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PHOTOSYNTHETIC PRODUCTION OF SCOTS
PINE IN THE NATURAL ENVIRONMENT

*MÄNNYN YHTEYTTÄMISTUOTOS LUONTAISESSA
KASVUYMPÄRISTÖSSÄ*

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Seloste

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The dependence of the rates of photosynthesis and transpiration are studied on the environmental factors and on the control of the plant metabolism with Scots pine in the natural environment. The importance of the different environmental factors to the photosynthetic production are evaluated. In modelling the dependence of the rates of photosynthesis and transpiration on the environmental factors and on the control processes, a dynamic system analysis approach is applied. Irradiance, temperature and water are explored during the annual cycle. Field measurements of the CO₂ exchange and environmental factors over three years are used in the analysis of the rate of the photosynthesis. The effect of different environmental factors on photosynthetic production is evaluated by model estimations using weather data in a 20-year period.

Tutkimuksessa tarkastellaan männyn fotosynteesi- ja haihduntanopeuden riippuvuutta ympäristökijöistä sekä aineenvaihdunnan säätymisestä. Fotosynteesi- ja haihduntanopeuden riippuvuutta ympäristökijöistä ja säätymistä kuvataan dynaamisen mallin avulla. Tutkimuksessa analysoidaan auringon säteilyn, lämpötilan ja veden vaikutusta. Fotosynteesinopeutta analysoidaan luonnon metsiköstä tehtyjen hiilidioksidin vaihdon ja ympäristökijöiden mittausten avulla. Eri ympäristökijöiden merkitystä yhteyttämistuotantoon arvioidaan mallin avulla käyttäen aineistona säähavaintoja 20 vuoden ajalta.

Key words: rate of photosynthesis, transpiration rate, stomatal regulation, irradiance response, annual cycle

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PREFACE

Ecophysiological research of forest trees has been carried on at the Department of Silviculture of the University of Helsinki since the 1970s. One of the main subjects of the investigations has been the process-oriented models of forest growth and yield. In the models, the stand development is derived from the metabolic functioning and structural regularities of the trees. The topic of my investigations has been the metabolic functioning of trees, for which research was needed to understand the causal relations of the environmental factors and metabolic processes. The research activities of this study have been carried out while I was working at the Forestry Field Station and at the Department of Silviculture of the University of Helsinki. The discussions and work, in close contact with colleagues who have given valuable support, ideas and criticism, have been fruitful for my work.

During my work and studies at the Department of Silviculture, Prof. Matti Leikola, head of the department, has encouraged and supported my efforts in many ways. The facilities provided by Prof. Rihko Haarlaa, head of the Forestry Field Station, have been greatly appreciated. I wish to thank them for their positive attitude.

Theoretical discussions with and advice given on the empirical work and on the preparation of the manuscript by Acting Prof. Pertti Hari have been valuable for completion of this work. I express my warmest thanks to him for inspiring and faithful support. My

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List of parameters

Parameter	Value	Explanation	Parameter	Value	Explanation
a_1	0.32 °C ⁻¹		e_1	5.56 cm s ⁻¹	
a_2	-5 °C		e_2	0.24 cm s ⁻¹	
A	1.0 m ⁻²		k	0.25 °C ⁻¹	
b	150-180 W m ⁻²		l_1	0.451	
B	1.6		l_2	0.084	
c_1	0.45-0.64 mg CO ₂ dm ⁻² h ⁻¹		m_1	4 h	
c_2	0.032 °C ⁻¹		P_m	5.9-6.2 mg CO ₂ dm ⁻² h ⁻¹	
c_3	-5 °C		R_{max}	1.0 g dm ⁻²	
d_1	6500	(Pelkonen 1981)	μ	0.59	
d_2	2	"	τ	0.715	transmittance of the atmosphere at the direction of the zenith
d_3	600	"			

List of main symbols

$c(I)$	utilization rate of carbon dioxide per leaf area and per carbon dioxide concentration (m s ⁻¹)	L_r	relative luminance of the line of sight
C	CO ₂ concentration of air in the chamber (g m ⁻³)	M	amount of soil water (mm)
C_a	ambient CO ₂ concentration (g m ⁻³)	N	amount of needles (kg)
D(z,t)	water vapour deficit in air (g m ⁻³)	p(x,t)	carbon dioxide exchange rate (mg CO ₂ dm ⁻² h ⁻¹)
e_a	ambient water vapour concentration (g m ⁻³)	q(t)	percolation rate (g m ⁻² h ⁻¹)
e_i	intercellular water vapour concentration (g m ⁻³)	q_h	gas flow rate (dm ³ h ⁻¹)
e(z,t)	evaporation rate at height z (g dm ⁻² h ⁻¹)	r(x,t)	specific respiration rate (mg CO ₂ dm ⁻² h ⁻¹)
E(x,t)	environmental factor, i.e. energy, water, carbon dioxide and nutrients	$R_a(z,t)$	intercepted water per unit needle area at height z (g dm ⁻²)
f(x,t)	specific rate of photosynthesis (mg CO ₂ dm ⁻² h ⁻¹)	s_s	throughfall rate to soil (g m ⁻² h ⁻¹)
$F_h(t_1,t_2)$	hypothetical photosynthetic production per unit of needle area (mg CO ₂ dm ⁻²)	$s_i(z,t)$	throughfall rate at height z (kg m ⁻² h ⁻¹)
$F_n(t_1,t_2)$	amount of photosynthesis of needles in a time interval $t_1 - t_2$ (mg CO ₂)	s_0	precipitation rate (kg m ⁻² h ⁻¹)
$F_p(t_1,t_2)$	photosynthetic production per unit of needle area in the summer phase (mg CO ₂ dm ⁻²)	S(t)	state of photosynthetic activity
$F_s(t_1,t_2)$	photosynthetic production per unit of needle area during the seasons (mg CO ₂ dm ⁻²)	S_0	solar constant (1360 W m ⁻²)
$F(t_1,t_2)$	amount of photosynthesis per unit of needle area in a time interval $t_1 - t_2$ (mg CO ₂ dm ⁻²)	t	time
$F_w(t_1,t_2)$	photosynthetic production per unit of needle area including stomatal regulation in the summer phase (mg CO ₂ dm ⁻²)	T(x,t)	temperature (°C)
g_0	conductance of open stomatas (m s ⁻¹)	u*	optimal degree of stomatal opening
h(x,t)	specific transpiration rate (mg H ₂ O dm ⁻² h ⁻¹)	V_c	volume of the canopy of a stand (m ³)
$h_c(t)$	transpiration rate of canopy (kg H ₂ O m ⁻² h ⁻¹)	V_h	volume of chamber (dm ³)
$H_c(t_1,t_2)$	amount of transpiration of canopy (kg m ⁻²)	V_s	soil volume (m ³)
$H_i(t_1,t_2)$	amount of transpired water by a tree (kg)	V_t	volume of the canopy of a tree (m ³)
i(z,t)	interception rate at height z (g dm ⁻² s ⁻¹)	w_s	mean water content of soil (kg m ⁻³)
I_d	diffuse sky irradiance (on a horizontal plane) (W m ⁻²)	W(t)	internal state (°C)
I_r	direct solar irradiance (on a horizontal plane) (W m ⁻²)	x	point in space
I_t	total incoming irradiance (on a horizontal plane) (W m ⁻²)	z	height (m)
I(x,t)	irradiance of incoming radiation (on a horizontal plane) (W m ⁻²)	α	angle between the sun and the line of sight (rad.)
I_z	irradiance at zenith (W m ⁻²)	β	solar elevation (angle of solar altitude) (rad.)
K(x,t)	concentration of a primary matter or a compound (kg m ⁻³)	γ	zenith angle of the sun (rad.)
		$\Gamma(t)$	state of chilling (°C)
		δ	declination of the sun (rad.)
		Θ	elevation angle of the line of sight (rad.)
		Q(x)	needle area density at x (m ² m ⁻³)
		τ^m	mean transmittance of atmosphere through the air mass m
		Φ	hour angle of the sun (rad.)
		φ	azimuth angle of the line of sight (rad.)
		Ω	latitude of the observer (rad.)
		λ	amount of carbon consumed per water unit (kg C/kg H ₂ O)

1. INTRODUCTION

1.1. Photosynthesis and its measurement

Photosynthesis is a key process in understanding the primary production in a plant ecosystem. The photosynthesis provides all the carbohydrates and therefore the energy that plants need to grow and to subsist. The photosynthesis per unit leaf area is characterized by a great temporal and spatial variation in natural conditions. This feature of the photosynthesis is incorporated in most plant ecosystems.

