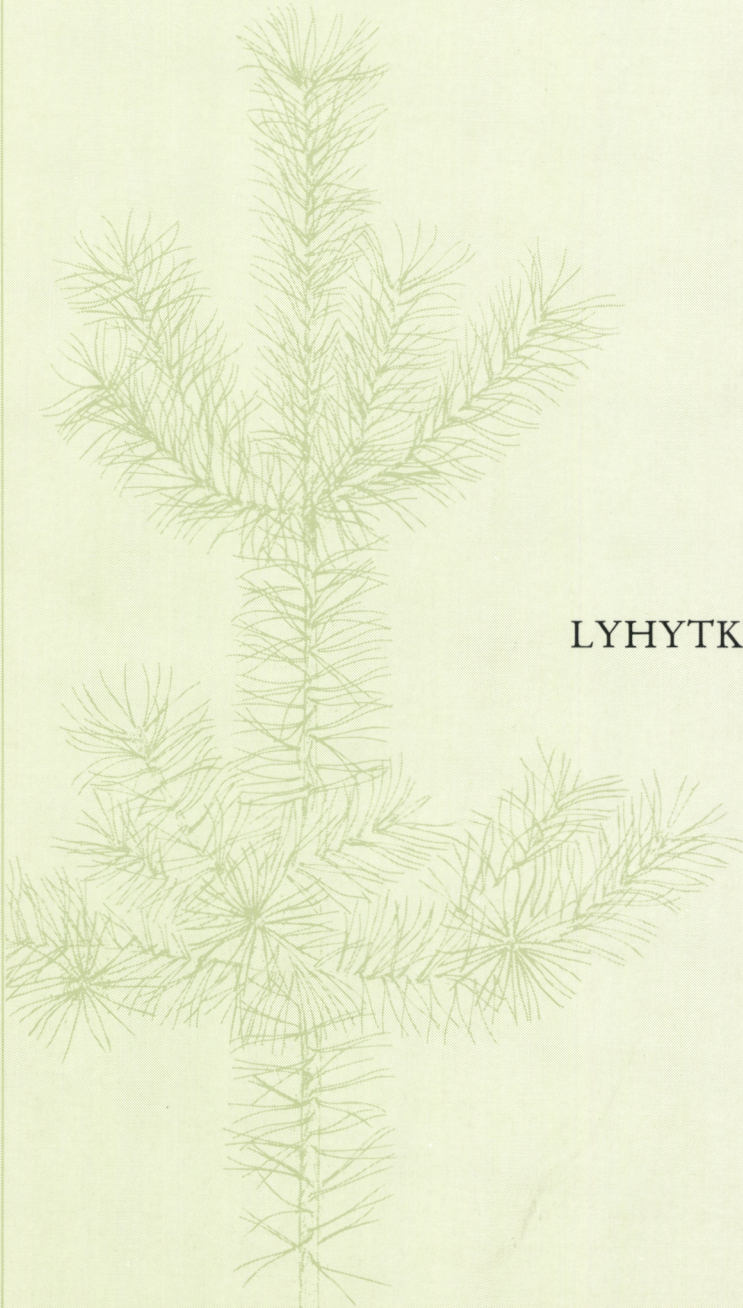


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GROWTH MODEL FOR MINI-ROTATION PLANTATIONS

RISTO SIEVÄNEN



SELOSTE

LYHYTKIERTOVIJELMÄN
KASVUMALLI

HELSINKI 1983

COMMUNICATIONES INSTITUTI FORESTALIS FENNIAE



THE FINNISH FOREST RESEARCH INSTITUTE (METSÄNTUTKIMUSLAITOS)

Unioninkatu 40 A
SF-00170 Helsinki 17
FINLAND

Director:
Professor Olavi Huikari

Head of Information Office:
Olli Kiiskinen

telex: 125181 hyfor sf
attn: metla/

phone: 90-661 401

Distribution and exchange of publications:

The Finnish Forest Research Institute
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Cover (front & back): Scots pine (*Pinus sylvestris* L.) is the most important tree species in Finland. Pine dominated forest covers about 60 per cent of forest land and its total volume is nearly 700 mil. cu.m. The front cover shows a young Scots pine and the back cover a 30-metre-high, 140-year-old tree.

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A simulation model for growth during one growing period in a mini-rotation plantation was constructed in the study. The model is based on results obtained in related biological (eco-physiological) research and the aim of the modelling was to connect some properties of the plants and some environmental factors to the accumulation of the yield.

The first step in the study is to analyse factors which bring about growth and development in a plant stand and their relationships. The main structure of the model is also obtained in the analysis. The main factors causing growth and development in a plant stand are: (1) the functioning of the plants as affected by environmental factors, (2) the micro-environment in the stand as affected by the external environment and the functioning of the plants and (3) the stand structure.

A submodel is constructed for each factor, rather large simplifications being made in the construction. The functioning of the plants is described with the aid of the flow of carbon, which is controlled by photosynthesis and respiration. Solar radiation and air temperature are considered as environmental variables. The assumption that the stand is horizontally homogeneous simplifies the treatment of the environmental factors in the stand and the stand structure.

Simulations are made with the model in order to demonstrate application of the model. The effect of weather and geographical location are studied. A sensitivity analysis of the model is made. The relative importance of some plant properties in improving the yield is studied using the results of the analysis. Finally, the role of the model as a tool in the study of plant productivity is discussed. Ways of improving the model, and the empirical studies suggested by the model are analysed.

Tutkimuksessa on laadittu malli, joka kuvaa lyhytkiertoviljelmän kasvua yhden kasvukauden aikana. Malli perustuu biologisessa (ekofysiologisessa) tutkimuksessa saatuihin tuloksiin ja sen tarkoitus on selvittää kasvien ominaisuuksien ja ympäristötekijöiden vaikutuksia sadon kertymisessä.

Ensiksi tutkimuksessa analysoidaan tekijöitä, jotka vaikuttavat kasvuston kasvuun ja kehitykseen. Näin määrytyy mallin yleinen rakenne. Tärkeimmät edellä mainituista tekijöistä ovat: (1) kasvien toiminta ympäristötekijöiden funktiona, (2) kasvuston sisäisten ympäristöolosuhteiden muodostuminen kasvien toiminnan ja säätökijöiden vaikutuksesta ja (3) kasvuston rakenne.

Jokaista tekijää kuvaamaan konstruoidaan osamalli tehden yksinkertaistuksia. Kasvien toiminta kuvataan hiilivirran avulla. Siihen vaikuttavat fotosynteesi ja respiratio. Ympäristötekijöinä käytetään säteilyn intensiteettiä ja ilman lämpötilaa.

Oletus, että kasvusto on vaakatasossa homogeeninen, yksinkertaistaa kasvuston ympäristöolosuhteiden ja rakenteen kuvausta.

Mallilla tehdään simulointeja, joilla osoitetaan miten mallia voi käyttää. Sään vaihtelun ja paikkakunnan vaikutusta satoon tutkitaan. Mallille tehdään herkkyyksianalyysi. Sen tuloksia käyttäen analysoidaan eräiden kasvien ominaisuuksien merkittävyyttä pyrittäessä parantamaan satoja. Lopuksi käsitellään mallien mahdollisuuksia toimia apuneuvona tutkittaessa kasvustojen tuottavuutta. Samalla analysoidaan mallin parantamista ja sen osoittamia empiirisen tutkimuksen tehtäviä.

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PREFACE

The main part of this work has been carried out as part of a project into the use of wood as an energy source (Pera-project) at the Department of Silviculture, the Finnish Forest Research Institute. The work has been financed for shorter periods of time by the Academy of Finland and has been completed at the Department of Mathematics, the Finnish Forest Research Institute. The related experimental work has been done at Suonenjoki Research Station of the Finnish Forest Research Institute.

The present work has been presented as a thesis for the degree of Lic. Tech. at the Helsinki University of Technology. On that occasion the manuscript was read by Dr.

Andrea Holmberg, Dr. Pertti Hari and Acting professor Paavo Pelkonen.

The manuscript of the present publication has been read by Professor Risto Seppälä, Dr. Erkki Lipas and Acting Professor Paavo Pelkonen, who also cooperated in carrying out the related measurements. The English language was checked by Mr. John Derome and the manuscript was typed and the figures drawn by Miss Outi Riikonen and Miss Marja Koskela.

I wish to extend my sincere thanks to all the persons mentioned above, as well as to the others who contributed to the accomplishment of the present study.

Helsinki
September 1983

Risto Sievänen

List of the main symbols

(in the order they occur in the text)

Chapter 2

q	total radiation sum during one hour	MJ/m ²	P_M	the maximum photosynthetic rate	mg CO ₂ · hr ⁻¹ dm ⁻²
q_0	total radiation sum during one hour under cloudless conditions	MJ/m ²	P_{m1}	function	—
z	parameter		P_{m2}	function	—
Q_0	irradiance caused by total radiation in mean conditions (reference)	W/m ²	T	air temperature	°C
Q	irradiance caused by total radiation	W/m ²	L_o	total leaf area in the stand per unit surface area of ground	
β	solar elevation	degrees	Q_a	the irradiance driving photosynthesis on the average at a horizontal plane	W/m ²
Z	parameter		Q_{da}	average irradiance on leaf surfaces caused by downward radiation	W/m ²
Q_t	daily total radiation sum	MJ/m ²	Q_{ua}	average irradiance on leaf surfaces caused by upward radiation	W/m ²
t_1	instant of sunrise	hours	P	daily photosynthesis in the stand per unit surface area of ground	kg CO ₂ /m ²
t_2	instant of sunset	hours	i_a	the first hour after sunrise	hours
			i_b	the last hour before sunset	hours
			R_p	respiration rate of the plant	kg starch
			w	dry-weight of the plant	kg starch
			T_m	the mean air temperature of the day	°C

Chapter 3

L	downward cumulative leaf area per unit surface area of ground		r_{11}, r_{12}	parameters	—
τ	attenuation coefficient of the total downward radiation averaged over a horizontal plane		R_m	amount of maintenance respiration during one day per unit surface area of ground	kg starch/m ²
K	parameter		W_l	dry-weight of leaves per unit surface area of ground	kg starch/m ²
Q_d	irradiance caused by downward radiation	W/m ²	W_r	dry-weight of current roots per unit surface area of ground	kg starch/m ²
Q_u	irradiance caused by upward radiation	W/m ²	R_g	amount of growth respiration per unit surface area of ground	kg starch/m ²
u_1, u_2	parameters	—	r_2	parameter	
T_s	daily mean temperature in the soil at a depth of 15 cm	°C	G	amount of photosynthates usable in growth per unit surface area of ground	kg starch/m ²
T_a	mean air temperature of the preceding day	°C			

d_1, d_2	parameters	—
p_n	CO ₂ uptake of a leaf	mg CO ₂ · hr ⁻¹ dm ⁻²
p_g	photosynthetic rate of a leaf	mg CO ₂ · hr ⁻¹ dm ⁻²
r	respiration rate of a leaf	mg CO ₂ · hr ⁻¹ dm ⁻²
P_m	the maximum photosynthetic rate at a moment	mg CO ₂ · hr ⁻¹ dm ⁻²
p_q	function	—
Q_s	saturating irradiance	W/m ²

Chapter 4

k	number of day	
D	growth substrate deficit	kg starch/m ²
W	the dry-weight of the stand per unit surface area of ground	kg starch/m ²
R	amount of respiration in the stand during one day per unit surface area of ground	kg starch/m ²

α_i	allocation ratio of photosynthates to the $i = l$ leaves $i = s$ stems $i = r$ roots		ΔT	the deviation of the monthly mean temperature from the long term mean	$^{\circ}\text{C}$
W_s	dry-weight of stems in the stand per unit surface area of ground	kg starch/m ²	ΔQ	the deviation of the monthly mean radiation sum from the long term mean	MJ/m ²
k_o	the day of growth initiation		Q_{t1}	the daily radiation sum in the simulation	MJ/m ²
\hat{P}	the same as P	kg CO ₂ /m ²	θ	any parameter of the model	
W_{i0}	the initial dry-weight per unit ground surface (Table 1) of $i = l$ leaves $i = s$ stems $i = r$ roots	kg starch/m ²	v_i	sensitivity of the dry-weight of the stand compartment with respect of a parameter $i = l$ leaves $i = s$ stems $i = r$ roots	—

1. INTRODUCTION

It has become evident following the oil crisis in 1973—74 that depleting fossil fuels will have to be replaced by other kinds of energy. The rising price of oil has speeded this up by making other sources of energy economically more viable, one of them being wood. Wood has some good properties as an energy source: it is renewable, the solar energy is stored in it in a stable form which can then be released at any time in the future using well known techniques, and its combustion does not change the global carbon dioxide balance of the atmosphere (Henry 1979), for instance. The limitations set on fuel wood production include the vast areas needed for this purpose owing to the low amount of energy stored in tree growth per unit area and unit of time.

The large area required for energy wood production puts different countries in a varying position as regards the possibility of using wood for energy. In densely populated countries wood is not likely to be an important energy source. However, in sparsely populated countries, like Finland, where suitable land areas for production are available, it can become a noticeable part of the national energy supply. Various estimates of the possibilities of using wood as an energy source in Finland have been put forward. An idea of the order of magnitude is well illustrated by two estimates of the potential annual energy supply as wood in Finland, which are 7 (Suomen ... 1981) and 10.5 (Energiametsäkomitean ... 1981) million tonnes of oil equivalent. The total energy consumption in Finland was 25.1 million tonnes of oil equivalent in 1981. It has been projected that part of the wood fuel will be obtained from silvicultural energy farms (Energiametsäkomitean ... 1981), the amount of wood obtainable from such sources in Finland being according, to one estimate (Lilleberg 1981), in the range 1.5—2.5 million tonnes of oil equivalent.

The idea of silvicultural energy farming has emerged from studies on intensified

wood production carried out using mini-rotation plantations (Malmivaara et al. 1971, Pohjonen 1974 and Sirén et al. 1974). Silvicultural energy farming involves the use of a high planting density, short rotation period (1—10 years) and multiple harvests from each planting (Henry 1979). The cultivation techniques used in preparing the sites, fertilization etc, is rather similar to that applied in agriculture. As several yields are to be harvested from one planting, those hardwoods which have a coppicing ability are therefore used as the plant material. Willow and poplar species have turned out to be most suitable for mini-rotation plantations in Finland. Research work is currently being carried out both in Finland (Pera-projektin ... 1979) and other countries (e.g. Henry 1979, Sirén and Sennerby 1980) on energy farming. The present study is connected to eco-physiological research being done at the Finnish Forest Research Institute on the CO₂ fixing properties of plants intended for use in energy plantations (Pera-projektin ... 1979, cf. also Sievänen 1980).

The information provided by eco-physiological measurements generally concerns a plant's immediate reactions to environmental factors. The dependence of the CO₂ uptake of leaves on temperature and radiation, for instance, is treated in many studies. On the other hand, the annual yield of a stand accumulates during the course of the whole growing period, when many varying factors have an effect on it. It is thus difficult to determine directly the effect of a certain factor on the yield; a factor exercising a strong influence at one moment may not be important over the whole period of growth. The measurements produce information about a factor's momentary influence, which then have to be generalized to cover the whole growing period. This, then, is the general problem associated with describing plant community development.

It has been possible, using computers, to

construct simulation models of growth in plant stands which are based on physiological data. The development of measuring devices has, in turn, increased the possibilities to gather data for the models. The simulation models have opened new possibilities for connecting the physiological information to the growth of a plant stand. During the last decade the construction of simulation models based on physiological information has been a method used widely in studies of plant productivity (e.g. Wit et al. 1978, Promnitz and Rose 1974, McKinion et al. 1974, Patefield and Austin 1971).

The aim of the present study has been to construct a growth model which is based on results obtained in related empirical (ecophysiological) research. The model is intended to act as a tool, which would provide a framework for organizing the information concerning the accumulation of the yield, which would reveal new research subjects and which could be used to make simulations. In addition, one of the aims in the writing of the manuscript has been to indicate how modelling — more generally the methods of systems analysis — can be used in the study of plant productivity.

The model described here depicts growth in an energy plantation of *Salix* cv. 'Aquatika' during the growing period following cutting. Photosynthesis is the most important process to be treated. Other processes considered are respiration,

allocation of photosynthates and attenuation of radiation in the canopy. Water and nutrients are omitted in the model and it is assumed that they are optimally supplied. The model is discrete with a time step of one day. The environmental variables used are either derived from meteorological measurements or simulated.

In the description of the model the modelling of plant communities is discussed first in Chapter 2 and the structure of the model to be built is then delineated on the basis of the discussion. The measurements pertaining to this study, as well as the generation of weather data is described. The construction of models for different processes in the stand are reported in detail in Chapter 3. In Chapter 4 the model is assembled and its performance analysed. Some possible applications are indicated by means of simulations. Finally, in Chapter 5 the use of the model as a tool in the study of plant productivity is discussed. Improvements to the model as well as the experiments suggested by the model are discussed, too.

