reed, 1991; Pretzsch, 1992). Mixed forest modelling should thus focus on simulating growth of individual trees and responses of individual trees to management (Pretzsch, 1992; Solomon & Leak, 1994).

The tree-level approach of Pretzsch (1992, 1995), though descriptive, forms an important attempt to model managed mixed forests. However, due to the infinite variety of possible species mixtures, coupled with the range of environmental conditions under which mixtures might be grown, a theoretical, process-oriented approach will be required to generalize competition relationships (Burkhart & Tham, 1992; Kelty & Cameron, 1994). Such an approach would result in mechanistic models, that can be used to simulate responses to silvicultural treatments that have never been performed in practice. Process-oriented models already appeared successful in simulating growth of monospecies stands (e.g. Mohren, 1987; Nikinmaa, 1992). For predicting the growth and development of mixed stands, however, no physiological tree models have been produced yet (Lavigne, 1992). The few process-oriented attempts made are gap- or stand-level based (e.g. Friend et al., 1993; Kramer, 1996). In this paper, a mechanistic model is presented that simulates growth of mixed-species forest stands, taking into account the effects of management on stand dynamics. Tree growth is dependent on radiation availability, and stand development is largely driven by the competition for radiation. The aim of the study was 1) to present the modelling concept, 2) to compare growth and yield of mixed stands with monospecies stands, and 3) to estimate effects of management on growth and yield. Data on monospecies and mixed stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and beech (*Fagus sylvatica* L.) were used for this study.

Material and methods

Structure of the simulation model: COMMIX

Time resolution, spatial arrangement, and tree representation

The simulation model is a FORTRAN-77 computer program, called COMMIX (COMpetition in MIXed stands). It is a process-based, tree-level, distance-dependent model of forest growth (Fig.5.1). The principal time-step of the model is one year.

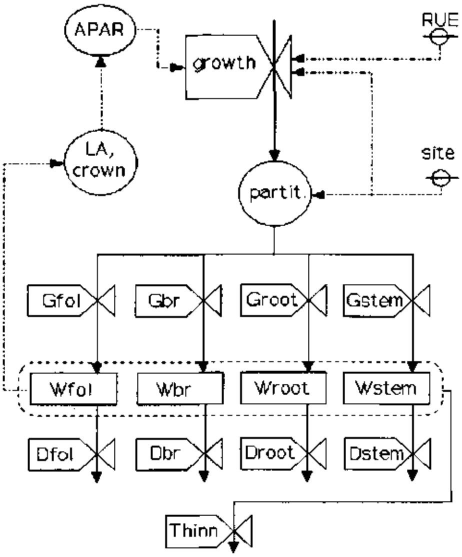


Figure 5.1: Flow diagram of COMMIX: APAR is absorbed PAR, LA is tree leaf area, RUE is radiation-use efficiency, 'site' represents site characteristics, 'partit' is partitioning, 'Thinn' is thinning, G is growth rate, W is dry weight, and D is turn-over.

In the model, individual trees were considered, characterized by the dry weights of the biomass components and the dimensions of stem and crown. In terms of biomass, a tree was divided into the following components: fine roots, coarse roots, stem, branches, and foliage. Structural characteristics were: stem diameter (at breast height: 1.30 m above the forest floor), tree height, crown base height, crown width, and crown form. Additional tree variables were sapwood area and foliage area. Tree crowns were represented by cones (Douglas-fir) and ellipsoids (beech), which were assumed to be symmetrical around the tree stem. Together, the individual crowns build up a three-dimensional canopy.

Basically, four steps can be distinguished in the dynamic simulation: 1) interception of radiation by a tree, 2) translation of the amount of absorbed photosynthetically active radiation (APAR) into an amount of dry matter, 3) partitioning of the dry matter (i.e. growth) over the different biomass components, and 4) updating the tree biomass status (integration) and calculating the changes in tree structure.

Radiation interception

Radiation attenuation is spatially explicit in COMMIX. To calculate absorption and transmission, a grid was defined on the forest floor; to connect the radiation beams with the grid points, virtual beams were defined, starting from the grid points, and heading in a direction determined by the orientation of the radiation (van Kraalingen, 1989). See Fig.5.2. When a beam crosses a crown, the flux density is partly attenuated. Whether intersection between the beam and a crown occurs depends on:
- the location of the grid-point
- the orientation of the beam
- the location and size of the tree crown.

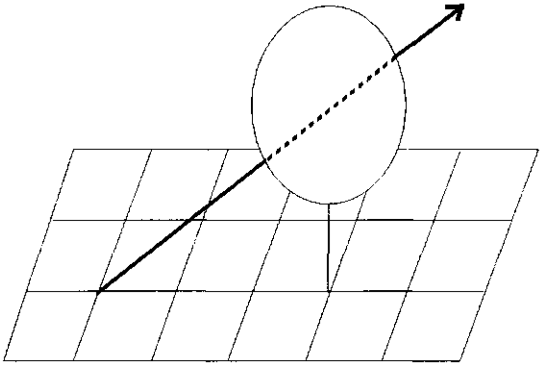


Figure 5.2: A two-dimensional grid at the forest floor is defined, from which beams extend upward through the forest canopy: the base of each beam originates from a defined grid-point (after Bartelink, 1996b).

The instantaneous radiation flux density, or irradiance (W m^{-2}) above a canopy, generally consists of both direct and diffuse radiation. To describe the diffuse conditions above the canopy, it was assumed that the sky has a uniform radiance, the so-called uniform overcast sky (UOC). To account for the geometric distribution of the diffuse radiation, the UOC was built up by 324 beam orientations (van Kraalingen, 1989). The angle of incidence in case of direct radiation follows from the position of the sun.
When a ray enters the canopy it may cross one or more tree crowns. In the model stem and branch intercepting areas were ignored, assuming that there is always foliage between the sun rays and the woody components. Leaves were assumed to be black i.e. reflection and transmission were ignored. The rate of radiation extinction inside a crown is thus dependent on:

1. the leaf angle distribution,
2. the leaf area density,
3. the radiation orientation,
4. the path length.

Assuming a uniform distribution of the foliage, the relationship between radiation regime, leaf characteristics, and radiation extinction was described by the Lambert-Beer equation. The relationship was modified to calculate the attenuation in the direction of the ray (Eq.5.1):

$$I_l = I_0 * \exp(-O_\beta * LAD * l) \qquad (5.1a)$$

$$O_\beta = K/\sin(\beta) \qquad (5.1b)$$

With	I_l	Irradiance at depth l (along ray direction) in the canopy (W.m^{-2})
	I_0	Irradiance outside the canopy (W.m^{-2})
	O_β	Projection coefficient
	β	Ray inclination
	LAD	Leaf area density ($m^2.m^{-3}$)
	l	Trajectory length; covered distance inside crown (m)
	K	Extinction coefficient

To calculate absorption, the beam was assigned a width equal to the grid cell size. When the heart of the beam intersects a crown, the beam cross-sectional area perpendicular to the beam direction (ß) is determined. The distance covered in the crown determines the attenuation rate. The difference between irradiance input and resulting irradiance after having passed the crown (in W m^{-2}), multiplied with the beam cross-sectional area, results in an estimate of the amount of radiation absorbed by that part of the crown (Fig.5.3).

About 50% of the radiation in The Netherlands comes from diffuse sky conditions (Spitters et al., 1986). For the present application, all radiation was considered to be diffuse, assuming that the angular variability of the direct radiation could be considered comparable with the distribution of a UOC. Average annual amount of photosynthetically active radiation (PAR) was derived from the weather station in Wageningen, the Netherlands (5°40'E, 51°58'N).

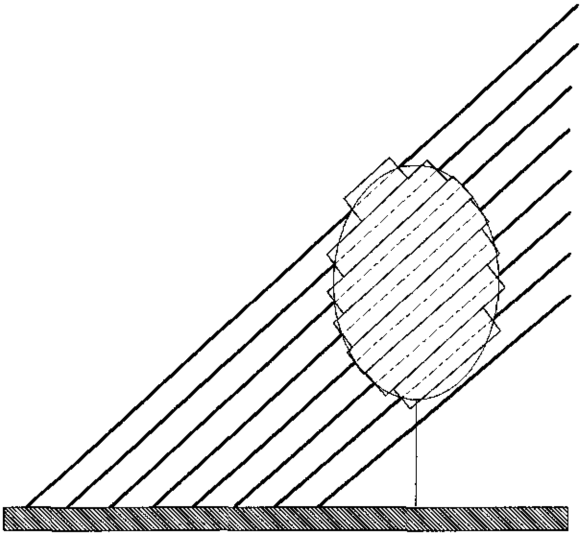


Figure 5.3: Crown form and cell width together determine the size of the beam-sections representing the crown volume (after Bartelink, 1996b).

Growth and dry matter partitioning

Based on results of many productivity studies, Monteith (1977) proposed the concept of radiation-use efficiency (RUE), stating that the ratio between the amount of APAR and the amount of dry matter produced would be a conservative parameter. In many productivity studies, a linear relationship between APAR and crop or forest growth has been found since (e.g. Gallagher & Biscoe, 1978; Stockle & Kiniry, 1990; Jarvis & Leverenz, 1983). This concept is applied in COMMIX (Eq.5.2). RUE-estimates were derived from Bartelink et al. (1997).

$$G_{DM} = I_a * \epsilon_{RU} \tag{5.2}$$

With G_{DM} growth rate i.e. dry matter increment (g [DM tree^{-1}] y^{-1})
I_a absorbed PAR (MJ [PAR tree^{-1}] y^{-1})
ϵ_{RU} radiation-use efficiency RUE (g [DM] MJ^{-1} [PAR])

The description of the assimilate allocation or dry matter partitioning plays a key role in mechanistic models of tree and forest growth (Landsberg, 1986; Cannell, 1989). The main concepts suitable for modelling purposes were summarized by Cannell & Dewar (1994). Though theoretically sound, most of the concepts are less suitable for forest modelling studies, since many included parameters are unknown (Cannell, 1989). In COMMIX a dynamic approach was used to simulate dry matter partitioning, based on the concept of maintaining structural balances (Mäkelä, 1986; Bartelink, 1997b). The partitioning coefficient f_i was defined as the fraction of the total dry matter growth apportioned to a certain biomass component 'i'; the sum of the partitioning coefficients equals 1. The net growth rate of a biomass component at time t then equals the difference between the gross absolute growth rate G and the loss due to the loss rate of the living biomass D (Eq.5.3):

$$dW_i/dt = f_i G - D_i \qquad (5.3)$$

With	dW_i/dt	net dry matter increment of component i (g [DM tree^{-1}] y^{-1})
	f_i	partitioning coefficient (-)
	G	growth rate (g [DM tree^{-1}] y^{-1})
	D_i	loss rate (g [DM tree^{-1}] y^{-1})

Tree structure

Height growth (primary growth) was modelled as an external driving variable, independent of dry matter growth rate. Height growth was estimated using the Chapman-Richards equation (Eq.5.4): site quality is expressed by the value of parameter Si, whereas the values of the other regression constants are assumed independent of site quality.

$$h = Si * (1-e^{-c1*t})^{c2} \qquad (5.4)$$

With	h	current tree height (m)
	Si	site index i.e. tree height at infinite age (m)
	t	tree age (a)
	c_i	regression constants (-)

The regression constants are species-specific and were derived from Jansen et al. (1997). The first-order derivative of Equation 5.4 was used to calculate height increment during each time-step.

Turn-over and mortality

In the present model, the loss rate of the biomass components was assumed to be proportional to the amount of biomass. Estimates on sapwood turn-over were needed because of the relationship between sapwood and foliage area in the partitioning model. The longevity of the sapwood was estimated to amount 20 years in case of Douglas-fir (Mohren, 1987), and 100 years for beech (Hillis, 1987). The relative needle loss per age-class increases linearly with age after the year in which the needles were formed, hence the needle weight per age-class decreases exponentially (Mohren & Bartelink, 1990).

Natural tree death is induced by an unbalanced tree structure; the concept was based on the buckling theory of Niklas (1992). The relationship between stem diameter on the one hand, and tree height and crown silhouette area on the other (Niklas, 1992) was used to define critical levels of stem diameter. The critical level reflects the stem diameter necessary to mechanically support the crown. If the stem diameter (dbh) is lower than this critical level, the tree has an increased probability of dying. An additional mortality criterium is the height/diameter-ratio (h/dbh-ratio), which was added because of its application in forestry practice. Trees with a h/dbh-ratio higher than 150 were assumed to have an increased probability of wind-throw, i.e. they die after three years if the ratio remains that high.

Thinning

In COMMIX, three thinning types can be chosen: 1) a systematic thinning, 2) a thinning from below, and 3) a thinning from above. Carrying out a systematic thinning implies that every n^{th} tree or n^{th} row is cut, irrespective of the tree characteristics. To simulate the other two thinning types, the stand area was split up in a number of blocks; the number is determined by the stand density, such that each block contains 4 trees on average. Within each block, trees are selected that need to be cut, depending on the thinning rule and on the fraction of stand basal area to be removed: because tree number is a non-continuous variable, a threshold was used, stating that at least 90% of the planned thinning should be carried out. Note that this might cause simulation results to deviate from the yield table data. A thinning-from-below ('low thinning') results in the cutting of the trees having the smallest stem diameter. A thinning-from above ('crown thinning' or 'high thinning') implies that, in order to benefit the best trees, the strongest competitors should be removed: in the model, the second-largest trees (in terms of diameter) are cut when a high thinning is simulated. Apart from thinning type, also thinning frequency and intensity (in terms of basal area) have to be indicated.

Data requirements and output

The species-specific parameters are crown form, specific leaf area, leaf angle distribution, and coefficients for the allometric and functional relationships in the partitioning sub-model (see Bartelink, 1997b). Table 5.1 gives an overview. Tree parameters needed are stem coordinates, species, tree height, crown base height, crown shape, and leaf area. The tree leaf area density (LAD: m^2 foliage per m^3 crown volume) is calculated from total leaf area and crown dimensions, assuming a homogeneous spatial foliage area distribution. Grid input data consist of grid size and cell width.

Output consist of both tree and stand level data, on annual states and rates, in terms of biomass, basal area, and stem volume.

Table 5.1: Main species parameters in COMMIX. RLR is relative loss rate of biomass. Root/shoot ratio represents the fine-root/foliage ratio. Values of other parameters, used in the dry matter partitioning module, can be found in Bartelink (1997b). I_{mV} is productivity (mean annual volume increment), derived from the yield table (Jansen et al., 1996).

		Douglas-fir		beech	
parameter	unit	value	ref¹⁾	value	ref¹⁾
radiation use-effic.	g MJ^{-1}	1.1	Ba2	1.2	Ba2
root/shoot ratio	kg kg^{-1}	0.35	Ol, K&G	2.0	H&B
leaf angle distr.	-	spheric.	-	horiz.	-
specific leaf area	m^2 kg^{-1}	5.63	Ba	17.20	Ba
wood basic density	kg m^{-3}	450	Z&Z	550	Bu
crown form	-	cone	-	ellips	-
foliage age classes	-	5	-	1	-
sapwood rings	-	20	Mo	100	Hi
foliage loss coeff.	y^{-2}	0.20	Ba	1.00	-
branch RLR	y^{-1}	0.03	Mo	0.03	-
coarse root RLR	y^{-1}	0.03	Mo	0.03	-
fine root RLR	y^{-1}	0.75	K&G	0.75	K&G
sapwood RLR	y^{-1}	0.05	Mo	0.01	Hi
I_{mV}	m^3 ha^{-1} y^{-1}	16	JSF	10	JSF

[1)] Abbreviations for authors: Ba = Bartelink (1996a, 1997a), Ba2 = Bartelink et al. (1997), Bu = Burger (1950), Hi = Hillis (1987), H&B = Hendriks & Bianchi (1995), JSF = Jansen et al. (1996), K&G = Keyes & Grier (1981), Mo = Mohren (1987), Ol = Olsthoorn (1991), Z&Z = van der Zwan & van de Zee (1991).

Field data

To evaluate model performance, field data were used that were collected as part of long-term growth and yield research. Data were derived from both temporary and permanent field plots. Other field data, especially on biomass and radiation, have been used in previous studies to evaluate some of the sub-models of COMMIX. The partitioning sub-model was evaluated based on biomass studies in Douglas-fir and beech (Bartelink, 1996a, 1997ab). The performance of the radiation sub-model was investigated using transmission measurements in a number of stands (Bartelink, 1997c).

Model runs

To investigate model performance, COMMIX was first applied to simulate growth and yield of monospecies Douglas-fir and beech stands, respectively, and compared with existing yield tables (Jansen et al., 1996). The thinning regimes as included in the yield tables (in terms of basal area to be removed) were applied in the model runs. Table 5.1 summarizes the main state parameters, and Table 5.2 shows the initial values of the tree variables. In general, the thinning regimes in the yield tables can be qualified as low thinning, i.e. smaller and poor-quality trees are removed, thereby preventing the canopy to become too open (Jansen et al., 1996). In this study, results of simulations imposing a low thinning were compared with the yield table data.

Table 5.2: Tree components distinguished in the COMMIX model and the initial values of the tree variables. Biomass amounts are dry weights. Foliage area is one-sided, projected area. Tree diameter (dbh) is measured at breast height (1.30m above the forest floor).

tree characteristic	unit	name	Douglas	beech
tree age	y	-	20	20
foliage biomass	kg	W_s	8.00	0.75
branch biomass	kg	W_{br}	7.10	2.16
stem biomass	kg	W_s	48.90	7.70
fine-root biomass	kg	W_{fr}	2.80	1.50
coarse-root biomass	kg	W_{cr}	10.90	1.56
sapwood area	m^2	A_s	0.0110	0.0040
foliage area	m^2	A_f	45.0	12.9
stem diameter	cm	dbh	14.3	7.2
tree height	m	h	12.9	7.0
crown radius	m	CRAD	1.45	0.85
crown base height	m	HCB	5.5	0.5

A well-known experimental design in studies of forest productivity is the 'substitutive' design, generally referred to as 'replacement series' (Kelty, 1992; see also de Wit, 1960). The effects of combining two species in a replacement series are analyzed by comparing the yield of each species in mixture with its yield in monoculture (de Wit, 1960; Harper, 1977). Here, total wood volume productions of 50-year periods of growth were compared. Following the approach of Kelty (1992), for the mixture of Douglas-fir (D) and beech (B), a relative yield (RY) of each species, and a relative yield total (RYT) can be calculated by:

$$RY_D = Y_{Dmix} / Y_{Dmono} \tag{5.5}$$

$$RYT = RY_D + RY_B \tag{5.6}$$

With Y_{Dmix} Yield (stand basal area) of Douglas-fir in the mixture ($m^3\ ha^{-1}$)
Y_{Dmono} Yield (stand basal area) of a Douglas-fir monoculture ($m^3\ ha^{-1}$)
RY_D Relative yield of Douglas-fir

To study the effects of stand composition on stand development, COMMIX was run according to a number of scenarios which together built up such a replacement series. In a sequence of stand compositions, the share of one species was gradually increased, until the monospecies stand of species A was completely replaced by monospecies stand B (Table 5.3). This resulted in five individual-tree mixtures, differing in species shares. High thinning was applied in the stands, in accordance with current forestry practice. Thinning intensity was expressed as fraction of the standing basal area; the same fractions as used in the low thinning were applied (the 'default' thinning scenario).

To determine the effects of management on productivity, the scenarios described above were also used imposing two alternative thinning regimes; in the first one thinning in beech amounted half the original intensity (in terms of basal area), and in the second one beech was not thinned at all (only natural mortality occurred).

Both in case of the investigation of the model performance and of the scenario analyses, simulated stands were built up by 400 trees, in a 20*20 square. Initial planting distance was 2.5m in the monospecies Douglas-fir stand and in the 5 scenario stands, and 1.7m for the monospecies beech stand. Stand amounts were calculated based on the sizes of the inner 256 (16x16) trees, to prevent border effects; the outer tree row was not thinned at all for the same reason. The model was set to simulate 50 years of stand growth, from age 20 to 70.

Table 5.3: Description of the initial stand compositions of the different scenarios. Stand differences are expressed in terms of the share of the species in the stand basal area (BA). Note that, because beech at age 20 has a smaller dbh than Douglas-fir at age 20, the share of beech in terms of stem number (N) is higher than in terms of basal area.

scenario	Douglas-fir		beech	
	%BA	%N	%BA	%N
1	100	100	0	0
2	75	50	25	50
3	50	25	50	75
4	25	10	75	90
5	0	0	100	100

Results

Model performance

In Figure 5.4 the simulation results for monospecies stands are compared with the data from the yield tables. In case of Douglas-fir, yield table data fitted well to the results of the simulated low thinning in the first decades. Differences occurred between table and model in the second part of the trajectory: the higher model estimates values, however, are in accordance with remarks of Schoonderwoerd & Daamen (1995), who found that the yield table under-estimates growth rates in stands older than approximately 40 years.

The simulated beech stand initially grew faster than described by the yield table, but slowed down at higher ages. Remarkably, the simulated stand productivity decreased at higher ages, which could be attributed to the opening up of the canopy. Apparently, the thinning intensity indicated by the yield table is rather large compared to the estimated basal area increment. Both discrepancies are probably due to uncertainties in the data or to errors in the assumptions used to build the yield table; this table has largely been based on Swedish and German tables, because of the lack of permanent sample plots in the Netherlands (Jansen et al., 1996). Since the data and relationships used in COMMIX are based on local field data instead, this will cause discrepancies between yield table predictions and simulation estimates.

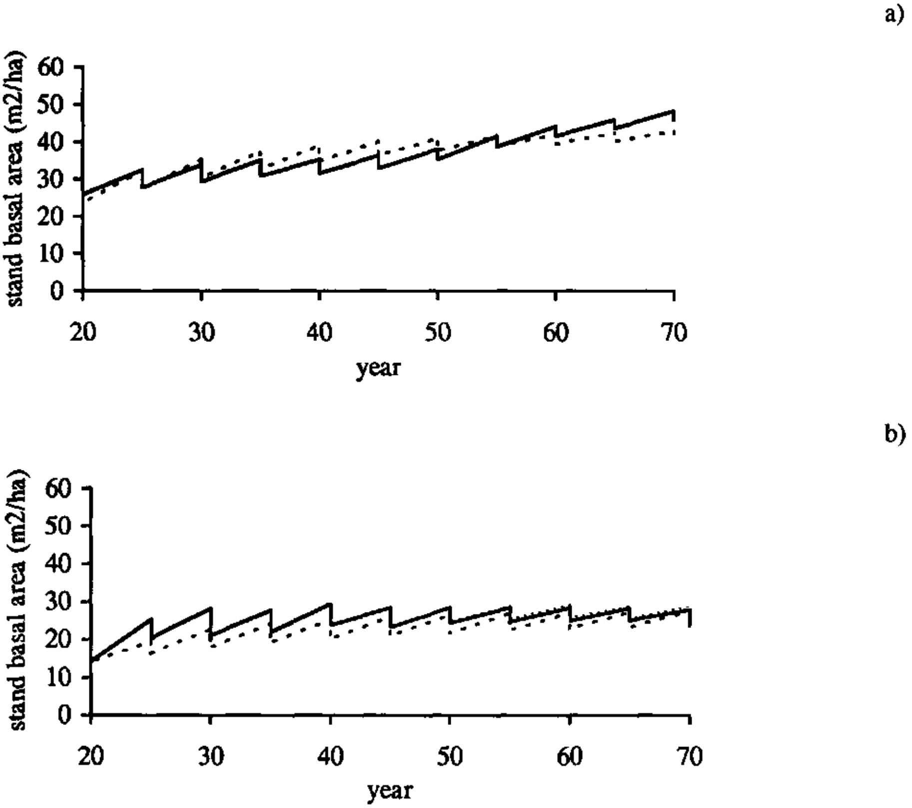


Figure 5.4: Temporal development of the stand basal area of monospecies stands: yield table data (solid line) compared with a simulated development assuming a low thinning (dotted line), for a) Douglas-fir, and b) beech. Yield tables were selected that best represent the productivities (in m^3 ha^{-1} y^{-1}) of the studied stands.

The initially low basal area presented by the yield table (see Fig.5.4) might be inaccurate: due to the lack of data, extrapolations were carried out, but a large uncertainty regarding the growth in the youth phase remains (Jansen, pers.comm.). It is remarkable that the basal area increment in the yield table is initially low (smaller slope of the line) compared to older ages; however, since growth rates are generally exponential, a faster growth rate would be expected. The decrease of the beech stand basal area after age 50 could be counterbalanced by lowering the thinning fraction; this implies that at higher ages the yield table over-estimates forest growth rate.

From the study of Schoonderwoerd & Daamen (1995) the variability of growth rates appears to be high for stands younger than 70 years; moreover, their study indicated that the yield table on average indeed over-estimates basal area increment (Jansen, pers.comm.).

Since overall simulation results agreed with the yield tables and because deviations could be attributed to uncertainties and errors in the tables, model performance was considered satisfying. COMMIX was thus applied to investigate the effects of stand composition and management on growth and yield, by simulating the replacement series.

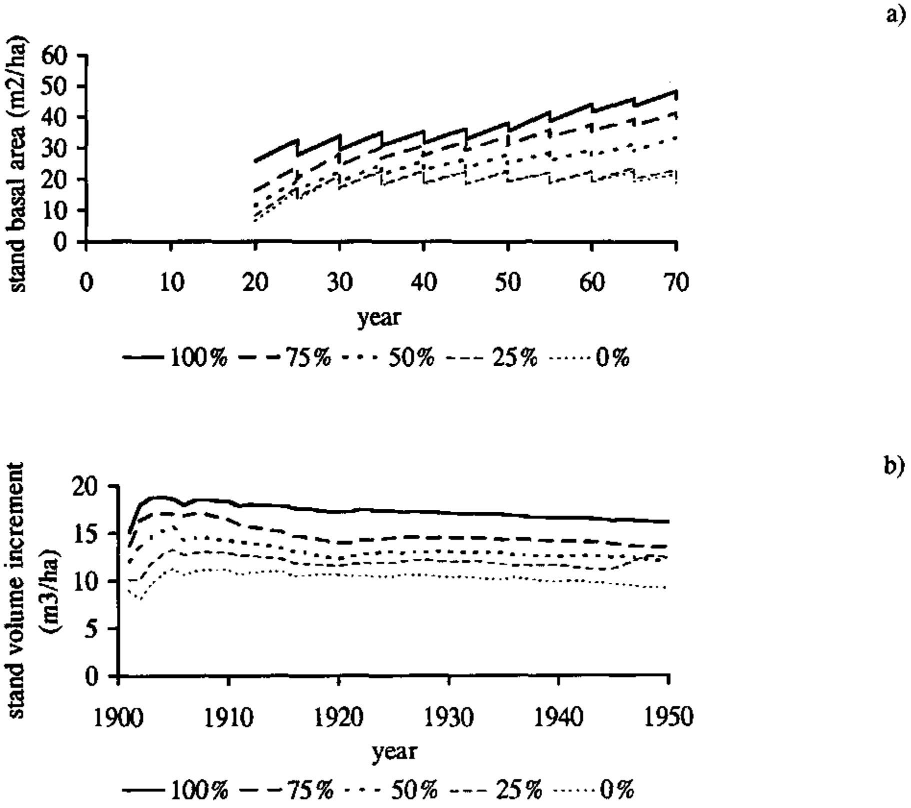


Figure 5.5: Modelled stand basal area development over time for the different simulated mixed stands. The legend indicates the basal area share of Douglas-fir at the start of the simulation: a) basal area development, b) basal area increment.

Results of the scenario study

The effects of stand composition on stand basal area development are presented in Figure 5.5a. Stand basal area was initially higher when the share of Douglas-fir was higher; the scenario study shows that, for the current thinning regimes, this difference was maintained during stand development. Fig.5.5b shows that volume increment was highest also in the stands containing the largest share of Douglas-fir. Absolute yields are presented in Figure 5.6.