The photosynthesis of Scots pine has been studied in most of the investigations of the CO₂ exchange of conifers (Linder 1979, 1981). But, there are still very few of the CO₂ exchange measurements in Scots pine trees under natural conditions for periods longer than a few days. Continuous measurements of the CO₂ exchange in the Scots pine have been carried out over longer periods in the SWECON project in central Sweden (Persson 1980) and in the research projects studying the primary production of a stand in central Finland (Hari et al. 1979, Pelkonen 1980 and 1981).

Photosynthetic carbon assimilation may be considered as a two-step process: first, the diffusion of the atmospheric CO₂ into the leaf intercellular space; second, the biochemical process of carbon fixation. The diffusion of the atmospheric CO₂ into the leaf intercellular space is governed by the physical laws of diffusion (Gaastra 1959). The biochemical process of carbon fixation is composed of the energy capture in light reactions and the formation of carbohydrates in the Calvin cycle. These reactions involve multiphase intermediates and an activation of enzymes (Farquhar and von Caemmerer 1982).

Energy is needed for many reactions in the cells. It is released from carbohydrates in the respiration. Respiration is expected to continue in the cells in the light similarly as in the dark (Farquhar and von Caemmerer 1982). Respiration causes the release of CO₂ from the cells of a leaf.

Photorespiration is light-dependent and intimately associated with the photosynthesis. Photorespiration is referred to gas exchange associated with glycolate metabolism (Foyer 1984). Carbon dioxide is partly recovered and partly lost in the photorespiratory pathway. Photorespiration results in the release of carbon dioxide.

The flow of carbon dioxide is further accompanied by the flow of water vapour from the leaf through the stomatas. This means that there is a close relationship between the photosynthesis and the transpiration. This complexity of the biochemical reactions and the flow of carbon dioxide and water vapour have been studied at different levels (e.g. Gaastra 1959, Reed et al. 1976, Charles-Edwards 1981, Jarvis 1981, Farquhar and von Caemmerer 1982, Cowan 1982).

The photosynthesis is not directly measurable, but the CO₂ exchange of a leaf or a shoot can be measured. It is possible to study the components of the carbon metabolism in laboratory conditions only, for example photorespiration, but its rate cannot be determined from field measurements (Luukkanen 1978). The respiration can be detected by the field measurements. Quantitatively, the respiration rate is a fraction of the rate of the photosynthesis in a one-year-old shoot of Scots pine.

Although detailed information is available of the components of the carbon metabolism of plants, information is still needed on the integrated activity of the gas exchange in natural conditions. The seasonal variation of the rate of the photosynthesis is suggestive of an annual cycle in conifers. The photosynthesis of Scots pine is principally exhausted during the winter period. However, Linder and Troeng (1980) have discovered photosynthesis for a couple of hours during the days with favourable weather in December – March in central Sweden. The photosynthesis of Scots pine gradually recovers in spring from winter dormancy to full activity (Pelkonen 1980, Linder and Troeng 1980).

The photosynthesis of pine has been found to continue in the weather conditions of central Sweden until late autumn (Linder and Troeng 1980). Autumn is the transition phase towards winter dormancy in the gas exchange.

1.2. The effect of the environmental factors on the photosynthesis

The rates of the carbon metabolic processes depend on the environmental factors. The variation of the environmental factors generates a variation in the rates of the carbon metabolic processes. The variation of the environmental factors can be characterized as spatial and temporal variation. The spatial and temporal variation is specific for each environmental factor. In principle, a change in the environmental factor can have an immediate or a delayed impact on the carbon metabolic processes. The impact of the environmental factor is related to the reactions stimulated and to the response of the reactions to the rate of the carbon metabolic processes.

The energy for the photosynthetic carbon assimilation is gained from the solar radiation in the photosynthetic light reactions. The photosynthetic carbon assimilation involves an energy supply. The photosynthetic carbon assimilation rapidly responds to the energy supply (Wierzbicki 1980). The dependence of the rate of the photosynthesis on the irradiance is non-linear. A temporal variation of the irradiance may be effective in the time interval when it is conceivable to measure the carbon dioxide exchange (Hari et al. 1983, Smolander 1984, Oker-Blom 1986 b). The spatial variation of the irradiance in the leaf area is often too large to be overlooked (Smolander 1984, Oker-Blom 1986 b). Thus, in order to estimate the rate of the photosynthesis per unit leaf area at a given moment, the irradiance at various points and at short time intervals is needed. An elevation of the sun and weather conditions generate a variation in the irradiance field above the canopy (Gates 1980, Ross 1981). The structure of the stand enhances the variation in the irradiance

field within the canopy (Andersson 1970, 1971, Nilson 1971, Ross 1981, Smolander 1984, Nilson et al. 1985, Oker-Blom 1986 b).

Temperature regulates most biochemical reactions. It affects the photosynthetic carbon assimilation, regulating dark reactions and having an effect on the light reactions as well. Temperature has an effect on the CO₂ exchange through the respiration. The temporal variation of the temperature within a stand is related to the diurnal course of the energy balance. The spatial component of the variation in the temperature may be influential in the different parts of the stand, but in most cases the diurnal variation of the temperature is bigger than the spatial variation within a pine stand (Shuttleworth 1975). The temporal variation is more significant within a shoot. A change in the temperature affects photosynthesis and respiration at a short time interval.

The variation of irradiance and temperature has an annual course. The annual cycle causes seasonal variations in the CO₂ exchange. The capability of the needles to endure the cold without damages requires changes in the composition of the cells compared with the active summertime. A change in temperature is obviously the signal for the effect of the annual cycle on the photosynthesis (Pelkonen and Hari 1980). Thus, temperature also has a long-term effect on the photosynthesis.

The inflow of carbon dioxide into the needles is closely related to the outflow of water vapour through the stomatas. The driving force of the gas diffusion is the difference in the partial pressure of the gas. The difference in the partial pressure of the water vapour between the ambient air and the intercellular space is the driving force of transpiration. Plants can regulate the gas flow by stomatas. The water available in foliage and the demand for transpiration in the air make up the requirement for stomatal regulation. In case of a water deficit the regulation of the transpiration is essential.

Soil water is a reservoir and a source of the transpiration flow. The transpiration may be considered as a continuous stream flowing from a periodically replenished source of a limited capacity, i.e. the reservoir of soil water, to a sink of a virtually unlimited capacity, the atmosphere (Hillel 1980). The reservoir

of soil water is replenished by the autumn rains, in spring by the water from melting snow and rains. It is conceivable to give an initial amount of soil water the value of the amount of the soil water in spring at the time of the melting of the snow. The size of the soil water reservoir in the growing season depends on the initial reservoir, the time development of the transpiration loss of the canopy, and on the replenishment by the rains. As long as the rate of the root uptake of soil water balances the rate of the canopy loss of transpiration, the stream continues unabated and governed by the meteorological conditions. Thenceforward the supply of water is not adequate to balance the transpiration, the regulation of the transpiration takes place. Transpiration begins to fall below the transpiration rate governed by the meteorological conditions. The beginning of the regulation depends on the combination of weather, plants and soil.

Regulation by closing the stomatas diminishes the inflow of carbon dioxide into the leaves. A decrease in the rate of the photosynthesis becomes apparent. The response of the photosynthetic rate to the environment changes in the course of the water deficit. This can be viewed as a change in the biological state of the plant during the water deficit. The water deficit has a long-term effect on the photosynthesis through the changed biological state during the inadequate water supply. The work of Gaastra (1959) introduced the coupling of the photosynthesis and the transpiration based on the diffusion of carbon dioxide and water vapour. This has been developed further by e.g. Chartier (1970), Charles-Edwards and Ludvig (1974), and Cowan and Farquhar (1977).

A new theoretical approach was introduced by Cowan (1977) and Cowan and Farquhar (1977), and it was further developed by Cowan (1982). They presented control of the gas exchange by means of optimization. According to this, the control of the gas exchange is considered optimal when maximal amounts of carbohydrates are produced per unit of water transpired in the prevailing environment. Hari et al. (1986) have given mathematical solutions to three formulations of the optimal stomatal control by introducing additional assumptions. They have described the procedures for empirical

testing of the solution of the first formulation.

The CO₂ concentration of the atmospheric air is the carbon resource of plants. The CO₂ concentration of the air has increased during the last decades (Lemon 1983). The changes in the CO₂ concentration of the atmospheric air are so slow that their effect on the photosynthesis cannot be observed in an annual inspection.

Carbon metabolism is interwoven with the metabolism of other inorganic nutrients taken from the soil. The availability of nutrients in association with carbohydrates effects the construction of enzymes and organs. The availability of nitrogen is combined to the cycle of organic matter on the growth site. The availability of other inorganic nutrients is related to the physical and chemical properties of the soil. Changes in the availability of most nutrients are extremely slow on a single growth site in a soil where the roots of a tree are growing. Therefore the effect of nutrients on the photosynthesis is not observable within a year on a single growth site.