The present study is related to the modelling done on plants and plant stands at the Systems Theory Laboratory, Helsinki University of Technology (Holmberg et al. 1979a, b, Hari et al. 1981, Kaitala 1982 and Mäkelä 1982) and at the Department of Silviculture, Helsinki University (Hari et al. 1982).

2. PREREQUISITIES FOR MODELLING

2.1 The modelling of plant communities

The plant community can be considered from several points of view, each of which is likely to result in a different model structure. The existing models of plant stands and plants can be roughly divided into three groups according to the use in question:

- 1) The yield tables (e.g. Koivisto 1959) used in forestry for providing directions for the management of forests are a set of plant community models. They are based on yield studies in which growth and yield models are constructed on the basis of extensive series of measurements (e.g. Vuokila and Väliaho 1980). In these models the stand development (i.e. changes in stand variables) is described using difference equations. The development of a stand during a short period of time (the discretization interval) depends on the state of the stand at the beginning of the period in question. Hence, the yield and growth models do not usually incorporate environmental variables directly. Different environmental conditions (soil conditions, climatic regions) are taken into consideration by means of equations or parameter values for each condition (Koivisto 1959). The yield tables thus depict the development and amount of growth in a forest stand having a certain structure, in a certain climatic region, on a certain site and under average climatic conditions. Thus, they comprise a large amount of information about forest stand development. They are based on descriptive models which do not depend on an understanding of the mechanisms involved in stand development.
- 2) The development process of plants is frequently studied with the aid of models (e.g. Hari 1972, Robertson 1973 and Sarvas 1972). Development and growth in plants are often linked together, and therefore the models describing development can also be used for predicting plant growth as well (e.g. Pohjonen 1975). The models are usually made for annual growth and development (cf. Abrami 1972, Sarvas 1972), but the growth over periods lasting for a number of years may be studied, too (Hari 1968). A variable of central importance in such models is the stage of development and its rate of change is usually described with the rate of development which, in turn, depends on environmental variables. The growth rate (rate of activity in general) depends on the stage of development and/or environmental variables which in most cases are temperature and day length (Holmberg et al. 1979a).
- 3) A large amount of quantitative data about plants has been accumulated during the last few decades. Modern measuring equipment and analysing techniques have promoted this growth of knowledge. The increase in

the amount of detailed information about plants and the advent of computers have enabled simulation models to be constructed, which are based on processes generating plant growth. The most important activity affecting growth is photosynthesis because the energy for plant growth is fixed by this process. Other important activities are transpiration, water and nutrient uptake. The most important submodel is therefore built for photosynthesis, other processes being treated to the extent permitted by the accuracy and complexity of the simulation model. The most convenient way of describing the activities affecting plant life is to use mass flows and the dependence of these flows on internal and external factors. Thus, a plant is described by means of the amounts of stored matter, and the changes in these amounts are governed by the flow rates (cf. Wit et al. 1970, Mäkelä 1982 and Thornley 1976). Simulation studies have primarily been done on agricultural crops (Wit et al. (1978), McKinion et al. (1974), Sheehy et al. (1979), Wann et al. (1978) and Patefield and Austin (1971)), but they have also been applied in forestry (Axelsson and Ågren (1976) and Mäkelä (1982)).

One of the most accurate and versatile simulation model of crop growth is that constructed by a research group in Wageningen in the Netherlands (Wit et al. 1978), called BACROS (Basic Crop Growth Simulation). It simulates an agricultural crop under optimal water and nutrients supply. The cultivated species is not specified and several different crops can be simulated by changing the parameter values. The model is based on the flows of carbon, water and nitrogen in the plants. Many of the activities of plants are connected to these flows and the micrometeorology of the canopy, which is important for describing a plant's relation to the environment, is treated accurately. The functioning of the roots is also included in the model.

The simulation models of crops (and plant communities in general) have shown the way for more and more accurate treatment of the processes occurring in plant communities. Simple and aggregated models like yield models or models of development, on the other hand, may be suitable for revealing principles governing community processes because they are not loaded with too many details.

The aim of modelling should basically determine the model structure but the knowledge available about plant processes sets limits on the model. Some problematic points, which may arise in the modelling of plant communities on the base of physiological

information, are listed in the following (cf. Ross 1970) and a way of overcoming them is discussed:

- (1) A large spatial and temporal variation is characteristic of the processes occurring in plant communities (cf. Hari et al. 1981), and further: The spatial variation takes place in three dimensions, which makes mathematical description difficult. The measurements needed for the estimation of community structure models are usually destructive, and hence it is difficult to measure structure dynamics. The environment of plants consists of two totally different elements, air and soil. The quantitative information about the processes occurring in the soil is poor. The processes in plants exhibit very different time constants, e.g. the chemical reactions of photosynthesis and the process of maturation have very different rates.
- (2) A large number of different activities are continuously taking place in plants. Accurate quantitative models have been constructed for some of them (photosynthesis, for example). However, there are processes which are less well known, and which may be important for the plant (processes in the roots, for example). Furthermore, the interconnections between processes are poorly understood.
- (3) The plants actively regulate their functioning, plants in different stages of development may react to similar environmental conditions in different ways. The quantitative information available about regulation is poor. The life cycle of a plant consists of phases which differ considerably from each other. Such phases are germination, vegetative growth, flowering, seed formation and the storage phase (tuber formation etc.). Different species undergo these phases in different ways.

When the above facts are summarized, it can be seen that a model builder is faced with a great diversity of processes and models of these processes, and the fact that the interconnections between the processes are poorly understood. Even when a very limited view of a plant community is taken, ad hoc assumptions have to be introduced to bridge lacunae in knowledge, in general, in order to ensure a functioning model. Hence, the subsequent models may contain large inaccuracies. In comparison to so-called technical systems, the use of models being an established practice in such studies, the ingredients with which a model builder of a plant community has to work with are poorer. The resulting model is therefore usually much more inaccurate than that of a technical system.

One possible way of applying dynamic models to plant communities has been delineated by Wit (1970). Plant communities exhibit many different modes of change in time; from rapid biochemical reactions to slow

changes in forest stand structure, for example. Different levels of biological knowledge are also associated with processes possessing different time constants. For example, biochemistry, physiology and ecology treat processes with increasing time constants, respectively. It is clear that it is impossible to build a simulation model which would be based on biochemistry and which would explain all the processes occurring in a plant community, because it would be far too large and cumbersome. Keeping this fact in mind, it can then be supposed that dynamic models could be effectively used in connecting different levels of knowledge (and hence different modes of change in time) together. That is; each arrow in Fig. 1 denotes a dynamic model. Fig. 1 depicts only one possible arrangement of dynamic models, the life of a plant can be dealt with in parts in other ways, too. The instant level is relative, new instants may also be distinguished in it (cf. Hari et al. 1981). In model building, an explainable level is fixed according to the basic aim of the study and then a model for a process in it is built using the information about an explanatory level, which is a level

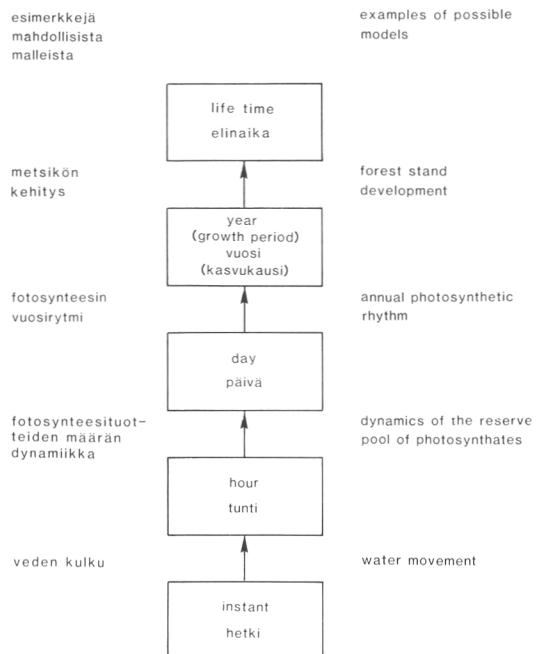


Figure 1. Plant life considered according to a time constant. Arrows indicate dynamic models.

Kuva 1. Ajallisen vaihtelun tasot kasvien toiminnassa. Nuolet tarkoittavat dynaamisia malleja.

with a suitably small time constant. The choice of the explanatory level naturally depends on the desired complexity of the model. It is the explainable level which determines what processes are taken into account and how. The choices can then be made rationally according a certain criteria and, hence, it may be assumed that the resulting model has a reasonable structure. It should be noted that this modelling strategy easily leads to discrete models: the events in the explanatory level are summed up to events in the explainable level.

2.2 The basic structure of the model

The present model is based on a preliminary model (Sievänen 1980). The experiences gained in its construction have been used to make the model more accurate at certain points (photosynthesis, respiration, environmental variables). However, some simplifications have also been made, perhaps the most important of them being the omittance of the role of photosynthate reserves. The structural relations of the present model are discussed in the following.

A plant community consists of single plants which interact with each other through the environment (cf. Hari et al. 1981). There are thus two main factors affecting the functioning of a plant community: 1. the way in which a plant reacts on environmental factors and 2. the way in which microenvironment in the community is formed under the effect of both the external climate and the plants. Two modes can be distinguished in the effect of plants: firstly, the environmental conditions are changed through the metabolism of plants and, secondly, the stand structure affects the nature of changes in the environmental conditions. On this basis the interconnections in a plant community can be depicted according to Fig. 2. The feedback loop through the stand structure in Fig. 2 is important for the dynamic development of plant community during an extended period of time.

Figure 2 presents a straightforward approach to the construction of a model of growth and stand structure development in a plant community. The submodels needed are (the term submodel (or model for short)

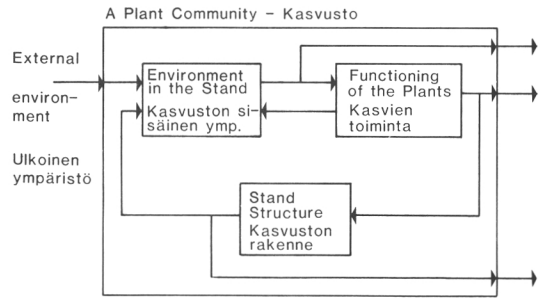


Figure 2. The connections between different factors in a plant community.

Kuva 2. Kasvuston kehitykseen vaikuttavien tekijöiden keskinäiset yhteydet.

is used in this report in a broad sense, it refers to relationships, be they dynamic, static, involved or simple, used in construction of the simulation model):

- 1) A model for the functioning of the plant as a function of environmental factors,
- 2) models describing the development of geometrical structure in a single plant as a function of environmental factors and the connection between structures of plant and stand and
- 3) a model of environmental conditions in the community.

When the explainable level is fixed, it can be used as a means for choosing suitable models for 1)–3). In the present case, the growth in a short rotation plantation during one growing period is studied, which determines the explainable level.

Owing to the aim of this modelling study, photosynthesis is the basic process taken into consideration in the submodel for the functioning of the plants. This means that it is based on the flow of carbon, and the other processes are treated to the extent that they affect it. In the present case the flow of carbon is described in a rather simple way (Fig. 3). The model of the carbon flow often includes two carbon stores (e.g. Wit et al. 1970): the reserve pool of photosynthates and structural matter. Here the use of the reserve pool has been omitted because it can be assumed that during the growing period photosynthesis and the formation of new structural matter are well balanced and the availability of photosynthates is the principal factor limiting growth. Structural dry-mass also contains an average amount of photosynthates which are not in the form of

structural matter. The photosynthesis in single leaves is assumed to depend on radiation and temperature. The model is therefore applicable to stands which are irrigated and supplied with sufficient nutrients.

In the submodel of the environment in the plant stand it is assumed that the plant stand is horizontally homogeneous. The extinction of radiation in the canopy is considered. Temperature is assumed to be spatially constant above the soil surface. In

the model an estimate is used for soil temperature.

The assumption that the stand is horizontally homogeneous means that the submodel for stand structure becomes very simple. The stand structure is described using the amounts of stems, leaves and roots; and is therefore determined by allocation ratios of photosynthates to the stems, leaves and roots. They are assumed to be constant throughout the growing period.

The activities described in the submodels are the following:

- 1) Dependence of the photosynthesis of single leaves on environmental factors,
- 2) changes in the photosynthetic efficiency of leaves during the photosynthetic production period,
- 3) effect of environmental factors on respiration in plants,
- 4) allocation of photosynthates to the stems, roots and leaves and
- 5) radiation and temperature in the stand.

When the submodels are connected together in the way indicated in Fig. 2, the relationships between the activities taken into account are as presented in Fig. 4.

The present model is discrete with a time step of one day. It is a natural time step for models having the growing period as the explainable level because of the diurnal rhythm of environmental factors. It is

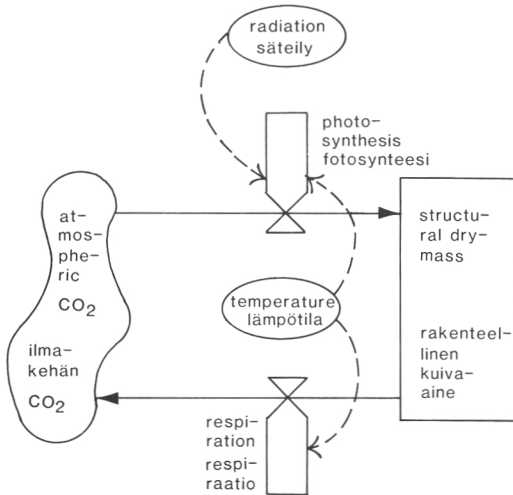


Figure 3. Flow of carbon in the model.
Kuva 3. Hiilen kulku mallissa.

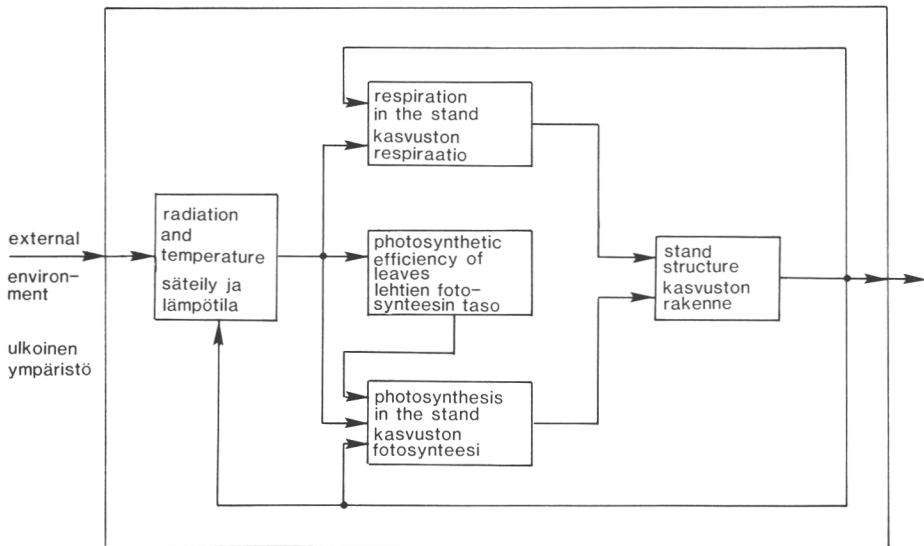


Figure 4. The relationships between the activities included in the model.
Kuva 4. Mallissa kuvattujen kasvustossa tapahtuvien toimintojen väliset yhteydet.

obvious that the photosynthetic capacity of leaves and the allocation ratios of photosynthates do not change considerably during one day. Photosynthesis, on the contrary, exhibits a marked diurnal variation because radiation and temperature vary considerably during one day. For this reason the diurnal variation of radiation is taken into account in the calculation of daily photosynthesis. Respiration also exhibits diurnal variation (Jones et al. 1978) but it is considered only in terms of one day.

2.3 Input weather data

The air temperature outside the canopy and the total irradiance on a horizontal surface at the upper level of the canopy comprise the environmental variables (input) for the model. The diurnal variation of environmental factors is taken into consideration in the photosynthesis submodel and hence the environmental factors have to be given with a smaller time step than one day. The environmental factors are most conveniently simulated when the use of the model is flexible (cf. Axelsson and Ågren 1976, Wit et al. 1978). The real course of environmental variables can be approximately reproduced in a weather simulator by using measured weather characteristics.

The weather simulator works as follows: the daily pattern of the change in temperature and radiation is described by means of functions which are adjusted so that the daily total radiation sum and the mean temperature are prescribed ones. They are taken either from measurements or simulated on the basis of weather statistics.