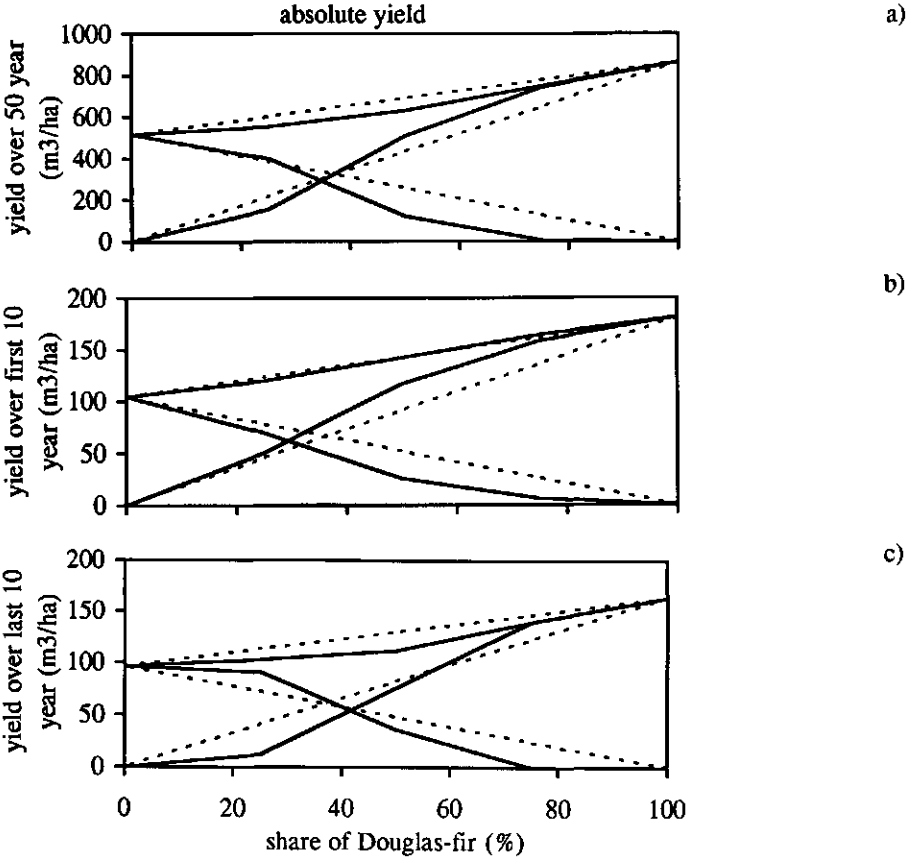


Figure 5.6: Estimated absolute yield over a fixed period of time for the stands of the scenario-study; thinning regime was equal to those applied in the monospecies stands of Douglas-fir and beech. Dashed lines represent expected yield if intra- and inter-specific interactions were equivalent. Solid lines represent model estimates. Stem volume production a) over a 50-year period, b) over the first decade, and c) over the last decade.

Considering the 50-year period, it appears that the productivity of the monospecies Douglas-fir stand is higher than both the beech and the mixed stands (Fig.5.6a). However, when the volume productions over the first (Fig.5.6b) and the last 10 years (Fig.5.6c) of the stand development are considered separately, it appears that initially a surplus value of the mixtures does exists in stands with a Douglas-fir basal area proportion higher than 50%, but that it disappears in the course of the stand development. The 'loss' of added value is partly due to the complete disappearance of beech in stands with high fractions of Douglas-fir. Fig.5.6a shows that in stands with a low proportion of Douglas-fir, the productivity of Douglas-fir is lower than could be expected from its basal area share in the mixture; in stands with more than 40% of Douglas-fir, the opposite is the case. The productivity of beech, in contrast, is lower than could be expected from its proportion of basal area, in almost any mixture. Fig.5.7, in addition, shows the absolute yields when no beeches in the mixed stands are thinned at all.

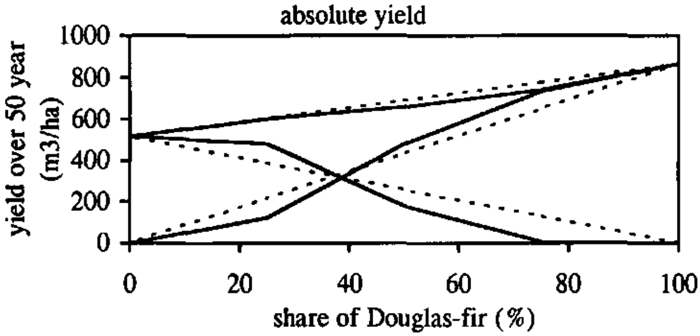
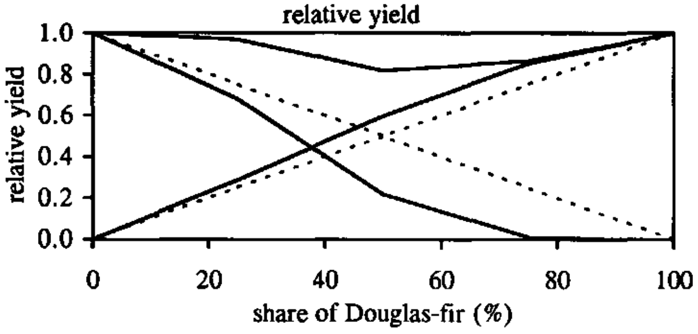


Figure 5.7: Estimated absolute yield for the stands of the scenario-studies in case of no thinning in beech. Dashed lines represent expected yield if intra- and inter-specific interactions were equivalent. Solid lines represent model estimates.

Figure 5.8 presents the relative yields (RY and RYT) of beech and Douglas-fir in the thinning scenarios. The scenario assuming a thinning intensity in beech equal to 50% of the default intensity is not presented, since these results were largely comparable with those of the no-thinning scenario. Obviously, thinning intensities in beech lower than the default thinning regime (copied from the yield table) result in an increased RYT in mixtures with a low proportion of Douglas-fir.

a)



b)

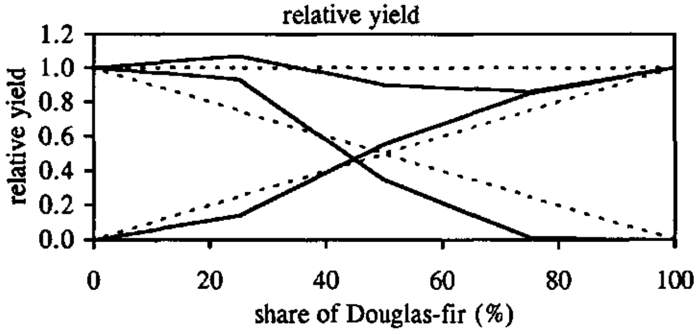


Figure 5.8: Estimated relative yield (RY) for the stands of the scenario-study, based on the stem volume production over a 50-year period, in case of a) the default thinning, b) no thinning in beech at all. Dashed lines represent expected yield if intra- and inter-specific interactions were equivalent. Solid lines represent model estimates.

In Fig.5.9 results of default thinning scenario's 2 and 4 are compared with field data on mixed stand basal area development. Field data were derived from Bartelink & Tünnissen (1996), and from Bartelink & Goudzwaard (unpublished). The stand composition in the research plots differed strongly in terms of basal area shares of the two species: the fraction of Douglas-fir varied between 30 and 85%. Although this variability can be expected to exaggerate differences in stand developments, the field data did not show a response to the proportion of (e.g.) Douglas-fir. Hence, no distinction was made here between field data from different stands. Fig.5.9 shows that the field data largely cover the simulated yield data, although in the field especially at young ages even larger basal areas are found.

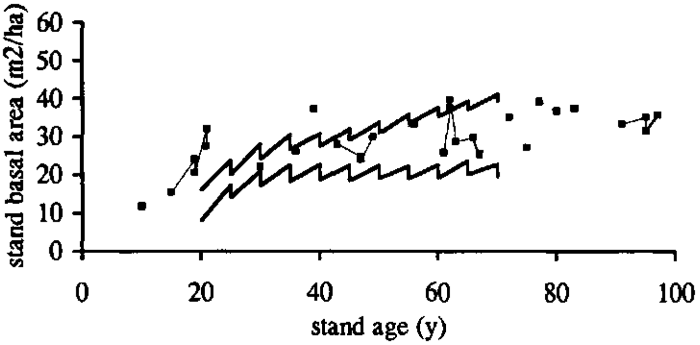


Figure 5.9: Comparison of scenario with field data on mixed stand basal area development. The upper line represents scenario 2, the lower line scenario 4. Connected symbols refer to total stand basal areas of the same stand. Data from Bartelink & Tünnissen (1996).

Discussion

Yield of mixtures versus monocultures

Two types of interactions between species have been identified that can cause yields in mixtures to exceed those in monocultures of the component species: 1) 'complementarity' in which species differences in height, crown form, rooting depth and phenology result in reduced competition and more complete use of a site's resources, 2) 'facilitation' in which the presence of one species directly benefits another (Kelty & Cameron, 1994). In the present study, complementarity is the most interesting feature, since competition for light is simulated. In forest studies, most evidence for the occurrence of complementarity comes from mixed stands with layered canopies which may intercept light more completely than canopies of a single species (Kelty & Cameron, 1994).

To compare the present simulations with field data from the literature, the restricted availability of data on Douglas-fir and beech mixtures makes it necessary to consider mixtures that are comparable with Douglas-fir/beech. Most suitable appear mixtures of beech with Norway spruce (*Picea abies*), and/or with fir (*Abies alba*). These type of mixtures can be expected to show stand dynamics comparable with the Douglas-fir/beech stands, because Douglas-fir, Norway spruce, and fir are all shade-tolerant, fast growing conifers, that cast deep shadows under their canopies.

Experience in central Europe has shown that a slight proportion of beech in spruce stands might increase the yield compared with spruce alone. Wiedemann (1950) and Assmann (1961) distinguished rich and poor soils. On the relatively rich soils, beech is able to run-up with the spruce; the yield of the mixture is equal to or lower than the yield of a monospecies spruce stand. On the relatively poor soils, beech remains in the lower part of the canopy without competing with the spruce; the productivity of the mixture can thus be larger than the yield of the monospecies spruce stand. Both Kennel (1965) and Zimmermann (1988) showed that the growth rate of spruce trees in mixed stands of spruce and beech is superior to the growth of spruce in pure stands, but that beeches in mixture with spruces are inferior to beeches in pure stands. Nusslein (1993), in accordance, found that a mixture containing 20-40% beech is most profitable in terms of wood production. Hladik & Dursky (1994) found the stand basal area in mixed stands of beech and spruce to be higher when the share of spruce was larger. Moreover, stand basal area of the mixture was always higher than that of monospecies beech, and also higher than monospecies spruce provided at least 60% of the basal area consisted of spruce. Bartelink & Tünnissen (1996) found the productivity of mixtures of beech and Douglas-fir to be generally higher than the yield of beech monocultures, but lower than those of Douglas-fir stands: in some cases, mixtures were found to be even more productive than pure Douglas-fir stands.

The general performance of mixed stands of spruce/fir and beech appearing from these studies is that, although on some sites the productivity of a mixture might slightly exceed the yield of a monospecies stand (but only when the proportion of the most productive species is not too low), the yield of the mixture will generally be somewhere in between the yield levels of the two monocultures (Kelty, 1992). These findings agree with results from the present simulation study. Referring to Fig.5.8, some of the presented mixtures seem to be more productive than the sum of the species' productivities (weighed using the basal area proportions) as well as than the monospecies Douglas-fir stand (Fig.5.8b). However, apart from relative yields, absolute values should be compared to identify the highest yielding stand in the experimental series: if one of the species is much more productive in monoculture than the other, the mixture can have a RYT exceeding 1.0, and yet not exceed the yield of the more productive species in monoculture (Kelty, 1992). Fig.5.7 shows the absolute yields when no thinning is carried out in the beech. It appears that, although RYT exceeds 1.0 in some mixtures, absolute yield is lower, implying that the productivity of all simulated stands is somewhere in between the productivities of monospecies stands of the contributing species. The productivity of a mixed stand of Douglas-fir and beech will not exceed the yield of a monospecies Douglas-fir stand; mixing the two species does hence not result in a more efficient use of the resources.

In order to have an effect on total yields in mixed stands, resource partitioning must involve those resources that are limiting tree growth on a particular site: thus, it would be expected that canopy stratification would have greatest effects in areas with ample growing season precipitation and soil nutrient levels, where light capture is the principal limiting factor (Kelty & Cameron, 1994). In the present situation, however, this is not the case; both the biomass data used to build the partitioning model, and the growth and yield data were derived from stands growing on sandy soils with deep water tables. It is likely that not only light but water too is a limiting factor on these sites. This shortage might camouflage a complementary effect with respect to radiation interception.

In case of complementarity, a fine-grained spatial pattern (e.g. tree-by-tree mixture) would be necessary to maximize the opportunity for optimal use of resources (Kelty & Cameron, 1994). The present results, however, do not confirm the occurrence of complementarity. To avoid the complete suppression of one of the contributing species (i.e. the beech), the trees could be planted in species groups; such a coarse-grained mixture would enable a species that has less competitive power, to remain part of the stand.

Modelling mixed species stands

From Figure 5.6-5.8 it appears that the yield of the mixtures was not linearly related to the basal area fraction of Douglas-fir present at the start of the simulations. Simply combining two yield tables, e.g. based on the fractions of the species present, will thus result in biased estimates of the yield of mixed stands. This stresses the necessity of using mechanistic approaches when predicting mixed stand development in relation to resource availability and/or management regimes.

The COMMIX mixed forest model was able to reproduce the development of monospecies stands as well as of mixed-species stands of Douglas-fir and beech. However, when simulating monospecies beech stands, it appeared that crown dynamics play a crucial role in stand growth and development. In mixed stands, timing and intensity of thinnings as well as the spatial distribution of the thinned trees will strongly affect the quality and composition of the growing stock (Solomon & Leak, 1994; Pretzsch, 1995). Both height growth (Opdahl, 1994) and horizontal crown expansion (Pretzsch, 1995), for example, are affected by stand structure and composition. When building a simulation model of mixed forest growth, much emphasis should thus be put on individual tree responses to resource availability. Moreover, species differences in phenology (e.g. timing of bud burst and leaf development) cause a temporal separation of light interception, which strongly affects competitive interrelationships (Kramer, 1996). Especially regarding the unknown responses of forests to climate change, including phenological aspects would increase the applicability of such a model.

In follow-up studies, COMMIX will be extended and used to estimate growth and yield for a wide range of mixed stands, among which Douglas-fir beech mixtures, by simulating different stand origins, species' shares, planting patterns, thinning regimes, and site conditions, in order to study stand dynamics and effects of human impacts, and ultimately to support the decision-making in forest management. The mechanistic approach enables to investigate the effects of thinnings on growth and yield, and to estimate responses to alternative silvicultural treatments in, from a growth and yield view-point, rather unknown forest ecosystems.

Chapter 6: Discussion and conclusions

6.1 Reflections on the approach

General

The aim of this research project was to analyse the effects of stand composition and forest management on growth and yield of mixed species forest stands, using a process-oriented model of forest growth. The main assumptions underlying the modelling approach were that radiation plays a key role in tree growth and forest development, and that (mixed) stand development can be described by quantifying the competition for radiation. Keddy (1989) defined 'competition' as:

> .. the negative effects which one organism has upon another by consuming, or controlling access to, a resource that is limited in availability.

In a forest stand, a tree's rate of success in obtaining scarce resources will be dependent on tree dimensions and stand structure.

As noted in Chapter 1, early mechanistic simulation models were stand-level approaches, describing relatively simple agro-ecosystems (even-aged, homogeneous, short-lived), and using elementary descriptions of the radiation regime and the water and nutrient availability (e.g. de Wit & Goudriaan, 1978). They ignored competition for resources. Stand-level modelling proved to be a suitable approach for such ecosystems. In order to simulate mixed stands too, in the last decade simulation modelling has moved towards stand-models that differentiate between species and are applicable to mixed crops (e.g. Kropff & van Laar, 1994) and mixed forest stands (Kramer, 1996). In complex systems like mixed forests, however, tree-level models will be necessary to account for competition: the differing characteristics of the species and the spatial distribution of the trees have a different and in most cases a much stronger impact on stand development than in is the case in monospecies forest stands. The descriptions of tree-to-tree interactions are thus necessary to provide reliable estimates of stand development.

As explained in Chapter 1, the development of the present simulation model COMMIX (COMpetition in MIXtures) was based on the following assumptions:

1. Radiation plays a key role in growth, and competition for radiation among trees determines stand development.
2. Dry matter production of a tree is related to the radiation it absorbs, and can be described by the radiation-use efficiency concept.
3. Partitioning of the dry matter growth over the biomass components is dependent both on tree state and on growing conditions, and is largely determined by the efforts of a tree to maintain its structural balances and its morphological growth pattern.

conditions. Soil conditions, for example, can be expected to strongly affect partitioning. In relatively poor soils, both the fine-root turn-over and the root-shoot ratio will be high; as a consequence, up to 80% of the available assimilates may go to the fine roots (Santantonio & Hermann, 1985). The main advantage of the present approach is that internal and external conditions that affect partitioning can be taken into account. A second advantage is that no respiration data are needed: the calculation of respiratory costs is one of the major pitfalls of mechanistic models (cf Cannell & Dewar, 1994).

Though the current partitioning model is useful, it could be extended and improved. A first point of concern is that in the model, tree height growth follows a predescribed pattern, being dependent only on species and site conditions. A better approach would be to relate height growth to resource availability, or to use site and growing conditions to describe height growth patterns over time (e.g. Kahn, 1994). However, the significance of height growth for a tree's survival is probably not in its contribution to the internal balance of growth, but rather to the tree's ability to compete for light and space (Mäkelä, 1986). Differences in height growth have a large impact on the intra- and inter-competitive interrelations in mixed stands. A better concept for height growth will be required to improve the confidence in model predictions (cf Lavigne, 1992).

The root-shoot ratio is another possible shortcoming in the present model. Plant nutrient status is probably the most important factor associated with carbon allocation; this feedback should thus be included in allocation models (Ågren & Wikström, 1993). The calculations with the present model showed that the ratio has a strong impact on partitioning in general, which is why reliable data on roots and shoots are needed to parameterize the model. However, there is the problem of quantifying the impact of site and growing conditions on allocation or partitioning. A number of links between partitioning and resource availability were established in the present model (e.g. through the root-shoot ratio and the incorporation of height in allometric relationships with dbh), but pipe-model ratios, basic wood densities, and allometric relationships will clearly also be affected by resource availabilities.

A third challenge is to incorporate structural mechanical principles. The structural theory for cantilever beams and the constant stress hypothesis would be especially useful for calculating the amount of growth to be partitioned to structural tissues (cf Cannell & Dewar, 1994).

Simulation of stand development

The COMMIX mixed forest model was able to reproduce the development of monospecies and mixed-species stands of Douglas-fir and beech. The research showed that a detailed description of the competition for radiation is necessary to simulate growth and development of (mixed) forest stands.

Using radiation availability as a measure of competitive status and growth rate is very appropriate for forestry practice: light availability (or canopy closure) is a very important criterium criterion for the forest manager when deciding about operations like thinnings. Although competition is currently expressed in terms of radiation availability only, this may also represent the tree's overall competitiveness: assuming a structural balance between the above- and below-ground tree parts implies that a tree's ability to intercept radiation reflects its below-ground competitiveness. For instance, the nutrient and water availability (below-ground competitiveness) will be reflected in above-ground crown characteristics like crown dimension and leaf area, and hence affect light interception.

To sum up: this research has shown that it is possible to describe competition by quantifying radiation availability using a spatial, mechanistic model of radiation interception. Because the concept is tree-based, it is suitable to simulate both even-aged and uneven-aged forest stands, and to estimate radiation availability for natural regeneration.

6.2 Mixed forest dynamics

Interactions in mixed stands

Mixed stands are widely believed to be potentially more productive than monospecies stands. Two types of positive interactions have been identified that might cause yields in mixtures to exceed those in monocultures of the component species (Kelty & Cameron, 1994):

1) 'complementarity' or 'competitive reduction', in which species differences in height, crown form, rooting depth and/or phenology result in a reduced competition and a more complete use of a site's resources,

2) 'facilitation' in which the presence of one species directly benefits another (symbiosis).

In studies on mixed forests, most of the evidence for the occurrence of complementarity has come from radiation absorption (Kelty, 1992). For example, stands consisting of a sun-adapted species that forms the overstorey with a shade-tolerant species that can survive in the sub-canopy layer might be able to absorb more PAR than monospecies stands. Evidence for complementarity in terms of other resources is scarce; it seem probable, however, that differences in rooting depth, for example, will increase the use of the soil resources.

Facilitation, on the other hand, principally functions through an increased availability of nutrients (Kelty, 1992). Binkley (1992), for instance, showed that mixing N_2-fixing species and non-N_2-fixing species resulted in significantly higher yields in mixed stands on relatively N_2-poor soils, because the litter from the N_2-fixing species contained more N_2 and decomposed faster. Morgan et al. (1992) concluded that differences in rooting patterns among species and differential mycorrhizal associations create conditions for enhanced availability of mineral N in mixed stands.

In this way, the yield of mixed stands can exceed the yields of the monospecies stands of the component species, for example:
- on rich soils, where the combination of shade-tolerant with sun-adapted species might create a multi-layered canopy, which will result in a greater radiation interception,
- on poor soils, where the incorporation of N-fixing species might increase productivity.

In most situations, however, the yield of the mixture will be somewhere in between the yield of the monocultures of the less productive and the most productive species, because the growing conditions are not optimal for both species (Burkhart & Tham, 1992), there are differences in height growth patterns (Kerr et al., 1992), or the species' shade tolerance is inappropriate for the situation (Kelty, 1992). For the present situation, i.e. Douglas-fir/beech mixtures growing on intermediate sites, hence no effect of mixing on stand productivity can be expected: both species tolerate shade or semi-shade, but water and nutrients were scarce (which excludes complementary), and facilitation was lacking.

Remarks on the case study: even-aged Douglas-fir/beech stands

Main reasons for choosing the even-aged Douglas-fir/beech stand for the case study were:
1) it is a relative simple system, compared to the uneven-aged mixed stand, and therefor suitable to start modelling with,
2) the data from permanent sample plots were available.

The present case-study, i.e. an even-aged mixture of Douglas-fir and beech, represents a rather artificial mixed stand type. Many natural forests consist of a mixture of species and ages (e.g. tropical rain forests), whereas other forest ecosystems are monospecific and virtually even-aged due to large-scale disturbances (e.g. boreal spruce forests). Though some examples of even-aged mixed-species stands occur, many stands of this type are artefacts, originating from forest operations (Smith, 1992), and probably the only way to maintain such mixtures is by permanently interfering in the stand development. The difference in height growth strategies is a serious problem: when species have comparable shade tolerance they must have similar height growth rates to avoid one suppressing the other (Kerr et al., 1992). The stratified canopy structure in mixtures tends to develop because the juveniles of sun-adapted species generally grow faster than shade-tolerant juveniles (Kelty, 1992; Smith, 1992).

Simulating stands of Douglas-fir and beech

The present simulation showed that competition between the species in the mixture generally resulted in a yield lower than the yield of a monoculture of the more productive species, the Douglas-fir. This might be because although both species are shade-tolerant (to a certain extent), there was heavy shading, which hampered the development of a sub-canopy layer. Moreover, to have a complementary effect of mixing species on stand yields, other resources (water, nutrients) have to be non-limiting (Kelty & Cameron, 1994): complementarity might have been hampered because competition for water and nutrients is likely to occur in the forest areas studied.

The simulation of mixed-stands of Douglas-fir and beech also revealed that the yield of a mixture was not linearly related to the initial basal area proportions of the contributing species. Simply combining two yield tables, e.g. based on the basal area fractions of the species present, will thus result in biased estimates of the yield of mixed stands.

The results presented in Chapter 5 indicate that when growing mixed stands of Douglas-fir and beech, the latter species might disappear from the system completely because of competition from Douglas-fir. In the case of uneven-aged conditions, competition pressure would be more variable within the stand, and some beeches would probably be able to survive. Clearly, the competitive interrelations will also depend on the spatial distribution of the species: the survival chance of beech can be expected to be higher when beech occurs in patches than when the stand is a tree-to-tree mixture.

In the case of Douglas-fir and beech, the maintenance of a mixed stand appeared to conflict with the maximization of wood production.

6.3 Model applications

In Western Europe, nowadays much attention is currently being paid to mixed forest management, to the natural conversion of monospecies stands, and to the natural regeneration of forests. This increased interest parallels the development of the 'close-to-nature' forestry in Europe, which involves forest managers trying to make more use of spontaneous processes. The Pro-Silva concept is an example of this movement (e.g. Zwart, 1992). The emphasis in forest operations has shifted from the stand towards the tree or tree group. As a consequence, to successfully manipulate forest development, decisions have to be taken on a much smaller scale (e.g. the tree) than in case of monospecies stands (the stand). This has encouraged the development and application of selection-forestry techniques such as single-tree harvesting.

The large variety of possible species mixtures, coupled with the range of environmental conditions under which mixtures might be grown and the different potential management regimes, make an empirical approach to estimate growth and development impracticable. In contrast, mechanistic models, quantify relationships between growing conditions, tree growth, and forest development in a more general way. Models like COMMIX provide insight into the dynamic processes of mixed stands, and enable forest managers to find out the consequences of their decisions in terms of growth, yield, and stand development.

6.4 Conclusions

The aim of the research project was to analyse the effects of stand composition and forest management on growth and yield of mixed species forest stands, using a process-oriented tree-level model of forest growth. The following conclusions are drawn, in relation to the research questions presented in Chapter 1:

1) Radiation interception by forest trees
In dense stands with a closed and homogeneous canopy, tree leaf area is closely related to radiation absorption (APAR); in the case of a heterogeneous non-closed canopy, however, locations of the trees and dimensions of the crowns strongly affect APAR. Grouping of foliage into individual crowns results in a considerable decrease in the interception of radiation per unit leaf area, implying that a spatial model is needed to estimate radiation absorption by individual forest trees.

2) Relationship between intercepted radiation and dry matter growth
The study revealed that RUE estimates can be derived from detailed eco-physiological process-models. Estimated RUE values can be used to estimate growth in models of (mixed) forest productivity.

3) Dry matter distribution
Assuming stable growing conditions, this research found the dry matter partitioning over the tree components to be rather constant. This suggests that the elementary approach of an annually fixed dry matter partitioning key might work well in mechanistic stand models. However, a dynamic approach is needed to account for effects of changing growing conditions. The partitioning model developed in this study, which includes feedback mechanisms between growing conditions and plant state, appears to be a suitable concept.

4) Mixed stand growth and development
The productivity of most mixed forest stands is generally somewhere in between the yield levels of the monocultures of the less productive and the most productive species. It will only be possible to achieve higher yields in mixed stands if these stands have a relatively small proportion of the sub-dominant species. In mixed stands of Douglas-fir and beech, Douglas-fir has the strongest competitive power, mainly due to its faster height growth. To maintain beech in a mixture with Douglas-fir, the proportion of Douglas-fir has to be reduced, resulting in a productivity being lower than that of the monospecific Douglas-fir stand: it is therefore difficult to reconcile the maintenance of a mixed stand with the maximization of wood production.

The present mechanistic approach appears to be promising to estimate the development of mixed forest stands and to quantify the impact of forest operations like thinnings on competitive interrelations and forest dynamics. The large variety of possible species mixtures, coupled with the range of environmental conditions under which mixtures might be grown, necessitates a mechanistic modelling approach based on underlying processes and emphasises the potential use of such models. Also of great importance, however, is the availability of suitable biomass data. Though data on stem dimensions can be derived from long-term research plots, data on other biomass components are less abundant. The collection of such data is important for building models and for evaluating their performance.

In follow-up studies, COMMIX will be extended and used to estimate growth and yield for a wide range of mixed stands by simulating different stand origins, species' shares, planting patterns, thinning regimes, and site conditions, in order to study stand dynamics and effects of human impacts, and ultimately to support the decision-making in forest management. The model's mechanistic approach enables the effects of thinnings on growth and yield to be investigated, and responses to be estimated of alternative silvicultural treatments in forest ecosystems whose growth and yield potential is largely unknown.

6.5 Recommendations

Data

For model predictions to become more accurate and valid under future conditions data are needed for calibration and for evaluating model performance. Traditional forest growth and yield research is an important data source: many data from long-term permanent field plots are available in Western Europe. Although they refer to monospecific, even-aged stands, these data are very useful for evaluating the performance of simulation models. They should therefore be made more accessible, for example by setting up common data bases. The major drawback of these data, however, is that they refer to the stem component only. Biomass data from other biomass components are also needed, both from above-ground and below-ground tree components. Especially the availability of data on roots is very restricted and needs serious attention.

Finally, data from forest reserves could be used; although forest management does not play a role in these areas, the data provide information on spontaneous forest dynamics, which could be used to test model performance.

Modelling

The present modelling approach is part of an ongoing development of models for mixed forest stands. For future applications, several aspects of COMMIX could be improved and extended. These are discussed below.

Species differences in phenology (e.g. timing of bud burst and leaf development) cause a temporal separation of light interception, which greatly affects competitive interrelationships (Kramer, 1995). Including phenological aspects would increase the applicability of such a model to the effects of climate change on forest growth.