The photosynthetic production per unit leaf area is an accumulation of carbon assimilated at the varying rate of the photosynthesis. Environmental factors affect the photosynthetic production through the rate of the photosynthesis. Environmental factors affect the photosynthetic rate and the accumulation of the photosynthetic production concurrently.

1.3. The objectives and structure of the study

The variation of the environmental factors is the environmental factor specific in nature. Environmental factors are also interrelated and have an annual cycle. Water is the environmental factor that affects the gas exchange through the soil water and through the water content of the air. The rate of the photosynthesis is affected concurrently by the environmental factors and the control of the plant metabolism. The control of the plant metabolism becomes operating in certain environmental conditions. In order to estimate the amount of photosynthesis, the response of

the rate of the photosynthesis to environmental factors and to the control of the plant metabolic processes needs to be known.

The aim of this study is

- to relate the response of the rate of photosynthesis and the transpiration rate to the environmental factors, i.e. irradiance, temperature, water content of air and soil, and to the control of the plant metabolic processes in Scots pine (*Pinus sylvestris* L.) in its natural environment
- to evaluate the consequences of different environmental factors in the photosynthetic production.

The study strives to establish the effect of the interaction of environmental factors and the regulation of the gas exchange on the photosynthesis in natural conditions. This is needed in order to estimate photosynthetic production over a long period. Photosynthesis and transpiration are described as dynamic processes. The complete model provides a framework for the understanding of the gas exchange of Scots pine during an entire annual cycle.

This study report consists of four parts. Chapter 2 comprises the theoretical approach to analyse the dynamic aspects of the gas exchange and the environment of the plant. Chapter 3 reports the empirical measurements of the gas exchange and the environmental factors. The empirical findings consist of measurements made on the research site in the years 1982, 1984 and 1985 and of a series of observations made by the Finnish Meteorological Institute.

The response of the rate of the photosynthesis to the environmental factors and the effect of the control on the photosynthesis are reported in Chapter 4. Irradiance, temperature and water are the environmental factors examined in summer and in autumn.

Chapters 5 and 6 characterize the environmental factors which make up the physical environment of a plant. Interactions of transpiration, the water content of the air and soil water are reported in Chapter 5 on the water regime of a pine stand.

The consequences of the environmental factors in the photosynthetic production per unit leaf area are evaluated in Chapter 7.

2. A THEORETICAL APPROACH TO THE ANALYSIS OF THE GAS EXCHANGE AND THE ENVIRONMENT

An environmental factor is a concept that incorporates primary matters, compounds and energy. Temporal and spatial variations are characteristic of many environmental factors. Environmental factors, except for solar irradiance and temperature, are a primary matter or a compound like water, carbon dioxide or nutrients. I denotes irradiance, T denotes temperature, K denotes the concentration of the primary matter or compound, x indicates a point in a space, and t stands for time. The environment of a plant, E , is

$$(1) \quad E(x,t) = (I(x,t), T(x,t), K(x,t))$$

The environment of a plant is composed of different environmental factors.

The exchange of carbon dioxide in the needles is formed by two metabolic processes, the photosynthesis and the respiration. The photosynthesis is here termed by the inflow of carbon dioxide into the needles and the respiration is termed by the outflow of carbon dioxide from the needles. The specific photosynthetic rate per unit needle area (per unit needle mass) is defined by a time derivative of the accumulated carbohydrates per unit needle area (per unit needle mass). The specific respiration rate per unit needle area (per unit needle mass) is defined respectively by a time derivative of the carbohydrates consumed in the respiration per unit needle area (per unit needle mass). Let f denote the specific photosynthetic rate, and r stands for the specific respiration rate. The rate of the carbon dioxide exchange, p , is formed by the photosynthesis and the respiration, i. e.

$$(2) \quad p(x,t) = f(x,t) - r(x,t)$$

The spatial variation of temperature is of minor importance in a pine stand, whereas the temporal variation of temperature is considerable (Shuttleworth 1975). Needles have a small size and a small heat capacity, but they have low reflectance and high absorpt-

ance of solar radiation due to the dark pigmentation. The cylindrical geometry of the pine needles results in less solar radiation being absorbed per unit surface area in contrast to broad leaves. The temperature of the needles is higher than the temperature of the ambient air in the high solar radiation. The temperature of the needles equals the ambient air temperature most of the time due to the small heat capacity of the needles and due to the wind (Gates 1981). The temperature of the needles is here assumed to be equivalent to the air temperature. Thus

$$(3) \quad T(x,t) = T(t)$$

Let us assume that the photosynthetic rate is determined by the environmental factors and the regulation of the plant metabolic processes, i.e. the state of the biochemical regulation system of the plant. The most important environmental factors affecting the photosynthesis are irradiance and temperature in conditions with no water deficit. Let us also assume that temperature is the only environmental factor that affects respiration. When the regulation of the plant metabolic processes do not operate, the rate of the exchange of carbon dioxide may be written as follows:

$$(4) \quad p(x,t) = f(I(x,t), T(t)) - r(T(t))$$

Regulation causes changes in the response of the metabolic processes to the environmental factors. The regulation operates at rates that depends on the state of the biochemical regulation system of the plant (Charles-Edwards 1981). The annual cycle and the water deficit are the primary regulations of the photosynthesis in the northern climate. The effect of water deficit is introduced into the analysis with the internal state of the plant, W . The effect of the annual cycle on the photosynthesis is introduced into the analysis with the state of the photosynthetic activity,

S, according to Pelkonen and Hari (1980), and Pelkonen (1981). When the regulations operate, the rate of the CO₂ exchange is written as follows:

$$(5) p(x,t) = f(I(x,t), T(t), W(t), S(t)) - r(T(t))$$

The regulation of the photosynthesis depends concurrently on the ambient environment and on the state of the biochemical regulation system, i.e. the internal state of the plant and the state of the photosynthetic activity. The stomatal regulation of the gas exchange depends on the internal state of the plant and on the temperature. The change in the state of the photosynthetic activity depends on the state itself and on the temperature. It is also assumed that a multiplicative model may be applied to approximate the specific photosynthetic rate. The specific photosynthetic rate is

$$(6) f(x,t) = f_1(I(x,t)) f_2(T(t)) f_3(W(t), T(t)) f_4(S(t), T(t))$$

where f_3 describes the stomatal regulation and f_4 describes the state of the photosynthetic activity. Each component of the model has to be determined. The components are determined hierarchically, i.e. the instantaneous responses to the photosynthesis are determined first. Thereafter, it is possible to analyse the slower responses of the environment to the photosynthesis.

The specific transpiration rate depends on the ambient concentration of water vapour, $e_a(x,t)$, on the intercellular concentration of water vapour, $e_i(x,t)$, and on the stomatal regulation. Let us assume that a multiplicative model can be applied. The specific transpiration rate, h , is

$$(7) h(x,t) = h_1(e_i(x,t) - e_a(x,t)) f_3(W(t), T(t))$$

where h_1 describes the dependence of the specific transpiration rate on the difference between the ambient and the intercellular concentration of the water vapour without the stomatal regulation, and f_3 describes the stomatal regulation respective to the photosynthetic rate.

The effect of the water deficit on the gas exchange is brought up by the internal state of the plant. Let us assume that the internal

state of the plant depends on the mean water content in the soil. Thus

$$(8) W(t) = g_1(w_s(t))$$

where w_s denotes the mean water content in the soil, and g_1 generally stands for a function to be determined.

The movement of the water in the soil-plant-atmosphere system can be described as a mass flow of water. The principal flows of water are throughfall to soil, transpiration and percolation, which affect the amount of soil water in the rooted layer of the soil. The density of the needle area is denoted by $\varrho(x)$ and the volume of the canopy by V_c . The transpiration rate of the canopy, $h_c(t)$, at a given moment is obtained by the integration

$$(9) h_c(t) = \int_{V_c} \varrho(x) h(x,t) dV_c$$

The amount of water in the soil is denoted by M and the volume of soil by V_s . The amount of soil water at a given moment is obtained from

$$(10) M(t) = V_s w_s(t)$$

The throughfall rate to soil is denoted by s_s and the percolation rate to ground water by q . The rate of change in the amount of soil water is

$$(11) dM/dt = s_s(t) - h_c(t) - q(t)$$

The amount of the photosynthesis per unit needle area in a time interval, $t_1 - t_2$, is defined by the integral of the photosynthetic rate over the time interval (Eq. 12),

$$(12) F(t_1, t_2) = \int_{t_1}^{t_2} f_1(I(x,t)) f_2(T(t)) f_3(W(t), T(t)) f_4(S(t), T(t)) dt$$

where $F(t_1, t_2)$ denotes the amount of photosynthesis per unit needle area. Determination of the Eq. (6) allows us to determine the integrals in the Eqs. (12) and (13).