On a cloudless day this approach succeeds in reproducing the real course of radiation and temperature, but on days when it is alternately cloudy and sunny temperature and radiation show no regular pattern. Functions used here are thus averages for sunshine and cloudy conditions.

2.3.1 The daily course of radiation

On a cloudless day the total radiation is clearly dependent on the solar elevation. Both theoretically derived and measured

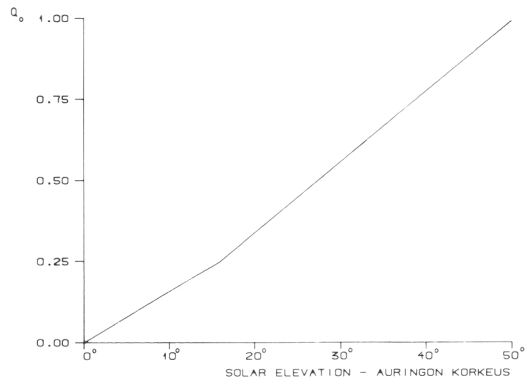


Figure 5. The estimated relationship between total irradiance, Q_0 , (relative values) and solar elevation.

Kuva 5. Estimoitu kokonaissäteilyn tunneittaisen summan, Q_0 , (suht. yks.) ja auringon korkeuden välinen yhteys.

relationships have been represented for this. For the prediction of the hourly total radiation sums, $q(t)$, from other meteorological data Saurio (1977) uses a model

$$q(t) = z \cdot q_0(t), \quad (2-1)$$

where $q_0(t)$ is the total radiation sum under cloudless conditions during the hour t , and z depicts the effect of other meteorological factors. It can be seen from (2-1) that if all other factors (i.e. z) remain constant throughout the course of a cloudy day, then the time course of the total radiation has a similar form to that of a clear day, only the level is different.

The method of (2-1) was used in this study. The reference radiation, Q_0 , was taken as the average time course of the irradiance caused by total radiation during one day in the summertime. It was estimated from weather statistics (Rossi 1976). The relationship between Q_0 and solar elevation is presented in Fig. 5.

Parameter Z is adjusted so that

$$\int_{t_1}^{t_2} Z Q_0(\beta(t)) dt = Q_t, \quad (2-2)$$

where β is solar elevation, t_1 and t_2 are the instants of sunrise and sunset and Q_t is the daily total radiation sum.

On a clear day the consistency of the model and the measurements is quite good (Fig. 6). The cloudiness on an overcast day has increased with time and therefore the

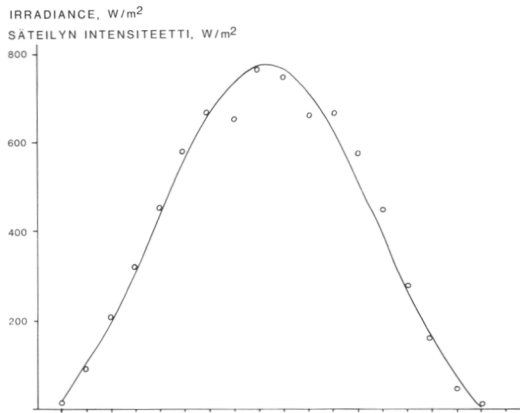


Figure 6. Total radiation sums measured on a clear (O) and overcast (*) day and simulated with model (2—1) (—).

Kuva 6. Kokonaissäteilyn tunneittaiset summat mitattuna kirkkaana (O) ja pilvisenä (*) päivänä sekä simuloituna mallilla (2-1) (—).

symmetrical pattern of model (2—1) does not fit very well the measurements because Z assumes a constant value for the whole day.

2.3.2 The daily total radiation sums

The average course of the daily total radiation sums during one year can be estimated from weather statistics (Rossi 1976). The approximation of the average course is done with a point graph (Fig. 7 giving an example) for different locations. In simulations (4.2.4), a stochastic component has been added to this average course in order to mimic the randomly varying weather.

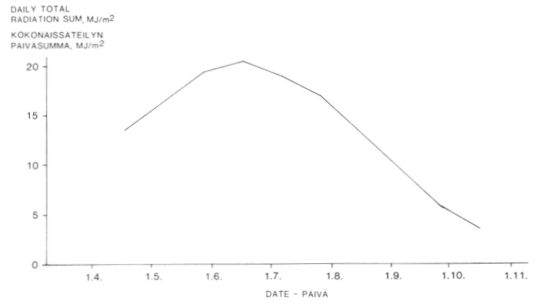


Figure 7. Approximation of the time course of the daily total radiation sums during the period May-October by at Luonetjärvi (62°28'N, 25°40'E).

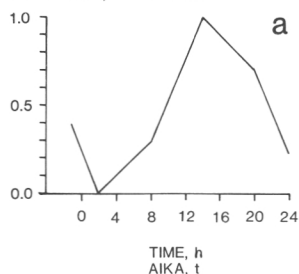
Kuva 7. Kokonaissäteilyn päivittäisen summan keskimääräinen kulku Luonetjärvellä (62°28'P, 28°40'I) ajalla toukokuu-lokakuu.

2.3.3 Temperature

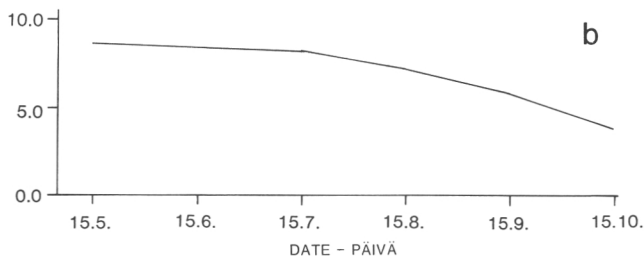
The temperature near the ground is mainly determined by the radiation balance and wind speed (Heino 1973). On clear days, the radiation balance follows a regular pattern of change, as does temperature. Cloudiness has an effect on the radiation balance, and wind causes turbulent exchange of heat in the air. Both these factors disturb the regular diurnal course of temperature. It is possible, however, to estimate the average diurnal course of temperature for summer months from weather statistics (Fig. 8a). In winter the diurnal course of temperature differs a lot from that in summer. The maximum difference between daily temperatures varies in the period April-October as depicted in Fig. 8b. All the above estimates were obtained from weather statistics recorded at the airport in Kuopio (63°01'N, 27°48'E), which is the nearest observation station to the experimental site in Suonenjoki with published results (Heino 1976). The mean temperature for one day is described using a sine function of time (Fig. 8c) for different locations, each having its own parameter values.

The diurnal course of temperature can now be simulated using the dependencies depicted in Fig. 8. In cases where measurements are available, then the mean temperature and the diurnal variation are obtained from them and only the diurnal pattern of change is simulated.

TEMPERATURE, REL. UNITS
LÄMPÖTILA, SUHT. YKS.



DIURNAL VAR. OF TEMP. °C
LÄMPÖTILAN VUOROKAUSVAIHT. °C



DAILY MEAN TEMP., °C
PÄIVÄN KESKILÄMPÖTILA, °C

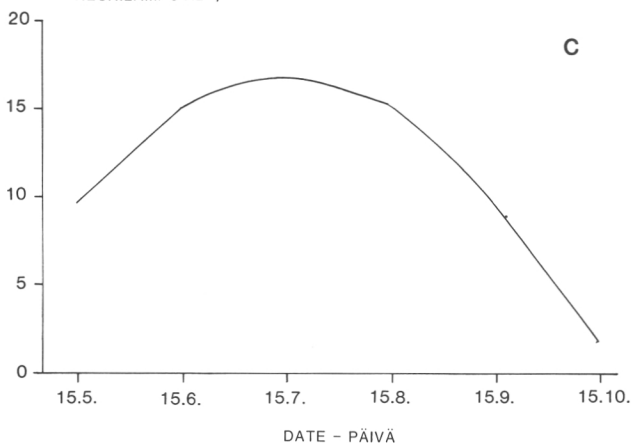


Figure 8. The diurnal course of temperature, relative values (a), the magnitude of the diurnal variation in temperature during the period May-October as estimated from weather statistics recorded at Kuopio airport (Heino 1976) (b) and daily mean temperature as a sine approximation at the same location during the period May-October (c).

Kuva 8. Kuopion lentokentän säätilastoista (Heino 1976) estimoitu lämpötilan vuorokausvaihtelu (suht. yks.) (a), lämpötilan vuorokausvaihtelun suuruus (b) ja vuorokauden keskilämpötilan riippuvuus ajasta (käytetty sini-funktiota) (c) ajalla toukokuu-lokakuu.

2.4 The measurements associated with the model

The empirical work from which the values for several of the parameters in the model have been obtained has been done at Suonenjoki Forest Research Station, the Finnish Forest Research Institute (62°37'N, 27°5'E) during 1978–1980. It has included observations of the CO₂ exchange of willow plants during the photosynthetic production period, radiation climate measurements and measurements of dry matter production and other characteristics of the stand and individual plants.

CO₂ exchange measurements

The measurements of CO₂ exchange had two main goals: to determine the relationship between the photosynthetic rate and momentary values of driving variables (light intensity and temperature), and to deter-

mine long term changes in the photosynthetic capacity. The measuring period usually comprised the period July-September, with some breaks.

The measuring equipments included assimilation chambers and an IRGA-apparatus for measuring the CO₂ concentration of gas samples (so-called open measuring system, see Hari et al. (1979)). The temperature in the canopy and the irradiance in the cuvettes were recorded. The irradiance was measured with equipment developed for measuring light in photosynthetic studies (Hari et al. 1976). In addition, the total short-wave radiation and temperature above the canopy were monitored. A data-logging unit was used to collect the data and to carry out the measurements at the desired frequency.

A closed-circulation, one-leaf assimilation chamber was also used. It was easier, using such a closed cuvette, to study, the responses of single leaves to environmental factors. This measuring system was used only occasionally for shorter periods.

The attenuation of the total short-wave radiation in the canopy was studied. The measurements were carried out using equipment for estimating the frequency distributions of light intensity within a stand (Salminen et al. 1983) during August 1979 in a willow stand with a leaf area index (leaf area per ground area unit) about 6. The sensors of the equipment were located at different heights inside and above the canopy. The vertical distribution of the leaf area within the canopy was evaluated in connection with the radiation climate measurements.

The phytometric characteristics of willow plants and stands have been measured in many studies carried out on energy plantations at the Suonenjoki Forest Research Station. All these measurements have been available for calculating willow stand characteristics. The following parameters were used in this modelling study: relationship between the dry-weight and length of the stems, relationship between the dry-weight of stems and their leaves, the dry-weight of leaves as a function of their area (specific leaf weight) and the length distribution of the stems in a stand.

3. SUBMODELS

The submodels were defined in the preceding chapter. The submodels are constructed in this part using the available information about the phenomena which they include. The values for parameters are also obtained during the construction of the submodels.

3.1 Allocation of photosynthates (Stand structure)

In the type of cultivation used at the experimental site the willow plantations were grown with a one year rotation cycle. In the spring the old stools produced new shoots. The number of stools per square meter varied between 4 and 16, and the number of shoots per stool was approximately 3–10, depending on the density of stools. Growth began at about the end of May and continued until the middle of September, at which time the longest stems had reached a length of 3–3.5 m. The final leaf area index was in the range of about 5–10.

The stand structure is described in the present case by means of the dry-weight of leaves, stems and roots as well as the leaf area index. The amount of plant material (leaves) that dies is so small that its role is neglected in the model. The construction of this submodel is therefore reduced to determining the allocation ratios of photosynthates to the leaves, stems and roots and the specific leaf weight. All these quantities were assumed to remain constant throughout the growing period. Their values were obtained on the basis of phytometric measurements (cf. 2.4), being 0.21, 0.69, 0.1 and 0.074 kg/m² for the allocation ratios of photosynthates to leaves, stems and roots and for specific leaf weight, respectively.

The allocation ratio of photosynthates to roots could not be measured. It can be assumed that during the first growing period following planting, it is about 0.3 in a sufficiently fertilized site (Sievänen et al. 1983). In subsequent years the root system has already been developed and the demand for photosynthates in the roots is obviously reduced. There is no information available about the allocation of photosynthates to

the roots, and so a value was obtained on the basis of some indirect evidence.

Even if the stand structure submodel in this case is very simple, it is an important part of the model of a plant stand (cf. Fig. 2). The description of stand structure formation, in general, consists of two parts: allocation of photosynthates and the formation of the geometrical structure of the plants.

3.2 Radiation and temperature in the stand

3.2.1 Attenuation of radiation in the stand

The model for the extinction of radiation is based on the assumption of horizontal homogeneity. It is usually made in radiation studies on plant stands (Ross 1970) and is realistic for a dense willow stand. Only changes in the vertical direction are, therefore, considered. The effect of the stems on the extinction of radiation is neglected.

The incoming radiation is composed of two components: direct and diffuse solar radiation. The diffuse radiation has been scattered in the atmosphere. The irradiance falling on the upper surface of a horizontal plane in a plant stand is determined by the proportion of directly penetrated and scattered components of the direct and diffuse solar radiation. The radiation impinging on the lower surface of a horizontal plane in the stand is composed of reflected direct and diffuse solar radiation. A large number of models have been constructed for the radiation regime in a plant stand (Ross 1981). The complex models take into consideration the different behaviour of the components of radiation, as well as the properties of the vegetation. Semi-empirical formulae are also available for the penetration of total radiation into a plant stand. In this study the total radiation impinging on both the lower and upper surface of a horizontal plane in the stand is considered. Simple semi-empirical formulae are applied.

The leaf area above a horizontal plane, rather than its height above the ground, determines the radiation regime on it. The attenuation of the radiation can then most suitably be described in terms of downward

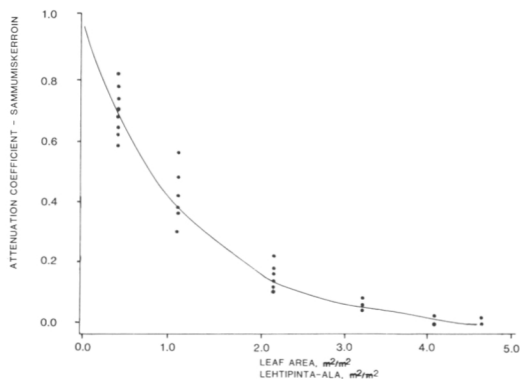


Figure 9. Comparison of model (3-1) (solid line) and measurements made at a solar elevation range of 26°–30°.

Kuva 9. Mallin (3-1) (yhtenäinen viiva) ja mittausten yhteensopivuus kun auringon korkeus, β , on välillä 26°–30°.

cumulative leaf area per ground area unit, L , that is, the leaf area above a horizontal plane. L is thus a measure of the shading leaf area. The extinction of radiation is measured with the attenuation coefficient, which is the irradiance in the canopy divided by the irradiance at the top of the canopy.

The attenuation coefficient of the total downward solar radiation averaged over a horizontal plane, τ , was found to obey exponential formula given by Tooming and Ross (1964) (cit. Ross 1981)

$$\tau(L) = e^{-\frac{K \cdot L}{\sin \beta}} \quad (3-1)$$

where K is a coefficient and β is the solar elevation. According to Ross (1981), K should vary with varying solar elevation but in this study a constant value of 0.37 is assumed. At low values of L , (3-1) seems to give too low values (Fig. 9) for τ . It may be due to different radiation penetration properties in the upper part of the stand in comparison to the lower part.

Measurements of the upward radiation revealed that it is a fraction of the downward radiation, and that this fraction decreases with increasing downward cumulative leaf area (Fig. 10). The irradiance caused by upward radiation, Q_u , is calculated from the irradiance caused by downward radiation, Q_d , with a multiplier, which depends on L ;

$$Q_u(L) = (u_1 - u_2L) \cdot Q_d(L), \quad (3-2)$$

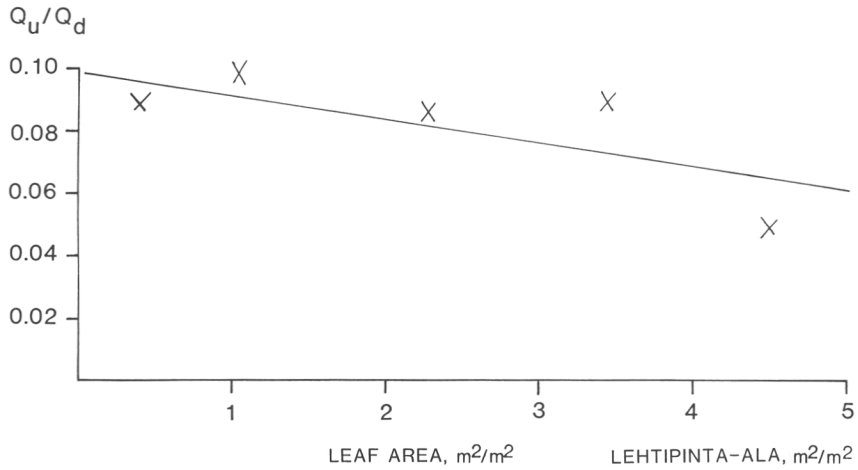


Figure 10. The fraction of upward radiation of downward radiation at different values of downward cumulative leaf area. The line is $y = 0.1 - 0.075x$.