Crown dynamics play a crucial role when modelling tree-to-tree interactions because crown size and position in the canopy together determine the tree's ability to intercept light. In turn, both height growth (Opdahl, 1994) and horizontal crown expansion (Pretzsch, 1995) are affected by stand structure and composition. When building a simulation model of mixed forest growth, much emphasis should thus be put on individual tree (crown) responses to resource availability. In COMMIX, an elementary approach was used to describe crown dynamics. A more mechanistic model could be built using mechanical relationships, i.e. assuming a structural balance between crown size, tree height, and stem diameter (see Niklas, 1992).

Mechanical relationships like the structural theory for cantilever beams and the constant stress hypothesis (Niklas, 1992) also form promising concepts when partitioning is simulated (Cannell & Dewar, 1994). The incorporation of mechanical relationships would optimize the functional link between growing conditions and growth partitioning.

In the past 20 years, the recognition of the importance of natural regeneration as a tool supporting forest management has increased considerably. It is now acknowledged that, when simulating the conversion of monospecies stands, or the regeneration of mixed stands, the process of natural regeneration should be incorporated in the model. Some models already take this process into account, e.g. the HYBRID gapmodel of Friend et al. (1993), and the SILVA2 model of Pretzsch (1992). The present study focused on the simulation of even-aged stands, ignoring regeneration. However, it would be relatively easy to quantify the growing conditions for regeneration because COMMIX already simulated light in detail. Incorporating this process in COMMIX would make the model suitable for simulating natural forest dynamics for a range of mixed stand types and under different management regimes.

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Summary

Introduction

Background

Without human interference, the largest part of Western Europe would be covered by mixed forests. Centuries of human activities, however, have resulted in huge changes in the structure and composition of the forests, and in much woodland being converted into agricultural land. In the 19th century and the first half of the 20th century, some of the former forest area was reforested with even-aged, monospecific stands, in order to produce wood on a regular basis. As a result, by the mid-20th century, much of the managed forest area in Western Europe consisted of even-aged, monospecific stands. Since then there has been a reaction against man-made monocultures, resulting in a move back to natural mixed forests which has lead to an increasing area of mixed-species stands. The main reasons for this move are: 1) mixed stands are believed to be closer to natural forests than single-species stands, and therefore to be more resistant to storms and less susceptible to insect attacks and diseases, 2) in terms of economics, mixed forests may mean a spread of financial risks, as fluctuations in the wood market can be accommodated much more easily, 3) exploiting spontaneous processes such as natural regeneration saves forest managers much money, and 4) mixed stands are preferred for reasons of amenity and biodiversity.

For a long time, the emphasis in silviculture in Western Europe was solely on even-aged, monospecific stands; many empirical stand-level growth models were developed and successfully used for managing such stands. In contrast, no generally accepted growth and yield approach has emerged so far for mixed forests. Moreover, the inexhaustible number of species combinations, management regimes, and site-dependent interactions make an empirical approach less suitable. In fact, a mechanistic model would be more suitable, because the reliability such a model depends more on the state of knowledge of physiological processes and responses to the growing conditions of the species involved than on a statistical fit to a particular set of empirical data.

Aim of the research and the questions posed

The aim of the present study was to analyse the effects of stand composition and forest management on the growth and yield of mixed species stands, using a process-oriented model of forest growth. It was intended that the results would benefit taking decisions about mixed forest stands, and support the research on mixed stand dynamics. The following research questions were therefore defined:

1. How is radiation interception by forest trees affected by a) crown size and dimension, and b) stand structure and composition?
2. What is the relationship between the amount of intercepted radiation and the growth rate of a tree (in terms of dry matter)?
3. How is growth (dry matter) distributed over the tree biomass components?
4. What are the effects of management treatments on mixed stand growth and development?

Prior to the modelling, biomass studies were carried out to establish relationships between tree components and to provide data to initialize the model.

Methodology

Modelling framework

A modelling approach that relates the growth of individual trees to their resource availability was chosen to analyse growth and yield of mixed stands. In this approach, competition between trees is quantified in terms of radiation availability. The COMMIX (COMpetition in MIXtures) simulation model was developed on the basis of three main assumptions:

1. Radiation plays a key role in growth: the radiation absorbed by a tree will strongly determine its growth rate, and competition for radiation among stand members will determine stand development.
2. Dry matter production of a tree is related to the radiation it absorbs, according to the radiation-use efficiency concept.
3. Partitioning of the dry matter growth over the biomass components is dependent both on tree state and on growing conditions, and is largely determined by the tree's attempts to maintain its structural balances.

Biomass studies were carried out to establish the relationships between tree components and to provide data to initialize the model.

Study sites and species

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and Common beech (*Fagus sylvatica* L.) were used in this research. Beech is an indigenous and commercially important species in the Netherlands and in a large part of north-western Europe. Douglas-fir, which was introduced in the Netherlands at the end of the 19th century, is the most important coniferous species after Scots pine in commercial terms. Mostly grown in large monospecific areas, Douglas-fir has occasionally been mixed, especially with Japanese larch, Norway spruce, and/or beech. Studying the Douglas-fir/beech mixture had extremely important methodological implications because it yielded a general idea of the interactions between coniferous and broadleaved species growing in mixed stands.

All the stands investigated were growing on well-drained, acid brown podsolic soils in ice-pushed preglacial deposits with deep water tables (>4m below surface). According to the yield tables, the sites were suitable or very suitable for both species, resulting in an estimated maximum mean annual stand volume increment (MMAI) of 14-16 m^3 ha^{-1} a^{-1} in the case of Douglas-fir, and 10-12 m^3 ha^{-1} a^{-1} for beech.

Biomass studies

Two biomass studies were carried out, on Douglas-fir and beech respectively, at the start of the research project, to establish allometric relationships among tree components, describe the above-ground dry matter distribution, and analyse the relationship between water transporting stem tissue (sapwood) and foliage area. This entailed sampling 23 Douglas-fir trees out of 4 stands and 38 beeches out of 6 stands.

Strong stand-independent correlations were found between stem and crown dimensions. Specific leaf area decreased with needle ageing and increased from tree top to crown base. Foliage area was linearly correlated with sapwood cross-sectional area at breast height in Douglas-fir, and with stem basal area at breast height in beech. The results of these biomass studies were used to initialize COMMIX, and to build a module of dry matter partitioning.

Simulating radiation interception by forest trees

The growth of a tree is dependent on the amount of absorbed radiation. The spatial model FORFLUX2 was developed to determine the role of crown characteristics on the absorption of photosynthetically active radiation (PAR) by individual forest trees and to analyse the effects of stand density and foliage clustering on transmission. The model's performance appeared to be accurate: simulated transmission patterns were largely comparable with field measurements. Analysis showed that PAR absorption by trees (APAR) is closely related to tree leaf area in closed canopy stands, but that this relationship is less clear in the open stand, indicating that in heterogeneous canopies spatial information on tree position and crown dimensions will strongly affect absorption by individuals. Analysis of the role of stand structure and density on the extinction-coefficient (K) showed that when the canopy is assumed to be horizontally homogeneous, K is generally overestimated because the foliage clusters around shoots and in individual crowns. This overestimation also depends on stand density: K increased with increasing LAI (leaf area index).

From this study it was concluded that a spatial radiation approach is necessary when estimating APAR in non-closed or heterogeneous canopies. FORFLUX2 is suitable for simulating the growth and development of mixed stands, because it enables the growing conditions of individual trees in the forest canopy to be taken into account. The radiation module was therefore incorporated into COMMIX.

Radiation-use efficiency (RUE)

The estimated amount of APAR can be used to calculate the growth rate of a tree. In this study, the 'radiation-use efficiency' (RUE) concept was adopted: a close relationship between APAR and dry matter production was assumed, thus circumventing the need for data on respiration, which are difficult to collect. The mechanistic forest growth model FORGRO was applied 1) to determine the suitability of applying the concept, 2) to investigate differences between RUE of beech and Douglas-fir, and 3) to analyse the effects of stand structure and stand composition on RUE in mixed species forest stands. Note that RUE was calculated using PAR: these RUE values were approximately double the RUE based on global radiation.

First, the net primary production (NPP) under optimum growing conditions was calculated using FORGRO. Comparing simulations with NPP data from literature revealed that FORGRO provided reliable estimates. FORGRO was therefore applied to estimate RUE for a range of scenarios. A sensitivity analysis showed that RUE is relatively insensitive to changes in photosynthetic parameters such as the maximum photosynthesis rate. Temperature had some effect: this lead to the hypothesis that species-specific responses to temperature affect competitive interrelationships if there is climate change.

Though RUE showed large daily variability, the RUE derived from cumulative absorbed photosynthetically active radiation (APAR) and NPP was virtually constant throughout the year and over a 10-year period, in both monospecific and mixed stands. It was thus concluded that the RUE is a useful concept for estimating dry matter production from absorbed radiation (APAR) by forest trees, and the concept was applied in COMMIX.

Partitioning of the dry matter

Having calculated the tree growth rate, the next step was to allocate the growth, either in terms of assimilates (allocation) or dry matter (partitioning). The existing theoretical concepts on allocation and partitioning include many unknown parameters. Many growth models therefore use descriptive keys, representing proportions of the carbohydrates or the dry matter that should go to a certain plant component. Because in COMMIX growth is expressed as dry matter increment (calculated using APAR and RUE), this study focused on partitioning of dry matter.

To be able to relate growing conditions to the partitioning pattern in Douglas-fir and beech, a model was developed that describes the dynamic partitioning of dry matter in individual trees. The model estimates the fractions of the total available dry matter that should go to certain plant parts, based on the concept of structural balances: both mechanistic and allometric relationships between tree components form conditions for the partitioning. The effects of dominance position, site conditions, and thinnings on the partitioning of growth were calculated.

First, model estimates of the temporal development of the stem diameter were compared with yield table data. The partitioning model appeared to perform well and was therefore applied in a scenario-study.

The results of the simulation runs showed that the partitioning of the annual total dry matter growth gradually changed with tree age: the changes were small, especially after age 20. Trees of average size (with respect to dbh) invested relatively more dry matter in the branches and less in the stem than suppressed trees did. Douglas-fir invested relatively more dry matter in its foliage, especially at the cost of the branch and stem components. Analysis of the effects of thinning revealed that a discontinuous reduction of stem number results in a gradual decrease in partitioning to the stem. The most obvious response to thinning consists of a sharp decrease in partitioning to fine roots and foliage and in an extra investment in the branches. Diameter growth appeared to be relatively constant: diameter will thus increase approximately linearly with time.

Because temporal changes in the dry matter partitioning were small, an elementary fixed partitioning key might work well in crop and forest growth models. However, to account for effects of changing growing conditions on the partitioning, a mechanistic and dynamic approach is needed. The study showed that the current partitioning approach is able to reproduce the development of an individual forest tree over time, both in terms of dbh and biomass. The approach was thus considered very suitable for modelling the effects of between-tree competition for resources on growth and development of (mixed) forest stands, and was therefore incorporated into COMMIX.

Simulating mixed stand growth

The biomass studies mentioned previously provided the research project with data to initialize COMMIX and to evaluate the radiation module, and with allometric and functional relationships for building the partitioning module. The three modules (on radiation, RUE, and partitioning, respectively) together built up the main model framework of COMMIX. Several other modules were added, e.g. those accounting for natural mortality and for thinning regimes.

Prior to scenario analyses, COMMIX was validated by being used to simulate growth of monospecific Douglas-fir and beech stands, respectively. It performed satisfactorily: some differences occurred when simulating beech monocultures, but these could be attributed to inaccuracies in the yield tables. The estimated productivity of older Douglas-fir stands was somewhat higher that the yield table data, due to underestimations of the table.

The next step was to apply COMMIX to compare growth and yield of mixed stands with monospecific stands, and to estimate the effects of management on growth and yield. A number of model stands that together made up a replacement series, were used to investigate model responses. Simulation results showed that initially there was a surplus yield in mixtures in which Douglas-fir made up over half of the basal area, but that this disappeared in the course of the stand development. The 'loss' of added value was partly attributed to the complete disappearance of beech in stands with high proportions of Douglas-fir. In stands with a low proportion of Douglas-fir, the productivity of Douglas-fir was lower than could be expected from its share of the basal area; in stands with more than 40% of Douglas-fir, the opposite was the case. The productivity of beech, in contrast, was lower than could be expected from its proportion of basal area, in almost any mixture. Thinning had a strong impact on growth and yield: thinning intensities in beech lower than the default thinning regime (copied from the yield table) resulted in an increased total relative yield (RYT) in mixtures with a low proportion of Douglas-fir. Although RYT exceeded 1.0 in some mixtures, absolute yield was always lower, implying that the productivity of the simulated stands was somewhere in between the productivities of monospecific stands of the contributing species. This led to the conclusion that growing mixed stands of Douglas-fir and beech will not result in a more efficient use of the available radiation.

Conclusions

The following conclusions are drawn in relation to the four research questions presented in Chapter 1:

1) Radiation interception by forest trees

In the case of a heterogeneous canopy, such as in mixed stands, foliage distribution, dimensions of the crowns, and clustering of foliage, strongly affect APAR. Therefore, a spatial model is needed to quantify competition for radiation and to estimate radiation absorption by individual trees in a forest.

2) Relationship between intercepted radiation and dry matter growth

A linear relationship between absorbed radiation and dry matter production was found. The study revealed that RUE estimates can be derived from detailed eco-physiological process-models and that RUE can be used to estimate growth in models of (mixed) forest productivity.

3) Dry matter distribution

Assuming stable growing conditions, the study found dry matter partitioning over the tree components to be rather constant. The elementary approach of an annually fixed dry matter partitioning key might thus work well in mechanistic stand models. However, a mechanistic, dynamic approach is needed to account for effects of changing growing conditions. The partitioning model developed appears to be a suitable concept.

4) Mixed stand growth and development

The productivity of most mixed forest stands is generally somewhere in between the yield levels of the monocultures of the less productive and the most productive species. It will only be possible to achieve higher yields in mixed stands if these stands have a relatively small proportion of the sub-dominant species. To maintain beech in a mixture with Douglas-fir, the proportion of Douglas-fir has to be reduced, resulting in a productivity being lower than that of the monospecific Douglas-fir stand. The maintenance of a mixed stand is thus on strained terms with the maximization of the wood production.

Insufficient data are available on mixed stands to directly support decision taking in forest management. It is therefore extremely important to establish new long-term research plots in mixed stands, to collect growth and yield data for evaluating growth and yield prediction models. However, the data per se will not satisfy forest managers: not only will they have to wait far too long before 'yield tables for mixed stands' can be developed, it is also impossible to set up permanent research plots to represent the huge number of growing conditions and stand compositions. New research tools capable of providing forest managers with information on possible management scenarios and on the consequences of certain management regimes are therefore urgently required. The infinite variety of possible species mixtures, coupled with the range of environmental conditions under which mixtures might be grown, not only necessitates a mechanistic modelling approach, but also stresses the applicability of such models.

Recommendations on the modelling approach

For future applications, COMMIX could be improved and extended on several aspects:

- Phenology: Species differences in phenology cause a temporal separation of light interception, which greatly affects competitive interrelationships. Including phenological aspects will increase the applicability of the model to simulate the effects of climate change on forest growth.
- Crown dynamics: Crown size and position in the canopy determine the tree's ability to intercept light. Much emphasis should thus be put on simulating individual tree crown responses to resource availability. A mechanistic model could be built using the structural balance between crown size, tree height, and stem diameter.
- Partitioning: Mechanical relationships like the structural theory for cantilever beams and the constant stress hypothesis also form promising concepts when partitioning is simulated. The incorporation of mechanical relationships would optimize the functional link between growing conditions and growth partitioning.
- Natural regeneration: In the past 20 years, the recognition of the importance of natural regeneration for forest management has increased considerably. The present study focused on the simulation of even-aged stands, ignoring regeneration. However, it would be relatively easy to quantify the growing conditions for regeneration because COMMIX already simulated light in detail. The concepts applied in COMMIX enable the extension of the model to simulate a variety of mixed stands, including natural regeneration, tree mortality, and management operations, on a range of sites.

Samenvatting

Simulatie van groei en concurrentie in gemengde opstanden van Douglas en beuk

Inleiding

Zonder sterke beïnvloeding van het landschap door de mens zou het grootste deel van West-Europa bedekt zijn met gemengd bos. Menselijke activiteiten door de eeuwen heen echter, hebben de structuur en samenstelling van het bos sterk veranderd, bovendien werd veel bos gekapt ten behoeve van de landbouw. Vanaf het begin van de 19de eeuw veranderde deze situatie: grote oppervlakten werden beplant, met als doel onder meer de georganiseerde productie van hout. De bosaanleg had tot gevolg dat halverwege de 20ste eeuw een groot deel van het West-Europese bos bestond uit gelijkjarige monocultures. De laatste decennia echter, is sprake van een kentering in het denken over bosbeheer, deels ingegeven door calamiteiten die deze eeuw plaats vonden in de monocultures (ziekten, stormen). Gelijkjarige monocultures worden nu door velen als kunstmatig gezien, waardoor er sprake is van een groeiende aandacht voor het (ongelijkjarige) gemengde bos. Dat gemengde bos wordt verondersteld een aantal voordelen te hebben boven de monocultuur: 1) gemengd bos wordt als 'natuur-bos' beschouwd, het zou resistenter zijn tegen stormen, ziekten en plagen, 2) de (hout-) producten uit gemengde bossen zijn gevarieerder waardoor beter ingespeeld kan worden op de houtmarkt, 3) het gebruik maken van spontane processen maakt beheer goedkoper (bijvoorbeeld natuurlijke verjonging in plaats van planten), 4) gemengd bos worden hoger gewaardeerd wanneer het gaat om zaken als biodiversiteit en recreatie.

In West-Europa heeft het bosbeheer zich lange tijd vooral bezig gehouden met gelijkjarige monocultures. Ten behoeve van het beheer werden empirische modellen zoals de opbrengsttabel ontwikkeld en algemeen gebruikt. Dergelijke beschrijvende benaderingen zijn erg bruikbaar gebleken om in de bosbouwpraktijk de groei en opbrengst van gelijkjarige monocultures te voorspellen. Voor gemengde opstanden echter, is er nog geen algemeen aanvaard concept. De grote variatie aan soorten-combinaties, groeiplaatsen en beheers-regimes maakt bovendien dat een empirische benadering niet erg vruchtbaar lijkt. Een functionele (mechanistische) benadering daarentegen, heeft als voordeel dat bij het voorspellen van de groei en ontwikkeling ingespeeld kan worden op die variabele groei-omstandigheden. Het gaat er in een dergelijke benadering om functionele verbanden tussen groei en groei-omstandigheden te kwantificeren. Voor gemengd bos lijkt daarbij het gebruik van boommodellen de voorkeur te verdienen boven opstandsmodellen, om de interactie tussen individuen van verschillende soorten te kunnen simuleren.

Doel van het hier beschreven onderzoek was het onderzoeken van de effecten van opstandssamenstelling en bosbeheer op de groei en ontwikkeling van gemengd bos, met gebruikmaking van een mechanistisch groeimodel. De resultaten van het onderzoek zouden een hulp moeten vormen bij het nemen van beslissingen over beheer van gemengd bos en zouden het onderzoek in gemengde bossen moeten ondersteunen.

De volgende onderzoeksvragen zijn gedefinieerd:

1. Wat is de rol van kroondimensies en opstandssamenstelling op de lichtonderschepping door individuele bomen in een opstand?
2. Welke relatie bestaat er tussen de hoeveelheid onderschept licht en de groei (uitgedrukt als drogestof-toename) van een boom?
3. Hoe wordt de drogestof verdeeld over de biomassa-componenten van een boom?
4. Welke invloed hebben beheersmaatregelen op groei en ontwikkeling van gemengd bos?

Methode

Een raamwerk voor de modellering

Om de groei en ontwikkeling in gemengde opstanden te kunnen voorspellen, is gekozen voor een functionele model-benadering. Op die manier is het mogelijk groei te kwantificeren en te relateren aan groei-omstandigheden. Het ontwikkelde mechanistische model, genaamd COMMIX (COMpetition in MIXtures), beschrijft de groei en dynamiek van een opstand, waarbij de concurrentie om licht tussen individuen centraal staat. De ontwikkeling van het simulatie model is gebaseerd op de volgende aannames:

1. Straling speelt een sleutelrol bij groei: de hoeveelheid straling die een boom absorbeert bepaalt in belangrijke mate diens groei-snelheid, bovendien stuurt concurrentie om straling de bosontwikkeling.
2. De groei van een boom is gerelateerd aan de hoeveelheid geabsorbeerde straling, in overeenstemming met het concept van de 'stralings-conversie-efficiëntie'.
3. De verdeling van de groei (drogestof) over de boomcomponenten is afhankelijk van boom- en groeiplaatscondities, en wordt gestuurd door het streven van een boom naar de instandhouding van interne (structurele) evenwichten.

Om het model te kunnen initialiseren en om model-onderdelen te kunnen verifiëren, zijn voorafgaand aan de modelbouw biomassa-studies uitgevoerd in Douglas en beuk.

Soorten en onderzoeks-locaties

In dit onderzoek zijn de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) en de beuk (*Fagus sylvatica* L.) gebruikt. Beide zijn in Nederland commercieel interessant, de beuk is dat ook in het overig deel van West-Europa. De Douglas is eind 19de eeuw geïmporteerd, en heeft zich sindsdien ontwikkeld tot de 'brood-boom' van de Nederlandse bosbouw. Douglas en beuk komen voor in monocultures, in mengingen met elkaar (met name in Nederland, in mindere mate in Duitsland en Frankrijk), en in mengingen met andere soorten. Het totale areaal Douglas en beuk is beperkt. In dit onderzoek gaat het echter niet zozeer om de soorten-keuze; het onderzoek moet antwoord geven op de vraag hoe in een menging van naaldbomen en loofbomen interacties tussen de soorten (concurrentie om licht) de groei en ontwikkeling van zo'n menging beïnvloeden.

De onderzochte opstanden zijn gelegen op holtpodzol-gronden, goed gedraineerd, met een diepe grondwater-spiegel (>4m beneden maaiveld). Gemeten naar de gangbare opbrengsttabellen zijn de bodems zeer geschikt voor de groei van Douglas (een maximale gemiddelde volume-bijgroei (I_{mv}) van 14-16 m^3 ha^{-1} $jaar^{-1}$ en beuk (10-12 m^3 ha^{-1} $jaar^{-1}$).

Biomassa-onderzoek

Voorafgaand aan de modelbouw is biomassa-onderzoek uitgevoerd in zowel Douglas- als beuken-monocultures, enerzijds om het uiteindelijke model (en modules daarin) te kunnen initialiseren en evalueren, anderzijds om functionele verbanden tussen bomen te kunnen bepalen, benodigd voor het voorspellen van de drogestof-verdeling. Drieëntwintig Douglas-sparren (uit 4 opstanden) en 38 beuken (uit 6) werden gekapt, waarna monsters van stam, takken en loof werden verzameld voor analyse en schatting van de biomassa-hoeveelheden per boom.
Diverse significante verbanden werden gevonden tussen boomkenmerken, biomassa-hoeveelheden en kroondimensies. Het specifieke bladoppervlak (SLA) nam toe van boomtop tot kroonbasis. Blad- respectievelijk naald-oppervlak waren lineair gecorreleerd met het spinthout-oppervlak (op 1.30 meter) van Douglas, en met het grondvlak (1.30m) van beuk. De gevonden allometrische relaties zijn gebruikt voor de ontwikkeling van een model van de drogestof-verdeling.

Simulatie van licht-onderschepping door bomen in bosverband

Groei van een boom is afhankelijk van de hoeveelheid onderschept licht. Voor het bepalen van de rol van kroon-afmetingen, kronendak-structuur, en bossamenstelling op de hoeveelheid door individuele bomen onderschepte fotosynthetisch actieve straling ('PAR'), is een ruimtelijk model ontwikkeld, genaamd FORFLUX2. Berekeningen toonden aan dat het model in staat is in het bos gemeten transmissies te voorspellen. FORFLUX2 is vervolgens gebruikt in een scenario-studie.
Uit de simulaties bleek dat in homogene (jonge) opstanden de geabsorbeerde PAR per boom (APAR) sterk gecorreleerd is aan het bladoppervlak; in heterogene opstanden (zoals gemengd bos) echter bleken ruimtelijke karakteristieken zoals kroonafmetingen en boomlocatie een sterke invloed te hebben op APAR. Model-berekeningen lieten bovendien zien dat wanneer het kronendak wordt voorgesteld als een horizontaal homogene laag, de extinctie-coëfficiënt (K) wordt overschat, als gevolg van clustering van loof om takken en in kronen. De overschatting is niet constant, maar neem toe met toenemende opstandsdichtheid of bladoppervlak (LAI).
Uit de resultaten bleek dat een ruimtelijke beschrijving van het licht-regime nodig is om APAR te schatten in heterogene opstanden. Het feit dat FORFLUX2 het mogelijk maakt om, in bos, APAR per boom te berekenen, maakt het tot een geschikt concept bij het schatten van de groei en ontwikkeling van gemengde bossen. Deze stralings-module is derhalve gebruikt in de ontwikkeling van het simulatie-model COMMIX.

Stralings-conversie-efficiëntie

Wanneer de hoeveelheid door een boom geabsorbeerde straling (APAR) bekend is, kan dit vervolgens gebruikt worden om de groeisnelheid te berekenen. Daarvoor is in deze deel-studie gebruik gemaakt van het concept van de stralings-conversie-efficiëntie (RUE). Dit concept stelt dat er een nauw verband bestaat tussen APAR en de drogestof-productie (net primary production NPP). Gebruik maken van RUE heeft als belangrijk voordeel dat geen ademhalings-gegevens nodig zijn om de groei van een boom te schatten: dergelijke gegevens zijn namelijk schaars en moeilijk te verkrijgen. Het gedetailleerde eco-fysiologisch groei-model FORGRO is gebruikt om 1) de aard van de relatie tussen APAR en NPP vast te stellen, 2) vast te stellen welke verschillen er bestaan tussen Douglas en beuk, en 3) te bepalen wat het effect is van opstandsstructuur en -samenstelling op RUE. Hierbij is RUE berekend op grond van (A)PAR: in geval van globale straling zou RUE dus circa de helft kleiner zijn.

Met behulp van FORGRO is NPP berekend, uitgaande van optimale groei-omstandigheden. Uit de vergelijking van FORGRO-schattingen met literatuur gegevens van de NPP bleek dat FORGRO betrouwbare schattingen van NPP voor Douglas en beuk levert; het model is daarom verder gebruikt in deze studie.

Vervolgens is FORGRO gebruikt om RUE te berekenen onder een aantal verschillende groei-omstandigheden. Een gevoeligheids-analyse liet zien dat RUE relatief onafhankelijk is van fotosynthese-parameters zoals de maximale fotosynthese-snelheid. Temperatuur had wel effect op RUE; de respons-verschillen tussen soorten zullen derhalve invloed hebben op de concurrentie-verhoudingen en dus een belangrijke rol spelen in geval van klimaat-veranderingen (broeikas-effect). RUE vertoonde veel variatie van dag-tot-dag; gebaseerd op cumulatieve waarden, echter, bleek RUE bij benadering constant te zijn, zowel in de loop van een jaar als bezien over meerdere jaren. Dit gold voor beide soorten, zowel in monocultures als in mengingen.

De conclusie van deze studie was dat RUE een bruikbaar concept is voor de simulatie van groei van (gemengd) bos, en dat RUE-schattingen verkregen kunnen worden door toepassing van gedetailleerde eco-fysiologisch modellen. Het concept is vervolgens ingebracht in COMMIX.

Verdeling van de groei (drogestof)

Nadat de groeisnelheid van een boom is berekend (de hoeveelheid voor groei beschikbare drogestof), is de vraag waar die groei wordt geïnvesteerd. Theoretische modellen die voorspellen hoe de groei wordt verdeeld (E: allocation, partitioning) zijn voorhanden, maar praktische concepten geschikt voor toepassing in groei-modellen zijn schaars. In deze studie is een model voor de verdeling van de drogestof ontwikkeld, gebaseerd op het concept van de 'structural balances', het streven van een boom naar de instandhouding van interne (structurele) evenwichten. Dit concept, dat gebaseerd is op functionele relaties zoals de 'pipe-model'-theorie en het 'root/shoot'-evenwicht, is aangevuld met een aantal allometrische relaties verkregen uit de eerdere biomassa-studies. Het model beschrijft de dynamische verdeling van de drogestof in Douglas-sparren en beuken op grond van boom-karakteristieken en groei-omstandigheden.

Om de geschiktheid van het model te testen werden schattingen van diametergroei (op 1.30m), verkregen uit berekende stambiomassa-groei, vergeleken met gegevens uit de gangbare opbrengst-tabellen. Omdat het model in staat bleek de diameter-ontwikkeling te reproduceren, is het gebruikt om verschillen tussen soorten en effecten van groeiplaats en sociale positie op de drogestof-verdeling te schatten aan de hand van een scenario-studie.