The density of the needle area in a volume (V) is denoted by $\varrho(x)$. The amount of photosynthesis assimilated by the needles in a time interval is obtained from

$$(13) F_n(t_1, t_2) =$$

$$\int_{t_1}^{t_2} \int \varrho(x) f_1(I(x,t)) f_2(T(t)) f_3(W(t), T(t)) f_4(S(t), T(t)) dt dV$$

The symbol F_n denotes the photosynthetic production of the needles.

The Eqs. (2), (4), (5) and (6) cover the dependence of the specific photosynthetic rate on the environmental factors. The Eqs. (12) and (13) are obtained by integrating the

specific photosynthetic rate. The Eq. (7) covers the dependence of the specific transpiration rate on the environmental factors. The Eq. (9) and the amount of transpiration are obtained respectively by integration. The Eqs. (8), (10) and (11) link the photosynthesis and the transpiration. The functions included in the above equations need to be known. The occupancy of photosynthesis, transpiration and their interaction results from the presented prerequisites.

3. MATERIALS

3.1. Field measurements

3.1.1. Overview

The study was based on simultaneous and continuous monitoring of the environmental factors and the gas exchange in the trees during the measuring periods. The data was collected in a Scots pine (*Pinus sylvestris*) stand situated at the Forestry Field Station of the University of Helsinki (lat. 61° 51'N, long. 24° 17'E, elev. 160 m asl.). The experimental stand was about twenty years old growing on a glacial drift. The topography of the site was somewhat irregular with a maximum difference in height of about 3 m. The density of the stand was approx. 2 200 stems per hectare and the mean height of the stand was 6.9 m. The experimental trees were situated on a slope facing south.

Two automatic measuring systems were used in the stand. The gas exchange in the trees and the environmental factors were measured by one measuring system and the micrometeorological measurements were made by another. The gas exchange measurements were carried out in three years, i.e. from 13 May to 30 November in 1982, from 26 June to 6 October in 1984, and from 1 July to 26 October in 1985. Micrometeorological measurements were carried out round the year.

3.1.2. Measurements of the CO₂ exchange and the environmental factors

The gas exchange measurements were made on two trees in 1982. One of the trees was growing on the lower slope and the other one on the upper slope. The difference in elevation was about 2 m. The gas exchange was measured on one tree both in 1984 and in 1985. This tree was growing on the upper slope. The gas exchange was studied on two shoots of each sample tree, the shoots facing south, southeast in 1982. Shoots parallel to the axis of the earth were measured in 1984 and 1985. The measurements were carried

out on one-year-old shoots in the second and fourth whorls.

The studied shoots were inserted in trap-type chambers, which closed automatically when the chamber came up for measuring. Each chamber was closed for a hundred seconds. The measuring system contained six chambers, which were measured in sequence. Two chambers were used for measuring the reference concentration of the CO₂ in the outside air. The opening and closing of the chambers took place by compressed air and by magnetic valves. The volume of the plexiglass chamber was 3.0 dm³.

The chambers were connected to the gas analyser by copper tubes. The gas analysing system is illustrated in Fig. 1 (cf. Hari et al. 1979). There was a continuous air flow of 1 dm³ min⁻¹ from all the chambers and through the analysing tubes. The tubes were warmed by electric cables to avoid condensation of water. The gas stream was steered from the closed chamber to the analysing system by the data logger controlled magnetic valves. Before the CO₂ content was analysed the water vapour was stabilized in the gas stream by passing it through a copper coil maintained at +1 °C. The CO₂ content was analysed by an infrared gas analyser (URAS I, Hartman and Braun). The gas flow was measured and controlled by a rotameter. New measuring chambers were used in 1984 and 1985. A fan was installed in the measuring chambers to mix the inside air.

The CO₂ exchange was measured in terms of a decrease in the CO₂ concentration of the air. The change in the CO₂ concentration in the chamber is governed by the following differential equation (Hari et al. 1983)

$$(14) \quad V_h \frac{dC}{dt} = - \int_{V_h} q(x) p(x,t) dV + q_h (C_a - C)$$

where C denotes the CO₂ concentration of the air in the chamber and C_a respectively in the outside air, q_h denotes the flow rate of the air, $q(x)$ the density of the leaf area, and V_h the volume of the chamber, p the specific CO₂ exchange rate, t time, and x a point in a

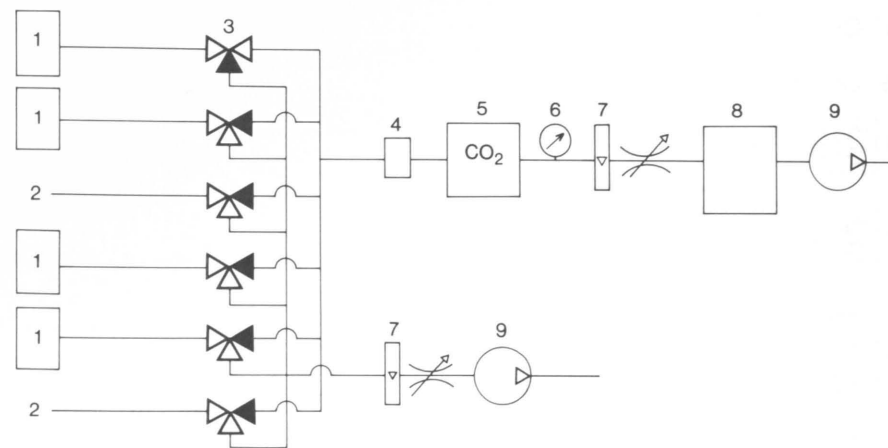


Figure 1. Diagram plan of the CO₂ analysing system: 1. chambers, 2. channels for the reference CO₂ measurements, 3. magnetic valves, 4. stabilizer for the concentration of water vapour in the air, 5. infrared gas analyser (IRGA, Hartman and Braun), 6. pressure gauge, 7. rotameter, 8. pressure stabilizer, and 9. pump.

space. t_0 denotes the moment of closing the chamber. The following relationship is obtained by integrating the above equation over the time interval Δ .

$$(15) \quad \int_{t_0}^{t_0+\Delta} \int_{V_h} q(x) p(x,t) dV dt = V_h (C(t_0) - C(t_0+\Delta)) + \int_{t_0}^{t_0+\Delta} q_h (C_a - C(t)) dt$$

The left side of the above equation denotes the amount of the CO₂ exchange in the chamber. The right side of the equation was obtained from the measurements of the gas analyser and from a correction factor to include the effect of air flowed in during the measuring.

The incoming irradiance was measured in each chamber using the ELP equipment (Hari et al. 1976). The five photo-voltaic cells (Siemens BPY 11) were inserted in each chamber. The equipment performed the integration of the incoming irradiance over time and approximated the integration over space with sums. Temperature was measured near each sample tree at the height of 3 m. Temperature was measured by copper-constantan thermocouples.

Total radiation and the diffuse sky radiation were measured above the canopy level using light sensors constructed at the Applied Electronics Laboratory, Helsinki University of Technology (Salminen et al. 1983). The sensors were calibrated by a Lambda pyranometer to have an output voltage of 0.1 mV/(Wm⁻²), with a tolerance of 1 %.

3.1.3. The data acquisition system

Total radiation, the diffuse sky radiation, the air temperature, the irradiance in the chambers and the CO₂ concentration were measured simultaneously. The measuring interval was a hundred seconds. The data acquisition system is illustrated in Fig. 2.