Kuva 10. Kasvustossa olevan vaakasuoran tason alapinnalle tulevan säteilyn intensiteetin osuus saman tason yläpinnalle tulevan säteilyn intensiteetistä varjostavan lehtipinta-alan funktiona. Kuvaan piirretty suora on $y = 0.1 - 0.075x$.

where u_1 and u_2 are coefficients, the values of which are deduced from Fig. 10.

(3—2) is a rather rough model for reflected radiation. It is known that solar elevation, among others (Goudriaan 1977), has a strong influence on the reflected radiation. However, due to the lack of more detailed information about the properties of the plants in question it serves as a first approximation.

3.2.2 Temperature

The spatial temperature differences in the canopy are neglected and the only temperature (air temperature above the canopy) is assumed to be that of the above-ground part of the stand. The spatial temperature differences in the soil are also neglected. The daily mean temperature at a depth of 15 cm, T_s , is used as the daily mean temperature of the soil. During the growing period it appears to depend on the mean air temperature of the preceding day, T_a , according to equation

$$T_s = d_0 + d_1 T_a, \quad (3-3)$$

where d_0 and d_1 are constants with values of 5 °C and 0.46, respectively.

3.3 Photosynthesis and respiration

The model of photosynthesis is based on the photosynthesis of single leaves which has been studied experimentally (cf. 2.4). Light and temperature are used as the environmental variables. The photosynthesis in the canopy is calculated with the aid of the radiation extinction model, spatial temperature differences in the canopy being neglected. Variation in the photosynthetic efficiency occurs during the growing period and is taken into consideration with a model in which temperature is a controlling factor. The respiration of the plants in the stand is described by means of a simple equation.

3.3.1 The photosynthetic rate of single leaves

The photosynthetic process utilizes light energy. The reaction constants in photosynthesis are temperature dependent and therefore the rate of process varies with temperature. Factors other than light and temperature are neglected in the model for photosynthesis. Therefore normal conditions as regards the CO₂ concentration in the air, air humidity, water and nutrient status of the plants etc. are assumed to hold.

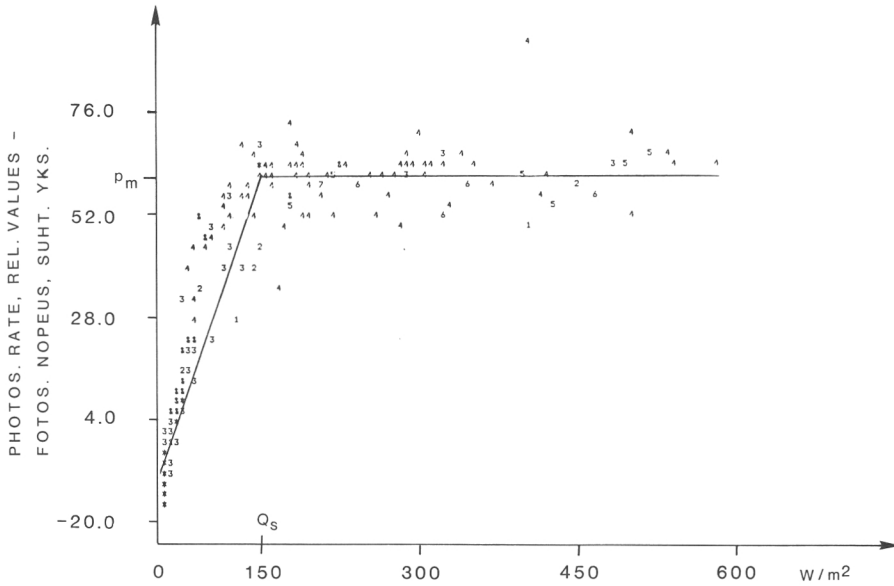


Figure 11. Measured relationship between CO₂ uptake (rel. units) in a leaf of willow and irradiance during one day. The solid line is p_n from (3—4), with p_q from (3—7) and with $r=6.4$, $p_m=69.0$, $Q_s=150$ W/m².

Kuva 11. Pajun lehden hiilidioksidin kulutuksen (suht. yks.) riippuvuus säteilyn intensiteetistä. Mittaukset on tehty yhden päivän aikana. Yhtenäinen viiva on p_n yhtälöstä (3-4), jossa on käytetty yhtälön (3-7) mukaista funktiota p_q . Käytetyt parametriarvot ovat $p_m=69$, $r=6.4$ ja $Q_s=150$ W/m².

The model thus applies to conditions with a sufficient supply of water and nutrients.

A characteristic light response curve of CO₂ uptake in a leaf, obtained from the measurements, is depicted in Fig. 11. The level of saturated CO₂ uptake varied, but the shape of the curve remained quite constant during the photosynthetic production period. The measured CO₂ uptake of a leaf consists of two opposite flows of CO₂: the CO₂ taken up in photosynthesis and the CO₂ released in respiration. The dependencies of the photosynthetic rate then have to be deduced from measurements of the CO₂ uptake in a leaf, p_n . It obeys the equation

$$p_n = p_g - r, \quad (3-4)$$

where p_g is the photosynthetic rate and r the respiration rate. When there is no light present,

$$p_n(0) = -r. \quad (3-5)$$

This is called the dark respiration. It is assumed that the dark respiration is not

considerably affected by the irradiance Q . From (3—4) and (3—5) is obtained (cf. Wit et al. 1978, p. 35)

$$p_g(Q) = p_n(Q) - p_n(0). \quad (3-6)$$

The Blackman curve

$$p_g(Q) = p_m \cdot p_q(Q) = p_m \cdot \begin{cases} \frac{Q}{Q_s}, & 0 \leq Q \leq Q_s \\ 1, & Q > Q_s \end{cases} \quad (3-7)$$

where p_m is the maximum photosynthetic rate at the moment and Q_s saturating irradiance, appeared to be suitable for describing the relation of p_g to irradiance (Fig. 11). The value for Q_s in Fig. 11 is typical for the measurements. Q_s assumed the same value throughout the growing period. p_m assumed a constant value in the middle of the growing period but declined in the autumn.

Photosynthesis is affected by temperature in two ways (Pelkonen 1981): first, it has an immediate effect on the photosynthetic rate and secondly, the photosynthetic efficiency at a certain moment may depend on the

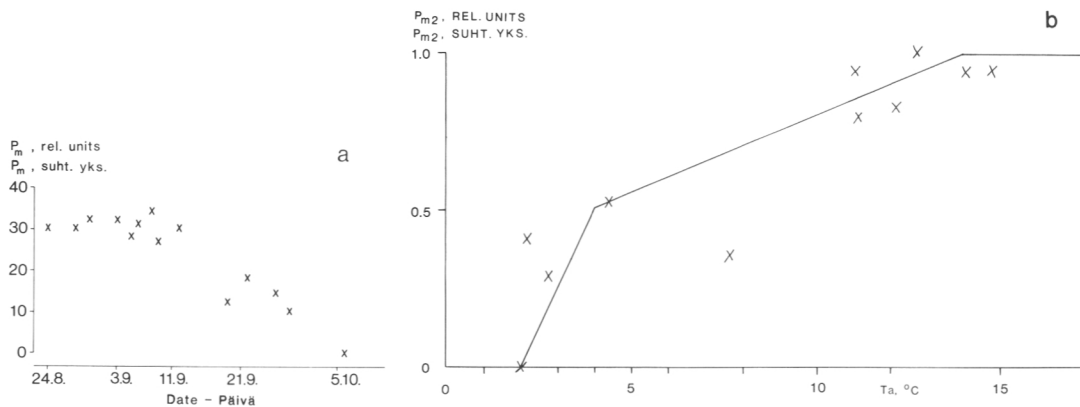


Figure 12. Variation in the maximum photosynthetic rate as a function of time (a) and as a function of the mean temperature of the preceding day (b). The solid line in (b) depicts function (3–10) (in relative values).
 Kuva 12. Maksimaalinen fotosynteesinopeus ajan (a) ja edellisen päivän keskilämpötilan (b) funktiona. Yhtenäinen viiva kuvassa (b) on yhtälö (3–10) (suht. yks.).

preceding temperature conditions. Both factors mainly have an effect on p_m , not on Q_s (Pelkonen 1981, Wit et. al. 1978). If it is supposed that the preceding temperatures do not affect the response to the prevailing temperature, then both effects can be incorporated into the model by defining

$$P_m = P_M \cdot P_{m1}(T) \cdot P_{m2}, \quad (3-8)$$

where P_M is the maximum photosynthetic rate, p_{m1} is the immediate effect of the prevailing air temperature, T , and p_{m2} is the dependence of the maximum photosynthetic rate on the preconditioning of the plants to prevailing temperatures.

The effect of the prevailing temperature is easily established under laboratory conditions (e.g. Mooney and Harrison 1979). However, in field conditions — where the measurements for this study were made — the plants seem to be very insensitive to temperature changes, which normally occur during the growing season. In this case, the effect of the prevailing air temperature was beyond the resolution capacity of the measuring instruments. An approximate formula

$$P_{m1} = \begin{cases} 1 & , T \geq 8 \\ T/8 & , 0 \leq T < 8 \\ 0 & , T < 0 \end{cases} \quad (3-9)$$

was then introduced. Wit et al. (1978) have had similar problems with the effect of the prevailing temperature. They have used a function of similar shape to (3–9).

The measurements showed that the photosynthetic efficiency was approximately constant from June to the end of August and then declined during September to zero (Fig. 12a). The leaves were shed during the first half of October. No measurements were made during June, but it may be supposed that the photosynthetic efficiency of the leaves is constant from the very beginning of the growing season until wintering starts in September. In the earlier study (Sievänen 1980), a model for the variation in the photosynthetic efficiency of Scots pine during spring, proposed by Pelkonen and Hari (1980), was applied. It is quite complicated and further measurements revealed that the variation in the photosynthetic efficiency of willow can be accounted for using a simpler model. The mean temperature of the preceding day was chosen to represent the previous temperatures in this model. When the maximum photosynthetic rate of one day is plotted against the average temperature of the previous day, T_a , Fig. 12b is obtained. The equation

$$P_{m2} = \begin{cases} 0 & , T_a \leq 2 \\ 0.25T_a - 0.5 & , 2 < T_a \leq 4 \\ 0.05T_a + 0.3 & , 4 < T_a \leq 14 \\ 1.0 & , T_a > 14 \end{cases} \quad (3-10)$$

was chosen to depict dependence of the variation in maximum photosynthetic rate on T_a (cf. Fig. 12b). The model thus depicts the dependence of the photosynthetic effi-

ency of the leaves on the prevailing temperatures. With this model, the photosynthetic rate approaches zero in the autumn and is constant during June-August in normal weather conditions. According to the measurements, parameter p_M was in the range 20–29 mgCO₂/h · dm².

3.3.2 Canopy photosynthesis

The photosynthetic rate of the stand can now be calculated with the aid of the light response curve for the photosynthetic rate of a single leaf, the radiation extinction model and the total leaf area, L_0 , in the stand. As the plantation is assumed to be well irrigated, the spatial temperature differences in the canopy are not likely to be very large (cf. Goudriaan 1977 and Wit et al. 1978). In addition, the photosynthetic rate of the leaves is rather insensitive to temperature, and on these grounds the temperature differences in the canopy are neglected and air temperature in the shade above the canopy is used in all the calculations.

Now, the photosynthetic rate of the stand is given by

$$p = p_m \cdot \int_0^{L_0} p_q(Q_a(L))dL, \quad (3-11)$$

where $Q_a(L)$ is the irradiance driving photosynthesis on the average at a horizontal plane with a shading leaf area of L and p_m and p_q are according to (3-7) (note: p does not depend on the particular vertical distribution of the leaf area).

The light response curve (3-7) was obtained for one leaf in the case where only one side is illuminated. Thus, when appropriate information is lacking, it can be supposed that if both sides of a leaf are exposed to radiation, then the irradiance values on both sides of the leaf can be summed up and the photosynthetic rate will respond to the summed radiation according to (3-7). This means that the photosynthetic rate of a leaf illuminated equally on both sides is less than, or equal, to the doubled photosynthetic rate for one side, because (3-7) is a saturating type of curve. $Q_a(L)$ in (3-11) is thus summed up from the downward and upward components.

The average irradiance values on the upper and lower surfaces of a horizontal

plane are obtained from the radiation extinction model. Deducing how these irradiance values relate to the irradiance driving photosynthesis (averaged over the plane) in leaves close to the horizontal plane is not a trivial task. The average irradiance on the upper surface is composed of the irradiance in sunflecks and the shaded area. The spatial variation in the light intensity can thus be considerable. The irradiance on the lower surface of the plane is likely to be more evenly distributed. Depending on the distribution of the sunflecks and shade, the photosynthesis of leaves close to a horizontal plane, which receives the same average irradiance, may proceed at rather different rates (Monteith 1965). In addition, the inclination of the leaves affects the irradiance which they are exposed to and thus the photosynthetic rate. The average irradiance falling on a leaf caused by both downward and upward radiation is used in calculating photosynthesis. A method proposed by Saeki (1963) is applied for calculating the average intensities which results in

$$Q_{da}(L) = -\frac{Q_d}{1-m} \cdot \frac{d}{dL}(\tau(L)) \quad (3-12)$$

for average irradiance on leaf surfaces caused by downward radiation, Q_{da} , where Q_d is the irradiance caused by downward radiation at the top of the stand, m is the transmission coefficient of the leaves (the value of 0.2 for a 'mean' green leaf according to Ross (1975) is assumed) and τ is the attenuation coefficient from (3-1).

In order to facilitate calculation of the average irradiance caused by upward radiation, Q_{ua} , it is supposed that the extinction of both downwards and upwards radiation is similar: that is, τ can be applied also for radiation passing upwards. The following now holds

$$Q_{ua} = (u_1 - u_2L)Q_{da} \quad (3-13)$$

which follows from (3-2). Now for Q_a in (3-11) it holds that

$$Q_a = Q_{da} + Q_{ua}. \quad (3-14)$$

It should be noted that because of the nonlinearity of the light response curve (3-7) (Hari et al. 1982), the average intensity on a leaf close to a horizontal plane is not the same as the intensity driving photosynthesis

on the average in leaves near to a horizontal plane. As a rule, the use of mean irradiance overestimates the photosynthetic rate because (3—7) is a saturating type of curve (cf. Ackcock et al. 1970). In this case, however, it is quite impossible to estimate the error.

Photosynthesis takes place during the light part of a day, and therefore the daily photosynthesis in the stand is given by

$$P = \sum_{i=i_a}^{i=i_b} p(i)\Delta t, \quad (3-15)$$

where $p(i)$ denotes the photosynthetic rate in the stand at time $t=i$, Δt is the time step of an hour and i_a and i_b denote the first hour after sunrise and the last hour before sunset, respectively.

3.3.3 Respiration in the stand

The model of respiration in the stand is based on models and measurements presented in the literature. Respiration can be regarded as the energy consumption of cells (cf. Penning de Vries 1975). As a rough approximation a plant needs energy for two purposes: for counteracting the decay of its constituents (maintenance respiration, which is proportional to plant mass) and for the synthesis of new organs (growth respiration, which is proportional to the growth rate of the plant) (Penning de Vries 1972, 1975). In this case the respiration rate, R_p , of a whole plant follows the law (cf. Hesketh et al. 1971)

$$R_p = r_1 w + r_2 \frac{dw}{dt}, \quad (3-16)$$

where w is the dry-weight of the plant and r_1 and r_2 are constants. The growth rate can also be replaced by the photosynthetic rate (cf. McCree 1970). It is generally known (Moldau and Karolin 1977) that r_1 depends on temperature and the plant species, and r_2 on the chemical composition of the plant.

Model (3—16) is used in this study with the time step of a day, because the accuracy of the model would have not been increased through the introduction of the diurnal course of temperature.

The application of (3—16) to willow should be done with care, because the studies on respiration are usually done on non-woody plants (cf. McCree 1970, Pen-

ning de Vries 1975). Leaves and most roots probably behave in the same manner as non-woody plants, but stems are likely to be less active as regards maintenance respiration. In addition, photosynthesis (counteracting respiration) may take place in the bark (Troeng 1980) and is not considered in the photosynthesis submodel. It is therefore assumed that maintenance respiration occurs only in the leaves and roots. Furthermore, the maintenance respiration rate is considered to depend on the daily mean temperature, T_m . The temperature dependency of the maintenance respiration is not very well known. A two-fold increase in the maintenance respiration with a 10 °C increase in temperature is assumed according to results represented by Troeng (1980) and Jones et al. (1978).