Uit simulaties volgde dat (co-) dominante bomen relatief meer investeren in takken en minder in de stam dan onderdrukte individuen. Vergeleken met beuk investeerde Douglas relatief meer in blad, vooral ten koste van takken en stam. Dunning bleek een duidelijk effect op de verdeling te hebben: de toedeling (fracties) naar fijne wortels en blad daalde sterk na elke ingreep, terwijl de toedeling naar takken sterk toenam. Dunnings-ingrepen leidden er bovendien toe dat de toedeling naar de stam relatief gezien afnam in tijd. In absolute zin resulteerde dit in een nagenoeg lineaire toename van de stamdiameter (1.30) in de tijd. Simulatie-resultaten lieten ook zien dat bij gelijkblijvende groei-omstandigheden de relatieve verdeling van de drogestof na verloop van tijd (na leeftijd 20 jaar) nauwelijks meer verandert. Dit maakt gebruik van vaste verdeelsleutels onder dergelijk omstandigheden mogelijk. Echter, om het effect van groei-omstandigheden op boomniveau te kunnen kwantificeren, is een functionelere benadering nodig zoals in dit deelonderzoek geschetst. Het gepresenteerde model is derhalve opgenomen in COMMIX.

Simulatie van groei van gemengd bos

De reeds genoemde biomassa-gegevens zijn gebruikt voor onder meer model-initialisatie en voor de analyse van de drogestof-verdeling. De drie ontwikkelde modules (voor stralings-onderschepping, voor groei-berekening met RUE en voor de verdeling van de drogestof) vormen samen de ruggengraat van COMMIX. Een aantal kleinere modules, onder meer voor de berekening van sterfte en dunning, zijn toegevoegd. COMMIX is eerst getest op bruikbaarheid door monocultures van Douglas en beuk te simuleren en de resultaten te vergelijken met de gangbare opbrengst-tabellen. Uit de vergelijking bleek dat COMMIX geschikt is voor gebruik; verschillen tussen beuk-simulaties en beuken-tabel konden deels worden verklaard uit onvolkomenheden in de tabel. Douglas-simulaties kwamen overeen met de gegevens uit de opbrengsttabel; kleine verschillen op hogere leeftijd konden worden teruggevoerd op onderschattingen van de opbrengsttabel. COMMIX is derhalve gebruikt voor een scenario-analyse, waarbij een aantal fictieve mengingen is samengesteld volgens het principe van de vervangingsreeks.

Simulatie-resultaten lieten zien dat in een enkele jonge menging met een groot aandeel Douglas de opbrengst van de menging hoger is dan de som van de opbrengsten van de fracties van de twee monocultures. In het algemeen echter lag de opbrengst tussen de niveaus van de monocultures beuk en Douglas in; dit is ten dele te wijten aan het verdwijnen van de beuk uit de menging.

De opbrengst van Douglas in opstanden met een laag aandeel Douglas was lager dan op grond van het grondvlak-aandeel kon worden verwacht; in opstanden met een hoog aandeel Douglas gold het tegenovergestelde. De productiviteit van beuk in menging, daarentegen, was bijna altijd lager dan op grond van het grondvlak-aandeel kan worden

verwacht.
Dunning bleek een grote invloed op de productiviteit en opstandssamenstelling te hebben. De conclusies luidden dat 1) het mengen van Douglas en beuk niet aantoonbaar leidt tot extra groei als gevolg van een (vermeende) vergrote licht-onderschepping, en 2) dat het handhaven van een menging ten koste gaat van de productiviteit.

Conclusies

Uit het onderzoek kunnen, refererend aan de gestelde onderzoeksvragen, de volgende conclusies getrokken worden:

1) Lichtonderschepping door individuen in bosverband

In homogene, gesloten opstanden bestaat een verband tussen het bladoppervlak van een boom en de daarmee onderschepte hoeveelheid licht. In het geval van heterogene opstanden echter, blijken posities van de bomen en afmetingen van individuele kronen een grote invloed te hebben op de lichtonderschepping en dus op de concurrentie. Clustering van bladeren en naalden resulteert in een sterke daling van de interceptie per eenheid bladoppervlak. Beide fenomenen duiden erop dat een ruimtelijk stralings-model nodig is om een goede schatting te krijgen van de lichtonderschepping door bomen in bosverband.

2) Het verband tussen onderschept licht en de drogestof-toename

Er bestaat een rechtlijnig verband tussen de hoeveelheid onderschept licht en de geproduceerde hoeveelheid straling, de RUE. Gedetailleerde ecofysiologische modellen kunnen gebruikt worden om deze RUE te schatten. De RUE-waarden kunnen vervolgens gebruikt worden om groei te schatten in modellen van bosgroei.

3) Drogestof-verdeling

De verdeling van de groei over de biomassa-componenten is constant zolang de groei-omstandigheden niet veranderen. Het gebruik van vaste verdeel-sleutels vormt derhalve een goede mogelijkheid in ecofysiologische modellen. Wanneer echter het effect van (veranderende) groei-omstandigheden op de drogestof-verdeling moet kunnen worden gekwantificeerd, dan is een dynamische benadering nodig. Het huidige sub-model, dat verbanden legt tussen verdeling en groei-omstandigheden, is een bruikbare benadering gebleken.

4) Groei en ontwikkeling van gemengd bos

De productiviteit van gemengde bossen ligt over het algemeen tussen de opbrengstniveaus van minst- en de meest-productieve monocultures van de participerende soorten in. Hogere opbrengsten in gemengde bossen zullen alleen gerealiseerd kunnen worden wanneer het aandeel van de laag-productieve soorten gering is. In gemengde Douglas-beuk opstanden is de Douglas in het voordeel, met name vanwege zijn snellere hoogtegroei. Om ontmenging te voorkomen (beuk te behouden) is het nodig het aandeel Douglas stelselmatig te reduceren, met als consequentie dat de productiviteit van de menging als geheel daalt tot onder het niveau van de monocultuur Douglas. Het handhaven van deze menging staat derhalve op gespannen voet met het streven naar een maximale houtproductie.

Hoewel gegevens van gemengde opstanden voorhanden zijn, is dit over het algemeen te weinig of te zeer gebonden aan lokale situaties om algemeen bruikbaar te zijn voor bosbeheer. Het instellen van proefperken in gemengde opstanden voor lange-termijn onderzoek, conform het traditionele groei- en opbrengst-onderzoek, is belangrijk om groeigegevens te verkrijgen, maar biedt, zeker op korte termijn, weinig soelaas voor beheer en onderzoek. Het op deze wijze verzamelen van informatie vergt erg veel tijd en een lange periode van onderzoek en is bovendien per definitie incompleet: het maken van 'opbrengst-tabellen' voor gemengde bossen heeft geen zin gezien de grote variatie aan groeiplaats-omstandigheden, mengingstypen, mengverhoudingen, dunnings-regimes en beheers-doelstellingen.

Er is derhalve behoeft aan nieuwe hulpmiddelen. Mechanistische modellen kunnen in deze behoefte voorzien omdat in deze benadering groei en ontwikkeling van individuele bomen gerelateerd worden aan groei-condities. Het effect van beheersmaatregelen op de ontwikkeling van gemengde bossen kan op die manier doorgerekend worden.

Aanbevelingen voor model-verbetering

De huidige model-benadering vormt een bijdrage in het proces van modelvorming voor gemengde bossen. Het model COMMIX zal verder ontwikkeld en uitgebreid worden, waarbij de nadruk zal liggen op de volgende aspecten:

- Fenologische verschillen tussen soorten; deze bepalen in belangrijke mate verschillen in concurrentie-positie. Effecten van klimaatveranderingen kunnen zo worden meegenomen.
- Kroon-dynamiek; de kroonomvang en -positie bepalen hoeveel licht wordt onderschept. Het beschrijven van de kroon-uitbreiding is tot nog toe vooral empirisch gebeurd: het gebruik van functionele relaties is gewenst, daarbij zijn met name mechanische verbanden veelbelovend.
- Diezelfde verbanden kunnen ook worden gebruikt om de beschrijving van de verdeling van de drogestof te optimaliseren: mechanische verbanden zouden het allometrische deel van de huidige benadering kunnen vervangen.
- Natuurlijke verjonging. In een aantal modellen wordt, aansluitend bij de gang van zaken in de bosbouw-praktijk, reeds rekening gehouden met natuurlijke verjonging. Gezien het stijgende belang van natuurlijke verjonging bij het beheer van gemengd bos, is uitbreiding van COMMIX met een regeneratie-module gewenst. Gezien het model-concept is het mogelijk COMMIX zo uit te breiden dat het model te gebruiken is voor simulatie van dynamiek in diverse soorten mengingen, met inbegrip van natuurlijke verjonging, sterfte en beheersmaatregelen, op een reeks van groeiplaatsen.