A data logger (Nokia Electronics) was the measuring unit used in the data acquisition system. The data logger also controlled the timing of the measuring sequence of chambers. The logger sent the measuring results to the minicomputer PDP 11/34. The transmission line (460 m) was optically coupled to the data logger and the computer in order to avoid damages due to lightning. The measuring system was turned off during thunder-

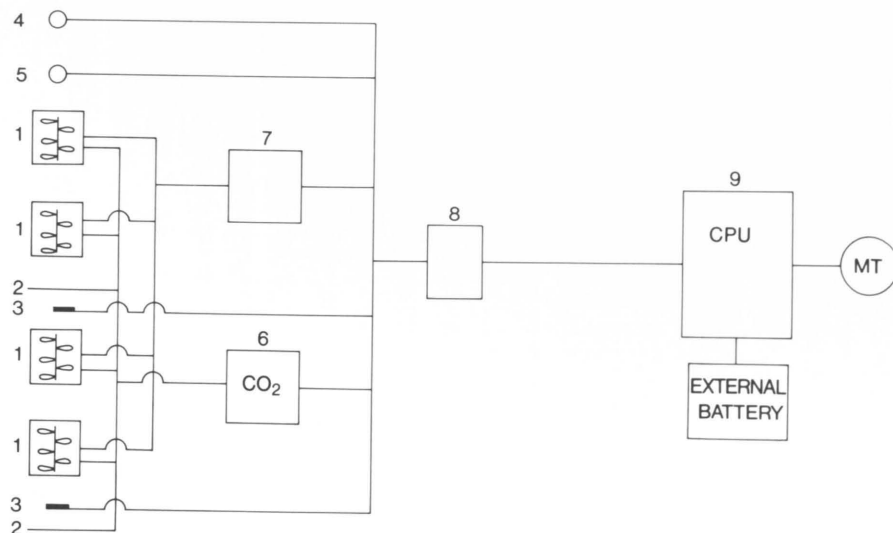


Figure 2. Measuring sensors and the data acquisition system: 1. irradiance sensors in chambers, 2. channels for the reference CO₂ measurements, 3. thermocouples, 4. total radiation, 5. diffuse sky radiation, 6. gas analyser for the CO₂ measurements (IRGA), 7. central unit of the ELP equipment, 8. logger central unit, and 9. computer.

storms. Otherwise the measuring system ran continuously.

The measuring system was checked every day. The measuring results were controlled and reported once a day by running the report program. The data was stored on magnetic tapes.

3.1.4. Micrometeorological measurements

The meteorological measurements were made by another automatic measuring system. A measuring mast was placed in the same pine stand. Sensors were installed on the mast, which was 12 m high.

Total radiation was measured above the canopy level by a light sensor constructed at the Applied Electronics Laboratory of the Helsinki University of Technology (Salminen et al. 1983). Wind velocity was measured by cup anemometers (Waisala) at the height of 3 m, 6 m and 9 m. Ventilated psychrometers constructed by the Finnish Meteorological

Institute were at the height of 3 m and 9 m. The dry and wet bulb temperatures of the psychrometers were measured by resistance temperature sensors (PT 100). Precipitation was measured by a rain gauge equipped with electric output. The rain gauge was placed at the top level of the canopy.

An analog data logger (VEKO) constructed at the Applied Electronics Laboratory of the Helsinki University of Technology was the measuring and controlling unit of the data acquisition system. All sensors were measured simultaneously. The measuring interval was 120 seconds. The data logger sent the measuring messages to the minicomputer PDP 11/34. The measuring results were checked and reported once a day by running the report program. The data was stored on magnetic tapes. The measurements were performed continuously throughout the year except for power failures. Monitoring of total radiation, precipitation and wet temperature was discontinued in winter.

3.2. Weather data supplied by the Finnish Meteorological Institute

Monitoring of the irradiance data was started in 1957 at the Jokioinen Observatory of the Finnish Meteorological Institute (lat. 60°48'N, long. 23°30'E, 103 m asl.) (Meteorological Yearbook of Finland 1963). The irradiance was measured by a pyranometer and the output was recorded continuously on a point recorder. The air temperature was measured and recorded by a

thermograph (Fuess). One sample per hour was taken from the irradiance and temperature measurements. The data used covered the period from 15 April to 15 October in the years 1958–1977.

Monthly precipitation data was available since 1883 from the Tampere Observatory of the Finnish Meteorological Institute (lat. 61°28'N, long. 23°44'E, 85 m asl.). The precipitation data was from the years 1883–1984.

4. THE RATE OF THE PHOTOSYNTHESIS

4.1. The response of the rate of the photosynthesis to irradiance and temperature

The rate of the photosynthesis is responsive to irradiance and temperature in the summer activity of the photosynthesis when the regulations of the gas exchange are not operating. The conditions prevail if there is no water deficit in the soil and if the demand for transpiration does not exceed the water supply to the needles. The rate of the photosynthesis is described by the following multiplicative model, where I denotes irradiance and T denotes temperature.

$$(16) \quad f(x,t) = f_1(I(x,t)) f_2(T(t))$$

Determination of the functions f_1 and f_2 is needed.

The response of the photosynthesis per unit of the needle area to irradiance is known to be non-linear. The response of the rate of the photosynthesis to irradiance is initially linear but tends to saturate when subjected to a high irradiance. The Michaelis-Menten function, which is widely used to describe a saturating response of a biological system to an input, was used to determine the function f_1 , i.e.

$$(17) \quad f_1(I(x,t)) = P_m \frac{I(x,t)}{I(x,t) + b}$$

where P_m and b are the specific parameters for a unit of the needle area in each shoot.

Temperature affects the photosynthesis through biochemical reactions in the photosynthesis and through the solubility of carbon dioxide in the intercellular water. The photosynthesis has a temperature response similar to that of other chemical reactions. An increase in temperature stimulates the photosynthesis. The solubility of carbon dioxide in water is higher at low temperatures than at high temperatures (Stumm and Morgan 1981). An increase in temperature reduces the photosynthesis at high temperatures. The response of the rate of the photosynthesis to

temperature was determined as follows:

$$(18) \quad f_2(T(t)) = \begin{cases} 0 & \text{if } T < a_2 \\ 1 - \exp(-a_1(T(t)-a_2)) & \text{if } T \geq a_2 \end{cases}$$

where a_1 and a_2 are parameters. The Eq. (18) covers the range of the temperatures occurring in the natural conditions of the studied area.

In order to estimate the parameters of the Eqs. (17) and (18), the specific respiration rate has to be determined. An increase in temperature increases respiration. The respiration rate in the light was assumed to continue in the same way as in the dark (Farquhar and von Caemmerer 1982). The response of the respiration rate to the temperature is known to be exponential in the dark. The dependence of the specific respiration rate on the temperature was determined as follows:

$$(19) \quad r(T(t)) = \begin{cases} 0 & \text{if } T \leq c_3 \\ c_1 (\exp(c_2(T(t)-c_3)) - 1) & \text{if } T > c_3 \end{cases}$$

where c_1 , c_2 and c_3 are parameters. The value of the parameter c_2 was derived from the measurements of the respiration of pine shoots in the dark. These measurements were made in laboratory conditions. The value used was $c_2 = 0.036 \text{ } ^\circ\text{C}^{-1}$.

The Eqs. (17), (18) and (19) were substituted in the Eq. (4) (Chapter 2) for the numerical estimation of the parameters. The data from 13 to 15 June in 1982, 29 to 30 June in 1984 and 2 to 3 July in 1985 were used to estimate the parameters.

The ELP equipment used to measure the irradiance inside the cuvette among needles performed the integration of irradiance over time using the Michaelis-Menten response and approximated the integration over space with sums. The criteria used to estimate the parameters were a linear relationship between the output of the ELP measurement and the measured rate of the CO_2 exchange (Hari et al. 1983). The parameters in the Eq. (17) were $b = 150 - 180 \text{ W m}^{-2}$ and the

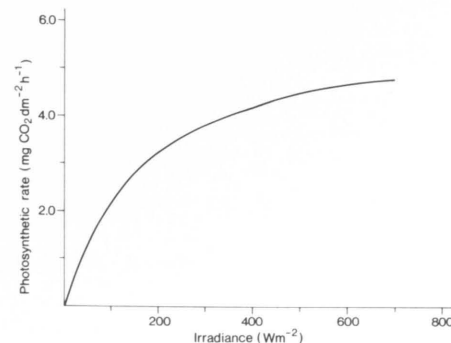


Figure 3. Dependence of the rate of the photosynthesis on irradiance Eq. (17) with parameters $P_m = 6.0 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ and $b = 170 \text{ W m}^{-2}$.

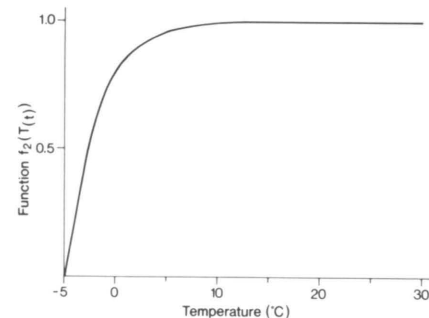


Figure 4. Dependence of the rate of the photosynthesis (function $f_2(T(t))$) on temperature Eq. (18) with parameters $a_1 = 0.32 \text{ } ^\circ\text{C}^{-1}$ and $a_2 = -5 \text{ } ^\circ\text{C}$.

parameter $P_m = 6.2 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ in 1984 and $5.9 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ in 1985. The values of the parameter P_m could not be estimated in 1982 due to measuring techniques. Thus the rates of the photosynthesis in 1982 should be considered as relative units. The dependence of the rate of the photosynthesis on irradiance (Eq. 17) is illustrated in Fig. 3.