For r_1 it then holds that

$$r_1 = r_{11} e^{r_{12}T_m}, \quad (3-17)$$

where $r_{12} = 0.0693/^\circ\text{C}$ to obtain the two-fold increase per 10 °C temperature rise. For r_{11} a value of 0.0017 g starch/g starch · 24 h is assumed, which means that 1 % of the mass of the leaves and roots is lost in maintenance at 25 °C every 24 h according to some measurements (Moldau and Karolin 1977). The amount of maintenance respiration during one day in the stand, R_m , is thus given by

$$R_m = r_{11} [e^{r_{12}T_m} W_l + e^{r_{12}T_s} W_r], \quad (3-18)$$

where T_s is the daily mean temperature in the soil (3.2) and W_l the dry-weight of the leaves in the stand. In an established plantation roots produced in previous years are present (see 3.1). Nevertheless, it is assumed that only new roots respire and W_r in (3—18) thus denotes the dry-weight of the roots grown during the current growing period.

It can be concluded from the second term on the right-hand side of (3—16) that when the dry-weight of the plant is increased by the amount ΔW , the amount $r_2\Delta W$ of assimilates is respired. Hence, the substrate utilizable in growth is used in the proportion $1/(1+r_2)$ and $r_2/(1+r_2)$ for mass increment and growth respiration, respectively (cf. Thornley 1976). Maintenance respiration obviously proceeds quite independently of other processes and there-

fore situations may occur where all the photosynthates are used in maintenance.

If assimilates usable in growth are present (see 4.1), growth and thus growth respiration will take place and for the amount of assimilates consumed in growth respiration in the stand, R_g , it holds that

$$R_g = \frac{r_2}{1+r_2} G, \quad (3-19)$$

where G denotes the amount of photosynthates.

Penning de Vries et al. (1974) have theoretically calculated that r_2 ranges approximately from 0.2 to 0.31 (original values compiled for the present notation). The value of 0.25 is assumed for r_2 in this study.

4. THE MODEL AND ITS PROPERTIES

The submodels have been constructed independently of each other using the information obtainable about the phenomena in question. In this chapter they are joined together in the manner depicted in Fig. 4. The equations defining the model are given and the equations used in the definitions of the submodels are summarized. A qualitative comparison is made using an experiment and then some examples of the possibilities of using the model as a tool in related research are given with the aid of simulations. The properties of the model are studied by means of sensitivity analysis.

4.1 The model

The interconnections between the submodels generally have a great influence on the performance of a model and therefore attention should be paid to them when submodels are combined. In the present case, the connection between photosynthesis, respiration and the amount of accumulated carbohydrates has to be considered in more detail. It is done in the following section.

4.1.1 *The carbohydrate pool neglected*

The time step of the model is one day and the assimilates produced during the light

part of the day are assumed to be consumed by the following morning (cf. Jones et al. 1978). This assumption is based on experiences gained with a preliminary model (Sievänen 1980) and hence the carbohydrate pool is neglected in this model (cf. 2.2). On the other hand, on some days the consumption in maintenance respiration may be higher than photosynthesis. Rather than making the assumption that maintenance is suppressed, a variable growth substrate deficit is defined. It is supposed that the deficit is compensated for — if possible — during subsequent days. This simple way of treating the dynamics of assimilates applies to normal growth conditions in which a growth substrate deficit occurs only exceptionally.

The photosynthates are supposed to be used primarily for maintenance respiration, then for compensating the growth substrate deficit and finally for growth if there are any still left. Let $P(k)$ and $R_m(k)$ denote the photosynthesis and maintenance respiration during day k and $D(k)$ the growth substrate deficit from the preceding days. Then either of the following two situations can occur during the day k :

1) Growth occurs, which is equal to the statement

$$P(k) - R_m(k) - D(k) > 0. \quad (4-1)$$

When the photosynthates utilizable in growth are consumed in the proportion $1/(1+r_2)$ and

$r_2/(1+r_2)$ (see 3.3.3) for the synthesis of new tissues and growth respiration, respectively, it holds for the dry-weight of the stand, W , that

$$W(k+1) = W(k) + \frac{1}{1+r_2} (P(k) - R_m(k) - D(k)) \quad (4-2)$$

and for the amount of respiration, R ,

$$R(k) = \frac{r_2}{1+r_2} [R_m(k) + r_2(P(k) - D(k))] \quad (4-3)$$

(cf. (3-17) and (3-18)). Then naturally

$$D(k+1) = 0. \quad (4-4)$$

2) No growth occurs when

$$P(k) - R_m(k) - D(k) \leq 0. \quad (4-5)$$

Then

$$W(k+1) = W(k) \quad (4-6)$$

and

$$R(k) = R_m(k), \quad (4-7)$$

and the growth substrate deficit attains a new value:

$$D(k+1) = D(k) + R_m(k) - P(k). \quad (4-8)$$

4.1.2 The equations

The growth in the stand can be calculated using (4-2) — (4-8). The equations which determine $P(k)$ and $R(k)$ (cf. Ch. 3), as well as the equations of the model, are summarized in the following.

P in the day k depends firstly on the total leaf area in the stand $L_o(k)$, which in turn is directly proportional to the dry-weight of the leaves. The average irradiance on the upper surface of a horizontal plane at the top of the stand, Q_d , depends on the daily total radiation sum and solar elevation, β , in the way given in 2.3. Then from 3.3

$$P(k) = P_{m1} (T_m(k-1)) \sum_{i=i_a(k)}^{i=i_b(k)} P_{m2} (T(i)) \cdot \frac{-KL}{\sin \beta(i)} \int_0^{L_o(k)} P_q [(1+u_1 - u_2L) \frac{Q_d(i)K}{(1-m) \sin \beta(i)} e^{-KL/\sin \beta(i)}] dL \Delta t, \quad (4-9)$$

where $i_a(k)$ and $i_b(k)$ denote the first hour after sunrise and the last hour before sunset,

respectively, and notation $x(i)$ denotes x when $t=i$.

For the maintenance respiration it holds that

$$R_m(k) = r_{11} [e^{r_{12}T_m(k)} W_l(k) + e^{r_{12}(d_0+d_1T_m(k-1))} W_r(k)] \quad (4-10)$$

from (3.3.3).

It is possible to write the equations for this model on the basis of (4-1) — (4-8). When f is a function for which it holds that

$$f(x) = \begin{cases} x, & x \geq 0 \\ 0, & x < 0 \end{cases} \quad (4-11)$$

then (4-2), (4-4), (4-6) and (4-8) can be transformed by incorporating the allocation ratios of photosynthates (cf. Mäkelä 1982) to the leaves, α_l , to the stems, α_s , and to the roots, α_r , into

$$W_i(k+1) = W_i(k) + \frac{\alpha_i}{1+r_2} f(P(k) - R_m(k) - D(k)) \quad (4-12)$$

$$D(k+1) = f(D(k) + R_m(k) - P(k))$$

where $i = l, s$ and r and W_l, W_s and W_r denote the dry-weights of the leaves, stems and roots, respectively. $P(k)$ depends on $W_l(k)$ and $R_m(k)$ is a function of both $W_l(k)$ and $W_r(k)$. (4-12) is thus a set of interconnected non-linear difference equations.

A closer inspection of (4-12) reveals, however, that in this case the dynamics of the model can be approximately represented in terms of W with only one difference equation: It can be seen that the case where it holds that $D(k+1) > 0$ occurs only a) in the autumn when growth has ceased or b) occasionally during the growing period on very cloudy days. The case a) is the condition for ending the simulation (cf. 4.1.3) and thus only case b) can affect the results of simulation. However, owing to the fact it is a rare occurrence case b) is neglected and thus $D=0$ all the time. If the initial values at time k_0 for the components of the stands are chosen in such a way that

$$W_i(k_0) = \alpha_i W(k_0), \quad (4-13)$$

where $i=l, s$ or r and $W(k_0)$ is the initial value for the total dry-weight of the stand, the relationship in (4-13) holds for all $W_i, i=l, s, r$ and all $k \geq k_0$ and k in the place of

k_0 . The dry-weights of the leaves, stems and roots are thus in constant proportions all the time.

With the above assumptions, (4—12) is reduced to

$$W(k+1) = (1 - \frac{a(k)}{1+r_2}) W(k) + \frac{\hat{P}(k, W(k))}{1+r_2} \quad (4-14)$$

where

$$a(k) = r_{11} [\alpha_l e^{r_{12}T(k)} + \alpha_r e^{r_{12}(d_0+d_1T(k-1))}] \quad (4-15)$$

and for $P(k)$ it is written

$$P(k) = \hat{P}(k, W(k)) \quad (4-16)$$

to indicate its dependence on $W(k)$.

If the initial values in (4—12) do not fulfil condition (4—13), $W_l(k)$, $W_s(k)$ and $W_r(k)$ are not in constant proportions for $k \geq k_0$ but

$$W_i(k) = W_i(k_0) + W'_i(k), \quad (4-17)$$

where $i=l, s$ or r and $W'_i(k)$, $i=l, s$ or r are such that condition (4—13) k in place of k_0 holds for them. Usually the magnitude of the initial values is very small in comparison to later values and hence

$$W_i(k) \cong W'_i(k) \quad (4-18)$$

for $i=l, s$ or r . The simulations have shown that with reasonable initial values, approximation (4—18) and assumption $D=0$ affect the result only very slightly and therefore the present model is described with (4—14). It can be seen that (4—14) describes a process in which the products of photosynthesis are summed up and the accumulated photosynthates are partly consumed in maintenance respiration. The term $a(k)$ in (4—14) (cf. 3.3.3) describes the effect of maintenance respiration. It can be seen from (4—12) and (4—17) that, if either the allocation ratios of photosynthates are not constant or the death of stand compartments takes place, it is no longer possible to reduce the equations (4—12) to (4—14).

4.1.3 The timing of growth

According to model (4—12), growth occurs when the carbohydrate balance is positive. In willows growth begins at the

time when the buds flush. The opening of the buds does not depend on the photosynthesis of the previous days, and therefore the day of growth initiation has to be specified as input.

In the autumn, in turn, the cessation of growth is described by means of the carbohydrate balance. It is supposed that the decline in the photosynthetic efficiency of the leaves (3.3.1) causes the cessation of growth. After growth cessation $D(k) > 0$ holds steadily. With increasing dry-weight increasing maintenance respiration also has a slight effect on the date of the cessation of growth.

4.2 Simulations

After a simulation model has been constructed, several kinds of numerical experiments can be made with it. Information about the real system itself can be obtained from these numerical experiments (cf. Shannon 1975, p. 2). Some of the possibilities of using a simulation model are: to predict the behaviour of the object, to study the effect of a factor when it is difficult to assess experimentally, to study the effect of a randomly varying factor (Monte Carlo simulation) or to study the general behaviour of the object. In the present case, a standard run is done for "mean conditions" in order to depict how the yield is accumulated. The effects of weather and the geographical location are then simulated as examples of the use of the model. However, the parameter values are first summarized and a qualitative comparison with an experiment is made.

The yield of the short rotation plantations in question is measured as the dry-weight of stems. In the following, the same quantity is used as the output of the model. As explained in 4.1.2, according to the model the dry-weights of all the compartments of the stand are, as an accurate approximation, in a constant ratio (given by (4—13)) to each other. The dry-weights of the leaves and roots formed during the current growing period are thus obtained from the yield by multiplication.

4.2.1 Parameter values

The present model has been put together by first considering the relationships which bring about growth in the plantation during one growing period and then modelling these relationships as submodels. Some of the relationships have been obtained as a result of the analysis of experiments and some of them have been taken from the literature. The estimates for parameter values have also been obtained in the analysis. It is clear that they are of different degrees of accuracy owing to their diverse sources. It is also clear that the set of parameter values does not apply directly to any single growing situation, but it does reflect some sort of mean values for the species and the growth conditions. It was not possible to give one single best value for the maximum photosynthetic rate and therefore a range of values is specified.

The parameters fall into three classes: parameters for plant functioning, for the environment in the stand and parameter functions for the diurnal variation in radiation and temperature. The dry-weights of the stand compartments at the beginning of the growing period are also included in the parameter set. The initial value for the dry-weight of the roots is derived from the assumption that only current roots respire (see 3.3.3), and from the fact that the

amount of roots does not have an effect on processes other than respiration. The values of the parameters are given in Table 1 and, whenever possible, the range within which the value lies is indicated.

4.2.2 Comparison with an experiment

The course of the development of the dry-weight of the stems in a mini-rotation stand, as well as the records of temperature and radiation (cf. 2.3) during one growing period are available for validating the model (Fig. 13). It is clear, therefore, that no extensive validation of the model can be made with such a limited amount of data. Whether the model's prediction is qualitatively in accordance with the experiment, only, can be studied.

No definite value has been given for the maximum photosynthetic rate (cf. Table 1). This parameter is quite important for the performance of the model and hence the simulations were made using different values of the parameter (Fig. 13a). It has been difficult to obtain reliable estimates for the initial values of the dry-weights of the stand compartments. The initial dry-weight of the leaves, W_{l0} , in particular, has a great influence on the behaviour of the model.

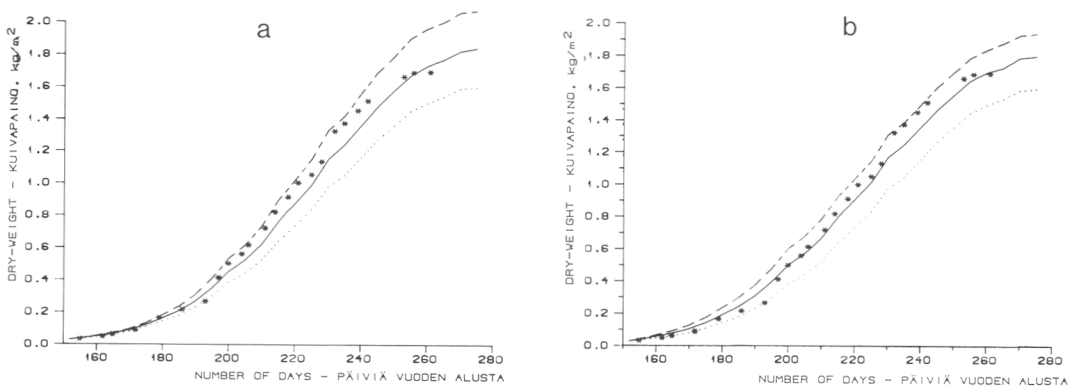


Figure 13. The measured (*) time course of the dry-weight of the stems during summer 1979 at the Suonenjoki Research Station. Simulated time course of the dry-weight of the stems for the same period when

(a) $W_{l0}=0.0091$ kg/m² and $p_M=25$ (···), 27 (—) and 29 (---) mgCO₂/h · dm²,

(b) $p_M=25$ mgCO₂/h · dm² and $W_{l0}=0.0091$ (···), 0.014 (—) and 0.018 (---) kg/m²

Kuva 13. Suonenjoen tutkimusasemalla kesällä 1979 mitattu varsien kuivapainon kasvu (*). Simuloitu varsien kuivapainon kasvu samalle ajalle, kun

(a) $W_{l0}=0.0091$ kg/m² and $p_M=25$ (···), 27 (—) and 29 (---) mgCO₂/h · dm²,

(b) $p_M=25$ mgCO₂/h · dm² and $W_{l0}=0.0091$ (···), 0.014 (—) ja 0.018 (---) kg/m²

Table 1. The parameter values.
Taulukko 1. Parametriarvot.