Listing of the COMMIX simulation model

```
*************************************************************************
* Structure of PROGRAM COMMIX-YR                                        *
*                                                                       *
* -- initial part --                                                    *
* CALL INITL          opens from input and output files                 *
* CALL INPUT          reads input-data from input-file(s)               *
* CALL UOC            help-variables for UOC-conditions                 *
* CALL GRIDP          grid size and coordinates of grid points          *
* CALL YRESET         resets annual totals to zero                      *
* CALL YSTATE         updates annual biomass amounts & tree structure   *
* CALL OUTPUT         writes annual totals to output file               *
* CALL YRESET         resets annual totals to zero                      *
* -- dynamic part --                                                    *
* DO year=1,nryears                                                     *
*   CALL FORFLX       determines DIF and DIR per tree per inclination   *
*   CALL PARABS       cumulates daily absorbed PARdif and PARdir        *
*   CALL FORFLX       radiation intensity below the crown               *
*   DO tree=1,N                                                         *
*     CALL HEIGHT     tree height and crown base height                 *
*     CALL TURNOV     biomass turn-over rates                           *
*     CALL GROWTH     annual dry matter increment based on RUE          *
*   CALL YSTATE       updates annual biomass amounts                    *
*   CALL MORTAL       determines whether natural tree death occurs      *
*   CALL THINNG       determines trees to be harvested                  *
*   CALL LITDYN       litter dynamics                                   *
*   CALL OUTPUT       writes annual totals to output file               *
*   CALL BOOKS        removes dead trees, updates tree arrays           *
*   CALL YRESET       resets annual totals to zero                      *
* -- terminal part --                                                   *
* CALL CLOSE          closes output files                               *
*                                                                       *
*************************************************************************

*     MAIN PROGRAM
      IMPLICIT REAL(A-Z)
      INTEGER TRI,CYR
      INTEGER MXSPEC,MXIND,MXTHIN,MXNRAY,MXSMPL,MXSAPR,MXFOLC,MXBLK
      INTEGER YR,STYEAR,ENYEAR
      INTEGER NRSPEC,LANGLE,BUDFLS,FOLFAL,NRSAP,NFOLC,SPAGE
      INTEGER THINYR,THINTP
      INTEGER NRIND,HSD,TNR,ONR,SPCD,VITAL
      INTEGER NRSAMP,NRAZ
      CHARACTER*4 SPILAB,SPEC
      LOGICAL ELLIPS,DEAD,HARVST,THTIME

      PARAMETER (MXSPEC=2,MXIND=400,MXTHIN=15,MXNRAY=324,MXSMPL=23104)
      PARAMETER (MXSAPR=100,MXFOLC=5,MXBLK=49)

      DIMENSION SPILAB(MXSPEC),SPAGE(MXSPEC),LANGLE(MXSPEC),
     &          BUDFLS(MXSPEC),FOLFAL(MXSPEC),SLA(MXSPEC),
     &          BADEN(MXSPEC),NLC(MXSPEC),BRTOR(MXSPEC),CRTOR(MXSPEC),
     &          FRTOR(MXSPEC),SMAX(MXSPEC),HCR1(MXSPEC),HCR2(MXSPEC),
     &          SH1(MXSPEC),SH2(MXSPEC),SH3(MXSPEC),RSH1(MXSPEC),
     &          RSH2(MXSPEC),RSH3(MXSPEC),TRUE(MXSPEC,10),
     &          ELLIPS(MXSPEC),PFRFL(MXSPEC),PFASA1(MXSPEC),
     &          PFASA2(MXSPEC),PFASA3(MXSPEC),PDHBR1(MXSPEC),
     &          PDHBR2(MXSPEC),PDHBR3(MXSPEC),PDWCR1(MXSPEC),
     &          PDWCR2(MXSPEC),PDWCR3(MXSPEC),PDWCR4(MXSPEC),
     &          PDWCR5(MXSPEC),NRSAP(MXSPEC),NFOLC(MXSPEC),
     &          SLAREA(MXSPEC),SWFL(MXSPEC),SWBRN(MXSPEC),SWST(MXSPEC),
     &          SWRT(MXSPEC),SBA(MXSPEC),SVOL(MXSPEC),SVINC(MXSPEC),
     &          MCM1(MXSPEC),MCM2(MXSPEC),
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     &          ACL1(MXSPEC),ACL2(MXSPEC),ACL3(MXSPEC)
      DIMENSION THINYR(MXTHIN),THINFR(MXSPEC,MXTHIN),
     &          THINTP(MXSPEC,MXTHIN)
      DIMENSION TNR(MXIND),ONR(MXIND),
     &          DBH(MXIND),SPEC(MXIND),SPCD(MXIND),
     &          HGT(MXIND),HINC(MXIND),HCB(MXIND),HCBOLD(MXIND),
     &          CRAD(MXIND),WST(MXIND),WBR(MXIND),WCR(MXIND),
     &          WFR(MXIND),WRT(MXIND),WNC(MXIND,MXFOLC),WFL(MXIND),
     &          VOL(MXIND),BA(MXIND),SA(MXIND),SAPR(MXIND,MXSAPR),
     &          XTRUNK(MXIND),YTRUNK(MXIND),ZTRUNK(MXIND),
     &          CSHAPE(MXIND),CRVOL(MXIND),CRL(MXIND),CRSA(MXIND),
     &          LAD(MXIND),VITAL(MXIND),DEAD(MXIND),HARVST(MXIND),
     &          YGDM(MXIND),ABSDIF(MXIND),ABSDIR(MXIND,MXNRAY),
     &          TRAPAR(MXIND),PARHCB(MXIND),GST(MXIND),GBR(MXIND),
     &          GFL(MXIND),GCR(MXIND),GFR(MXIND),GSA(MXIND),
     &          DBR(MXIND),DFL(MXIND),DCR(MXIND),DFR(MXIND),DSA(MXIND),
     &          DNC(MXIND,MXFOLC)
      DIMENSION UCOSIS(MXNRAY),UCOCOS(MXNRAY),SINCLI(MXNRAY),
     &          CONTIL(MXNRAY)
      DIMENSION XSAMP(MXSMPL),YSAMP(MXSMPL),ZSAMP(MXSMPL)


* * * * * * * * * * * * * * * INITIAL PART * * * * * * * * * * * * * * *

*     read run control data
      CALL INITL

*     read input data from the inputfiles:
      CALL INPUT (MXSPEC, MXIND,MXTHIN,MXSAPR,MXFOLC,
     &                              NRSPEC, NRIND, NRSAP, NFOLC,
     &                         NRAZ,STYEAR,ENYEAR,    YR, START,
     &                       SPILAB, SPAGE,LANGLE,BUDFLS,FOLFAL,
     &                          SLA, BADEN,   NLC, BRTOR, CRTOR, FRTOR,
     &                         SMAX,  HCR1,  HCR2,   SH1,   SH2,
     &                          SH3,  RSH1,  RSH2,  RSH3,  TRUE,
     &                       ELLIPS, PFRFL,PFASA1,PFASA2,PFASA3,
     &                       PDHBR1,PDHBR2,PDHBR3,PDWCR1,PDWCR2,
     &                       PDWCR3,PDWCR4,PDWCR5,  MCM1,  MCM2,
     &                        ACL1, ACL2, ACL3,THINYR,THINFR,THINTP,
     &                          ONR,    TNR,SPEC,   SPCD,    HGT,    HCB,
     &                         CRAD,    WST,    WBR,    WCR,    WFR,
     &                          WRT,    WNC,    WFL,     SA,   SAPR,
     &                       XTRUNK,YTRUNK,ZTRUNK,    CRL,  VITAL,
     &                         DEAD,HARVST,
     &                         XORI,  YORI,   XMAX,   YMAX,
     &                         X1P,X2P,Y1P,Y2P,
     &                         CWID,PLOTAR,   X1C,X2C,Y1C,Y2C,CPLOT)

*     Initial calculations for radiation sub-model
*     Help-variables for diffuse light conditions
      CALL UOC (  MXNRAY,  NRAZ,
     &                       UCOSIS,UCOCOS,SINCLI,CONTIL)

*     Coordinates of the gridpoints at the forest floor
      CALL GRIDP (MXSMPL,
     &                         XORI,  YORI,   XMAX,   YMAX,   CWID,
     &                 NRSAMP, XSAMP, YSAMP, ZSAMP)

*     Reset annual totals
      CALL YRESET (MXSPEC, MXIND,MXNRAY,MXFOLC,NRSPEC,
     &                              YR, START,
     &                          SPAGE,
     &                    HINC,ABSDIF,ABSDIR,TRAPAR,PARHCB,
     &                           GST,    GBR,    GFL,    GCR,    GFR,
```

```
     &                       GSA,   DBR,   DFL,   DCR,   DFR,
     &                       DSA,   DNC,
     &   SLAREA,SWST,SWBRN,SWFL,SWRT,SBA,SVOL,SVINC,
     &   HLAI,HWST,HWBRN,HWFL,HWRT,HBA,HVOL,
     &   TOTGDM,YIELDG,YIELDV,TVINC,LITTER)

*     Calculate states and stand structure
      CALL YSTATE (MXSPEC, MXIND,MXSAPR,MXFOLC,NRSPEC, NRSAP,
     &                     NFOLC, NRIND,    YR,STYEAR,PLOTAR,
     &          cplot,START,SLA,BADEN,
     &          RSH1,RSH2,RSH3,
     &          ELLIPS,
     &          SLAREA,SWFL,SWBRN,SWST,
     &          SWRT,SBA,SVOL,SVINC,MCM1,MCM2,
     &          ONR,DBH,SPCD,
     &          HGT,
     &          CRAD,WST,WBR,WCR,
     &          WFR,WRT,WNC,WFL,LAD,
     &          VOL,BA,SA,SAPR,
     &          XTRUNK,YTRUNK,
     &          CSHAPE,CRVOL,CRL,CRSA,
     &          YGDM,
     &          GST,GBR,GFL,GCR,
     &          GFR,GSA,
     &          DBR,DFL,DCR,DFR,DSA,DNC,DEAD,
     &          X1C,X2C,Y1C,Y2C,
     &      TVINC,TOTGDM,
     &      HSD,HLAI,HWST,HWBRN,HWFL,HWRT,HBA,HVOL)

*     Output of starting values
      CALL OUTPUT (MXSPEC, MXIND,NRSPEC, NRIND,THTIME,
     &                      YR,CPLOT,PLOTAR,
     &                    SPAGE,SPILAB,   ONR,
     &                TNR,   DBH,  SPEC,  SPCD,   HGT,
     &                       HCB,  CRAD,  CRSA,PARHCB,
     &                     VITAL,  YGDM,   GST,   GBR,
     &                       GFL,   GCR,   GFR,   GSA,   DBR,
     &                       DFL,   DCR,   DFR,   DSA,
     &                    XTRUNK,YTRUNK,ZTRUNK,
     &                    SLAREA,  SWFL, SWBRN,  SWST,  SWRT,
     &                       SBA,  SVOL, SVINC,
     &             HSD,HWST,HWBRN,HWFL,HWRT,HLAI,HBA,HVOL,LITTER,
     &             TOTGDM,TVINC,YIELDG,YIELDV)

*     Reset annual totals
      CALL YRESET (MXSPEC, MXIND,MXNRAY,MXFOLC,NRSPEC,
     &                         YR, START,
     &                      SPAGE,
     &               HINC,ABSDIF,ABSDIR,TRAPAR,PARHCB,
     &                       GST,   GBR,   GFL,   GCR,   GFR,
     &                       GSA,   DBR,   DFL,   DCR,   DFR,
     &                       DSA,   DNC,
     &   SLAREA,SWST,SWBRN,SWFL,SWRT,SBA,SVOL,SVINC,
     &   HLAI,HWST,HWBRN,HWFL,HWRT,HBA,HVOL,
     &   TOTGDM,YIELDG,YIELDV,TVINC,LITTER)


* * * * * * * * * * * * * * DYNAMIC PART * * * * * * * * * * * * * * *

*     Start of main time-loop
      DO 1000 CYR=1,(ENYEAR-STYEAR+1)

*        Screen counter
         PRINT '(''+'',30X,A,I7)', 'YEAR=',CYR
```

```
          CALL FORFLX (MXSPEC, MXIND,MXNRAY,MXSMPL, NRIND,NRSAMP,
     &                             1,  NRAZ,  CWID,LANGLE,ELLIPS,
     &                           TNR,  SPCD,   HGT,   HCB,  CRAD,
     &                        XTRUNK,YTRUNK,ZTRUNK,CSHAPE,   CRL,
     &                           LAD, XSAMP, YSAMP, ZSAMP,UCOSIS,
     &                        UCOCOS,SINCLI,CONTIL,   CYR,
     &                 ABSDIF,ABSDIR,PARHCB)

*         Calculate absolute amount of absorbed diffuse PAR per tree
          CALL PARABS ( MXIND, NRIND,
     &                        ABSDIF,   ONR,
     &                 TRAPAR)

*         Estimate remaining radiation intensity below the crownbase
          CALL FORFLX (MXSPEC, MXIND,MXNRAY,MXSMPL, NRIND,NRSAMP,
     &                             2,  NRAZ,  CWID,LANGLE,ELLIPS,
     &                           TNR,  SPCD,   HGT,   HCB,  CRAD,
     &                        XTRUNK,YTRUNK,ZTRUNK,CSHAPE,   CRL,
     &                           LAD, XSAMP, YSAMP, ZSAMP,UCOSIS,
     &                        UCOCOS,SINCLI,CONTIL,   CYR,
     &                 ABSDIF,ABSDIR,PARHCB)

          DO 1200 TRI=1,NRIND

*             Calculate new tree height and crown base height
              CALL HEIGHT (MXSPEC, MXIND,   TRI,
     &                             SPAGE,  SMAX,  HCR1,  HCR2,  SPCD,
     &                               HGT,   HCB,PARHCB,   DBH,  ACL1,
     &                              ACL2,  ACL3,
     &                       HINC,HCBOLD,   CRL)

*             Calculate turn-over rates
              CALL TURNOV (MXSPEC, MXIND,MXSAPR,MXFOLC,   TRI,
     &                         BRTOR,CRTOR,FRTOR, NRSAP,  SPCD,   WFL,
     &                               WNC,   WBR,   WCR,   WFR,  SAPR,
     &                             NFOLC,   NLC,
     &                        DFL,   DNC,   DBR,   DCR,   DFR,   DSA)

*             Calculate dry matter growth per tree
              CALL GROWTH (MXSPEC, MXIND,   TRI,    YR,
     &                               SLA, BADEN,  HCR1,  HCR2,   SH1,
     &                               SH2,   SH3,  TRUE, PFRFL,PFASA1,
     &                            PFASA2,PFASA3,PDHBR1,PDHBR2,PDHBR3,
     &                            PDWCR1,PDWCR2,PDWCR3,PDWCR4,PDWCR5,
     &                               DBH,  SPCD,   HGT,   HCB,HCBOLD,
     &                               WST,   WBR,   WCR,  YGDM,TRAPAR,
     &                               DBR,   DFL,   DCR,   DFR,   DSA,
     &                        GST,   GBR,   GFL,   GCR,   GFR,   GSA,
     &                              DEAD, VITAL)

 1200     CONTINUE

*         Update tree biomass amounts and crown dimensions
          CALL YSTATE (MXSPEC, MXIND,MXSAPR,MXFOLC,NRSPEC, NRSAP,
     &                         NFOLC, NRIND,    YR,STYEAR,PLOTAR,
     &        cplot,START,SLA,BADEN,
     &        RSH1,RSH2,RSH3,
     &        ELLIPS,
     &        SLAREA,SWFL,SWBRN,SWST,
     &        SWRT,SBA,SVOL,SVINC,MCM1,MCM2,
     &        ONR,DBH,SPCD,
     &        HGT,
     &        CRAD,WST,WBR,WCR,
```

```
     &        WFR,WRT,WNC,WFL,LAD,
     &        VOL,BA,SA,SAPR,
     &        XTRUNK,YTRUNK,
     &        CSHAPE,CRVOL,CRL,CRSA,
     &        YGDM,
     &        GST,GBR,GFL,GCR,
     &        GFR,GSA,
     &        DBR,DFL,DCR,DFR,DSA,DNC,DEAD,
     &          X1C,X2C,Y1C,Y2C,
     &    TVINC,TOTGDM,
     &    HSD,HLAI,HWST,HWBRN,HWFL,HWRT,HBA,HVOL)

*         Natural mortality, sapwood turn-over, needle age-classes
          CALL MORTAL (MXSPEC, MXIND, NRIND,
     &                          MCM1,  MCM2,   DBH,  SPCD,
     &                           HGT,  CRSA, VITAL,
     &                   DEAD)

*         Carry out a thinning (when necessary)
          CALL THINNG (MXSPEC, MXIND,MXTHIN, MXBLK,
     &                        NRSPEC, NRIND,PLOTAR,THTIME,
     &                         SPAGE,THINYR,THINFR,THINTP,
     &                           TNR,   DBH,  SPCD,    BA,
     &                        XTRUNK,YTRUNK,  DEAD,
     &                           X1P,   X2P,   Y1P,   Y2P,
     &                           X1C,   X2C,   Y1C,   Y2C,
     &                        HARVST)

*         Summarize biomass losses due to mortality
          CALL LITDYN (MXSPEC, MXIND, NRIND,PLOTAR,
     &                         BADEN,   DBH,  SPCD,   WST,   WBR,
     &                           WCR,   WFR,   WFL,  DEAD,HARVST,
     &                           DBR,   DFL,   DCR,   DFR,
     &                        XTRUNK,YTRUNK,
     &                           X1C,   X2C,   Y1C,   Y2C,
     &                 YIELDG,YIELDV,LITTER)



*         Write annual results to output files
          CALL OUTPUT (MXSPEC, MXIND,NRSPEC, NRIND,THTIME,
     &                       YR,CPLOT,PLOTAR,
     &                        SPAGE,SPILAB,   ONR,
     &                    TNR,   DBH,  SPEC,  SPCD,   HGT,
     &                          HCB,   CRAD,  CRSA,PARHCB,
     &                         VITAL,  YGDM,   GST,   GBR,
     &                           GFL,   GCR,   GFR,   GSA,   DBR,
     &                           DFL,   DCR,   DFR,   DSA,
     &                        XTRUNK,YTRUNK,ZTRUNK,
     &                        SLAREA,  SWFL, SWBRN,  SWST,  SWRT,
     &                           SBA,  SVOL, SVINC,
     &                 HSD,HWST,HWBRN,HWFL,HWRT,HLAI,HBA,HVOL,LITTER,
     &                 TOTGDM,TVINC,YIELDG,YIELDV)

*         Remove dead trees, reshuffle arrays
          CALL BOOKS ( MXIND,MXNRAY,MXSAPR,MXFOLC, NRIND,
     &                       ONR,   TNR,   DBH,  SPEC,  SPCD,   HGT,
     &                         HINC,   HCB,HCBOLD,  CRAD,   WST,
     &                          WBR,   WCR,   WFR,   WRT,   WNC,
     &                          WFL,   VOL,    BA,    SA,  SAPR,
     &                       XTRUNK,YTRUNK,ZTRUNK,CSHAPE, CRVOL,
     &                          CRL,  CRSA,   LAD, VITAL,  DEAD,
     &                       HARVST,  YGDM,
     &                       ABSDIF,ABSDIR,TRAPAR,PARHCB,   GST,
```

```
     &                          GBR,   GFL,   GCR,   GFR,   GSA,
     &                          DBR,   DFL,   DCR,   DFR,   DSA,
     &                          DNC)

*         Reset annual amounts, update year counter
          CALL YRESET (MXSPEC, MXIND,MXNRAY,MXFOLC,NRSPEC,
     &                            YR, START,
     &                         SPAGE,
     &                   HINC,ABSDIF,ABSDIR,TRAPAR,PARHCB,
     &                           GST,   GBR,   GFL,   GCR,   GFR,
     &                           GSA,   DBR,   DFL,   DCR,   DFR,
     &                           DSA,   DNC,
     &      SLAREA,SWST,SWBRN,SWFL,SWRT,SBA,SVOL,SVINC,
     &      HLAI,HWST,HWBRN,HWFL,HWRT,HBA,HVOL,
     &      TOTGDM,YIELDG,YIELDV,TVINC,LITTER)

 1000 CONTINUE

      CALL CLOSE
      PRINT*,'  Run finished. '

      END

************************************************************************
*                         SUBROUTINES                                  *
************************************************************************

*----------------------------------------------------------------------*
*  SUBROUTINE BOOKS                                                    *
*  Author: H.H. Bartelink                                              *
*  Date of last revision: Autumn 1995                                  *
*  Purpose: In this subroutine dead trees are removed from the tree    *
*           arrays, and the arrays are reshuffled                      *
*----------------------------------------------------------------------*
      SUBROUTINE BOOKS ( MXIND,MXNRAY,MXSAPR,MXFOLC, NRIND,
     &                         ONR,   TNR,   DBH,  SPEC,  SPCD,   HGT,
     &                           HINC,   HCB,HCBOLD,  CRAD,   WST,
     &                            WBR,   WCR,   WFR,   WRT,   WNC,
     &                            WFL,   VOL,    BA,    SA,  SAPR,
     &                         XTRUNK,YTRUNK,ZTRUNK,CSHAPE, CRVOL,
     &                            CRL,  CRSA,   LAD, VITAL,  DEAD,
     &                         HARVST,  YGDM,
     &                         ABSDIF,ABSDIR,TRAPAR,PARHCB,   GST,
     &                            GBR,   GFL,   GCR,   GFR,   GSA,
     &                            DBR,   DFL,   DCR,   DFR,   DSA,
     &                            DNC)
      IMPLICIT REAL(A-Z)
      INTEGER I,TRI,NRLIVE,MPTY
      INTEGER MXIND,MXNRAY,MXSAPR,MXFOLC
      INTEGER NRIND,TNR,ONR,SPCD,VITAL
      LOGICAL DEAD,HARVST
      CHARACTER*4 SPEC
      DIMENSION TNR(MXIND),ONR(MXIND),
     &          DBH(MXIND),SPEC(MXIND),SPCD(MXIND),
     &          HGT(MXIND),HINC(MXIND),HCB(MXIND),HCBOLD(MXIND),
     &          CRAD(MXIND),WST(MXIND),WBR(MXIND),WCR(MXIND),
     &          WFR(MXIND),WRT(MXIND),WNC(MXIND,MXFOLC),WFL(MXIND),
     &          VOL(MXIND),BA(MXIND),SA(MXIND),SAPR(MXIND,MXSAPR),
     &          XTRUNK(MXIND),YTRUNK(MXIND),ZTRUNK(MXIND),CSHAPE(MXIND),
     &          CRVOL(MXIND),CRL(MXIND),CRSA(MXIND),LAD(MXIND),
     &          VITAL(MXIND),DEAD(MXIND),HARVST(MXIND),YGDM(MXIND),
     &          ABSDIF(MXIND),ABSDIR(MXIND,MXNRAY),TRAPAR(MXIND),
     &          PARHCB(MXIND),GST(MXIND),GBR(MXIND),GFL(MXIND),
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```
     &          GCR(MXIND),GFR(MXIND),GSA(MXIND),DBR(MXIND),DFL(MXIND),
     &          DCR(MXIND),DFR(MXIND),DSA(MXIND),DNC(MXIND,MXFOLC)

*     Reshuffling of tree-arrays to account for tree mortality
      NRLIVE=0
      DO 100 TRI=1,NRIND
          IF (DEAD(TRI).OR.HARVST(TRI)) GOTO 100
          NRLIVE=NRLIVE+1
          TNR(NRLIVE)=NRLIVE
          ONR(NRLIVE)=ONR(TRI)
          SPEC(NRLIVE)=SPEC(TRI)
          SPCD(NRLIVE)=SPCD(TRI)
          XTRUNK(NRLIVE)=XTRUNK(TRI)
          YTRUNK(NRLIVE)=YTRUNK(TRI)
          ZTRUNK(NRLIVE)=ZTRUNK(TRI)
          WFL(NRLIVE)=WFL(TRI)
          DO 110 I=1,MXFOLC
              WNC(NRLIVE,I)=WNC(TRI,I)
 110      CONTINUE
          WBR(NRLIVE)=WBR(TRI)
          WST(NRLIVE)=WST(TRI)
          WCR(NRLIVE)=WCR(TRI)
          WFR(NRLIVE)=WFR(TRI)
          WRT(NRLIVE)=WRT(TRI)
          DBH(NRLIVE)=DBH(TRI)
          SA(NRLIVE)=SA(TRI)
          DO 120 I=1,MXSAPR
              SAPR(NRLIVE,I)=SAPR(TRI,I)
 120      CONTINUE
          BA(NRLIVE)=BA(TRI)
          HGT(NRLIVE)=HGT(TRI)
          HINC(NRLIVE)=HINC(TRI)
          HCB(NRLIVE)=HCB(TRI)
          HCBOLD(NRLIVE)=HCBOLD(TRI)
          CRL(NRLIVE)=CRL(TRI)
          VOL(NRLIVE)=VOL(TRI)
          CSHAPE(NRLIVE)=CSHAPE(TRI)
          CRAD(NRLIVE)=CRAD(TRI)
          CRVOL(NRLIVE)=CRVOL(TRI)
          CRSA(NRLIVE)=CRSA(TRI)
          TRAPAR(NRLIVE)=TRAPAR(TRI)
          ABSDIF(NRLIVE)=ABSDIF(TRI)
          DO 130 I=1,MXNRAY
              ABSDIR(NRLIVE,I)=ABSDIR(TRI,I)
 130      CONTINUE
          PARHCB(NRLIVE)=PARHCB(TRI)
          YGDM(NRLIVE)=YGDM(TRI)
          LAD(NRLIVE)=LAD(TRI)
          VITAL(NRLIVE)=VITAL(TRI)
          DEAD(NRLIVE)=DEAD(TRI)
          HARVST(NRLIVE)=HARVST(TRI)
          GST(NRLIVE)=GST(TRI)
          GBR(NRLIVE)=GBR(TRI)
          GFL(NRLIVE)=GFL(TRI)
          GCR(NRLIVE)=GCR(TRI)
          GFR(NRLIVE)=GFR(TRI)
          GSA(NRLIVE)=GSA(TRI)
          DBR(NRLIVE)=DBR(TRI)
          DFL(NRLIVE)=DFL(TRI)
          DCR(NRLIVE)=DCR(TRI)
          DFR(NRLIVE)=DFR(TRI)
          DSA(NRLIVE)=DSA(TRI)
          DO 140 I=1,MXFOLC
              DNC(NRLIVE,I)=DNC(TRI,I)
```

```
  140     CONTINUE
  100 CONTINUE
*     Fill up tree arrays with zero values
      if (nrind.le.0) stop ' All trees died ............'
      NRIND=NRLIVE
      MPTY=NRIND+1
      DO 200 TRI=MPTY,MXIND
          TNR(TRI)=0
          SPEC(TRI)=' UNK'
          SPCD(TRI)=0
          XTRUNK(TRI)=0.
          YTRUNK(TRI)=0.
          ZTRUNK(TRI)=0.
          WFL(TRI)=0.
          DO 210 I=1,MXFOLC
              WNC(TRI,I)=0.
  210     CONTINUE
          WBR(TRI)=0.
          WST(TRI)=0.
          WCR(TRI)=0.
          WFR(TRI)=0.
          WRT(TRI)=0.
          DBH(TRI)=0.
          SA(TRI)=0.
          DO 220 I=1,MXSAPR
              SAPR(TRI,I)=0.
  220     CONTINUE
          BA(TRI)=0.
          HGT(TRI)=0.
          HINC(TRI)=0.
          HCB(TRI)=0.
          HCBOLD(TRI)=0.
          CRL(TRI)=0.
          VOL(TRI)=0.
          CSHAPE(TRI)=0.
          CRAD(TRI)=0.
          CRVOL(TRI)=0.
          CRSA(TRI)=0.
          TRAPAR(TRI)=0.
          ABSDIF(TRI)=0.
          DO 230 I=1,MXNRAY
              ABSDIR(TRI,I)=0.
  230     CONTINUE
          PARHCB(TRI)=0.
          YGDM(TRI)=0.
          LAD(TRI)=0.
          VITAL(TRI)=0
          DEAD(TRI)=.FALSE.
          HARVST(TRI)=.FALSE.
          GST(TRI)=0.
          GBR(TRI)=0.
          GFL(TRI)=0.
          GCR(TRI)=0.
          GFR(TRI)=0.
          GSA(TRI)=0.
          DBR(TRI)=0.
          DFL(TRI)=0.
          DCR(TRI)=0.
          DFR(TRI)=0.
          DSA(TRI)=0.
          DO 240 I=1,MXFOLC
              DNC(TRI,I)=0.
  240     CONTINUE
  200 CONTINUE
```

```
      RETURN
      END


*------------------------------------------------------------------*
*  SUBROUTINE CLOSE                                                *
*  Author:  Hank Bartelink                                         *
*  Date of last revision:                                          *
*          Januari 1995                                            *
*  Purpose : this subroutine closes the output units               *
*------------------------------------------------------------------*
      SUBROUTINE CLOSE

*     Close output units
      CLOSE (UNIT=30)
      CLOSE (UNIT=31)
      CLOSE (UNIT=32)
      CLOSE (UNIT=33)
      CLOSE (UNIT=34)
      CLOSE (UNIT=50)

      RETURN
      END


* ------------------------------------------------------------------- *
*     Subroutine FORFLX has been derived from program FORFLUX2        *
*     Author:        H.H. Bartelink                                   *
*                    Dept. of Forestry                                *
*                    Wageningen Agricultural University               *
*     Last revision: June 1996                                        *
*                                                                     *
*     Subroutine FORFLUX-2 calculates the attenuation of radiation    *
*     passing the canopy of a (mixed) forest stand.                   *
*     The absorption by individual trees as well as the radiation     *
*     intensity just below the living crown are calculated. Radiation *
*     interception by trees is calculated from the path length of a beam *
*     traversing through the crowns. Starting points form a grid at the *
*     forest floor.                                                   *
*     FI = Function Indicator:                                        *
*               FI=1    calculate APAR                                *
*               FI=2    calculate PAR below the crown                 *
* ------------------------------------------------------------------- *
      SUBROUTINE FORFLX (MXSPEC, MXIND,MXNRAY,MXSMPL, NRIND,NRSAMP,
     &                              FI,  NRAZ,  CWID,LANGLE,ELLIPS,
     &                             TNR,  SPCD,   HGT,   HCB,  CRAD,
     &                          XTRUNK,YTRUNK,ZTRUNK,CSHAPE,   CRL,
     &                             LAD, XSAMP, YSAMP, ZSAMP,UCOSIS,
     &                          UCOCOS,SINCLI,CONTIL,    CYR,
     &                   ABSDIF,ABSDIR,PARHCB)

      IMPLICIT REAL(A-Z)
      INTEGER FI,I,GP,S
      INTEGER MXSPEC,MXIND,MXNRAY,MXSMPL,CYR
      INTEGER LANGLE
      INTEGER NRIND,TNR,SPCD
      INTEGER NRSAMP,NRAZ
      LOGICAL ELLIPS
      DIMENSION LANGLE(MXSPEC),ELLIPS(MXSPEC)
      DIMENSION TNR(MXIND),SPCD(MXIND),HGT(MXIND),HCB(MXIND),
     &          CRAD(MXIND),XTRUNK(MXIND),YTRUNK(MXIND),ZTRUNK(MXIND),
     &          CSHAPE(MXIND),CRL(MXIND),LAD(MXIND),ABSDIF(MXIND),
```

```
     &          ABSDIR(MXIND,MXNRAY),PARHCB(MXIND)
      DIMENSION XSAMP(MXSMPL),YSAMP(MXSMPL),ZSAMP(MXSMPL)
      DIMENSION UCOSIS(MXNRAY),UCOCOS(MXNRAY),SINCLI(MXNRAY),
     &          CONTIL(MXNRAY)

*     Available flux through horizontal plane (J/m2): presently set to 1
*     to calculate relative absorptions. Multiply ABSDIF & ABSDIR with
*     absolute flux to arrive at absolute amounts of absorbed PAR.
      ACAPAR=1.
      IF (FI.EQ.1) THEN
*         Radiation absorption by individual trees is calculated
*         Initializing
          DO 20 I=1,NRIND
              ABSDIF(I)=0.
              DO 21 S=1,MXNRAY
                  ABSDIR(I,S)=0.
  21          CONTINUE
  20      CONTINUE
*         Calculation of tree absorption: rays move upwards from gridpoints
          DO 100 GP=1,NRSAMP
*             Screen counter
C              PRINT '(''+'',30X,A,I5,A,I7)', 'YEAR=',CYR,', GP=',GP
              GPX=XSAMP(GP)
              GPY=YSAMP(GP)
              GPZ=ZSAMP(GP)
*             Determine which trees are intersected, and for these trees
*             the relative amount of absorbed radiation
              DO 110 S=1,(9*NRAZ)
                  COSIS=UCOSIS(S)
                  COCOS=UCOCOS(S)
                  SICL=SINCLI(S)
                  CTS=CONTIL(S)
*                 Radiation on plane perpendicular to inclination
                  TRANS=ACAPAR/SICL
                  CALL XCROWN (MXSPEC, MXIND,MXNRAY, NRIND,     S,
     &                                 COSIS, COCOS,   GPX,   GPY,
     &                                   GPZ,  SICL,   CTS,  CWID,
     &                                LANGLE,ELLIPS,   TNR,  SPCD,
     &                                   HGT,   HCB,  CRAD,XTRUNK,
     &                                YTRUNK,CSHAPE,   CRL,   LAD,
     &                         ABSDIF,ABSDIR, TRANS)
 110          CONTINUE
 100      CONTINUE

        ELSE
*         Radiation intensity just below the living crown is determined,
*         for diffuse conditions only
          DO 200 I=1,NRIND
              GPX=XTRUNK(I)
              GPY=YTRUNK(I)
              GPZ=ZTRUNK(I)+HCB(I)
*             Determine which trees are intersected,
              DO 210 S=1,(9*NRAZ)
                  COSIS=UCOSIS(S)
                  COCOS=UCOCOS(S)
                  SICL=SINCLI(S)
                  CTS=CONTIL(S)
*                 Radiation on plane perpendicular to inclination
                  TRANS=ACAPAR/SICL
                  CALL XCROWN (MXSPEC, MXIND,MXNRAY, NRIND,     S,
     &                                 COSIS, COCOS,   GPX,   GPY,
     &                                   GPZ,  SICL,   CTS,  CWID,
     &                                LANGLE,ELLIPS,   TNR,  SPCD,
     &                                   HGT,   HCB,  CRAD,XTRUNK,
```

```
     &                                YTRUNK,CSHAPE,   CRL,   LAD,
     &                         ABSDIF,ABSDIR, TRANS)
*                 Transmission through a horizontal plane
                  TRANS=TRANS*SICL
*                 Remaining intensity (MJ/m2) in point below crown
                  PARHCB(I)=PARHCB(I)+TRANS*CONTIL(S)
  210           CONTINUE
  200       CONTINUE
      ENDIF

      RETURN
      END



* ---------------------------------------------------------------------- *
*     SUBROUTINE GRIDP                                                   *
*     Author:  H.H. Bartelink                                            *
*              Dept. of Forestry                                         *
*              Wageningen Agricultural University                        *
*     Date:    Summer 1995                                               *
*                                                                        *
*     Subroutine GRIDP calculates the X-and Y-position of a number of    *
*     gridpoints at the forest floor, based on the plot area and the     *
*     size of the square grid-cells, indicated by the cell-width CWID    *
* ---------------------------------------------------------------------- *
      SUBROUTINE GRIDP (MXSMPL,
     &                           XORI,  YORI,  XMAX,  YMAX,  CWID,
     &                  NRSAMP, XSAMP, YSAMP, ZSAMP)
      IMPLICIT REAL(A-Z)
      INTEGER X,Y,GP,NRX,NRY
      INTEGER MXSMPL,NRSAMP
      DIMENSION XSAMP(MXSMPL),YSAMP(MXSMPL),ZSAMP(MXSMPL)

      DO 100 GP=1,MXSMPL
          XSAMP(GP)=0.
          YSAMP(GP)=0.
          ZSAMP(GP)=0.
  100 CONTINUE

      GP=0
      NRX=NINT((XMAX-XORI)/CWID)
      NRY=NINT((YMAX-YORI)/CWID)
      DO 200 X=1,(NRX+1)
          DO 210 Y=1,(NRY+1)
              GP=GP+1
              IF (GP.GT.MXSMPL) STOP ' Too many gridpoints for memory!'
              XSAMP(GP)=XORI+REAL(X-1)*CWID
              YSAMP(GP)=YORI+REAL(Y-1)*CWID
              ZSAMP(GP)=0.
  210     CONTINUE
  200 CONTINUE
      NRSAMP=GP
      PRINT*,' Number of sample points: ',NRSAMP
      PRINT*,' '

      RETURN
      END


*---------------------------------------------------------------------*
*  SUBROUTINE GROWTH                                                  *
*  Author: H.H. Bartelink                                             *
```

```
*  Date of last revision: Spring 1996                                 *
*  Purpose: This subroutine calculates the distribution keys for      *
*           partitioning of the dry matter available for growth,      *
*           and the resulting growth rates.                           *
*           Partitioning is based on claims of the different biomass *
*           components, which are derived from functional and         *
*           allometric relationships:                                 *
*           - root/shoot-balance: WFR/WFL=f(APAR)                     *
*           - pipe-model theory: FLA/SA=constant                      *
*           - height = f(t,site)                                      *
*           - WBR = f(d,h)                                            *
*           - WCR = f(d)                                              *
*---------------------------------------------------------------------*
      SUBROUTINE GROWTH (MXSPEC, MXIND,   TRI,    YR,
     &                             SLA, BADEN,  HCR1,  HCR2,   SH1,
     &                             SH2,   SH3,  TRUE, PFRFL,PFASA1,
     &                          PFASA2,PFASA3,PDHBR1,PDHBR2,PDHBR3,
     &                          PDWCR1,PDWCR2,PDWCR3,PDWCR4,PDWCR5,
     &                             DBH,  SPCD,   HGT,   HCB,HCBOLD,
     &                             WST,   WBR,   WCR,  YGDM,TRAPAR,
     &                             DBR,   DFL,   DCR,   DFR,   DSA,
     &                      GST,   GBR,   GFL,   GCR,   GFR,   GSA,
     &                            DEAD, VITAL)
      IMPLICIT REAL(A-Z)
      INTEGER I,TRI,SPI,T
      INTEGER MXSPEC,MXIND,YR
      INTEGER SPCD,VITAL
      LOGICAL DEAD
      PARAMETER (PI=3.1416)
      DIMENSION TRUHLP(10)
      DIMENSION SLA(MXSPEC),BADEN(MXSPEC),HCR1(MXSPEC),HCR2(MXSPEC),
     &          SH1(MXSPEC),SH2(MXSPEC),SH3(MXSPEC),TRUE(MXSPEC,10),
     &          PFRFL(MXSPEC),PFASA1(MXSPEC),PFASA2(MXSPEC),
     &          PFASA3(MXSPEC),PDHBR1(MXSPEC),PDHBR2(MXSPEC),
     &          PDHBR3(MXSPEC),PDWCR1(MXSPEC),PDWCR2(MXSPEC),
     &          PDWCR3(MXSPEC),PDWCR4(MXSPEC),PDWCR5(MXSPEC)
      DIMENSION DBH(MXIND),SPCD(MXIND),HGT(MXIND),HCB(MXIND),
     &          HCBOLD(MXIND),WST(MXIND),WBR(MXIND),WCR(MXIND),
     &          YGDM(MXIND),TRAPAR(MXIND),GST(MXIND),GBR(MXIND),