The data from 13 to 15 June 1982 was used to estimate the parameters a_1 and a_2 in the temperature dependence. The period also included minimum daytime temperatures of $+3 \text{ } ^\circ\text{C}$. The value of the parameter $a_2 = -5 \text{ } ^\circ\text{C}$ was derived from the measurements made

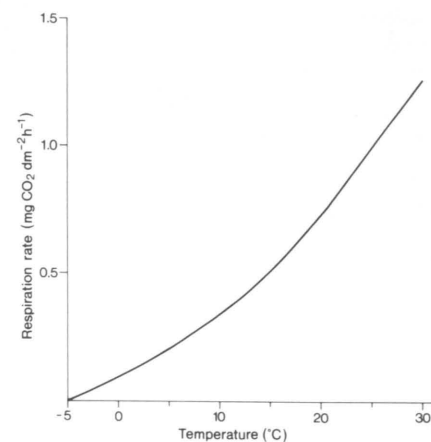


Figure 5. Dependence of the respiration rate on temperature Eq. (19) with the parameter $c_1 = 0.50 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$.

in autumn. The parameter a_1 was $0.32 \text{ } ^\circ\text{C}^{-1}$. The above response to the temperature with fixed parameters was used in the analyses of all the shoots and in the measuring periods 1982, 1984 and 1985. Figure 4 illustrates the used dependence of the rate of the photosynthesis on the temperature (Eq. 18).

The parameter c_3 in the response of the specific respiration rate to the temperature (Eq. 19) was derived from the measurements made in autumn. The value of the parameter c_3 was $-5 \text{ } ^\circ\text{C}$. The parameter c_1 was specific for each shoot. It was $0.45 - 0.64 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ in 1984 and 1985. The dependence of the respiration rate on the temperature is shown in Fig. 5.

The validity of the model was tested by predicting the rate of the CO_2 exchange by the temperature and irradiance measurements using Eq. (17), Eq. (18) and Eq. (19) for the model of the CO_2 exchange (Eq. 4). The predicted values of the CO_2 exchange were compared to the measured values of the CO_2 exchange which were obtained simultaneously with the temperature and irradiance measurements. The rate of the CO_2 exchange could be predicted fairly well by the model as shown in Fig. 6 at 29 May. The predicted rate of the CO_2 exchange was con-

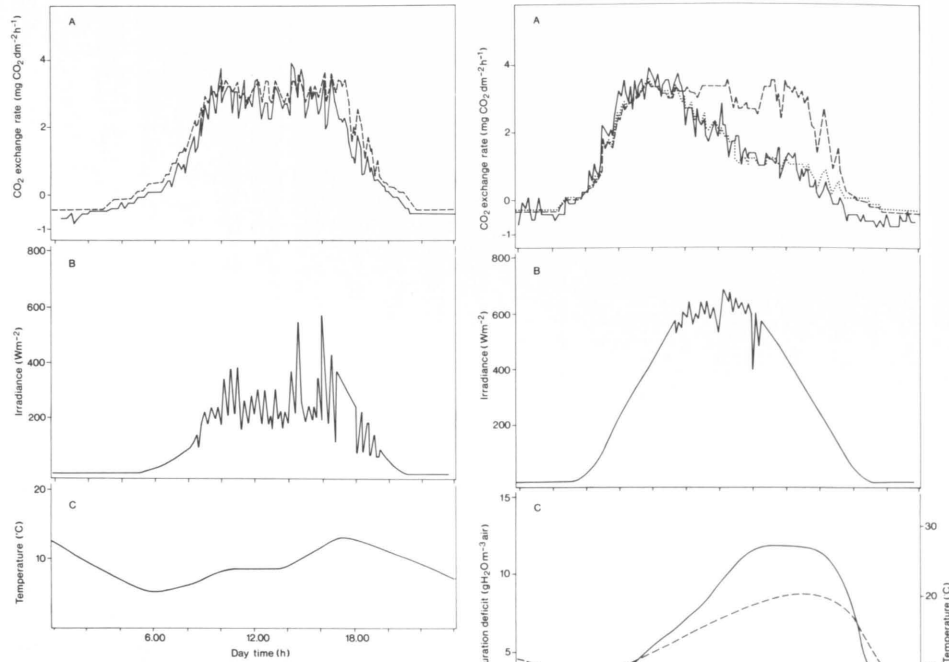


Figure 6. A. Measured rate of the CO₂ exchange (solid line), and according to the Eqs. (4) and (16), predicted rate of the CO₂ exchange (broken line) on 29 May 1982. B. Irradiance and C. temperature on 29 May 1982. (Korpilahti and Hari 1988 a).

sistent with the diurnal course of the measured rate of the CO₂ exchange.

On some summer days, decrease occurred in the measured rate of the CO₂ exchange in the afternoon. The deficit of water vapour in the air increased strongly or it was high on those days. The measured rate of the CO₂ exchange decreased for a few hours in the afternoon compared to the predicted rate of the CO₂ exchange. The rate of the CO₂ exchange could not be predicted by the model in such conditions (Fig. 7). The measured rate of the CO₂ exchange decreased for example on 22 May, 1 June (Fig. 7), 2 June and 3 June in 1982. In the early and late morning, the predicted rate of the CO₂ exchange was consistent with the measured rate of the CO₂

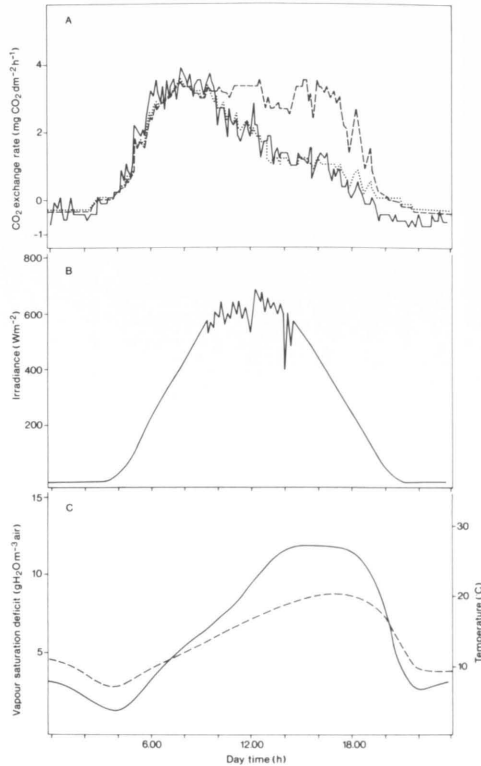


Figure 7. A. Measured rate of the CO₂ exchange (solid line), according to the Eqs. (4) and (16) predicted rate of the CO₂ exchange (broken line), and according to Eqs. (5), (6) and (20) predicted rate of the CO₂ exchange (dotted line) on 1 June 1982. B. Irradiance, C. temperature (broken line) and water vapour saturation deficit (solid line) on 1 June 1982.

exchange. The predicted rate of the CO₂ exchange diverged from the course of the measured rate of the CO₂ exchange when the deficit of water vapour in the air exceeded 7–9 gm⁻³. The deficit of water vapour remained high on such warm and sunny days until late evening. Usually the deficit of water vapour decreased rapidly during the late evening hours. The rate of the CO₂ exchange recovered during those hours. If irradiance was available, the rate of the CO₂ exchange could be predicted by the model.

After a number of warm and sunny days in the early part of June 1982, the weather turned cloudier and cooler. The deficit of water vapour in the air remained low all day in such weather. The predicted rate of the CO₂ exchange was again consistent with the measured rate of the CO₂ exchange through the day as for example on 10 June 1982 (Fig. 8). The measured rate of the CO₂ exchange was predictable by the model used for the rate of the CO₂ exchange with the same parameter values later in the summer, for instance on 30 June 1982 (Fig. 9) and on 28 August 1982 (Fig. 10).