Parameter Parametri	Meaning Merkitys	Source Lähde	Value Arvo	Possible range Mahd. vaiht. väli
P_M	maximum photosynthetic rate (3.3.1) <i>max. fotosynteesinopeus</i>	experiments <i>koe</i>	20—29 $\frac{\text{mgCO}_2}{\text{h} \cdot \text{dm}^2}$	17.3.—28.8.*
P_{m1}	relationship of photos, rate on temp. (3.3.1) <i>fotos. nopeuden riippuvuus lämpöt.</i>	estimate, literature, <i>arvio, kirjall.</i>	Function-funktio Eq. (3—9) — <i>yht. (3—9)</i>	
P_{m2}	dependency of maximum photos. rate on previous temperature conditions (3.3.1) <i>max. fotos. nopeuden riippuvuus edeltävistä lämpöt.</i>	experiments <i>koe</i>	Function-funktio Fig. 12 — <i>kuva 12</i>	
Q_s	irradiance at which photosynthesis, saturates (3.3.1) <i>fotosynteesin kyllästysintensiteetti (3.3.1)</i>	”	150 Wm^{-2}	100—250
r_{11}	relation of maintenance respiration to temperature	literature	0.0017	
r_{12}	<i>ylläpitohengityksen riipp. lämpöt.</i>	<i>kirjallisuus</i>	0.0693 $^{\circ}\text{C}^{-1}$	
r_2	growth respiration coefficient (3.3.3) <i>kasvuhengityksen vakio</i>	”	0.25	0.2—0.31
α_l	allocation ratio of photosynthates to leaves (3.1) <i>fotosynteesituotteiden jakosuhte lehtiin</i>	experiments <i>koe</i>	0.21	
α_s	” stems ” <i>varsiin</i>	”	0.69	
α_r	” roots ” <i>juuriin</i>	estimate <i>arvio</i>	0.1	< 0.5
s_l	specific leaf weight (3.1) <i>lehden paino/pinta-ala</i>	experiments <i>koe</i>	0.074 kgm^{-2}	
d_0	regression of soil temperature on mean	”	5 $^{\circ}\text{C}$	
d_1	temperature of preceding day (3.2) <i>maan lämpötilan riippuvuus edellisen päivän lämpötilasta</i>	”	0.46	
K	radiation extinction coefficient (3.2) <i>säteilyn sammumiskerroin</i>	”	0.37	0.3—0.5
u_1	dependency of upward radiation on downward	”	0.1	
u_2	radiation (3.2) <i>heijastuneen säteilyn osuus heijastumattomasta säteilystä</i>	”	0.0075	
m	transmission coefficient of a leaf (3.3.2) <i>lehden läpäisykerroin</i>	literature <i>kirjallisuus</i>	0.2	
W_{l0}	initial value of the dry-weight leaves (4.2.2) <i>lehtien kuivapainon alkuarvo</i>	estimate <i>arvio</i>	0.0091 kg/m^2	
W_{s0}	same as above, but for stems (4.2.2) <i>sama varsilille</i>	experiments <i>koe</i>	0.03 kg/m^2	
W_{r0}	same as above, but for roots (4.2.2) <i>sama juurille</i>	estimate <i>arvio</i>	0.0	
	dependency of radiation on solar elevation (2.3.1) <i>säteilyn riippuvuus auringon korkeudesta</i>	literature <i>kirjallisuus</i>	Function-funktio Fig. 5 - <i>kuva 5</i>	
	diurnal variation of temperature (2.3.3) <i>lämpötilan vuorokausivaihtelu</i>	”	Function-funktio Fig. 8 - <i>kuva 8</i>	

* Estimated from Larcher (1980) with an assumption of dark respiration being 15 % of net photosynthesis
Estimoitu Larcherilta (1980) olettaen, että pimeähengitys on 15 % hiilidioksidin kulutuksesta

Simulations were therefore made using different values of this parameter, too (Fig. 13b).

It can be seen that with relevant values for the parameters (cf. Table 1), the model behaves in a qualitatively similar way to the experiment. However, according to the model growth continues for a longer time than in the experiment and the increase in the yield in the field in the middle of the growing period is faster than in the simulations. These discrepancies may be due to the submodel for the level of the photosynthetic efficiency of the leaves or to the invalidity of the assumption that the allocation ratios of photosynthates are constant (see Ch. 5).

4.2.3 The standard run

The courses of the daily radiation sums and the mean temperature during the growing period were established in section 2.3 for the nearest possible locations to the experimental site at Suonenjoki. They represent mean weather conditions for Central Finland, and when they are put into the model the yield under mean conditions is obtained for the same area — it is not necessarily the mean yield.

The yield in different years varied between about 1.4 kg/m² and 1.6 kg/m² in the experimental plots (P. Pelkonen, pers.

comm.). In order to make the simulations comparable with the real situation, a value (21.8 mgCO₂/h · dm²) was chosen for the maximum photosynthetic rate so that the yield in the standard run equals 1.4 kg/m². The values of the other parameters are given in Table 1. The date for the initiation of growth was the same (152, corresponds to 1.6.) as in 4.2.2.

The simulated growth of the dry-weight of the stems (Fig. 14a) continues up until the first part of October. This is due to the fact that the reproduced mean temperature (Fig. 8c) drops quite slowly to values which result in the cessation of photosynthesis. In the field growth ceases earlier (cf. 4.2.2). Photosynthesis (Fig. 14b) shows a peak at the period of maximum growth rate around the middle of August (about day 225). The radiation and temperature at that time are no longer the best possible values for photosynthesis. The slow accumulation of the leaf area at the beginning of the growing period has shifted the time of maximal photosynthetic production in the stand towards the autumn. This shows that a plantation using a rotation cycle of one year is not able to use effectively the good growth conditions prevailing during the first part of the growing period. Plantations in which longer rotation cycles are used are in a better position in this respect.

The curve of respiration as a function of time (Fig. 14b) is of a rather similar shape to that for photosynthesis: the level is naturally

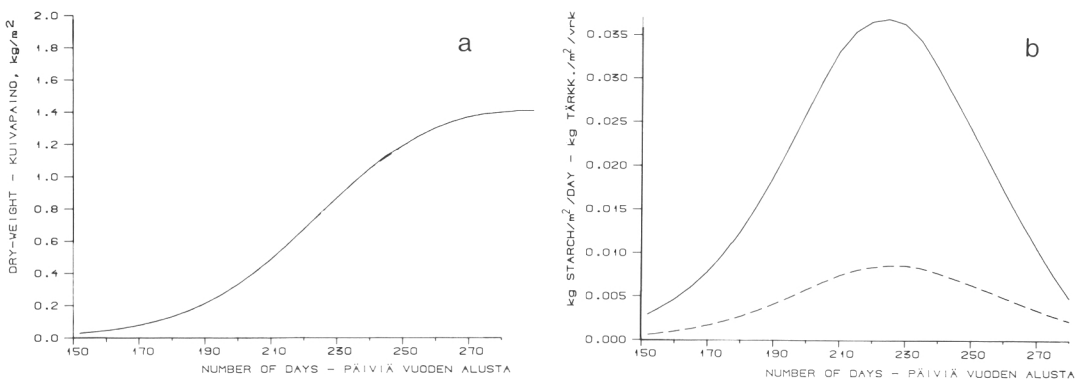


Figure 14. Simulated time course of the dry-weight of the stems (solid line) (a), the daily amounts of photosynthesis (broken line) and respiration (dashed line) (b). Reproduced values (cf. 2.3) for the daily radiation sums and mean temperature were used.

Kuva 14. Simuloitu varsien kuivapainon kasvu (yhtenäinen viiva) (a), päivittäisen fotosynteesin (katkoviiva) ja respiration (pisteviiva) määrä (b). Säteilylle ja lämpötilalle on käytetty laskettuja arvoja (katso 2.3).

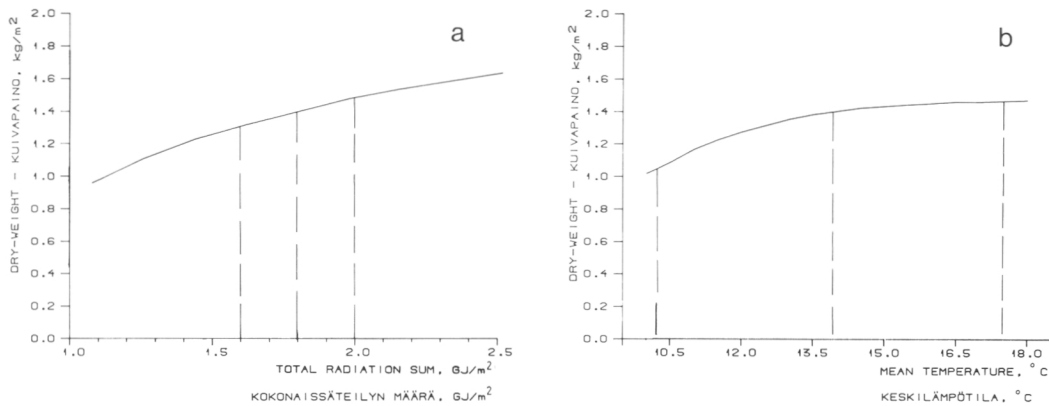


Figure 15. The simulated effects of the radiation sum during the period June—September (a) and the annual mean temperature (b) on yield. The mean values (condition of the standard run) as well as the possible ranges of variation and indicated with a dashed line.

Kuva 15. Kesä-syyskuussa tulleen säteilyn määrän (a) ja vuoden keskilämpötilan (b) simuloitu vaikutus satoon. Säätilastoista arvioidut keskiarvot ja vaihteluvälien rajat on merkitty katkoviivoiin. Simuloinnissa 4.2.3 on käytetty keskiarvoja.

different. The maximum rate of respiration occurs at a slightly later date than that of photosynthesis. This is quite natural because the maintenance respiration increases along with an increase in the dry-weight of the stand. During the first half of the growing period the level of respiration is about 21 % that of photosynthesis. During the period of maximal growth it is 23 % and increases to 100 % towards the end of the growing period.

4.2.4 The effect of weather

The influence of weather on the growth of plants can be roughly divided into two categories: the effect of normally occurring variation in growth conditions, which do not damage plants, and the damaging effects of extreme conditions. Such simulation models are not directly applicable without modifications to the study of the latter case, but the yield as a function of normally occurring growth conditions can easily be calculated by simulation. An important part of the analysis is the description of the climatic fluctuation for the simulations. In this case it is done in a simple manner.

The radiation is the most important environmental factor in the present model. It turns out, however, that in nature the variation in the radiation, measured in terms of the radiation sum during the period June-

September is rather small. The maximum and minimum radiation sums during that period were 2.0 GJ/m² and 1.6 GJ/m², respectively, in 1958—1967 at Luonetjärvi (Rossi 1976). The mean was 1.8 GJ/m². The radiation sum during the growing period can be used as a measure of the radiation regime during that time. It can be seen from Fig. 15a, that the corresponding variation in the yield is small when the radiation sum is in the normal range.

The annual mean temperature varied between -0.8 °C and 6.5 °C during 1961—1975 at Kuopio airport (Heino 1976). When the mean temperature of period June—September is assumed to vary as much as the annual mean temperature does, it induces (Fig. 15b) a change of the same order of magnitude in the yield (ca. 7 %) as the variation caused by radiation. It can be seen that the increased mean temperature of the period June—September does not, in practice, increase the yield. This may be partly due to the increased maintenance respiration, which consumes additional photosynthates.

The distribution of the radiation and temperature during the growing period clearly affects the yield. One figure is thus not good enough for describing the radiation or temperature conditions during plant growth. The next step was to take the variation in radiation and temperature during the growing period into consider-

ation. It was done by means of Monte Carlo simulation.

The sum of the radiation and mean temperature for each month from June to October was assumed for this purpose. This choice is based on the fact that longer periods of good and bad weather occur alternately during the growing period. In addition, it was assumed that when good weather is prevailing both the radiation and the temperature are above the mean, and vice versa. For this purpose the variation in the monthly mean temperature and in the monthly radiation sum were related to each other. The variation was calculated with respect to the observed long term means using meteorological statistics for Luonetjärvi (published by The Finnish Meteorological Institute). The approximation

$$\Delta T = 5.1 \cdot 10^{-1} \Delta Q, \quad (4-19)$$

where ΔT ($^{\circ}\text{C}$) and ΔQ (MJ/m^2) denote the deviations of the monthly mean temperature and radiation sum from the long term mean, respectively, appeared to be suitable for this study. Furthermore, the ranges of variation in the monthly radiation sums for June—October in 1958—1967 (Rossi 1976) were determined. The width of the ranges was multiplied by a deliberately chosen factor,

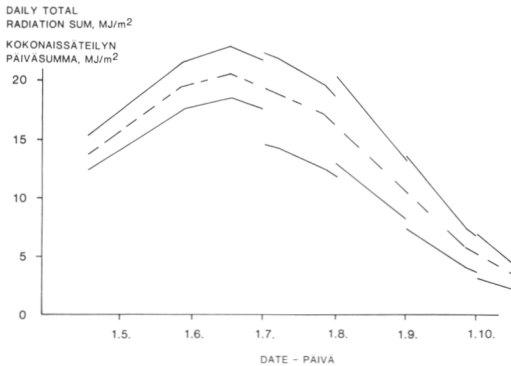


Figure 16. The range of the daily radiation sums used in the simulation. The dashed line is the normal course of the radiation (the same as Fig. 7). The range of variation in the monthly radiation sums is the distance between the upper and lower curves.

Kuva 16. Simuloinnissa käytetty päivittäisen säteilysumman vaihteluväli. Katkoviiva kuvaa säteilyn normaalia kulkua (sama kuin kuvassa 7). Kuukautisten säteilysummien vaihteluväli on ylemmän ja alemman käyrän välinen etäisyys.

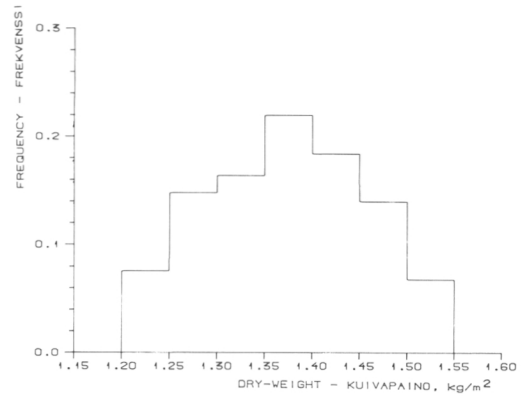


Figure 17. The simulated distribution of the yield.
Kuva 17. Sadon määrän simuloitu jakauma.

1.3, so to obtain the "real" range of variation. For the daily radiation sum in the simulation, Q_{t1} , it now holds that

$$Q_{t1} = Q_t + \Delta Q, \quad (4-20)$$

where Q_t is the normal course of radiation from 2.3 and ΔQ attains the same value during the whole month. This gives possible values for the daily radiation sums as depicted in Fig. 16.

It was assumed in the Monte Carlo simulation that the deviation of the radiation sum is evenly distributed in the range of variation, and for each month its own value was drawn. The corresponding deviation of the monthly mean temperature was calculated with the aid of (4-19).

The resulting distribution of the yield (Fig. 17) is quite even and rather narrow. The range of variation is 12 % around the mean yield of $1.37 \text{ kg}/\text{m}^2$. The mean yield is a slightly lower than the yield in the standard run. This can be clearly seen in Fig. 15; the bad weather conditions lower the yield more than the good conditions increase it. According to this model, variations in radiation and temperature which normally occur do not decrease the yield to any practical extent below 90 % of the mean. The variation is thus smaller than that in the series of measurements. According to Mikola (1978) the annual ring indices of Scots pine varied between about 77 and 130 during the period 1900—1974 in Southern Finland. Thammincha (1981) re-

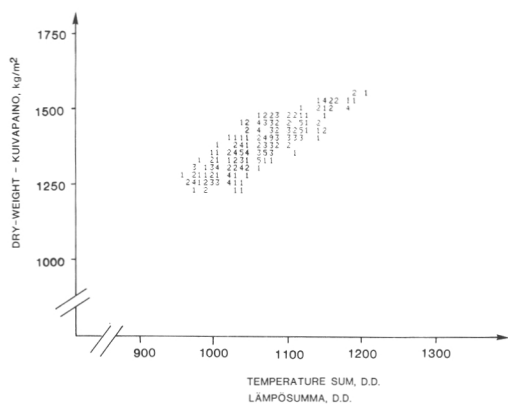


Figure 18. The simulated dry-weight of stems as a function of the temperature sum. The numbers in the plot indicate frequencies.

Kuva 18. Varsien kuivapaino lämpösunnan funktiona kasvukauden lopussa simuloimnin mukaan. Numerot kuvassa ilmaisevat frekvenssejä.

ports even larger variations in series of annual ring indices. The annual fluctuation in harvest yields of crops can be as high as 50 % of the mean (Varjo 1978). Nevertheless, it should be noted that the yield in the case of the present model is not the same as the annual ring indices nor the harvest yield of a crop. It is quite natural that the annual variation in the yield predicted here is smaller than that in the field; the model contains only some of the several affecting factors. The description of climatic variations should be made more complete in further studies.

Radiation measurement series are not readily available in Finland and yield studies have had to be carried out without radiation data. The most commonly used variable is temperature (cf. Lunelund 1942). When the simulated yield is plotted as a function of the temperature sum (calculated with the aid of the model), the curve in Fig. 18 is obtained. It can be seen that, depending on the distribution of warm and cold periods, the yield can be different even when the value of temperature sum is the same. It is interesting to note that a similar result is arrived at when measured harvest yields of crops are plotted as a function of the temperature sums (cf. Varjo 1978).