     &          GFL(MXIND),GCR(MXIND),GFR(MXIND),GSA(MXIND),
     &          DBR(MXIND),DFL(MXIND),DCR(MXIND),DFR(MXIND),DSA(MXIND),
     &          DEAD(MXIND),VITAL(MXIND)

*     Leave the subroutine when no light is intercepted
      IF (TRAPAR(TRI).LE.0.) RETURN

*     Total dry matter increment depends on RUE (species-dependent)
*     and on absorbed PAR
      DO 100 T=1,10
         TRUHLP(T)=TRUE(SPCD(TRI),T)
  100 CONTINUE
*     RUE is in g/MJ, TRAPAR in MJ/year, GDM in Kg(!)/year
*     RUE depends on foliage efficiency: APAR per unit foliage area
      FE=1.
      RUE=LINT(TRUHLP,10,FE)
*     Total annual amount (Kg/year)
      YGDM(TRI)=RUE*TRAPAR(TRI)/1000.

*     Help-variables
      SPI=SPCD(TRI)
      C11=  HCR1(SPI)
      C12=  HCR2(SPI)
      C21=PFASA1(SPI)
      C22=PFASA2(SPI)
```

```
      C23=PFASA3(SPI)
      C3 = PFRFL(SPI)
      C41=PDHBR1(SPI)
      C42=PDHBR2(SPI)
      C43=PDHBR3(SPI)
      C51=PDWCR1(SPI)
      C52=PDWCR2(SPI)
      C53=PDWCR3(SPI)
      C54=PDWCR4(SPI)
      C55=PDWCR5(SPI)
      C61=   SH1(SPI)
      C62=   SH2(SPI)
      C63=   SH3(SPI)
*     GFL is calculated iteratively, based on the functional relationships
*     Starting value of GFL
      GFL(TRI)=0.1*YGDM(TRI)
      GOLD=GFL(TRI)
      RATIO=0.
      I=0
*     Start of the iterative loop:
  200 IF (RATIO.LT.0.99.OR.RATIO.GT.1.01) THEN
*         Avoid endless loop due to small differences between GFL and GOLD
          I=I+1
          IF (I.GT.100) THEN
              WRITE(50,'(2I5,2F10.3)') YR,TRI,GFL(TRI),GOLD
              GOTO 201
          ENDIF
          GFL(TRI)=0.99*GOLD+0.01*GFL(TRI).
*         Here the heart of the rate calculation starts
          GOLD=GFL(TRI)
          SQRD2=((DBH(TRI)/100.)**2.)+((4.*SLA(SPI))/(PI*C21))
     &       *(GFL(TRI)-DFL(TRI))+((4.*C22)/(PI*C21))
     &       *(HCB(TRI)-HCBOLD(TRI)) +(4./PI)*DSA(TRI)
*         Avoid root of negative value: when DFL exceeds GFL, tree dies
          IF (SQRD2.LT.0.) THEN
              GFL(TRI)=99.9
              DEAD(TRI)=.TRUE.
              RETURN
            ELSE
              D2=100.*(SQRD2**0.5)
          ENDIF
          GFL(TRI)=YGDM(TRI)
     &         -(C41*(D2**C42)*(HGT(TRI)**C43) -WBR(TRI)+DBR(TRI))
     &         -((BADEN(SPI)/1000.)*(D2**C61)*(HGT(TRI)**C62)
     &                                    *EXP(C63)-WST(TRI))
     &         -(C3*(GFL(TRI)-DFL(TRI)) +DFR(TRI))
     &         -(C51 +C52*(D2**C53) +C54*(D2**C55) -WCR(TRI)+DCR(TRI))
          RATIO=0.
          IF (GFL(TRI).NE.0.) RATIO=GOLD/GFL(TRI)
          GOTO 200
      ENDIF
*     The outcome of the iterative process is an estimate for GFL:
  201 D2=100.*(((DBH(TRI)/100.)**2.)+((4.*SLA(SPI))/(PI*C21))
     &   *(GFL(TRI)-DFL(TRI))+((4.*C22)/(PI*C21))*(HCB(TRI)-HCBOLD(TRI))
     &   +(4./PI)*DSA(TRI))**0.5
*     Dry matter partitioned to branches, stem, and roots, and sapwood
*     area increment
      GBR(TRI)=C41*(D2**C42)*(HGT(TRI)**C43) -WBR(TRI)+DBR(TRI)
      GST(TRI)=(BADEN(SPI)/1000.)*(D2**C61)*(HGT(TRI)**C62)*EXP(C63)
     &         -WST(TRI)
      GFR(TRI)=C3*(GFL(TRI)-DFL(TRI)) +DFR(TRI)
      GCR(TRI)=C51 +C52*(D2**C53) +C54*(D2**C55) -WCR(TRI)+DCR(TRI)
      GSA(TRI)=(SLA(SPI)/C21)*(GFL(TRI)-DFL(TRI))
     &         +(C22/C21)*(HCB(TRI)-HCBOLD(TRI)) +DSA(TRI)
```

```
      RETURN
      END


*----------------------------------------------------------------------*
*  SUBROUTINE HEIGHT                                                   *
*  Author:  Hank Bartelink                                             *
*  Date of last revision:                                              *
*           December 1995                                              *
*  Purpose: Calculates new tree heights and crown dimensions in an     *
*           annual time-step. Height and crown base are used to        *
*           determine partitioning.                                    *
*           Upward crown-shift is dependent on APAR.                   *
*----------------------------------------------------------------------*
      SUBROUTINE HEIGHT (MXSPEC, MXIND,   TRI,
     &                           SPAGE,  SMAX,  HCR1,  HCR2,  SPCD,
     &                             HGT,   HCB,PARHCB,   DBH,  ACL1,
     &                            ACL2,  ACL3,
     &                     HINC,HCBOLD,   CRL)

      IMPLICIT REAL(A-Z)
      INTEGER TRI
      INTEGER MXSPEC,MXIND
      INTEGER SPAGE,SPCD
      PARAMETER (PI=3.14159265359,DGRD=0.017453292)
      DIMENSION SPAGE(MXSPEC),SMAX(MXSPEC),HCR1(MXSPEC),HCR2(MXSPEC),
     &          ACL1(MXSPEC),ACL2(MXSPEC),ACL3(MXSPEC)
      DIMENSION SPCD(MXIND),HGT(MXIND),HINC(MXIND),HCB(MXIND),
     &          HCBOLD(MXIND),CRL(MXIND),PARHCB(MXIND),DBH(MXIND)

*     Height increment follows from Chapman-Richards-curve
      AGE=SPAGE(SPCD(TRI))
      HINC(TRI)=-SMAX(SPCD(TRI))*((1.-EXP(HCR1(SPCD(TRI))*AGE))
     &      **(HCR2(SPCD(TRI))-1.))*HCR1(SPCD(TRI))*HCR2(SPCD(TRI))
     &      *EXP(HCR1(SPCD(TRI))*AGE)
*     New tree height
      HGT(TRI)=HGT(TRI)+HINC(TRI)

*     Shifting-up of crown base depends on radiation intensity below crown
*     Save the old value for calculations in the partitioning routine
      HCBOLD(TRI)=HCB(TRI)
*     Move up the crown base 0.5m if annual transmission is less than 5%
      IF (PARHCB(TRI).LT.0.05) HCB(TRI)=HCB(TRI)+0.5
*     Crown length (m)
      CRL(TRI)=HGT(TRI)-HCB(TRI)

*     Alternative approach: allometric relationships
      CRL(TRI)=ACL1(SPCD(TRI))+ACL2(SPCD(TRI))*DBH(TRI)+
     &         ACL3(SPCD(TRI))*DBH(TRI)**2.
      CRL(TRI)=AMIN1(AMAX1(0.33*HGT(TRI),CRL(TRI)),HGT(TRI))
      HCB(TRI)=AMAX1(HCBOLD(TRI),(HGT(TRI)-CRL(TRI)))

      RETURN
      END


*----------------------------------------------------------------------*
*  SUBROUTINE INITL                                                    *
*  Date of last revision:                                              *
*           Januari 1995 by Hank Bartelink                             *
*  Purpose: This subroutine opens input data-files & output files,     *
```

```
*           and writes headings to the output files                  *
*--------------------------------------------------------------------*
      SUBROUTINE INITL

      IMPLICIT REAL(A-Z)

      OPEN (UNIT=23,FILE=  'RUNMIX.DAT',STATUS='OLD')
      OPEN (UNIT=24,FILE=   'STAND.DAT',STATUS='OLD')
      OPEN (UNIT=25,FILE=  'MANAGE.DAT',STATUS='OLD')
      OPEN (UNIT=30,FILE=  'TRGROW.OUT',STATUS='OLD')
      OPEN (UNIT=31,FILE=  'TRDIMS.OUT',STATUS='OLD')
      OPEN (UNIT=32,FILE=  'TRLOSS.OUT',STATUS='OLD')
      OPEN (UNIT=33,FILE=  'SPBIOM.OUT',STATUS='OLD')
      OPEN (UNIT=331,FILE=  'SPPROD.OUT',STATUS='OLD')
      OPEN (UNIT=34,FILE=  'STBIOM.OUT',STATUS='OLD')
      OPEN (UNIT=35,FILE=  'STPROD.OUT',STATUS='OLD')
      OPEN (UNIT=36,FILE=  'YLDTBL.OUT',STATUS='OLD')
      OPEN (UNIT=50,FILE=  'WARNNG.MSG',STATUS='OLD')

      WRITE(30,'(A)') 'Growth rates'
      WRITE(30,'(2A35)')
     &'tree species  age  dbh  Gtot  Gfl  ',
     &'  Gbr   Gst   Gcr   Gfr    Gsa     '
      WRITE(30,'(2A35)')
     &' nr     #      yr   cm   kg    kg  ',
     &'   kg    kg    kg    kg     dm2    '

      WRITE(31,'(A)') 'Tree structure and condition'
      WRITE(31,'(2A35)')
     &'tree species  age  dbh height  hcb ',
     &' crrad crsharea  PARcb  Vital      '
      WRITE(31,'(2A35)')
     &' nr     #      yr   cm     m      m  ',
     &'   m      m2     fract    #        '

      WRITE(32,'(A)') 'Turn-over'
      WRITE(32,'(A)')
     &'tree species  age  dbh  Dfol  Dbr   Dcr   Dfr     Dsa'
      WRITE(32,'(A)')
     &' nr     #      yr   cm  kg     kg    kg    kg     dm2'

      WRITE(33,'(A)') 'Amounts per species'
      WRITE(33,'(2A37)')
     &'  age    spec foliage  branch    stem',
     &'   root      LA    BA      volume     '
      WRITE(33,'(2A37)')
     &'   #       #     ton      ton     ton',
     &'    ton      m2     m2      m3       '

      WRITE(34,'(A)') ' Amounts per stand'
      WRITE(34,'(2A37)')
     &' year    stem  branch  foliage  roots',
     &'    LAI      BA     V      litter    '
      WRITE(34,'(2A37)')
     &'   #      ton    ton    ton     ton  ',
     &'     -       m2     m3      ton      '

      WRITE(35,'(A)') '  Stand composition and growth rate: per ha'
      WRITE(35,'(A61)')
     &'  Stand composition        Growth             Yield        '
      WRITE(35,'(A61)')
     &'  year   N     BA      V   drymatter   V      BA     V     '
      WRITE(35,'(A61)')
     &'   #     #     m2     m3      ton     m3      m2    m3     '
```

```
      WRITE(36,'(A)') '  Yield table info: per ha'
      WRITE(36,'(A30)')
     &'  year   N     BA      V     '
      WRITE(36,'(A30)')
     &'   #     #     m2     m3     '

      WRITE(50,'(A)') ' Iterative growth calculation interrupted at:'
      WRITE(50,'(A)') ' Year Tree    GFL       GOLD'

      RETURN
      END


*-----------------------------------------------------------------------*
*  SUBROUTINE INPUT                                                     *
*  Author: Hank Bartelink                                               *
*  Date of revision:                                                    *
*          Januari 1997                                                 *
*  Subroutine INPUT reads the variables from the input data-files,      *
*  calculates some derived variables, and declares some constants.      *
*-----------------------------------------------------------------------*
      SUBROUTINE INPUT (MXSPEC, MXIND,MXTHIN,MXSAPR,MXFOLC,
     &                                NRSPEC, NRIND, NRSAP, NFOLC,
     &                           NRAZ,STYEAR,ENYEAR,    YR, START,
     &                         SPILAB, SPAGE,LANGLE,BUDFLS,FOLFAL,
     &                            SLA, BADEN,   NLC,
     &                          BRTOR, CRTOR, FRTOR,
     &                           SMAX,  HCR1,  HCR2,   SH1,   SH2,
     &                            SH3,  RSH1,  RSH2,  RSH3,  TRUE,
     &                         ELLIPS, PFRFL,PFASA1,PFASA2,PFASA3,
     &                         PDHBR1,PDHBR2,PDHBR3,PDWCR1,PDWCR2,
     &                         PDWCR3,PDWCR4,PDWCR5,  MCM1,  MCM2,
     &                           ACL1,  ACL2,  ACL3,THINYR,THINFR,
     &                         THINTP,   ONR,
     &                            TNR,  SPEC,  SPCD,   HGT,   HCB,
     &                           CRAD,   WST,   WBR,   WCR,   WFR,
     &                            WRT,   WNC,   WFL,    SA,  SAPR,
     &                         XTRUNK,YTRUNK,ZTRUNK,   CRL, VITAL,
     &                           DEAD,HARVST,
     &                           XORI,  YORI,  XMAX,  YMAX,
     &                           X1P,X2P,Y1P,Y2P,
     &                           CWID,PLOTAR,  X1C,X2C,Y1C,Y2C,CPLOT)

      IMPLICIT REAL(A-Z)
      INTEGER TRI,I,SP,ILEN,SPUN,STRLEN,FCSPEF,WSSTAR,RINGS,SPI
      CHARACTER*15 SPEFIL
      INTEGER MXSPEC,MXIND,MXTHIN,MXSAPR,MXFOLC
      INTEGER YR,STYEAR,ENYEAR
      INTEGER NRSPEC,LANGLE,BUDFLS,FOLFAL,NRSAP,NFOLC,SPAGE
      INTEGER THINYR,THINTP
      INTEGER NRIND,TNR,ONR,SPCD,VITAL
      INTEGER NRAZ
      CHARACTER*4 SPILAB,SPEC
      LOGICAL ELLIPS,DEAD,HARVST
      PARAMETER (PI=3.141592654,DGRD=0.017453292)
      DIMENSION SPILAB(MXSPEC),SPAGE(MXSPEC),LANGLE(MXSPEC),
     &          BUDFLS(MXSPEC),FOLFAL(MXSPEC),SLA(MXSPEC),
     &          BADEN(MXSPEC),NLC(MXSPEC),
     &          BRTOR(MXSPEC),CRTOR(MXSPEC),FRTOR(MXSPEC),
     &          SMAX(MXSPEC),HCR1(MXSPEC),HCR2(MXSPEC),SH1(MXSPEC),
     &          SH2(MXSPEC),SH3(MXSPEC),RSH1(MXSPEC),RSH2(MXSPEC),
     &          RSH3(MXSPEC),TRUE(MXSPEC,10),ELLIPS(MXSPEC),
     &          PFRFL(MXSPEC),PFASA1(MXSPEC),PFASA2(MXSPEC),
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```
     &          PFASA3(MXSPEC),PDHBR1(MXSPEC),PDHBR2(MXSPEC),
     &          PDHBR3(MXSPEC),PDWCR1(MXSPEC),PDWCR2(MXSPEC),
     &          PDWCR3(MXSPEC),PDWCR4(MXSPEC),PDWCR5(MXSPEC),
     &          NRSAP(MXSPEC),NFOLC(MXSPEC),MCM1(MXSPEC),MCM2(MXSPEC),
     &          ACL1(MXSPEC),ACL2(MXSPEC),ACL3(MXSPEC)
      DIMENSION THINYR(MXTHIN),THINFR(MXSPEC,MXTHIN),
     &          THINTP(MXSPEC,MXTHIN)
      DIMENSION TNR(MXIND),ONR(MXIND),
     &          SPEC(MXIND),SPCD(MXIND),HGT(MXIND),
     &          HCB(MXIND),CRAD(MXIND),WST(MXIND),WBR(MXIND),
     &          WCR(MXIND),WFR(MXIND),WRT(MXIND),WNC(MXIND,MXFOLC),
     &          WFL(MXIND),SA(MXIND),SAPR(MXIND,MXSAPR),
     &          XTRUNK(MXIND),YTRUNK(MXIND),ZTRUNK(MXIND),
     &          CRL(MXIND),VITAL(MXIND),DEAD(MXIND),HARVST(MXIND)

      PRINT*,'  Reading data-files....... '


*     Number of azimuthal directions:
      NRAZ=12

*     Reading run specifications from RUNMIX.DAT:
*     Starting year, ending year:
      CALL MOFILP(23)
      READ(23,*) STYEAR,ENYEAR
*     Grid size, number of species, & species file-names;
*     species data are derived from the specified files
      CALL MOFILP(23)
      READ(23,*) XORI,YORI,XMAX,YMAX,CWID
*     Origin should indicate lower left corner of the grid
      IF (XORI.GT.XMAX.OR.YORI.GT.YMAX) STOP ' Impossible grid-size! '
      CALL MOFILP(23)
      READ(23,*) NRSPEC
      IF (NRSPEC.GT.MXSPEC) STOP ' Too many species!'
      DO 100 SP=1,NRSPEC
          CALL MOFILP(23)
          READ(23,'(A)') SPEFIL
          STRLEN=ILEN(SPEFIL)
          SPUN=230+SP
          OPEN(UNIT=SPUN,FILE=SPEFIL(1:STRLEN),STATUS='OLD')
*         Species identification label and species code
          FCSPEF=WSSTAR(SPEFIL)
          SPILAB(SP)=SPEFIL(FCSPEF:FCSPEF+4)
*         Species age
          CALL MOFILP(SPUN)
          READ (SPUN,*) SPAGE(SP)
*         Radiation-use efficiency in relation to temperature:
          CALL MOFILP(SPUN)
          READ (SPUN,*) (TRUE(SP,I),I=1,9,2)
          READ (SPUN,*) (TRUE(SP,I),I=2,10,2)
*         Date of bud-flush & leaf fall
          CALL MOFILP(SPUN)
          READ (SPUN,*) BUDFLS(SP),FOLFAL(SP)
*         Number of needle age-classes & needle loss-coefficient
          CALL MOFILP(SPUN)
          READ (SPUN,*) NFOLC(SP),NLC(SP)
          IF(NFOLC(SP).GT.MXFOLC) STOP ' Too many foliage age-classes!'
*         Crown-form, leaf angle-distribution & specific leaf area
          CALL MOFILP(SPUN)
          READ (SPUN,*) ELLIPS(SP),LANGLE(SP),SLA(SP)
*         Basic density of stemwood & number of sapwood rings
          CALL MOFILP(SPUN)
          READ (SPUN,*) BADEN(SP), NRSAP(SP)
          IF(NRSAP(SP).GT.MXSAPR) STOP ' Too many sapwood rings!'
```

```
*         Annual root biomass turnover rates (branches and roots):
          CALL MOFILP(SPUN)
          READ (SPUN,*) BRTOR(SP),CRTOR(SP),FRTOR(SP)
*         Root-shoot ratio (kg/kg) & foliage/sapwood area ratio (m2/m2)
          CALL MOFILP(SPUN)
          READ (SPUN,*) PFRFL(SP), PFASA1(SP),PFASA2(SP),PFASA3(SP)
*         Coefficients for allometric relationship on branch biomass
          CALL MOFILP(SPUN)
          READ (SPUN,*) PDHBR1(SP),PDHBR2(SP),PDHBR3(SP)
*         Coefficients for allometric relationship on coarse root biomass
          CALL MOFILP(SPUN)
          READ (SPUN,*) PDWCR1(SP),PDWCR2(SP),PDWCR3(SP),
     &                  PDWCR4(SP),PDWCR5(SP)
*         Maximum tree height for the region, and the regression
*         coefficients for Chapman-Richards height equation:
          CALL MOFILP(SPUN)
          READ (SPUN,*) SMAX(SP),HCR1(SP),HCR2(SP)
*         Regression-coefficients for Shumacher and Hall volume equation:
          CALL MOFILP(SPUN)
          READ (SPUN,*) SH1(SP),SH2(SP),SH3(SP)
*         Reversed Shumacher and Hall coefficients:
          RSH1(SP)=(EXP(SH3(SP)))**(-1./SH1(SP))
          RSH2(SP)=1./SH1(SP)
          RSH3(SP)=-SH2(SP)/SH1(SP)
*         Coefficients on relationship between crown size and dbh (McMahon)
          CALL MOFILP(SPUN)
          READ (SPUN,*) MCM1(SP),MCM2(SP)
*         Coefficients on relationship between crown length and dbh
          CALL MOFILP(SPUN)
          READ (SPUN,*) ACL1(SP),ACL2(SP),ACL3(SP)
          CLOSE (SPUN)
 100  CONTINUE

*     Reading tree data from STAND.DAT:

*     Tree number at the beginning of the simulation,
      CALL MOFILP(24)
      READ (24,*) NRIND
      IF (NRIND.GT.MXIND) STOP ' Too many trees!'
*     Plot size
*     Boundaries of the plot and the central plot area (target trees)
      CALL MOFILP(24)
      READ (24,*) X1P,X2P,Y1P,Y2P
      CALL MOFILP(24)
      READ (24,*) X1C,X2C,Y1C,Y2C
*     Area of the total plot
      PLOTAR=(X2P-X1P)*(Y2P-Y1P)
*     Area of the central plot
      CPLOT=(X2C-X1C)*(Y2C-Y1C)
*     Initial data on tree age, size (height, height of the crown
*     base, crown radius), and dry weight of biomass components
*     (Note: dbh is calculated from WST and tree height!)
      DO 200 TRI=1,NRIND
          CALL MOFILP(24)
          READ (24,*) TNR(TRI),XTRUNK(TRI),YTRUNK(TRI),ZTRUNK(TRI),
     &                SPCD(TRI),CRAD(TRI),HGT(TRI),HCB(TRI),WFL(TRI),
     &                WBR(TRI),WST(TRI),WCR(TRI),WFR(TRI),SA(TRI)
*         Save original tree number
          ONR(TRI)=TNR(TRI)
*         Species identification label
          SPI=SPCD(TRI)
          SPEC(TRI)=SPILAB(SPI)
*         Crown length (m)
          CRL(TRI)=HGT(TRI)-HCB(TRI)
```

```
*         Total root biomass
          WRT(TRI)=WCR(TRI)+WFR(TRI)
*         Evergreens: distribute foliage over age-classes
*         Initial (daily) foliage biomass per age-class
*         using Mohren's (1987) approach; no mortality in new foliage
          IF (NFOLC(SPI).GT.1) THEN
              IF (NFOLC(SPI).EQ.2) THEN
                  WNC(TRI,1)=0.
                  WNC(TRI,2)=1.0*WFL(TRI)
                ELSE
                  X=0.
                  DO 210 I=1,NFOLC(SPI)-2
                      X=X+EXP(-(0.5*NLC(SPI)*(I**2.)))
  210             CONTINUE
                  WNC(TRI,1)=0.
                  WNC(TRI,2)=WFL(TRI)/(1.+X)
                  DO 211 I=3,NFOLC(SPI)
                      WNC(TRI,I)=WNC(TRI,2)*EXP(-(0.5*NLC(SPI)*
     &                           ((I-2)**2.)))
  211             CONTINUE
              ENDIF
            ELSE
                DO 212 I=1,MXFOLC
                    WNC(TRI,I)=0.
  212           CONTINUE
          ENDIF
*         Sapwood cross-sectional area at breast height:
*         Initially, sapwood area is assumed equal for all annual rings
          DO 220 I=1,MXSAPR
              SAPR(TRI,I)=0.
  220     CONTINUE
          IF (SPAGE(SPCD(TRI)).GE.NRSAP(SPI)) THEN
              RINGS=NRSAP(SPI)
            ELSE
              RINGS=SPAGE(SPCD(TRI))
          ENDIF
          DO 230 I=1,RINGS
              SAPR(TRI,I)=SA(TRI)/REAL(RINGS)
  230     CONTINUE
*         Labels indicating tree vitality
          VITAL(TRI)=0
          DEAD(TRI)=.FALSE.
          HARVST(TRI)=.FALSE.
  200 CONTINUE

*     Reading thinning data from MANAGE.DAT:
*     Stand-ages at which thinning occurs:
      CALL MOFILP(25)
      READ(25,*) (THINYR(I),I=1,15)
*     Species-specific thinning regimes
      DO 300 SP=1,NRSPEC
*         Thinning intensity (fraction of species basal area in the stand)
          CALL MOFILP(25)
          READ(25,*) (THINFR(SP,I),I=1,15)
*         Thinning type
          CALL MOFILP(25)
          READ(25,*) (THINTP(SP,I),I=1,15)
  300 CONTINUE

*     Initialize year number
      YR=STYEAR
      START=0.

*     End of input subroutine
```

```
*     Close used units:
      CLOSE (23)
      CLOSE (24)
      CLOSE (25)

      PRINT*,'  ..finished.  Start run...'
      PRINT*,' '

      RETURN
      END



*----------------------------------------------------------------------*
*  SUBROUTINE LITDYN                                                   *
*  Author: H.H. Bartelink                                              *
*  Date of last revision: Winter 1995/96                               *
*  Purpose: This subroutine determines total amount of litter          *
*----------------------------------------------------------------------*
      SUBROUTINE LITDYN (MXSPEC, MXIND, NRIND,PLOTAR,
     &                           BADEN,   DBH,  SPCD,   WST,   WBR,
     &                             WCR,   WFR,   WFL,  DEAD,HARVST,
     &                             DBR,   DFL,   DCR,   DFR,
     &                          XTRUNK,YTRUNK,
     &                             X1C,   X2C,   Y1C,   Y2C,
     &                   YIELDG,YIELDV,LITTER)

      IMPLICIT REAL(A-Z)
      INTEGER TRI
      INTEGER MXSPEC,MXIND
      INTEGER NRIND,SPCD
      LOGICAL DEAD,HARVST
      PARAMETER (PI=3.1415927)

      DIMENSION BADEN(MXSPEC)
      DIMENSION DBH(MXIND),SPCD(MXIND),WST(MXIND),
     &          WBR(MXIND),WCR(MXIND),WFR(MXIND),WFL(MXIND),
     &          DEAD(MXIND),HARVST(MXIND),DBR(MXIND),DFL(MXIND),
     &          DCR(MXIND),DFR(MXIND),XTRUNK(MXIND),YTRUNK(MXIND)

      DO 100 TRI=1,NRIND
*         Only trees in the center are used to calculate stand totals
          IF (XTRUNK(TRI).LT.X1C.OR.XTRUNK(TRI).GT.X2C.OR.
     &        YTRUNK(TRI).LT.Y1C.OR.YTRUNK(TRI).GT.Y2C) GOTO 100
*         Biomass loss due to turn-over
          LOSTUO=DFL(TRI)+DBR(TRI)+DCR(TRI)+DFR(TRI)
*         Biomass loss due to tree mortality: dead stems not harvested
          IF (DEAD(TRI)) THEN
              LOSMOR=WFL(TRI)+WBR(TRI)+WST(TRI)+WCR(TRI)+WFR(TRI)
            ELSE
              LOSMOR=0.
          ENDIF
*         Biomass loss due to harvesting: stems are removed
*         Total harvested stem biomass (in m3/ha and m2/ha)
          IF (HARVST(TRI)) THEN
              LOSHAR=WFL(TRI)+WBR(TRI)+WCR(TRI)+WFR(TRI)
              YIELDV=YIELDV+
     &               (WST(TRI)/BADEN(SPCD(TRI)))*10000./PLOTAR
              YIELDG=YIELDG+
     &               ((PI*(0.005*DBH(TRI))**2.))*10000./PLOTAR
            ELSE
              LOSHAR=0.
          ENDIF
*         Increase total amount of litter (ton/ha)
```

```
          LITTER=LITTER+(LOSTUO+LOSMOR+LOSHAR)*(10000./PLOTAR)/1000.
  100 CONTINUE

      RETURN
      END



*-----------------------------------------------------------------------*
*  SUBROUTINE MORTAL                                                    *
*  Author: H.H. Bartelink                                               *
*  Date of last revision: Winter 1995/96                                *
*  Purpose: This subroutine determines natural tree death               *
*-----------------------------------------------------------------------*
      SUBROUTINE MORTAL (MXSPEC, MXIND, NRIND,
     &                            MCM1,  MCM2,   DBH,  SPCD,
     &                             HGT,  CRSA, VITAL,
     &                     DEAD)
      IMPLICIT REAL(A-Z)
      INTEGER TRI
      INTEGER MXSPEC,MXIND
      INTEGER NRIND,SPCD,VITAL
      LOGICAL DEAD
      DIMENSION MCM1(MXSPEC),MCM2(MXSPEC)
      DIMENSION DBH(MXIND),SPCD(MXIND),HGT(MXIND),CRSA(MXIND),
     &          VITAL(MXIND),DEAD(MXIND)

      DO 100 TRI=1,NRIND
      IF (DEAD(TRI)) GOTO 100
*         Tree mortality based on wind exposure (elasticity theory)
          CRIT=(CRSA(TRI)*HGT(TRI)/MCM1(SPCD(TRI)))**
     &         (1./MCM2(SPCD(TRI)))
*         Tree becomes susceptible to wind when actual dbh is less than
*         67% of the mechanically required dbh
          IF (0.67*CRIT.GT.DBH(TRI)) VITAL(TRI)=VITAL(TRI)-1
*         Tree mortality due to extreme h/dbh-ratio
          HDR=HGT(TRI)/DBH(TRI)
          IF (HDR.GT.1.5) VITAL(TRI)=VITAL(TRI)-1
*         Re-vitalisation
          IF (VITAL(TRI).LT.0.AND.CRIT.LE.DBH(TRI).AND.HDR.LE.1.5)
     &        VITAL(TRI)=VITAL(TRI)+1
          IF (VITAL(TRI).GT.0) VITAL(TRI)=0
*         Mortality occurs after 3 consecutive years of un-balance
          IF (VITAL(TRI).LE.-3) THEN
              DEAD(TRI)=.TRUE.
            ELSE
              DEAD(TRI)=.FALSE.
          ENDIF
  100 CONTINUE

      RETURN
      END



*-----------------------------------------------------------------------*
*  SUBROUTINE OUTPUT                                                    *
*  Author:  Hank Bartelink                                              *
*  Date of last revision:                                               *
*           Januari 1995                                                *
*  Purpose : this subroutine writes results to the output files         *
*-----------------------------------------------------------------------*
      SUBROUTINE OUTPUT (MXSPEC, MXIND,NRSPEC, NRIND,THTIME,
     &                       YR,CPLOT,PLOTAR,
```

```
     &                         SPAGE,SPILAB,   ONR,
     &                      TNR,   DBH,  SPEC,  SPCD,   HGT,
     &                             HCB,  CRAD,  CRSA,PARHCB,
     &                           VITAL,  YGDM,   GST,   GBR,
     &                             GFL,   GCR,   GFR,   GSA,   DBR,
     &                             DFL,   DCR,   DFR,   DSA,
     &                          XTRUNK,YTRUNK,ZTRUNK,
     &                          SLAREA,  SWFL, SWBRN,  SWST,  SWRT,
     &                             SBA,  SVOL, SVINC,
     &                   HSD,HWST,HWBRN,HWFL,HWRT,HLAI,HBA,HVOL,LITTER,
     &                   TOTGDM,TVINC,YIELDG,YIELDV)
      IMPLICIT REAL(A-Z)
      INTEGER TRI,SP
      INTEGER MXSPEC,MXIND,YR
      INTEGER NRSPEC,SPAGE
      INTEGER NRIND,HSD,TNR,ONR,SPCD,VITAL
      LOGICAL THTIME
      CHARACTER*4 SPILAB,SPEC
      DIMENSION SPILAB(MXSPEC),SPAGE(MXSPEC),SLAREA(MXSPEC),
     &          SWFL(MXSPEC),SWBRN(MXSPEC),SWST(MXSPEC),SWRT(MXSPEC),
     &          SBA(MXSPEC),SVOL(MXSPEC),SVINC(MXSPEC)
      DIMENSION TNR(MXIND),ONR(MXIND),XTRUNK(MXIND),YTRUNK(MXIND),
     &          ZTRUNK(MXIND),DBH(MXIND),SPEC(MXIND),
     &          SPCD(MXIND),HGT(MXIND),HCB(MXIND),CRAD(MXIND),
     &          CRSA(MXIND),PARHCB(MXIND),VITAL(MXIND),
     &          YGDM(MXIND),GST(MXIND),GBR(MXIND),GFL(MXIND),
     &          GCR(MXIND),GFR(MXIND),GSA(MXIND),
     &          DBR(MXIND),DFL(MXIND),DCR(MXIND),DFR(MXIND),DSA(MXIND)

*     Amounts are calculated per central plot CPLOT, not per plot PLOTAR
      DO 1 SP=1,NRSPEC
          SWFL(SP)=SWFL(SP)*PLOTAR/CPLOT
          SWBRN(SP)=SWBRN(SP)*PLOTAR/CPLOT
          SWST(SP)=SWST(SP)*PLOTAR/CPLOT
          SWRT(SP)=SWRT(SP)*PLOTAR/CPLOT
          SLAREA(SP)=SLAREA(SP)*PLOTAR/CPLOT
          SBA(SP)=SBA(SP)*PLOTAR/CPLOT
          SVOL(SP)=SVOL(SP)*PLOTAR/CPLOT
          SVINC(SP)=SVINC(SP)*PLOTAR/CPLOT
    1 CONTINUE
      HWST=HWST*PLOTAR/CPLOT
      HWBRN=HWBRN*PLOTAR/CPLOT
      HWFL=HWFL*PLOTAR/CPLOT
      HWRT=HWRT*PLOTAR/CPLOT
      HLAI=HLAI*PLOTAR/CPLOT
      HBA=HBA*PLOTAR/CPLOT
      HVOL=HVOL*PLOTAR/CPLOT
      HSD=HSD*PLOTAR/CPLOT
      TOTGDM=TOTGDM*PLOTAR/CPLOT
      TVINC=TVINC*PLOTAR/CPLOT
      YIELDG=YIELDG
      YIELDV=YIELDV
      LITTER=LITTER

*     Annual growth rates per tree
 30   FORMAT(I5,A6,I5,7(F6.1),F8.2)
      DO 100 TRI=1,NRIND
          WRITE(30,30) ONR(TRI),SPEC(TRI),SPAGE(SPCD(TRI)),DBH(TRI),
     &                 YGDM(TRI),GFL(TRI),GBR(TRI),GST(TRI),GCR(TRI),
     &                 GFR(TRI),GSA(TRI)*100.
  100 CONTINUE

*     Resulting tree structure
 31   FORMAT(I5,A6,I5,4(F6.1),F8.1,F9.3,I5)
```

```
      DO 200 TRI=1,NRIND
          WRITE(31,31) ONR(TRI),SPEC(TRI),SPAGE(SPCD(TRI)),DBH(TRI),
     &                 HGT(TRI),HCB(TRI),CRAD(TRI),CRSA(TRI),
     &                 PARHCB(TRI),VITAL(TRI)
  200 CONTINUE

*     Annual turnover rates per tree (kg, m2)
 32   FORMAT(I5,A6,I5,5(F6.1),F8.2)
      DO 300 TRI=1,NRIND
          WRITE(32,32) TNR(TRI),SPEC(TRI),SPAGE(SPCD(TRI)),DBH(TRI),
     &                 DFL(TRI),DBR(TRI),DCR(TRI),DFR(TRI),DSA(TRI)*100.
  300 CONTINUE

*     Results summarized per species (ton, m2, m3)
 33   FORMAT(I5,A8,7(F8.2))
      DO 400 SP=1,NRSPEC
          WRITE(33,33) SPAGE(SP),SPILAB(SP),SWFL(SP),SWBRN(SP),
     &                 SWST(SP),SWRT(SP),SLAREA(SP),SBA(SP),SVOL(SP)
  400 CONTINUE
      WRITE(331,*) SPAGE(1),SVINC(1),SVINC(2)

*     Amounts per stand (per ha)
 34   FORMAT(I5,8(F8.2))
      WRITE(34,34) YR,HWST,HWBRN,HWFL,HWRT,HLAI,HBA,HVOL,LITTER

*     Stand composition, growth, and yield (per ha)
 35   FORMAT(I6,I5,4(F8.2),2X,2(F6.2))
 36   FORMAT(I6,I5,4(F8.2))
 362  FORMAT(I6,A5,2(F8.2))
      WRITE(35,35) YR,HSD,HBA,HVOL,TOTGDM,TVINC,YIELDG,YIELDV
      IF (THTIME) THEN
          FG=YIELDG/HBA
          WRITE(36,36) YR,HSD,HBA,HVOL,YIELDG,FG
          WRITE(36,362) YR,' ....',HBA-YIELDG,HVOL-YIELDV
      ENDIF

      RETURN
      END


*----------------------------------------------------------------------*
*  SUBROUTINE PARABS                                                    *
*  Author:  Hank Bartelink                                              *
*  Date of last revision:                                               *
*           December 1996                                               *
*  Purpose: This subroutine determines the daily total amount of        *
*  absorbed PAR per tree.                                               *
*----------------------------------------------------------------------*
      SUBROUTINE PARABS ( MXIND, NRIND,
     &                          ABSDIF,   ONR,
     &                   TRAPAR)
      IMPLICIT REAL(A-Z)
      INTEGER TRI,n
      INTEGER MXIND,NRIND,ONR
      DIMENSION ONR(MXIND),ABSDIF(MXIND),TRAPAR(MXIND)

*     Total amount of absorbed diffuse radiation per tree,
*     estimated by sub-program FORFLX. Annual PAR is 1718 MJ/m2;
*     DIFYR is in MJ PAR/m2 per year.
      DIFYR=1718.
      DO 100 TRI=1,NRIND
          TRAPAR(TRI)=DIFYR*ABSDIF(TRI)
  100 CONTINUE
```

```
      RETURN
      END


*---------------------------------------------------------------------*
*  SUBROUTINE TURNOV                                                  *
*  Author: H.H. Bartelink                                             *
*  Date of last revision: Autumn 1995                                 *
*  Purpose: The subroutine calculates biomass turn-over rates         *
*---------------------------------------------------------------------*
      SUBROUTINE TURNOV (MXSPEC, MXIND,MXSAPR,MXFOLC,   TRI,
     &                      BRTOR,CRTOR,FRTOR, NRSAP,  SPCD,   WFL,
     &                             WNC,   WBR,   WCR,   WFR,  SAPR,
     &                           NFOLC,   NLC,
     &                      DFL,   DNC,   DBR,   DCR,   DFR,   DSA)
      IMPLICIT REAL(A-Z)
      INTEGER TRI,SPI,I
      INTEGER MXSPEC,MXIND,MXSAPR,MXFOLC
      INTEGER NRSAP,SPCD,NFOLC
      DIMENSION BRTOR(MXSPEC),CRTOR(MXSPEC),FRTOR(MXSPEC),
     &          NRSAP(MXSPEC),NFOLC(MXSPEC),NLC(MXSPEC)
      DIMENSION SPCD(MXIND),WFL(MXIND),WNC(MXIND,MXFOLC),WBR(MXIND),
     &          WCR(MXIND),WFR(MXIND),SAPR(MXIND,MXSAPR),DFL(MXIND),
     &          DNC(MXIND,MXFOLC),DBR(MXIND),DCR(MXIND),DFR(MXIND),
     &          DSA(MXIND)

      SPI=SPCD(TRI)

*     Fixed turn-over rates are expressed as fractions of living biomass
*     Foliage life-span differs between evergreen and broadleaved trees
      IF (NFOLC(SPI).GT.1) THEN
          DO 100 I=1,NFOLC(SPI)
              DNC(TRI,I)=(I-1)*NLC(SPI)*WNC(TRI,I)
              DFL(TRI)=DFL(TRI)+DNC(TRI,I)
  100     CONTINUE
        ELSE
          DFL(TRI)=1.0*WFL(TRI)
      ENDIF
      DBR(TRI)=BRTOR(SPI)*WBR(TRI)
      DFR(TRI)=FRTOR(SPI)*WFR(TRI)
      DCR(TRI)=CRTOR(SPI)*WCR(TRI)
*     Sapwood mortality is equal to the area of the oldest sapwood ring
      DSA(TRI)=SAPR(TRI,NRSAP(SPI))

      RETURN
      END


* ---------------------------------------------------------------------- *
*     SUBROUTINE UOC                                                     *
*     Author:  H.H. Bartelink                                            *
*              Dept. of Forestry                                         *
*              Wageningen Agricultural University                        *
*     Date:    Autumn 1991                                               *
*                                                                        *
*     This subroutine calculates three helpvariables, based on           *
*     several combinations of inclination and azimuth.                   *
*     A diffuse light environment is simulated, represented by           *
*     the Uniform Overcast Sky (UOC).                                    *
* ---------------------------------------------------------------------- *
      SUBROUTINE UOC (  MXNRAY,  NRAZ,
     &                         UCOSIS,UCOCOS,SINCLI,CONTIL)
```

```
      IMPLICIT REAL(A-Z)
      INTEGER S,AZ,IN,STEP
      INTEGER MXNRAY,NRAZ
      PARAMETER (DGRD=0.017453292)
      DIMENSION UCOSIS(MXNRAY),UCOCOS(MXNRAY),SINCLI(MXNRAY),
     &          CONTIL(MXNRAY)

*     Coefficient NRAZ should be a multiple of 324 and 360
      IF(NRAZ.NE.3.AND.NRAZ.NE.4.AND.NRAZ.NE.6.AND.NRAZ.NE.9
     &   .AND.NRAZ.NE.12.AND.NRAZ.NE.18.AND.NRAZ.NE.36)
     &   STOP ' Illegal NRAZ: change value in subroutine INPUT. '

*     Counter S is used to fill arrays UCOSIS and UCOCOS
      STEP=360/NRAZ