The variance of the measured rate of the CO₂ exchange varied in a wide range daily over a long period. The variance of the measured rate of the CO₂ exchange is related to

weather conditions on that day. For technical reasons and due to changes in the CO₂ concentration of the air, a varying number of measurements per day were available. Figure (11) illustrates the mean of the measured rate of the CO₂ exchange in periods of 10 days and the variance of the measured rate of the CO₂ exchange in the respective periods in 1982. The residual sum of the squares of the model for the CO₂ exchange was computed daily to quantify the validity of the model (Fig. 12 and 13). The periods when the saturation deficit of water vapour in the air exceeded 7 gm⁻³, and the dry period in July and in the early August 1982, were restricted from this computation. The residual sum of the squares of the model was below 15 % of the mean of the variance of the measured rate of the CO₂

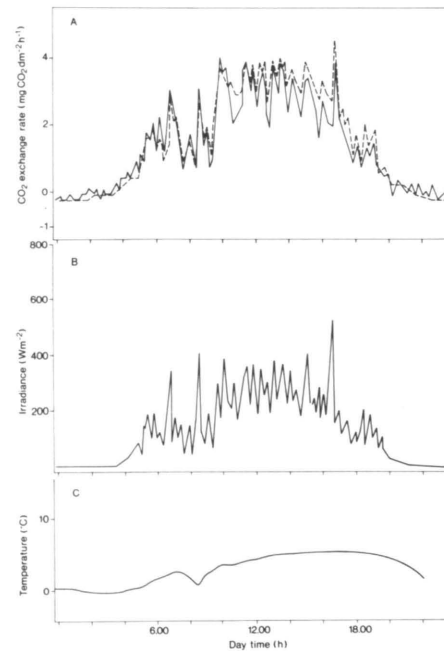


Figure 8. A. Measured rate of the CO₂ exchange (solid line) and, according to the Eqs. (4) and (16), predicted rate of the CO₂ exchange (broken line) on 10 June 1982. B. Irradiance and C. temperature (broken line) and water vapour saturation deficit (solid line) on 10 June 1982.

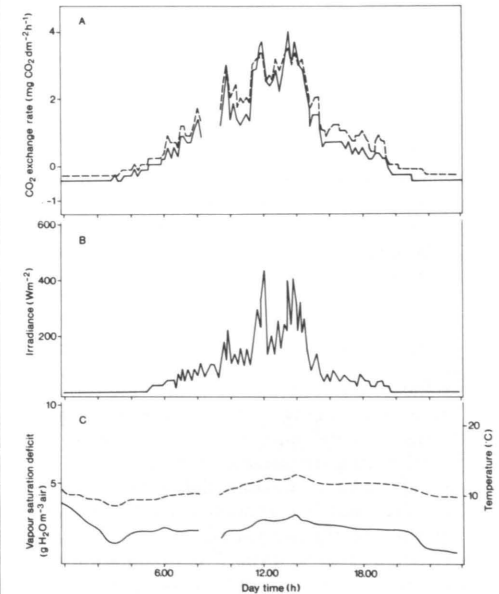


Figure 9. A. Measured rate of the CO₂ exchange (solid line) and, according to the Eqs. (4) and (16), predicted rate of the CO₂ exchange (broken line) on 30 June 1982. B. Irradiance, C. temperature (broken line) and water vapour saturation deficit (solid line) on 30 June 1982.

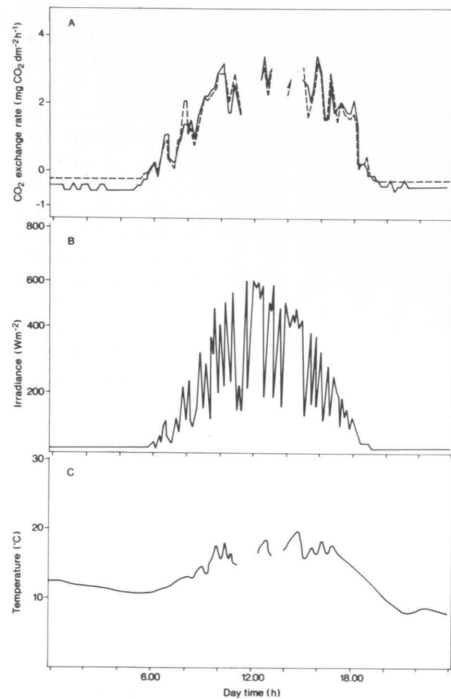


Figure 10. A. Measured rate of the CO₂ exchange (solid line) and, according to the Eqs. (4) and (16), predicted rate of the CO₂ exchange (broken line) on 28 August 1982. B. Irradiance and C. temperature on 28 August 1982. (Korpilahti and Hari 1988 b).

exchange on most days in 1982 (Fig. 12 and 13). Any changing trend was not observable in the residual sum of the squares of the model during the summer. The model for the rate of the CO₂ exchange defined by the Eqs. (17), (18) and (19) explained 80–95 % of the variance of the measured rate of the CO₂ exchange on most days. The predictability of the model was the same in different shoots. The predictability of the model with fixed values of the parameters remained stable in summer and was at the same level also in late summer. The validity of the model of the CO₂ exchange was respective also in 1984 and 1985. The number of days was slightly lower in 1984 and 1985 than in 1982 when the

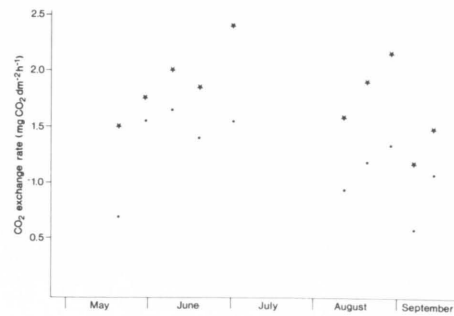


Figure 11. The means of the measured rate of the CO₂ exchange in the periods of 10 days and the variances of the measured rate of the CO₂ exchange in the respective periods in 1982. Mean marked by (●) and variance marked by (*) (Korpilahti and Hari 1988 a).

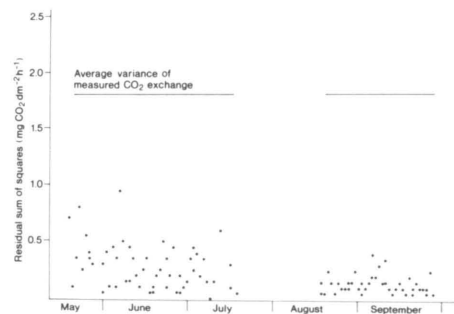


Figure 12. The residual sum of the squares of the model for the CO₂ exchange (Eqs. 4 and 16) per day in 1982 for the shoot of the tree on the upper slope. The mean variance of the measured rate of the CO₂ exchange excluding the dry period in June and in early August. (Korpilahti and Hari 1988 a).

percentage of the explained variance of the model was 80–95 % of the variance of the measured CO₂ exchange. The accuracy of the measurements of the CO₂ exchange was slightly lower in 1984 and 1985 than in 1982 due to changed technics.

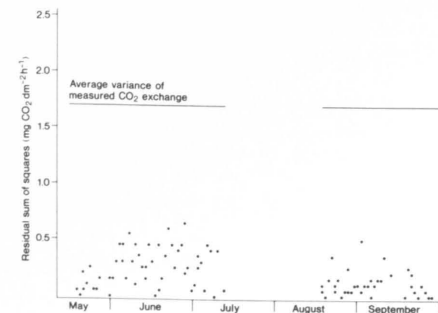


Figure 13. The residual sum of the squares of the model for the CO₂ exchange (Eqs. 4 and 16) per day in 1982 for the shoot of the tree on the lower slope. The mean variance of the measured rate of the CO₂ exchange excluding the dry period in June and in early August.

4.2. The effect of the water deficit on the photosynthesis

4.2.1. The response of the rate of the photosynthesis to the water deficit

The inflow of carbon dioxide into the needles is accompanied by the outflow of water vapour from the needles through the stomata. The intercellular concentration of water vapour is considered to be saturated. Thus the difference in the partial pressure of the water vapour between the ambient air and the intercellular space is the driving force of transpiration. Plants regulate the transpiration by closing the stomata. If the demand for transpiration exceeds the water supply to the needles, the resulting condition generates the regulation of the gas exchange to operate. The water deficit changes the biological state of the plant in a time interval. The state of the plant affects the response to the environment.

Regulation of the gas exchange is included in the analysis with the internal state of the plant, *W*. The water deficit affects the internal state. The internal state is assumed to change slowly. It has a constant value during the day. The stomatal regulation of the photosynthesis is assumed to depend on the internal state and on the ambient temperature as follows:

$$(20) f_3(W(t), T(t)) = \begin{cases} \exp(-k(T(t)-W(t))) & \text{if } T > W \\ 1 & \text{if } T \leq W \end{cases}$$

where *k* is a parameter. The value of the parameter *k* was 0.25.

Greenhouse data of alder (*Alnus incana* (L.) Moench) seedlings and field data of birch (*Betula pendula* Roth) seedlings have been analysed with this method by Hari and Luukkanen (1973 and 1974). Field data of Scots pine seedlings have been analysed respectively by Hallman et al. (1978) and Korpilahti (1982).

On a number of days in the measuring periods 1982 and 1985, the measured rate of the CO₂ exchange decreased for a few hours at midday and in the afternoon. The daily value of the internal state was estimated from the measurements of the CO₂ exchange using the Eqs. (17), (18), (19) and (20). Estimation of the daily value of the internal state requires high enough temperature. If the maximum temperature is not high enough to provoke the depression of the gas exchange, the value of the internal state, *W*, cannot be estimated.