This demonstrates one possible use for simulation models: as a tool in developing (aggregated) simpler models for the same phenomena which they are describing. When

the phenomenon is reproduced with the aid of the simulations, it is possible to investigate, for example, which variables should be included in the simpler model. Laaksonen (1979), for instance, uses a regression model for the calculation of the effects of climatic factors on the hectare yield of cereals. The model contains the following variables: a modified temperature sum, precipitation, favourable weather at the end of the growing period and the weather conditions at the harvest time. The effect of including the mean temperature for June, for instance, in the set of variables could be estimated by a simulation model which is based on the daily increments of the yield and their dependence on temperature, even though no measurements of this variable were available. Other properties of simpler models can also be studied in this way.

4.2.5 Production potentials at different locations

The simulations made so far have been for Central Finland. Further simulations can be used to estimate the extent to which the production potential varies in different parts of the country as a result of the differences in radiation and temperature conditions. Here, again, the observed variation should be larger, since other factors besides radiation and temperature also affect the yield.

The differences in the climate in Finland are evidently strongest in the direction south-north. In order to study the changes in production potential in this direction, the courses of the daily radiation sums and the daily mean temperatures were determined (Heino 1976 and Rossi 1976) for Helsinki (60°12'N, 24°55'E), Jokioinen (60°49'N, 23°30'E) and Sodankylä (67°22'N, 26°39'E). Besides Luonetjärvi (62°28'N, 25°40'E) which was the fourth location, these were the only locations where extensive radiation measurements have been made. The determination was carried out in the same manner as was done in Section 2.3. The temperature conditions are clearly different at these four locations. However, the amounts of radiation vary quite little; the mean radiation sums during June—September are 1.93 GJ/m², 1.80 GJ/m² and 1.63

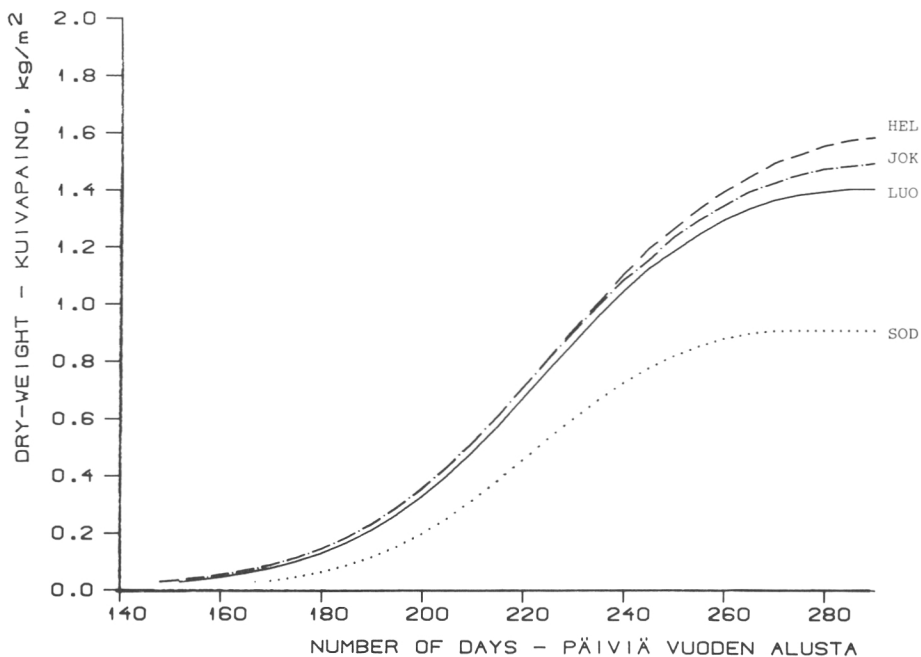


Figure 19. The increase in the dry-weight of stems at different locations.
 Kuva 19. Simuloitu varsien kuivapainon kasvu eri paikkakunnilla.

GJ/m² at Helsinki, Luonetjärvi and Sodankylä, respectively. In addition to the differences in radiation and temperature, the dates when the growing period started are different in different parts of the country. This was taken into consideration in the simulation by specifying growth initiation days

Helsinki	Jokioinen	Luonetjärvi	Sodankylä
28.5.	28.5.	1.6.	16.6.

on the basis of Keränen (1942). The other initial values were the same as those in the standard run.

The result shows (Fig. 19) that the differences in the yield in the southern half of Finland are rather small. Up in the north, in turn, the yield is considerably lower. Both the late onset and early cessation of growth decrease the yield. The simulation suggests, therefore, that short rotation plantations of the kind in question will not be very effective in Northern Finland, although they receive relatively large amounts of radiant energy during the summer.

4.3 Sensitivity analysis

Sensitivity analysis is a tool for studying the properties of a model. It reveals the effect of small changes in parameter values on the output of the model. Thus, sensitivity analysis can be used to find those parameters (or submodels) which have the greatest effect on the performance of the model. This information can then be used, for example, in the planning of experiments such that the most important parts of the model can be identified most accurately. In the following the equations for the sensitivity functions are first derived. They are then used in assessing the relative importance of some plant properties for the accumulation of the yield.

4.3.1 Sensitivity functions

The effect of small variations in a parameter on a particular variable of the model can be evaluated using sensitivity

functions. For a variable y , which is a function of time, t , the sensitivity, v , with respect to a parameter, θ , is defined by (Tomovic and Vukobratovic 1972)

$$v(t, \theta) = \lim_{\Delta\theta \rightarrow 0} \frac{y(t, \theta + \Delta\theta) - y(t, \theta)}{\Delta\theta} = \frac{\partial y(t, \theta)}{\partial \theta} \quad (4-21)$$

The sensitivity of the present model is considered only in the case where $D=0$, that is, only equations (4-12) are used. The sensitivity functions are calculated with respect to the parameters in Table 1 (except for the parameter functions describing the diurnal variation in radiation and temperature and the initial dry-weight of stems). The parameter functions in photosynthesis submodel were parametrized for sensitivity analysis (see legend of Fig. 20). The calculation of sensitivity with respect to the initial dry-weight of the stems was omitted because it has no effect on the dynamic behaviour of the model.

The sensitivity of the model (4-12) is defined through the sensitivity functions

$$v_i(k, \theta) = \frac{\partial W_i(k)}{\partial \theta} \quad (4-22)$$

where $i=1, s$ and r , $k \geq k_0$ and θ denotes any parameter of the model. Using (4-12) and the definitions of the sensitivity functions (cf. Mäkelä 1982) the following is obtained for the parameters in Table 1 and for $i=1, s$ and r

$$v_i(k+1, \theta) - v_i(k, \theta) = \frac{\alpha_i}{1+r_2} \left[\left(\frac{\partial P(k)}{\partial W_1} - \frac{\partial R_m(k)}{\partial W_1} \right) v_i(k, \theta) - \frac{\partial R_m}{\partial W_r} v_r(k, \theta) \right] + \frac{\partial}{\partial \theta} \left[\frac{\alpha_i(P(k) - R_m(k))}{1+r_2} \right] \quad (4-23)$$

with initial values $v_i(k_0, \theta) = 0$. When the initial values of W_1 and W_r ($\theta=W_{10}$ or $\theta=W_{r0}$) are considered it holds for $i=1, s$ and r that

$$v_i(k+1, \theta) - v_i(k, \theta) = \frac{\alpha_i}{1+r_2} \left[\left(\frac{\partial P(k)}{\partial W_1} - \frac{\partial R_m}{\partial W_1} \right) v_i(k, \theta) - \frac{\partial R_m(k)}{\partial W_r} v_r(k, \theta) \right]$$

with initial values

$$v_i(k_0, \theta) = \begin{cases} 1, & \theta = W_{i0} \\ 0, & \text{otherwise} \end{cases} \quad (4-25)$$

(4-23) and (4-24) each give three equations for one parameter. When the

equations for each parameter are solved simultaneously with the model equations (4-12) the sensitivity functions for the growing period are obtained. This was done in connection with the standard run (4.2.3). In the following, the sensitivity of the dry-weight of the stems is considered only, the sensitivities of other plant compartment behaving in the same manner. Instead of the functions v_s , the relative sensitivities, $v_s \cdot \theta$ are plotted (Fig. 20). This makes it easier to compare the sensitivities with each other because the plotted value shows the change in W_s when the parameter is changed by 1 %.

The time courses of the sensitivities are quite similar with regard to the shape; their absolute value increasing toward the end of the time interval. This is understandable: (4-12) is a set of weakly interconnected equations, the solutions of which being rather simply-shaped functions. Hence the sensitivity functions can be expected to be simple, too. The maximum rate of photosynthesis is evidently the parameter which has the greatest influence on the yield (Fig. 20a). It shows the importance of the photosynthesis submodel, even more so as some other parameters (Q_s, K) in it also show a rather high relative sensitivity. The parameters (α_1, α_s and s_1) which are involved in the growth of the leaf area and yield accumulation are another set of important parameters. This shows that the stand structure submodel is central for the growth dynamics of the plantation. It has to be kept in mind that the allocation ratios of photosynthates sum up to one, and thus depend on each other. It can be seen that the model is quite insensitive to parameters in the respiration submodel, Fig. 20b, d. This shows that respiration is of lesser importance in the model. The same applies to roots.

The conclusions arrived at with the help of the relative sensitivities is impaired by the fact that the possible range of variation is different in different parameters. It is estimated (Table 1), for instance, that Q_s can be as small as 50 % of its nominal value when the corresponding figure for r_2 is 80 %. In some cases, therefore, a better insight can be obtained by comparing the values of the sensitivity functions, given in Table 2.

It can be seen that α_1 is the most important allocation ratio of the photo-

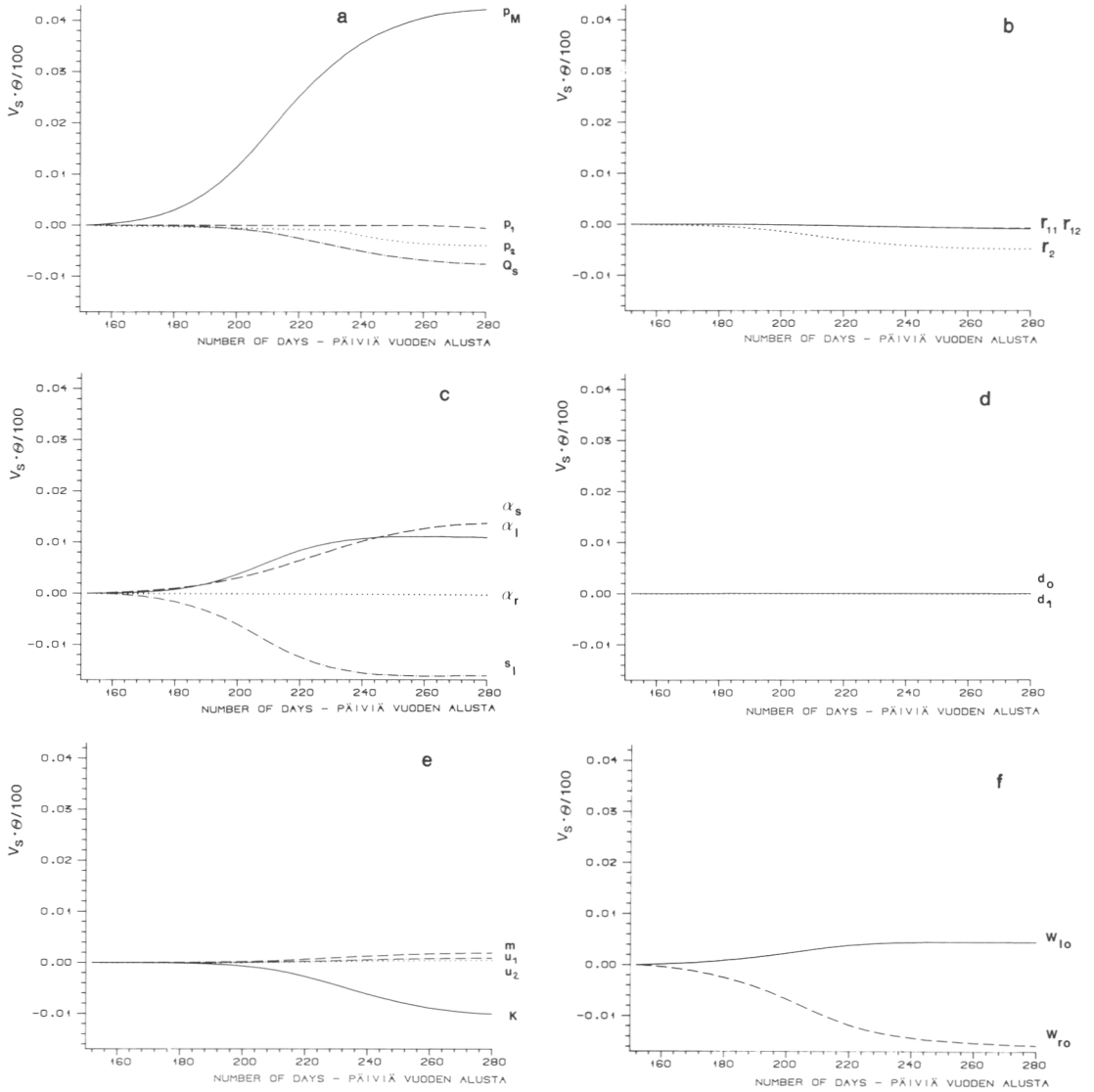


Figure 20. Relative sensitivities of the dry-weight of the stems ($v_s \theta / 100$) with regard to parameters. The plotted value shows the change in W_s when the parameter is changed by 1 %.

- (a) $\theta = p_M, p_1, p_2, Q_s$, where p_1 and p_2 are the corner points of the dependence of the photosynthetic rate on temperature (Eq. (3–9)) and on the temperature history (Fig. 3–4b), respectively. Their nominal values are $p_1 = 8 \text{ }^\circ\text{C}$, $p_2 = 14 \text{ }^\circ\text{C}$.
- (b) $\theta = r_{11}, r_{12}, r_2$
- (c) $\theta = \alpha_1, \alpha_s, \alpha_r, s_1$
- (d) $\theta = d_1, d_0$
- (e) $\theta = k, u_1, u_2, m$
- (f) $\theta = W_{10}, W_{r0}$; in the latter case the values $v_s/50$ are depicted

Kuva 20. Varsien kuvapainon suhteellinen herkkyyys ($v_s \theta / 100$) mallin parametrien suhteen. Kuva ilmaisee muuttujan W_s arvon muutoksen, kun parametrin arvo kasvaa 1 %.

- (a) $\theta = p_M, p_1, p_2, Q_s$, where p_1 and p_2 ovat kulman paikat fotosynteesinopeuden riippuvuudessa lämpötilasta (yhtälö (3–9)) ja lämpötilahistoriasta (kuva 12b). Niiden normaaliarvot ovat $p_1 = 8 \text{ }^\circ\text{C}$ ja $p_2 = 14 \text{ }^\circ\text{C}$.
- (b) $\theta = r_{11}, r_{12}, r_2$
- (c) $\theta = \alpha_1, \alpha_s, \alpha_r, s_1$
- (d) $\theta = d_1, d_0$
- (e) $\theta = k, u_1, u_2, m$
- (f) $\theta = W_{10}, W_{r0}$; jälkimmäisessä tapauksessa on piirretty $v_s/50$.

Table 2. The values of the sensitivity functions on day 280 (corresponds to 7.10.). The functions are calculated in connection with the standard run (4.2.3).

Taulukko 2. Herkkyyshfunktioiden arvot päivänä 280 (päivä 7.10.) Funktiot on laskettu simuloinnin 4.2.3 yhteydessä.

param. param.	v(280, θ)	param. param.	v(280, θ)
p_M	$7.00 \cdot 10^6$	s_j	$-2.19 \cdot 10^2$
p_1^{**}	$-6.70 \cdot 10^{-3}$	d_0	$-1.86 \cdot 10^{-3}$
p_2^{**}	$-2.76 \cdot 10^{-2}$	d_1	$-2.30 \cdot 10^{-2}$
Q_s	$-5.07 \cdot 10^{-3}$	K	-2.73
r_{11}	$-5.84 \cdot 10^{-1}$	u_1	$4.71 \cdot 10^{-1}$
r_{12}	-1.24	u_2	$1.15 \cdot 10^1$
r_2	-1.95	m	$9.50 \cdot 10^{-1}$
α_1	5.19	W_{10}	$4.96 \cdot 10^1$
α_s	1.99	W_{r0}	$-7.90 \cdot 10^{-1}$
α_r	$-2.70 \cdot 10^{-1}$		

* see legend of Fig. 20
katso kuvan 20 kuvateksti

synthates, and α_s in turn is of minor importance in the model because all the allocation ratios can be assumed to have variation of the same magnitude. The relative sensitivities give a different impression (Fig. 20c). According to the above observation, the initial value of dry-weight of the leaves has a far greater influence on the yield than that of the roots.