      S=0
      DO 100 IN=5,85,10
          INCL=IN*DGRD
          SINC=SIN(INCL)
*         The contribution to the irradiance of a horizontal surface
          CTR=(COS((IN-5.)*DGRD))**2.-(COS((IN+5.)*DGRD))**2.
          DO 110 AZ=0,(360-STEP),STEP
              S=S+1
              AZIM=AZ*DGRD
              SINCLI(S)=SINC
              UCOSIS(S)=COS(INCL)*SIN(AZIM)/SINC
              UCOCOS(S)=COS(INCL)*COS(AZIM)/SINC
              CONTIL(S)=CTR/NRAZ
 110      CONTINUE
 100  CONTINUE

      RETURN
      END


* ---------------------------------------------------------------------- *
*     SUBROUTINE XCROWN                                                  *
*     Author:  H.H. Bartelink                                            *
*              Dept. of Forestry                                         *
*              Wageningen Agricultural University                        *
*     Date:    Spring 1992                                               *
*                                                                        *
*     Subroutine XCROWN checks for a certain light beam (described by    *
*     azimuth and inclination) whether it reaches the gridpoint GP       *
*     unintercepted or is intercepted by neighbouring tree crowns,       *
*     which are either represented by cones or ellipsoides.              *
*     Final aim of this subroutine is to calculate the coordinates of    *
*     the intersection between cone mantle and light beam                *
*     (XOUT,YOUT,ZOUT) and to derive the lenght of the light beam        *
*     inside the tree crowns.                                            *
* ---------------------------------------------------------------------- *
      SUBROUTINE XCROWN (MXSPEC, MXIND,MXNRAY, NRIND,      S,
     &                            COSIS, COCOS,   GPX,    GPY,
     &                              GPZ,  SICL,   CTS,   CWID,
     &                           LANGLE,ELLIPS,   TNR,   SPCD,
     &                              HGT,   HCB,  CRAD,XTRUNK,
     &                           YTRUNK,CSHAPE,   CRL,    LAD,
     &                    ABSDIF,ABSDIR, TRANS)
      IMPLICIT REAL(A-Z)
      INTEGER I,SPI,S,J,NRXX,RANK,R,LI,LR,HLP
      INTEGER MXSPEC,MXIND,MXNRAY
      INTEGER LANGLE
      INTEGER NRIND,TNR,SPCD
      LOGICAL ELLIPS
```

```
      PARAMETER (LI=400,LR=324)
      DIMENSION LINS(LI),CRIT(LI),RANK(LI),IR(LR)
      DIMENSION LANGLE(MXSPEC),ELLIPS(MXSPEC)
      DIMENSION TNR(MXIND),SPCD(MXIND),HGT(MXIND),HCB(MXIND),
     &          CRAD(MXIND),CSHAPE(MXIND),CRL(MXIND),LAD(MXIND),
     &          XTRUNK(MXIND),YTRUNK(MXIND),ABSDIF(MXIND),
     &          ABSDIR(MXIND,MXNRAY)

*     Check dimensions of local variables
      IF (LI.NE.MXIND.OR.LR.NE.MXNRAY) STOP ' Too few space for locals'

*     Start calculations
      NRXX=0
      DO 10 I=1,NRIND
          LINS(I)=0.
          CRIT(I)=0.
   10 CONTINUE

      DO 100 I=1,NRIND
          RANK(I)=TNR(I)
          HG=HGT(I)
          XTR=XTRUNK(I)
          YTR=YTRUNK(I)
          HC=HCB(I)
          CL=CRL(I)
          CRD=CRAD(I)
          SPI=SPCD(I)
*     Ignore trees below the grid (in case of elevated grid-points)
          IF (GPZ.GE.HG) GOTO 100
*     Start of the calculation of the path lenghts of a certain
*     beam inside intersected trees, and calculation of the resulting
*     light intensity in gridpoint GP.

*     Discriminate between cone-shaped and ellipsoidal crowns
          IF (ELLIPS(SPI)) THEN
*     Height position (ZELC) of ellipsoid center (maximum crown radius)
              HCL=0.5*CL
              ZELC=HC+HCL
*     Parameters for determining the determinant are calculated
              ADET=COSIS**2.+COCOS**2.+(CRD/HCL)**2.
              BDET=2.*(COSIS*(GPX-COSIS*GPZ)-XTR*COSIS+COCOS*(GPY-
     &             COCOS*GPZ)-YTR*COCOS-ZELC*(CRD/HCL)**2.)
              CDET=(GPX-COSIS*GPZ)**2.+XTR*(-2.*GPX+2.*COSIS*GPZ+XTR)
     &            +(GPY-COCOS*GPZ)**2.+YTR*(-2.*GPY+2.*COCOS*GPZ+YTR)
     &            -(1.-(ZELC/HCL)**2.)*CRD**2.
              DET=BDET**2.-4.*ADET*CDET
*     If DET is lower than zero, no intersection occurs
              IF (DET.LE.0.) GOTO 100
              Z1=(-BDET+SQRT(DET))/(2.*ADET)
              Z2=(-BDET-SQRT(DET))/(2.*ADET)
              ZIN=MIN(Z1,Z2)
              ZOUT=MAX(Z1,Z2)
*     Neglect trees below the grid-point
              IF (ZOUT.LE.GPZ) GOTO 100
            ELSE

*     Program execution arrives here when crown appears to be cone-shaped.
              TANC=2.*CSHAPE(I)
              CMANGL=ATAN(TANC)
*     Parameters for determining the determinant are calculated
              ADET=COSIS**2.+COCOS**2.-1./TANC**2.
              BDET=2.*(COSIS*(GPX-COSIS*GPZ)-XTR*COSIS+COCOS*
     &             (GPY-COCOS*GPZ)-YTR*COCOS+HG/TANC**2.)
              CDET=(GPX-COSIS*GPZ)**2.+XTR*(-2.*GPX+2.*
```

```
     &             COSIS*GPZ+XTR)+(GPY-COCOS*GPZ)**2.+YTR*
     &             (-2.*GPY+2.*COCOS*GPZ+YTR)-(HG/TANC)**2.
*     Check if light beam parallels the angle of the cone mantle CMANGL;
*     in that case ADET will be zero, hence ZOUT becomes -C/B
              IF (ABS(SICL-SIN(CMANGL)).LT.0.00001) THEN
                  Z1=-CDET/BDET
*     Ignore intersection in the upper part of the hour-glass
                  IF (Z1.GE.HG) GOTO 100
*     Ignore intersection if it occurs below the crown base
                  IF (Z1.LE.HC) GOTO 100
                  ZIN=HC
                  ZOUT=Z1
                ELSE
*     Calculate the value of DET; ignore trees with no intersection
                  DET=BDET**2.-4.*ADET*CDET
*     If DET is lower than zero, no intersection occurs
                  IF (DET.LT.0.) GOTO 100
*     Program execution arrives here when intersection occurs
                  IF (DET.GT.-0.0001.AND.DET.LT.0.0001) THEN
*     One intersection occurs when the ray cuts the cone-top:
*     intersection is then only relevant in case the ray inclination
*     exceeds the cone mantle-angle
                      IF (SICL.LE.SIN(CMANGL)) GOTO 100
                      ZIN=HC
                      ZOUT=HG
                    ELSE
*     Program execution arrives here when DET is positive, hence two
*     intersections occur
                      Z1=(-BDET+SQRT(DET))/(2.*ADET)
                      Z2=(-BDET-SQRT(DET))/(2.*ADET)
*     Ignore tree when only the upper part of the hour-glass is cut:
                      IF (Z1.GE.HG.AND.Z2.GE.HG) GOTO 100
                      ZMIN=MIN(Z1,Z2)
                      ZMAX=MAX(Z1,Z2)
*     Ignore the intersection in the upper part of the hour-glass
                      IF (ZMAX.GT.HG) THEN
*     The cone is only cut when intersection occurs above the crown base
                          IF (ZMIN.LT.HC) GOTO 100
                          ZIN=HC
                          ZOUT=ZMIN
                        ELSE
*     Ignore tree if both intersections occur below the cone description
                          IF (ZMAX.LE.HC) GOTO 100
                          ZOUT=ZMAX
                          ZIN=ZMIN
*     Cut the cone description at the crown base
                          IF (ZIN.LT.HC) ZIN=HC
                     ENDIF
                  ENDIF
              ENDIF
          ENDIF
c         XIN=GPX+(ZIN-GPZ)*COSIS
c         XOUT=GPX+(ZOUT-GPZ)*COSIS
*     Crownform-specific loops are left now: Z-coordinates are known
*
*     Determine the length of the covered distance (LINS) in the crown
*     of tree I, and count the total number of intersected crowns (NRXX)
          LINS(I)=(ZOUT-ZIN)/SICL
          CRIT(I)=ZOUT
          NRXX=NRXX+1
  100 CONTINUE

      IF (NRXX.EQ.0) RETURN
```

```
*     Determine the tree-order of intersection: the first intersected tree
*     is the one having the highest ZOUT value (=CRITerion)
      IF (NRIND.EQ.1) GOTO 299
      DO 200 I=2,NRIND
          J=I
  210     IF (J.LE.1) GOTO 200
          IF (CRIT(RANK(J)).GT.CRIT(RANK(J-1))) THEN
              HLP=RANK(J)
              RANK(J)=RANK(J-1)
              RANK(J-1)=HLP
              J=J-1
              GOTO 210
            ELSE
              GOTO 200
          ENDIF
  200 CONTINUE

*     Above-canopy flux: through a plane perpendicular to the inclination
  299 IIN=TRANS
*     Calculate transmission and interception per intersected tree
      DO 300 R=1,NRXX
          I=RANK(R)
          IF(LINS(I).LE.0.) GOTO 300
          SPI=SPCD(I)
*         Calculate the species-specific projection-coefficient
          IF (LANGLE(SPI).EQ.1) THEN
*         A horizontal leaf angle distribution is assumed
              OB=SICL
            ELSE
*         A spherical distribution is assumed
              OB=0.5
          ENDIF
*         Shoot clustering according to Goudriaan (1977):
          OB=OB/1.515
*         Absorption (exponential light extinction), in fraction per m2
          IOUT=IIN*EXP(-OB*LAD(I)*LINS(I))
          ABSOR=IIN-IOUT
*         Relative amount of intercepted radiation per cross-section
          IR(S)=ABSOR*((CWID**2.)*SICL)
*         In case of a UOC, the contribution to the illuminance,
*         depending on the radiation direction, is taken into account
          RAYUOC=IR(S)*CTS
*         Absorbed radiation in case of UOC-conditions
          ABSDIF(I)=ABSDIF(I)+RAYUOC
*         Absorbed radiation (MJ) per ray direction (direct light)
          ABSDIR(I,S)=ABSDIR(I,S)+IR(S)
*         New radiation input-intensity for next tree cut by ray
          IIN=IOUT
  300 CONTINUE
*     Resulting transmission
      TRANS=IOUT

      RETURN
      END


*----------------------------------------------------------------------*
*  SUBROUTINE YRESET                                                   *
*  Author:  Hank Bartelink                                             *
*  Date of last revision:                                              *
*           December 1996                                              *
*  Purpose:                                                            *
*      Resets annual totals                                            *
```

```
*-----------------------------------------------------------------------*
      SUBROUTINE YRESET (MXSPEC, MXIND,MXNRAY,MXFOLC,NRSPEC,
     &                             YR, START,
     &                          SPAGE,
     &                    HINC,ABSDIF,ABSDIR,TRAPAR,PARHCB,
     &                            GST,    GBR,    GFL,    GCR,    GFR,
     &                            GSA,    DBR,    DFL,    DCR,    DFR,
     &                            DSA,    DNC,
     &     SLAREA,SWST,SWBRN,SWFL,SWRT,SBA,SVOL,SVINC,
     &     HLAI,HWST,HWBRN,HWFL,HWRT,HBA,HVOL,
     &     TOTGDM,YIELDG,YIELDV,TVINC,LITTER)

      IMPLICIT REAL(A-Z)
      INTEGER I,TRI,SP,S
      INTEGER MXSPEC,MXIND,MXNRAY,MXFOLC
      INTEGER YR
      INTEGER NRSPEC,SPAGE

      DIMENSION SPAGE(MXSPEC),SLAREA(MXSPEC),
     &          SWST(MXSPEC),SWBRN(MXSPEC),SWFL(MXSPEC),
     &          SWRT(MXSPEC),SBA(MXSPEC),SVOL(MXSPEC),SVINC(MXSPEC)
      DIMENSION HINC(MXIND),ABSDIF(MXIND),
     &          ABSDIR(MXIND,MXNRAY),TRAPAR(MXIND),PARHCB(MXIND),
     &          GST(MXIND),GBR(MXIND),GFL(MXIND),GCR(MXIND),
     &          GFR(MXIND),GSA(MXIND),DBR(MXIND),DFL(MXIND),
     &          DCR(MXIND),DFR(MXIND),DSA(MXIND),DNC(MXIND,MXFOLC)

*     Reset growth & mortality rates and APAR to zero
      DO 100 TRI=1,MXIND
          GST(TRI)=0.
          GBR(TRI)=0.
          GFL(TRI)=0.
          GCR(TRI)=0.
          GFR(TRI)=0.
          GSA(TRI)=0.
          HINC(TRI)=0.
          DFL(TRI)=0.
          DO 110 I=1,MXFOLC
              DNC(TRI,I)=0.
  110     CONTINUE
          DBR(TRI)=0.
          DCR(TRI)=0.
          DFR(TRI)=0.
          DSA(TRI)=0.
          ABSDIF(TRI)=0.
          DO 120 S=1,MXNRAY
              ABSDIR(TRI,S)=0.
  120     CONTINUE
          TRAPAR(TRI)=0.
          PARHCB(TRI)=0.
  100 CONTINUE

*     Reset annual amounts to zero
      DO 200 SP=1,MXSPEC
          SLAREA(SP)=0.
          SWST(SP)=0.
          SWBRN(SP)=0.
          SWFL(SP)=0.
          SWRT(SP)=0.
          SBA(SP)=0.
          SVOL(SP)=0.
          SVINC(SP)=0.
  200 CONTINUE
      HLAI=0.
```

```
      HWST=0.
      HWBRN=0.
      HWFL=0.
      HWRT=0.
      HBA=0.
      HVOL=0.
      TOTGDM=0.
      YIELDG=0.
      YIELDV=0.
      TVINC=0.
      LITTER=0.

*     Keep track of age
      START=START+1.
      IF (START.GE.2.) THEN
*         Update age of species
          DO 300 SP=1,NRSPEC
             SPAGE(SP)=SPAGE(SP)+1
  300     CONTINUE
*         Update year counter
          YR=YR+1
      ENDIF

      RETURN
      END


*----------------------------------------------------------------------*
*  SUBROUTINE YSTATE                                                   *
*  Author:  Hank Bartelink                                             *
*  Date of last revision:                                              *
*           December 1996                                              *
*  Purpose: Calculates annual totals                                   *
*----------------------------------------------------------------------*
      SUBROUTINE YSTATE (MXSPEC, MXIND,MXSAPR,MXFOLC,NRSPEC, NRSAP,
     &                           NFOLC, NRIND,    YR,STYEAR,PLOTAR,
     &          cplot,START,SLA,BADEN,
     &          RSH1,RSH2,RSH3,
     &          ELLIPS,
     &          SLAREA,SWFL,SWBRN,SWST,
     &          SWRT,SBA,SVOL,SVINC,MCM1,MCM2,
     &          ONR,DBH,SPCD,
     &          HGT,
     &          CRAD,WST,WBR,WCR,
     &          WFR,WRT,WNC,WFL,LAD,
     &          VOL,BA,SA,SAPR,
     &          XTRUNK,YTRUNK,
     &          CSHAPE,CRVOL,CRL,CRSA,
     &          YGDM,
     &          GST,GBR,GFL,GCR,
     &          GFR,GSA,
     &          DBR,DFL,DCR,DFR,DSA,DNC,DEAD,
     &          X1C,X2C,Y1C,Y2C,
     &      TVINC,TOTGDM,
     &      HSD,HLAI,HWST,HWBRN,HWFL,HWRT,HBA,HVOL)

      IMPLICIT REAL(A-Z)
      INTEGER I,TRI,SPI,SP,NLIVE
      INTEGER MXSPEC,MXIND,MXSAPR,MXFOLC
      INTEGER YR,STYEAR
      INTEGER NRSPEC,NRSAP,NFOLC
      INTEGER NRIND,HSD,ONR,SPCD
      LOGICAL ELLIPS,DEAD
```

```
      PARAMETER (PI=3.14159265359,DGRD=0.017453292)

      DIMENSION SLA(MXSPEC),BADEN(MXSPEC),RSH1(MXSPEC),RSH2(MXSPEC),
     &          RSH3(MXSPEC),ELLIPS(MXSPEC),NRSAP(MXSPEC),NFOLC(MXSPEC),
     &          SLAREA(MXSPEC),SWFL(MXSPEC),SWBRN(MXSPEC),SWST(MXSPEC),
     &          SWRT(MXSPEC),SBA(MXSPEC),SVOL(MXSPEC),SVINC(MXSPEC),
     &          MCM1(MXSPEC),MCM2(MXSPEC)
      DIMENSION ONR(MXIND),DBH(MXIND),SPCD(MXIND),HGT(MXIND),
     &          CRAD(MXIND),WST(MXIND),WBR(MXIND),WCR(MXIND),
     &          WFR(MXIND),WRT(MXIND),WNC(MXIND,MXFOLC),WFL(MXIND),
     &          VOL(MXIND),BA(MXIND),SA(MXIND),SAPR(MXIND,MXSAPR),
     &          XTRUNK(MXIND),YTRUNK(MXIND),
     &          CSHAPE(MXIND),CRVOL(MXIND),CRL(MXIND),CRSA(MXIND),
     &          YGDM(MXIND),LAD(MXIND),DEAD(MXIND),
     &          GST(MXIND),GBR(MXIND),GFL(MXIND),GCR(MXIND),
     &          GFR(MXIND),GSA(MXIND),DBR(MXIND),DFL(MXIND),DCR(MXIND),
     &          DFR(MXIND),DSA(MXIND),DNC(MXIND,MXFOLC)

*     Initializing the number of survival trees
      NLIVE=0

      DO 100 TRI=1,NRIND
          IF (DEAD(TRI)) GOTO 100
          SPI=SPCD(TRI)
*         Integration: calculate new amounts of biomass and tree sizes
*         Foliage dynamics differ between broadleaves and evergreens
          IF (NFOLC(SPI).GT.1) THEN
*           Update biomass in the old needle age-classes
            DO 110 I=2,NFOLC(SPI)
                WNC(TRI,I)=WNC(TRI,I)-DNC(TRI,I)
  110       CONTINUE
          ENDIF
          WFL(TRI)=WFL(TRI)+GFL(TRI)-DFL(TRI)
          WBR(TRI)=WBR(TRI)+GBR(TRI)-DBR(TRI)
          WST(TRI)=WST(TRI)+GST(TRI)
          WCR(TRI)=WCR(TRI)+GCR(TRI)-DCR(TRI)
          WFR(TRI)=WFR(TRI)+GFR(TRI)-DFR(TRI)
          WRT(TRI)=WCR(TRI)+WFR(TRI)
          SA(TRI)=SA(TRI)+GSA(TRI)-DSA(TRI)
*         Stem dry weight in kg, stem fresh volume in dm3,
*         dbh in cm, basal area in m2
          VOL(TRI)=1000.*WST(TRI)/BADEN(SPI)
*         Save former diameter
          DBHOLD=DBH(TRI)
          DBH(TRI)=RSH1(SPI)*(VOL(TRI)**RSH2(SPI))*
     &             (HGT(TRI)**RSH3(SPI))
          DINC=DBH(TRI)-DBHOLD
          BA(TRI)=(PI/4.)*(DBH(TRI)/100.)**2.
*         Crown dimensions (m, m2, & m3)
          IF (YR.NE.STYEAR) THEN
*             Maximum supported crown silhouette area CMX
              CMX=MCM1(SPI)*(DBH(TRI)**MCM2(SPI))/HGT(TRI)
*             Crown radius is supposed not to decrease
              IF (ELLIPS(SPI)) THEN
                  CRAD(TRI)=MAX(CRAD(TRI),CMX/(PI*CRL(TRI)/2.))
                ELSE
                  CRAD(TRI)=MAX(CRAD(TRI),CMX/CRL(TRI))
              ENDIF
          ENDIF
*         Calculate actual crown silhouette area CRSA (m2)
          IF (ELLIPS(SPI)) THEN
              CRSA(TRI)=PI*CRAD(TRI)*CRL(TRI)/2.
            ELSE
              CRSA(TRI)=CRAD(TRI)*CRL(TRI)
```

```
          ENDIF
*         Crown shape (-) and volume (m3)
          CSHAPE(TRI)=0.5*CRL(TRI)/CRAD(TRI)
          IF (ELLIPS(SPI)) THEN
              CRVOL(TRI)=(4.*PI/3.)*CSHAPE(TRI)*CRAD(TRI)**3.
            ELSE
              CRVOL(TRI)=(PI/3.)*CRL(TRI)*CRAD(TRI)**2.
          ENDIF
*         Leaf area density (m2/m3)
          LAD(TRI)=WFL(TRI)*SLA(SPI)/CRVOL(TRI)

*         Stand structure per species (S); in ton, m2, or m3 per ha
*         Only trees in the center are used to calculate stand totals
          IF (XTRUNK(TRI).LT.X1C.OR.XTRUNK(TRI).GT.X2C.OR.
     &        YTRUNK(TRI).LT.Y1C.OR.YTRUNK(TRI).GT.Y2C) GOTO 100
*         Number of living individuals in the center area
          NLIVE=NLIVE+1
          SLAREA(SPI)=SLAREA(SPI)+WFL(TRI)*SLA(SPI)/PLOTAR
          SWST(SPI)=SWST(SPI)+(WST(TRI)/1000.)*(10000./PLOTAR)
          SWBRN(SPI)=SWBRN(SPI)+(WBR(TRI)/1000.)*(10000./PLOTAR)
          SWFL(SPI)=SWFL(SPI)+(WFL(TRI)/1000.)*(10000./PLOTAR)
          SWRT(SPI)=SWRT(SPI)+(WRT(TRI)/1000.)*(10000./PLOTAR)
          SBA(SPI)=SBA(SPI)+BA(TRI)*(10000./PLOTAR)
          SVOL(SPI)=SVOL(SPI)+(VOL(TRI)/1000.)*(10000./PLOTAR)
          SVINC(SPI)=SVINC(SPI)+(GST(TRI)/BADEN(SPI))*(10000./PLOTAR)
*         Total stem volume increment
          TVINC=TVINC+(GST(TRI)/BADEN(SPI))*(10000./PLOTAR)
*         Total absolute amount of produced dry matter (tons/year)
          TOTGDM=TOTGDM+(YGDM(TRI)/1000.)*10000./PLOTAR
  100 CONTINUE

*     Biomass and structure per ha (H)
*     Stand density (N/ha)
      HSD=NINT(REAL(NLIVE)*(10000./PLOTAR))
      DO 200 SP=1,NRSPEC
          HLAI=HLAI+SLAREA(SP)
          HWST=HWST+SWST(SP)
          HWBRN=HWBRN+SWBRN(SP)
          HWFL=HWFL+SWFL(SP)
          HWRT=HWRT+SWRT(SP)
          HBA=HBA+SBA(SP)
          HVOL=HVOL+SVOL(SP)
  200 CONTINUE

*     Skip annual updates at start of the simulation
      IF (START.LE.1.) RETURN

      DO 300 TRI=1,NRIND
*         Push needle biomass amounts in the next age-class
          IF (NFOLC(SPCD(TRI)).GT.1) THEN
            DO 310 I=NFOLC(SPCD(TRI)),2,-1
                WNC(TRI,I)=WNC(TRI,I-1)
  310       CONTINUE
*           New needles (GFL) are added to class 1 in next growing season
            WNC(TRI,1)=GFL(TRI)
          ENDIF
*         Push annual sapwood into next sapwood age-class
          SA(TRI)=0.
          DO 320 I=NRSAP(SPCD(TRI)),2,-1
              SAPR(TRI,I)=SAPR(TRI,I-1)
              SA(TRI)=SA(TRI)+SAPR(TRI,I)
  320     CONTINUE
          SAPR(TRI,1)=GSA(TRI)
          SA(TRI)=SA(TRI)+SAPR(TRI,1)
```

```
  300 CONTINUE

      RETURN
      END


*----------------------------------------------------------------------*
*  Include sub-programs                                                *
*  These sub-programs contain functions presently called for.          *
*----------------------------------------------------------------------*
      INCLUDE 'SERVCE.FOR'
      INCLUDE 'WEATHR.FOR'
      INCLUDE 'THINNG.FOR'
*----------------------------------------------------------------------*



*----------------------------------------------------------------------*
*  SUBROUTINE THINNG                                                   *
*  Author: H.H. Bartelink                                              *
*  Date of last revision: Summer 1997                                  *
*  Purpose: The subroutine determines which trees are thinned          *
*  Type of thinning to be simulated:                                   *
*    1 = systematic: every x-th tree, depending on species             *
*    2 = from below: smallest trees per sub-area, up to a certain      *
*        fraction of the basal area of the species concerned           *
*  At maximum, 15 thinning moments can be described. Information on   *
*  the thinnings is derived from file MANAGE.DAT in subroutine INPUT. *
*----------------------------------------------------------------------*
      SUBROUTINE THINNG (MXSPEC, MXIND,MXTHIN, MXBLK,
     &                          NRSPEC, NRIND,PLOTAR,THTIME,
     &                           SPAGE,THINYR,THINFR,THINTP,
     &                             TNR,   DBH,  SPCD,    BA,
     &                          XTRUNK,YTRUNK,  DEAD,
     &                          X1P,X2P,Y1P,Y2P,
     &                          X1C,X2C,Y1C,Y2C,
     &                       HARVST)
      IMPLICIT REAL(A-Z)
      INTEGER I,J,TRI,SP,POSIT,COUNT,LI,LS,THTP,CRIT
      INTEGER I2,B,V,IV,ANTBL,NBR,NTBL,NTBLS,BLK,BPOSIT
      LOGICAL THIN,GOTCHA,SECOND
      INTEGER MXSPEC,MXIND,MXTHIN,MXBLK
      INTEGER NRSPEC,SPAGE
      INTEGER BLKNR,NRBLK
      INTEGER THINYR,THINTP
      INTEGER NRIND,TNR,SPCD
      LOGICAL DEAD,HARVST,THTIME
      PARAMETER (PI=3.1416,LI=400,LS=2,LB=49)
      DIMENSION POSIT(LI),CUMBA(LS),THFR(LS),THTP(LS),THIN(LS),
     &          BLK(LI),GOTCHA(LI),BPOSIT(LB),NTBL(LB),GBLK(LB),
     &          NTBLS(LB,LS),SPBA(LS)
      DIMENSION BLKNR(LB),X1BLK(LB),X2BLK(LB),Y1BLK(LB),Y2BLK(LB)
      DIMENSION SPAGE(MXSPEC)
      DIMENSION THINYR(MXTHIN),THINFR(MXSPEC,MXTHIN),
     &          THINTP(MXSPEC,MXTHIN)
      DIMENSION TNR(MXIND),DBH(MXIND),SPCD(MXIND),BA(MXIND),
     &          XTRUNK(MXIND),YTRUNK(MXIND),DEAD(MXIND),
     &          HARVST(MXIND)


*     Check dimensions of local variables
      IF (LI.NE.MXIND.OR.LS.NE.MXSPEC.OR.LB.NE.MXBLK)
     &    STOP ' Too few space for locals'
```

```
*     Check whether or not a thinning should be carried out
      THTIME=.FALSE.
      DO 100 SP=1,NRSPEC
          THIN(SP)=.FALSE.
          DO 110 I=1,MXTHIN
              CHCK=ABS(REAL(THINYR(I)-SPAGE(SP)))
              IF (CHCK.LT.0.5) THEN
                  THFR(SP)=THINFR(SP,I)
                  THTP(SP)=THINTP(SP,I)
                  THIN(SP)=.TRUE.
                  THTIME=.TRUE.
                  GOTO 101
              ENDIF
  110     CONTINUE
*         Initializing species total and thinned basal area
  101     SPBA(SP)=0.
          CUMBA(SP)=0.
  100 CONTINUE
*     Thinning routine is left when no thinning occurs
      IF (.NOT.THTIME) RETURN

*     In case thinning does occur, in one or more of the species:

*     Calculate species basal area (m2/ha), to determine fraction
*     to be thinned: actual cut is based on the BA of the center
      CAREA=(X2C-X1C)*(Y2C-Y1C)
      DO 150 TRI=1,NRIND
*         Ignore dead and harvested trees
C          IF (DEAD(TRI).OR.(HARVST(TRI))) GOTO 150
          IF (XTRUNK(TRI).LT.X1C.OR.XTRUNK(TRI).GT.X2C.OR.
     &        YTRUNK(TRI).LT.Y1C.OR.YTRUNK(TRI).GT.Y2C) GOTO 150
          SPI=SPCD(TRI)
          SPBA(SPI)=SPBA(SPI)+BA(TRI)*(PLOTAR/CAREA)
  150 CONTINUE


*     Initialize tree ranking positions
      DO 200 COUNT=1,NRIND
          POSIT(COUNT)=COUNT
  200 CONTINUE
*     Trees are sorted according to their dbh
      DO 300 COUNT=2,NRIND
          J=COUNT-1
*         Ignore dead and harvested trees
C          IF (DEAD(J).OR.(HARVST(J))) GOTO 300
  310     IF (J.GE.NRIND) PRINT*,' Error in dimensions'
          IF (DBH(POSIT(J+1)).GT.DBH(POSIT(J))) GOTO 300
          HLP=POSIT(J)
          POSIT(J)=POSIT(J+1)
          POSIT(J+1)=HLP
          J=J-1
          IF (J.LE.0) GOTO 300
          GOTO 310
  300 CONTINUE

*     Carry out the systematic thinning (THTP=1)
      DO 500 SP=1,NRSPEC
          IF (THTP(SP).NE.1) GOTO 500
          IF (SPBA(SP).LE.0.) GOTO 500
          IF (.NOT.THIN(SP)) GOTO 500
*         Percentage of thinning determines which trees will be removed
          CRIT=NINT(1./THFR(SP))
          COUNT=0
          DO 510 TRI=1,NRIND
```

```
                IF (SPCD(TRI).NE.SP) GOTO 510
*               Only trees in PLOTAR are thinned
                IF (XTRUNK(TRI).LT.X1P.OR.XTRUNK(TRI).GT.X2P.OR.
     &              YTRUNK(TRI).LT.Y1P.OR.YTRUNK(TRI).GT.Y2P) GOTO 510
                COUNT =COUNT+1
                IF (COUNT.EQ.CRIT) THEN
                    HARVST(TRI)=.TRUE.
                    COUNT=0
                ENDIF
  510       CONTINUE
  500 CONTINUE

*     Program arrives here when low-thinning is applied in 1 or all species

*     Blok size is variable, to guarantee on average ANTBL trees per block
*     Average number of trees per block
      ANTBL=4
*     Number of blocks
      NRBLK=NRIND/ANTBL
*     Number of blocks can be 9, 16, 25, 36, 49
      IF (NRBLK.GE.49) THEN
        NRBLK=49
        GOTO 123
      ENDIF
      IF (NRBLK.GE.36) THEN
        NRBLK=36
        GOTO 123
      ENDIF
      IF (NRBLK.GE.25) THEN
        NRBLK=25
        GOTO 123
      ENDIF
      IF (NRBLK.GE.16) THEN
        NRBLK=16
        GOTO 123
      ENDIF
      IF (NRBLK.LT.16) NRBLK=9
 123  IF (NRBLK.GT.LB) STOP ' Too few local memory for LB'
*     Calculate block width, assuming a square PLOTAR
      BLW=SQRT(PLOTAR)/SQRT(REAL(NRBLK))
*     Now determine the x- and y-coordinates per block
      B=0
*     Number of blocks per row
      NBR=NINT(SQRT(REAL(NRBLK)))
      DO 20 I=1,NBR
          DO 21 J=1,NBR
              B=B+1
              BLKNR(B)=B
              X1BLK(B)=X1P+REAL(I-1)*BLW
              X2BLK(B)=X1P+REAL(I)*BLW
              Y1BLK(B)=Y1P+REAL(J-1)*BLW
              Y2BLK(B)=Y1P+REAL(J)*BLW
   21     CONTINUE
   20 CONTINUE

*     Assign each tree to a block; avoid double-counting of trees
*     using variable GOTCHA
      DO 677 TRI=1,NRIND
          GOTCHA(TRI)=.FALSE.
          BLK(TRI)=0
 677  CONTINUE
      DO 600 V=1,MXBLK
          DO 610 TRI=1,NRIND
*             Ignore trees already assigned to a block
```

```
                IF (GOTCHA(TRI)) GOTO 610
*               Only trees in block V are taken into account
                IF (XTRUNK(TRI).LT.X1BLK(V).OR.XTRUNK(TRI).GT.
     &              X2BLK(V).OR.YTRUNK(TRI).LT.Y1BLK(V).OR.
     &              YTRUNK(TRI).GT.Y2BLK(V)) GOTO 610
                GOTCHA(TRI)=.TRUE.
                BLK(TRI)=V
  610       CONTINUE
  600 CONTINUE

*     Carry out the thinning from below (THTP=2) or above (THTP=3)
      DO 900 SP=1,NRSPEC
          IF (THTP(SP).NE.2.AND.THTP(SP).NE.3) GOTO 900
          IF (SPBA(SP).LE.0.) GOTO 900
          IF (.NOT.THIN(SP)) GOTO 900
*         Determine basal area and tree number per block
  999     DO 650 V=1,MXBLK
*             Re-setting block tree number and basal area to zero
              NTBL(V)=0
              GBLK(V)=0.
              NTBLS(V,SP)=0
              DO 651 TRI=1,NRIND
                  IF (BLK(TRI).NE.V) GOTO 651
                  IF (HARVST(TRI)) GOTO 651
                  GBLK(V)=GBLK(V)+BA(TRI)
                  NTBL(V)=NTBL(V)+1
                  SPI=SPCD(TRI)
                  NTBLS(V,SPI)=NTBLS(V,SPI)+1
  651         CONTINUE
  650     CONTINUE
*         Arranging the blocks according to their basal area
*         Initialisation
          DO 700 COUNT=1,NRBLK
              BPOSIT(COUNT)=COUNT
  700     CONTINUE
*         Putting blocks with low basal area in front
          DO 800 COUNT=2,NRBLK
              J=COUNT-1
  810         IF (J.GE.NRBLK) PRINT*,' Error in dimensions'
              IF (GBLK(BPOSIT(J+1)).GT.GBLK(BPOSIT(J))) GOTO 800
              HLP=BPOSIT(J)
              BPOSIT(J)=BPOSIT(J+1)
              BPOSIT(J+1)=HLP
              J=J-1
              IF (J.LE.0) GOTO 800
              GOTO 810
  800     CONTINUE
*         Amount of basal area to be cut
          BATHIN=THFR(SP)*SPBA(SP)
*         Determine in (up to) which blocks a tree has to be cut
          I=NRBLK+1
          I2=0
  910     IF (CUMBA(SP).LT.0.90*BATHIN) THEN
*             Choose block with highest GBLK to start cutting
              I=I-1
*             CUMBA might be still too low after passing all blocks:
              IF (I.LE.0) THEN
*                 Either all blocks contain 1 or no trees of the species

                  IF (I2.GE.NRBLK) GOTO 950
*                 Or it is still possible to take a next-smallest tree
                  GOTO 999
              ENDIF
*             Determine in which block thinning should occur
```

```
              DO 920 V=1,NRBLK
                  IF (V.EQ.BPOSIT(I)) THEN
*                     Now the block to be thinned is known (V)
*                     Ignore blocks with 1 or no trees, if possible
c                      IF (NTBL(V).LE.1) THEN
                      IF (NTBLS(V,SP).LE.1) THEN
                          I2=I2+1
                          GOTO 910
                      ENDIF
*                     Within this block V, the smallest tree is cut
*                     in case of low thinning, and the second-largest
*                     in case of high thinning
                      IF (THTP(SP).EQ.2) THEN
*                         A low thinning is carried out
                          DO 930 IV=1,NRIND
                              IF (BLK(POSIT(IV)).NE.V) GOTO 930
                              IF (SPCD(POSIT(IV)).NE.SP) GOTO 930
*                             Only trees in PLOTAR are thinned
                              IF (XTRUNK(POSIT(IV)).LT.X1P.OR.
     &                            XTRUNK(POSIT(IV)).GT.X2P.
     &                            OR.YTRUNK(POSIT(IV)).LT.Y1P.OR.
     &                            YTRUNK(POSIT(IV)).GT.Y2P) GOTO 930
*                             Harvest tree, update total harvest:
*                             skip when tree is already harvested
                              IF (HARVST(POSIT(IV))) GOTO 930
                              HARVST(POSIT(IV))=.TRUE.
                              CUMBA(SP)=CUMBA(SP)+BA(POSIT(IV))
*                             Check total harvest and go to next block
*                             if necessary (i.e. when CUMBA<BATHIN)
                              GOTO 910
  930                     CONTINUE
                        ELSE
*                         A high thinning is carried out
                          SECOND=.FALSE.
                          DO 940 IV=NRIND,1,-1
                              IF (BLK(POSIT(IV)).NE.V) GOTO 940
                              IF (SPCD(POSIT(IV)).NE.SP) GOTO 940
*                             Only trees in PLOTAR are thinned
                              IF (XTRUNK(POSIT(IV)).LT.X1P.OR.
     &                            XTRUNK(POSIT(IV)).GT.X2P.
     &                            OR.YTRUNK(POSIT(IV)).LT.Y1P.OR.
     &                            YTRUNK(POSIT(IV)).GT.Y2P) GOTO 940
                              IF (.NOT.SECOND) THEN
                                  SECOND=.TRUE.
                                  GOTO 940
                              ENDIF
*                             Harvest second-best tree, update total
*                             harvest: skip when tree is already harvested
                              IF (HARVST(POSIT(IV))) GOTO 940
                              HARVST(POSIT(IV))=.TRUE.
                              CUMBA(SP)=CUMBA(SP)+BA(POSIT(IV))
*                             Check total harvest and go to next block
*                             if necessary (i.e. when CUMBA<BATHIN)
                              GOTO 910
  940                     CONTINUE
                      ENDIF
                      GOTO 910
                  ENDIF
  920         CONTINUE
          ENDIF
*         Step to other species if CUMBA equals BATHIN
          GOTO 1000

*         When NTBL.LE.1 choose smallest tree to cut
```

```
  950     DO 960 TRI=1,NRIND
              IF (SPCD(POSIT(TRI)).NE.SP) GOTO 960
*             Only trees in PLOTAR are thinned
              IF (XTRUNK(POSIT(TRI)).LT.X1P.OR.
     &            XTRUNK(POSIT(TRI)).GT.X2P.
     &            OR.YTRUNK(POSIT(TRI)).LT.Y1P.OR.
     &            YTRUNK(POSIT(TRI)).GT.Y2P) GOTO 960
*             Harvest tree, update total harvest:
*             skip when tree is already harvested
              IF (HARVST(POSIT(TRI))) GOTO 960
              HARVST(POSIT(TRI))=.TRUE.
              CUMBA(SP)=CUMBA(SP)+BA(POSIT(TRI))
*             Check total harvest: skip if enough BA is thinned
              IF (CUMBA(SP).GE.(0.90*BATHIN)) GOTO 1000
  960     CONTINUE
 1000     CONTINUE
  900 CONTINUE

      RETURN
      END
```

Appendix 2: List of acronyms

aaa

ABSDIF	--	R	Relative amount of absorbed diffuse radiation per tree
ABSDIR	--	R	Relative amount of absorbed direct radiation per tree
ACL1	--	R	Allometric constant in dbh - crown length relationship
ACL2	--	R	Allometric constant in dbh - crown length relationship
ACL3	--	R	Allometric constant in dbh - crown length relationship
ANTBL	--	I	Average amount of trees per thinning block

bbb

BA	m2	R	Tree basal area
BADEN	kg/m3	R	Stemwood basic density
BATHIN	m2	R	Amount of a species' basal area to be removed by thinning
BLK	--	I	Number of the block the tree is assigned to
BLKNR	--	I	Block number
BLW	m	R	Block width
BPOSIT	--	I	Rank in a block series, determined by block basal area: used in thinning

ccc

CMX	m2	R	Maximum supportable crown silhouette area
CONTIL	--	R	Contribution to the irradiance of a horizontal surface: depends on sun inclination
COUNT	--	I	Local tree counter
CRAD	m	R	Crown radius
CRL	m	R	Crown length
CRSA	m2	R	Crown silhouette area
CRTOR	1/y	R	Coarse root biomass turn-over rate
CRVOL	m3	R	Crown volume
CSHAPE	--	R	Crown shape: ratio between crown length and crown diameter
CUMBA	--	R	Local variable: cumulative species-specific basal area

ddd

DBH	cm	R	Tree diameter at breast height
DBR	kg/y	R	Annual turn-over rate of branches
DCR	kg/y	R	Annual turn-over rate of coarse roots
DEAD	--	B	Label indicating whether or not a tree will die
DFL	kg/y	R	Annual turn-over rate of foliage
DFR	kg/y	R	Annual turn-over rate of fine roots
DIFYR	MJ/m2	R	Available amount of PAR per year
DNC	kg/y	R	Mortality rate per foliage age-class
DSA	m2/y	R	Transition of sapwood to heartwood

eee

ELLIPS	--	L	Indicator of crown shape: cone or ellipsoid
ENYEAR	--	I	Last year of the simulation run

fff

FCSPEF	--	I	Counter, used to determine length of file-names
FE	MJ/m2	R	Foliage PAR-interception efficiency: APAR per unit foliage
FRTOR	1/y	R	Fine root biomass turn-over rate

ggg

GBLK	m2	R	Basal area per block
GBR	kg/y	R	Dry matter allocated to the branches
GCR	kg/y	R	Dry matter allocated to the coarse roots
GDM	kg/y	R	Dry matter growth rate per tree
GFL	kg/y	R	Dry matter allocated to the foliage
GFR	kg/y	R	Dry matter allocated to the fine roots
GOTCHA	--	L	Indicates whether a tree has been assigned to a block already
GSA	m2/y	R	Growth rate of the sapwood area
GST	kg/y	R	Dry matter allocated to the stem

hhh

HARVST	--	L	Indicates whether or not a tree is thinned
HBA	m2/ha	R	Stand basal area
HCB	m	R	Height of the crown base
HCBOLD	m	R	Former height of the crown basel
HCR1	--	R	Coefficient for the Chapman-Richards height-equation
HCR2	--	R	Coefficient for the Chapman-Richards height-equation
HGT	m	R	Tree height
HINCR	m/y	R	Tree height growth
HLAI	--	R	Leaf area index (hectare)
HSD	/ha	I	Stand density
HVOL	m3/ha	R	Stand volume
HWBRN	ton/ha	R	Stand branch biomass
HWFL	ton/ha	R	Stand foliage biomass
HWRT	ton/ha	R	Stand root biomass
HWST	ton/ha	R	Stand stem biomass

iii

ILEN	--	I	Length of text string
IR	--	R	Relative amount of intercepted radiation per gridpoint, per ray
IYR	--	I	Year counter

lll

LAD	m2/m3	R	Leaf area density
LANGLE	--	R	Leaf angle distribution
LITTER	ton	R	Total biomass loss due to turn-over, mortality, or harvest (excl. stems)
LOSHAR	kg	R	Biomass losses due to harvest (excluding stems)
LOSMOR	kg	R	Biomass losses due to natural mortality
LOSTUO	kg	R	Biomass losses due to turn-over of components (excluding stems)

mmm

MCM1	--	R	Coefficient for the McMahon-relationship between crown and dbh
MCM2	--	R	Coefficient for the McMahon-relationship between crown and dbh
MXBLK	--	I	Maximum number of thinning blocks
MXFOLC	--	I	Maximum number of foliage age-classes
MXIND	--	I	Maximum number of individuals
MXNRAY	--	I	Maximum number of rays
MXSAPR	--	I	Maximum number of sapwood rings
MXSMPL	--	I	Maximum amount of sample points
MXSPEC	--	I	Maximum number of species

MXTHIN	--	I	Maximum number of thinning moments

nnn

NFOLC	--	I	Number of foliage age-classes
NLC	--	R	Needle loss coefficient
NRAZ	--	I	Number of azimuthal directions to be simulated
NRBLK	--	I	Actual number of thinning blocks
NRIND	--	I	Actual number of trees
NRSPEC	--	I	Actual number of species
NRSAMP	--	I	Actual number of sample points
NRSAP	--	I	Actual number of sapwood rings
NTBL	--	I	Total number of trees per block
NTBLS	--	I	Number of trees per block per species

ooo

OB	--	R	Projection coefficient

ppp

PAR	J/m2/s	R	Instantaneous amount of incoming PAR
PARHCB	--	R	Relative radiation intensity below the crown base
PDHBR1	--	R	Partitioning: constant in dbh/h - branch biomass relationship
PDHBR2	--	R	Partitioning: constant in dbh/h - branch biomass relationship
PDHBR3	--	R	Partitioning: constant in dbh/h - branch biomass relationship
PDWCR1	--	R	Partitioning: constant in dbh - coarse root biomass relationship
PDWCR2	--	R	Partitioning: constant in dbh - coarse root biomass relationship
PDWCR3	--	R	Partitioning: constant in dbh - coarse root biomass relationship
PDWCR4	--	R	Partitioning: constant in dbh - coarse root biomass relationship
PDWCR5	--	R	Partitioning: constant in dbh - coarse root biomass relationship
PFASA1	--	R	Partitioning: constant in foliage - sapwood area relationship
PFASA2	--	R	Partitioning: constant in foliage - sapwood area relationship
PFASA3	--	R	Partitioning: constant in foliage - sapwood area relationship
PFRFL	--	R	Partitioning: root/shoot or fine root/foliage ratio
PLA	m2	R	Absolute amount of projected leaf area
PLOTAR	m2	R	Total plot area (excluding unthinned border)
POSIT	--	I	Rank in a tree series, determined by tree dbh: used in thinning

rrr

RANK	--	I	Tree rank according to order of intersection by ray
RAYUOC	--	R	Counter: summing IR in case of a UOC
RINGS	--	I	Initial number of sapwood rings: help-variable
RSH1	--	R	Coefficient for the reversed Schumacher-Hall volume-equation
RSH2	--	R	Coefficient for the reversed Schumacher-Hall volume-equation
RSH3	--	R	Coefficient for the reversed Schumacher-Hall volume-equation
RUE	g/MJ	R	Species-specific radiation-use efficiency

sss

SA	m2	R	Sapwood area per tree
SAPR	m2	R	Sapwood area per sapwood-ring per tree
SBA	m2/ha	R	Species basal area
SH1	--	R	Coefficient for the Schumacher-Hall volume-equation
SH2	--	R	Coefficient for the Schumacher-Hall volume-equation

SH3	--	R	Coefficient for the Schumacher-Hall volume-equation
SINCLI	--	R	Sine of the sun inclination
SLA	m2/kg	R	Specific leaf area (species-specific)
SLAREA	--	R	Leaf area index per species
SMAX	m	R	Site index: species-specific maximum tree height
SPAGE	y	I	Species age
SPBA	m2	R	Species basal area (local variable)
SPCD	--	I	Species code
SPEFIL	--	C	Name of the species data file
SPILAB	--	R	Species identification label
SPUN	--	I	File unit number
STRLEN	--	I	Length of the name of the input-file
STYEAR	--	R	Starting year of the simulation run
SVOL	m3	R	Stem volume per species
SWBRN	ton/ha	R	Branch biomass per species
SWFL	ton/ha	R	Foliage biomass per species
SWRT	ton/ha	R	Root biomass per species
SWST	ton/ha	R	Stem biomass per species

ttt

THIN	--	L	Indicates whether or not a thinning should be carried out in a species
THINFR	--	R	Fraction of basal area of the species to be removed by thinning
THINTP	--	I	Type of thinning to be applied on the species concerned
THINYR	--	I	Species age at which thinning has to be carried out
THTIME	--	L	Indicates whether or not a thinning should be carried out
TOTGDM	ton	R	Total annual dry matter production
TOTINC	m3	R	Total annual stem volume production
TRANS	--	R	Resulting relative light intensity (fraction)
TRAPAR	MJ/y	R	Annual amount of intercepted PAR per tree
TRUE	--	R	Species-specific dependency of RUE on FE
TRUHLP	--	R	Help-variable: see TRUE

uuu

UCOCOS	--	R	Intermediate variable
UCOSIS	--	R	Intermediate variable

vvv

VITAL	--	I	Tree vitality label
VOL	dm3	R	Stem volume

www

WST	kg	R	Stem dry weight
WBR	kg	R	Branch dry weight
WCR	kg	R	Coarse root dry weight
WFR	kg	R	Fine root dry weight
WFL	kg	R	Foliage dry weight
WNC	kg	R	Foliage biomass per foliage age-class
WRT	kg	R	Total root dry weight

xxx			
X1BLK	m	R	Minimum X-coordinate of the thinning block
X2BLK	m	R	Maximum X-coordinate of the thinning block
X1C	m	R	Minimum X-coordinate of the sub-plot containing target trees
X2C	m	R	Maximum X-coordinate of the sub-plot containing target trees
X1P	m	R	Minimum X-coordinate of the plot
X2P	m	R	Maximum X-coordinate of the plot
XSAMP	m	R	Coordinate of the sample-point
XTRUNK	m	R	Coordinate of stemfoot
XTR	m	R	Intermediate variable: see XTRUNK
yyy			
Y1BLK	m	R	Minimum Y-coordinate of the thinning block
Y2BLK	m	R	Maximum Y-coordinate of the thinning block
Y1C	m	R	Minimum Y-coordinate of the sub-plot containing target trees
Y2C	m	R	Maximum Y-coordinate of the sub-plot containing target trees
Y1P	m	R	Minimum Y-coordinate of the plot
Y2P	m	R	Maximum Y-coordinate of the plot
YGDM	kg/y	R	Annual total amount of produced dry matter per tree
YIELD	m3	R	Total annual stem volume production
YSAMP	m	R	Coordinate of the sample-point
YR	--	R	Year counter
YTRUNK	m	R	Coordinate of stemfoot
YTR	m	R	Intermediate variable: see YTRUNK
zzz			
ZTRUNK	m	R	Coordinate of stemfoot
ZSAMP	m	R	Coordinate of the sample-point

Appendix 3: List of other publications by the author

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Curriculum vitae

Hank (Hendrik Herman) Bartelink werd geboren op 22 maart 1963 te Winterswijk. Na het behalen van het Atheneum-diploma aan de Rijksscholengemeenschap in Zwolle, begon hij in 1982 aan de studie Bosbouw van de toenmalige Landbouwhogeschool Wageningen. Als onderdeel van deze studie verbleef hij 3 maanden in Wales (UK), voor een stage en onderzoek in een bosreservaat, en 3 maanden in Duitsland, om ervaring op te doen met de zogenaamde 'naturgemässe Waldwirtschaft'. Afstudeervakken hadden o.a. betrekking op Wildbeheer, Fotogrammetrie en Luchtfoto-interpretatie, Bosecologie, en Theoretische Produktie-ecologie. Dat laatste onderzoek, uitgevoerd bij de toenmalige Dorschkamp (het huidige IBN-DLO), wekte de interesse voor de modelmatige benadering van bosgroei. Dit resulteerde, na het behalen van het doctoraal-examen aan de Landbouwuniversiteit Wageningen in juni 1988, in een tijdelijke aanstelling bij de Dorschkamp (IBN-DLO) als vervangende dienst. Gedurende deze periode, van juli 1988 tot oktober 1989, was hij werkzaam als onderzoeker, met name op het gebied van de simulatie van bosgroei.
In november 1989 werd hij aangesteld als universitair docent bij de vakgroep Bosbouw van de Landbouwuniversiteit Wageningen (0.8 weektaak), met als taak het verzorgen van onderwijs en onderzoek op het gebied van de Groei- & Productieleer en de Luchtfoto-interpretatie. Van 1990 tot 1995 was hij tevens aangesteld (0.2 taak) als onderzoeker bij het IBN-DLO in het Bosbegrazings-programma. In 1996 is zijn taken-pakket veranderd en uitgebreid (1.0 taak), en omvat thans de Groei- & Opbrengstleer en de Eco-fysiologie. Sinds 1 februari 1998 is hij, voor een periode van 7 maanden, voor 0.8 taak gedetacheerd bij het IBN-DLO als onderzoeker Bosmodellen.