4.3.2 The importance of some plant properties

The yield in a short rotation plantation can be increased by both changing the growth environment and by selecting plants with suitable properties. The environment can be changed by fertilization, irrigation/drainage and spacing, for instance. It is practically impossible to influence radiation and temperature directly in large scale cultivation. Selection and breeding are the means of affecting the plant material used in short rotation plantation in a way which is commonly applied to agriculture, and which has given large increases in the yield of agricultural crops.

The models can be used as a tool for both optimizing growth conditions and developing plant material in research directed at yield improvement. It is quite obvious

that a model can be used to delineate optimal actions needed for changing the environment in yield improvement. The result can be then used in directing field experiments at important tasks. The models can be used in the same manner in developing plant material: such properties or combinations of properties can be looked for which are likely to increase the yield. For instance, it has been shown theoretically (Duncan 1971) and verified experimentally that more erect leaves of plants increase photosynthesis in some closely-spaced agricultural stands. The models thus serve as a tool for expressing the effect of the property on the size of the yield.

What this model indicates about the effect of some plant properties on the yield is analysed in the following. The analysis is based on the sensitivity functions given above. As many of the parameters in the model depend on the properties of the plants, the effect of these properties on the yield can therefore be assessed by considering the sensitivity functions. The fact that many of the properties may be interconnected has to be taken into consideration in the analysis. The increase in photosynthetic efficiency seems to be related to the increase in respiration (Kallis and Tooming 1974), for example. It also has to be kept in mind that only first order approximations are obtained from the sensitivity functions when the direction in which the parameter should be changed is obtained, but not the absolute value of the optimum. The photosynthetic efficiency, allocation ratios and growth initiation are considered.

It is expected on the basis of this model that an increase in photosynthetic efficiency (which corresponds approximately to the maximum photosynthetic rate) should increase the yield (Fig. 20a). The measurements have shown (Kallis and Tooming 1974) that in several species, the maximum photosynthetic rate as well as the dark respiration rate increase by about 1 % when the specific leaf weight is increased by the same amount. All these properties should then be analysed simultaneously. An increase in p_M of 1 % increases the yield by 0.042 kg/m^2 (3 %), cf. Fig. 20a. That means an increase of 0.042 kg/m^2 in the yield if the photosynthetic rate only is increased by 1

%). If the effect of increased respiration (r_{11} and r_2 , which determine the level of respiration) and specific leaf weight (s_l) are taken into consideration, then the gain in yield is as much as 0.02 kg/m^2 (1.4 %). That is

$$v_s(p_M, 280) p_M/100 + v_s(s_l, 280) s_l/100 + v_s(r_{11}, 280) r_{11}/100 + v_s(r_2, 280) r_2/100 = 0.02 \text{ kg/m}^2. \quad (4-26)$$

It is possible that increased specific leaf weight affects the attenuation of radiation through thick leaves. In order to incorporate also this effect, the parameter K was increased by 1 %. In this case the increase in yield is as much as 0.01 kg/m^2 (0.7 %).

We have to be cautious in this kind of analysis because the sensitivity functions have been calculated using nominal values for the parameters and when one or several values of the parameters are changed the functions themselves change. Nevertheless, when the changes in the values of the parameters are small, it can be assumed that the functions do not vary to any great extent. Hence, the analysis suggests that even if the connections between the properties are as described above, then the photosynthetic efficiency is a good selection criterium for yield improvement. It should be noted that the seasonal variation in photosynthesis also affects the yield and should hence be taken into consideration if it turns out to be related to the above properties.

By examining the sensitivities with respect to the allocation ratios of photosynthates (Table 2), it can be seen that the yield increases with increasing α_l . If α_l is increased by 0.05, α_s is correspondingly

decreased by 0.05 and α_r remains intact (the allocation ratios sum up to one), the yield is increased by 0.16 kg/m^2 . The additional investment in leaves thus results in such a good increase in the growth of the whole plant, that in spite of the decrease in their share of growth, the dry-weight of the stems is greater.

The sensitivity of the model with respect to the initial dry-weight of the leaves and roots shows that the timing of growth has quite a strong effect on the yield. It can be deduced from Table 2 and the standard run (4.3.2), that if the growth (simulation) begins one day earlier than day 152 (corresponds to 1.6.), then the yield is increased by 1.8 %. Starting 5 days earlier causes an increase of 11 %. This is due to the favourable growth conditions in early summer. This shows that early growth initiation is a good property, if other factors, such as night frosts, are excluded from the analysis. This analysis also shows that strong allocation of photosynthates to the leaves in the beginning of the growth period increases the yield.

The above analysis of some growth factors is quite tentative and the set of properties considered does not include all the plant properties which can potentially be changed. It does show, however, how such a model can be used in the connection of the biological research made on yield improvement. The hypothesized relationships can be evaluated in advance and the biological research concentrated on central problems. The results of the biological studies can then, in turn, be used for making the model more precise in answering new questions.

5. CONCLUDING REMARKS

Although the possibilities of using the model as a tool are discussed in the previous sections (4.2 and 4.3), this subject is also touched on here, too. Ways of improving the model and the study topics for related research suggested by the model are also discussed in this context.

The development of a model can be regarded as consisting of two steps (Majkowski et al. 1981): (1) formulation and modification of the model and (2) validation. These steps are iteratively repeated. The validation consists of both experimentation and comparing the results with the simulations. When the above classification is further elaborated and the role of experimentation is taken into consideration, a picture of the modelling process is obtained (Fig. 21). The role of modelling as a tool in the research carried out on the accumulation of the yield can be also viewed with the aid of Fig. 21. The answer to the question "a good fit?" (Fig. 21) can be interpreted as both negative and affirmative. The model can be inadequate in some respect, but in another respect it can function adequately enough. The experimental results of the related biological research are utilized in the development of the model (inadequate parts of it) and the comparisons between simulations and experiments reveal both deficiencies in the model and new experiments which should be performed. The model guides the experimental work and hence is a means for directing the research. It also develops and incorporates new information as the research progresses. Besides this, the model can also be used to produce simulations suitable for investigating the properties of the study object without having to carry out any experiments. The simulations can naturally only provide relevant information about the study object within the boundaries of the validity of the model.

The present work has passed through the

phases from modelling to simulation, and by comparing the simulations and experiments (Fig. 21) some of the experiences already gained with a preliminary model (Sievänen 1980) have been utilized in the construction of the present model (cf. 2.2). Simulations have been made so as to indicate some future uses for the model. The research process is now in the phase where the information about the simulation, and comparison with experiments should be used in further modelling and experimentation. In the following both the improvement of the model and the experiments suggested by this study are discussed.

As many processes (transpiration, nutrient uptake etc.) are omitted in the present model, one way of improving it would be to include some of them in it. This would mean broadening the range of the applicability of the model (to conditions of water deficit, for instance). If such broadening is required then the process in question should be included in the model. However, this topic does not come within the scope of this discussion. Comparison of the model's prediction and the experiment, the simulations and the sensitivity analysis provide the following information:

- The variable growth substrate deficit does not in practice affect the behaviour of the model. It can be neglected as a superfluous variable.
- The growth predicted by the model lasts longer than in the experiment. This can be due to validities in the submodel for the photosynthetic efficiency of the leaves, or to changes in the allocation of photosynthates (taking place in the experiment).
- The simulated growth rate (of the dry-weight of the stems) is less than the measured growth rate in the middle of the growing period. This discrepancy may be caused by errors in the calculation of photosynthesis in the stand or by changes in the allocation of the photosynthates during the growing period. The error in the calculation of photosynthesis in the stand may be due to the model of light extinction in the stand (it would not be equally valid for a low and for a tall stand).
- The sensitivity analysis shows that the most important parameter in the model is the maximum

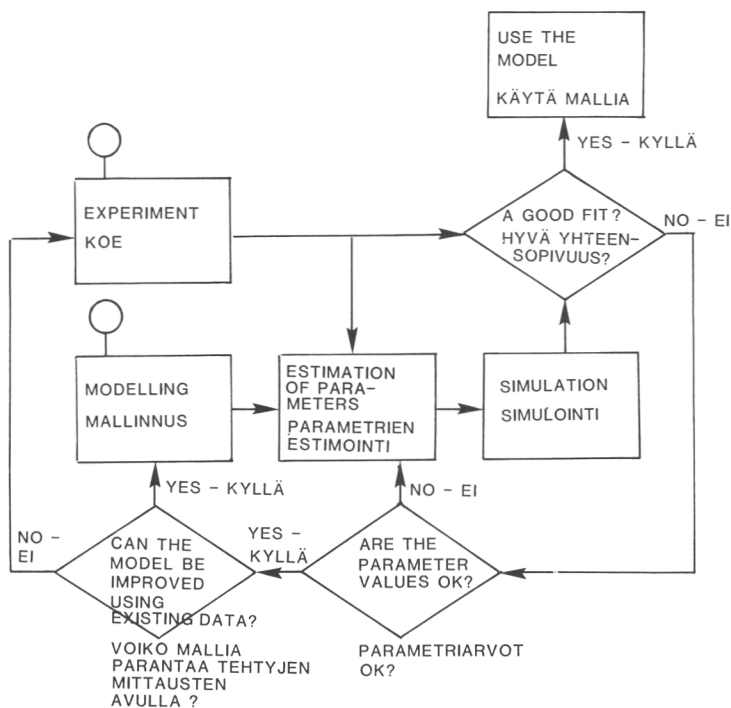


Figure 21. The process of modelling. Adopted from Holmberg (1982) with slight modifications.

Kuva 21. Mallinnusprosessi, otettu mukaillen Holmbergilta (1982).

rate of photosynthesis. Other important parameters are the allocation ratios of photosynthates, specific leaf weight, the extinction coefficient for radiation and the initial amount of leaves.

In conclusion, it can be stated that the photosynthesis in the stand and the allocation of photosynthates should be modelled more accurately. It should be noted that no definite answers to the questions "are the parameter values OK?" and "can the model be improved using existing data?" in Fig. 21 could be given, but the submodels and the values for parameters have to be studied simultaneously.

Suggestions for further experimental work can be derived from the above analysis. The main ones are:

- The study of processes pertaining to the photosynthesis submodel. A closer determination of values for parameters, especially for the maximum photosynthetic rate. The cessation of photosynthesis should be studied too.

- The seasonal variation in the allocation of photosynthates is an important subject to study. The initial amounts of dry-weight in the different compartments of the stand should also be measured accurately.
- The applicability of the model for the extinction of radiation of stands of different sizes should be studied.

The aim of this modelling study has been to construct a growth model for a mini-rotation plantation which is based on data obtained from related empirical research and which can be used as a tool in the study of the accumulation of the yield. The construction of the model as well as simulations made with it have been described in the previous chapters. In this chapter it was shown, how the modelling can generally serve as a tool in a research process and how the present model can guide research in this particular case. In conclusion, it can be stated that this report shows how modelling (the methods of systems analysis) can be used in research into plant productivity.

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SELOSTE

Lyhytkiertoviljelmän kasvumalli

Tutkimuksessa on laadittu lyhytkiertoviljelmän kasvun simulointimalli. Se perustuu pääosin ekofysiologisiin mittaustuloksiin. Mallin tarkoituksena on kuvata sadon kertymistä niin, että sen avulla voi tutkia kasvien ominaisuuksien ja ympäristötekijöiden vaikutusta sadon määrään.

Mallinrakennuksessa analysoidaan ensiksi tekijöitä, jotka merkittävimmin vaikuttavat kasvuston kehitykseen (luku 2). Päätekijät ovat: (1) kasvien toiminta ympäristötekijöiden funktiona, (2) kasvuston sisäisten ympäristöolosuhteiden muodostuminen kasvien toiminnan ja säätekijöiden vaikutuksesta ja (3) kasvuston rakenne. Näiden tekijöiden keskinäiset vaikutukset on esitetty kuvassa 2. Jokaiselle em. tekijälle konstruoidaan osamalli. Kasvien toiminta kuvataan hiilivirran avulla. Siihen vaikuttavia toimintoja ovat fotosynteesi ja respiratio (kuva 3). Ympäristötekijöinä käytetään säteilyn intensiteettiä ja ilman lämpötilaa. Kastelun ja lannoituksen oletetaan olevan optimaalisia. Kasvuston oletetaan olevan vaakatasossa homogeeninen. Tämä oletus yksinkertaistaa kasvuston sisäisten ympäristöolosuhteiden kuvausta. Lämpötila oletetaan vakioksi koko kasvustossa. Säteilyn vaimeneminen varjostavan lehtipintalan funktiona on otettu huomioon. Kasvuston rakenne kuvataan yksinkertaisesti lehtien, varsien ja juurten kuivapainolla. Kasvuston rakenteeseen olennaisesti vaikuttava tekijä on fotosynteesituotteiden jakautuminen (allokointi) kasvien eri osiin. Mallissa tarkasteltujen tekijöiden keskinäiset kytkennät on esitetty kuvassa 4. Luvussa 3 on esitetty osamallien yksityiskohtainen rakentaminen.

Luvussa 4 kootaan malli osista yhteen ja tehdään sillä simulointeja, joilla osoitetaan, miten mallia voidaan käyttää. Syöttämällä malliin ympäristötekijöiden keskimääräinen kulku kasvukauden aikana simuloidaan kasvuston käyttäytymistä normaaliolosuhteissa. Voidaan todeta, että simuloinnin mukaan yksivuotinen kasvusto ei pysty tehokkaasti käyttämään alkukesän hyviä kasvuolosuhteita, koska tällaisessa kasvustossa yhteyttävä lehtipinta-ala on riittävä vasta loppukesällä. Simulointien mukaan normaalista auringonpaisteen ja lämpötilan vaihtelusta johtuvat sadon vaihtelut ovat melko pieniä Etelä- ja Keski-Suomessa. Simulointien mukaan myös sääolosuhteiden paikallisesta vaihtelusta johtuvat sadon erot ovat pieniä samalla alueella. Pohjois-Suomessa on mallin mukaan sen sijaan odotettavissa pienempiä satoja.

Mallille tehdään herkkyyksianalyysi, jonka avulla voidaan tutkia sen ominaisuuksia. Analyysi osoittaa, että tärkein osa mallia on kasvuston fotosynteesin osamalli. Herkkyyksianalyysin tulosten perusteella tutkitaan myös kasvien eräiden ominaisuuksien merkitystä sadon parantamisessa.

Lopuksi tarkastellaan mallinrakennuksen mahdollisuuksia toimia apuneuvona kasvustojen tuottavuuden tutkimuksessa. Tarkastelussa osoitetaan, kuinka malli voi toimia tutkimuksen suuntaajana sekä viitekehystenä johon uudet tutkimustulokset voidaan suhteuttaa. Tässä yhteydessä käsitellään myös mallin parantamista simuloinneista saatujen kokemusten perusteella ja mallin osoittamia empiirisen tutkimuksen kohteita. Fotosynteesinopeuden riippuvuus ympäristötekijöistä ja fotosynteesituotteiden jakautuminen ovat tärkeimpiä niistä.

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Author's address: The Finnish Forest Research Institute, Unioninkatu 40 A, SF-00170 Helsinki 17, Finland.

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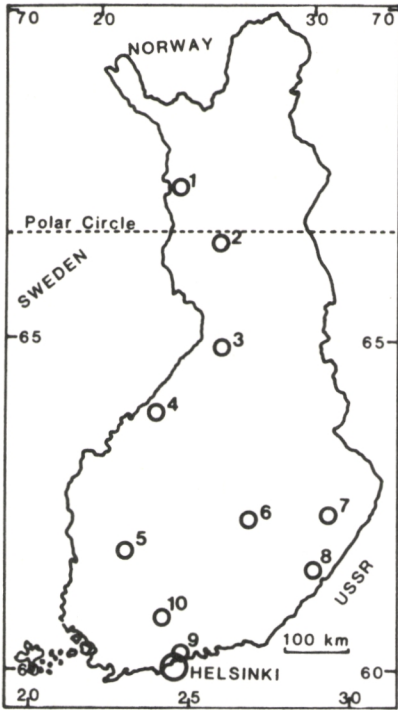


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FACTS ABOUT FINLAND

Total land area: 304 642 km² of which 60—70 per cent is forest land

Mean temperature, °C:	Helsinki	Joensuu	Rovaniemi
January	-6,8	-10,2	-11,0
July	17,1	17,1	15,3
annual	4,4	2,9	0,8

Thermal winter
 (mean temp. <0°C): 20.11.—4.4. 5.11.—10.4. 18.10.—21.4.

Most common tree species: *Pinus sylvestris*, *Picea abies*, *Betula pendula*, *Betula pubescens*



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