The validity of the model for the CO₂ exchange with the regulation function was tested by predicting the rate of the CO₂ exchange by the temperature and irradiance measurements using the Eqs. (17), (18), (19) and (20), and the estimated value of the internal state. The predicted rate of the CO₂ exchange was compared with the simultaneously measured rate of the CO₂ exchange. The predicted rate of the CO₂ exchange seemed to be consistent with the measured rate of the CO₂ exchange through the day, for example on 1 June 1982 (Fig. 7).

June and July of 1982 were exceptionally dry in Finland. Precipitation on the research site amounted in June to 32 mm and in July to 28 mm. The average precipitation at the Forestry Field Station from 1931 to 1960 is in June 53 mm and in July 77 mm. On four days from 15 June to 9 August in 1982 the daily precipitation was over 5 mm. There were 38 days in the period without any rain.

The decrease in the measured rate of the CO₂ exchange increased in the dry period. The measured rate of the CO₂ exchange decreased first at midday and in the afternoon until mid-July. The rate of the photosynthesis showed for example on 16 July (Fig. 14) in

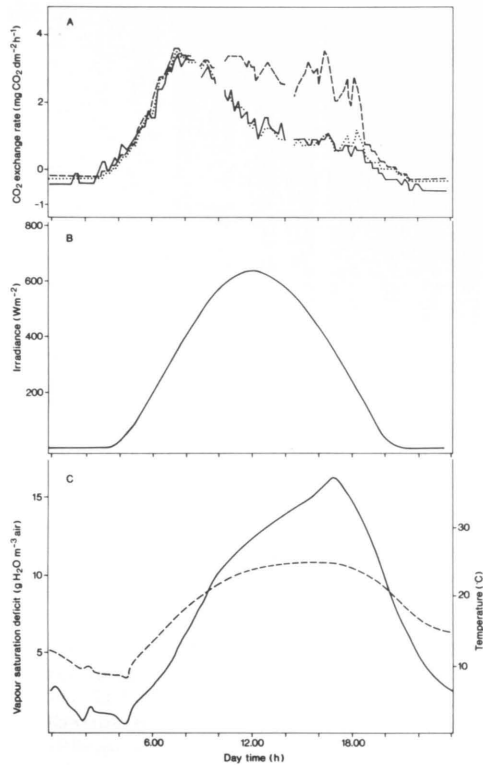


Figure 14. A. Measured rate of the CO_2 exchange (solid line), according to the Eqs. (4) and (16) predicted rate of the CO_2 exchange (broken line), and according to the Eqs. (5), (6) and (20) predicted rate of the CO_2 exchange (dotted line) on a clear day, i.e. on 16 July 1982. A decrease occurred in the CO_2 exchange rate when the ambient temperature exceeded $+20^\circ\text{C}$. B. Irradiance, C. temperature (broken line) and vapour saturation deficit (solid line) on 16 July 1982.

the late morning hours dependence on irradiance and temperature until the ambient temperature exceeded $+20^\circ\text{C}$. The stomatal regulation was not operational at temperatures below $+20^\circ\text{C}$; it was operational at temperatures above $+20^\circ\text{C}$. The water deficit increased in the dry period. The weather was somewhat cloudy on 24 July. The maximum temperature was $+19^\circ\text{C}$. A decrease in the rate of the CO_2 exchange

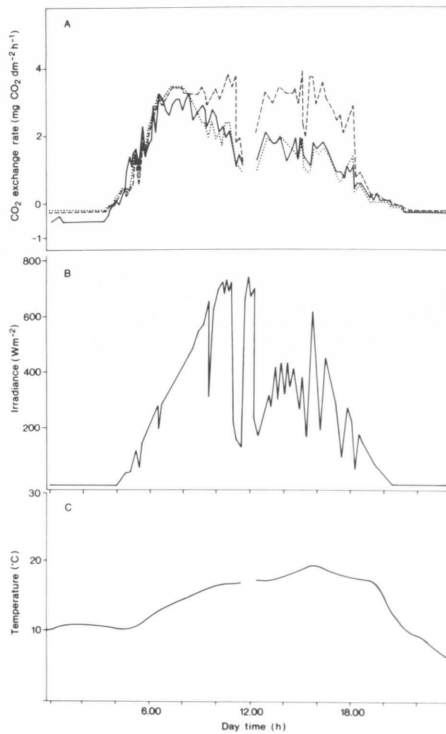


Figure 15. A. Measured rate of the CO_2 exchange (solid line), according to the Eqs. (4) and (16) predicted rate of the CO_2 exchange (broken line), and according to the Eqs. (5), (6) and (20) predicted rate of the CO_2 exchange (dotted line) on 24 July 1982, when the weather was somewhat cloudy. A decrease occurred in the CO_2 exchange rate when the ambient temperature exceeded about $+16^\circ\text{C}$. B. Irradiance and C. temperature on 24 July 1982. (Korpilahti and Hari 1988 b).

occurred when the ambient temperature rose to $+16^\circ\text{C}$ (Fig. 15). Late July and early August the CO_2 exchange decreased strongly from late morning until late evening. The CO_2 exchange decreased strongly for example on 1 August (Fig. 16). Only in the early morning did the rate of the photosynthesis follow the dependence on irradiance and temperature. The CO_2 exchange decreased when the ambient temperature rose above

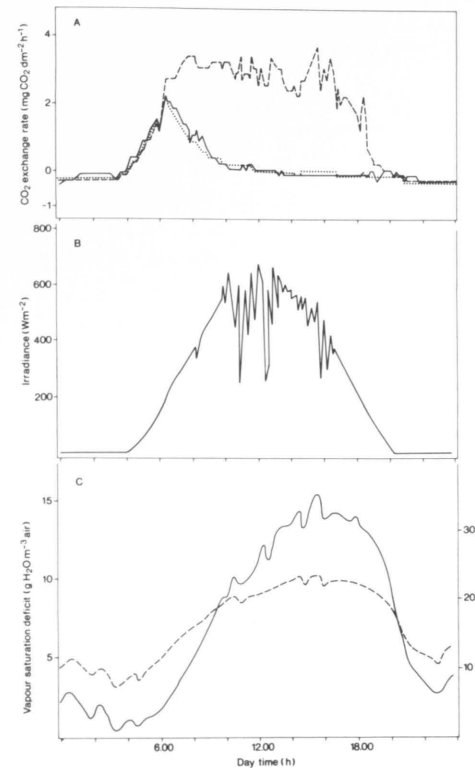


Figure 16. A. Measured rate of the CO_2 exchange (solid line), according to the Eqs. (4) and (16) predicted rate of the CO_2 exchange (broken line), and according to the Eqs. (5), (6) and (20) predicted rate of the CO_2 exchange (dotted line) on a warm and rather clear day, i.e. on 1 August 1982. A decrease occurred in the CO_2 exchange rate when the ambient temperature exceeded $+15^\circ\text{C}$. B. Irradiance, C. temperature (broken line) and water vapour saturation deficit (solid line) on 1 August 1982.

$+15^\circ\text{C}$. The rate of the CO_2 exchange decreased after this all day.

The regulation function, f_3 , of the model for the CO_2 exchange improved essentially the fitness of the predicted rate of the CO_2 exchange for the measured rate of the CO_2 exchange in the dry period. The decrease in the rate of the CO_2 exchange could be predicted by the model through the day in increasing water deficit conditions. The residu-

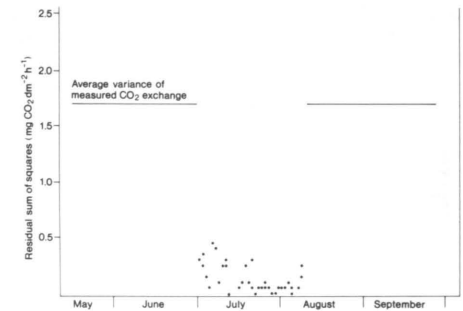


Figure 17. The residual sum of the squares of the model for the CO_2 exchange with the stomatal regulation (Eqs. 5, 6, 17, 18, 19, and 20) per day in July and in early August 1982. The mean of the variance of the measured rate of the CO_2 exchange excluding the dry period in June and early August.

al sum of the squares of the model was below 15 % of the mean of the variance of the measured rate of the CO_2 exchange, (excluding the measurements in the dry period), on most days in July and in the early August 1982 (Fig. 17). The variance of the measured rate of the CO_2 exchange was small in the dry period due to the decrease in the rate of the CO_2 exchange.

The estimated daily values of the internal state are presented in Fig. 18 for the period from 13 May to 10 September 1982. The daily values of the internal state could not be estimated on the days when the ambient temperature was not high enough to require the stomatal regulation. The daily values of the internal state could be estimated on 1 June, 2 June, 5 June and 6 June, and from 9 July to 8 August in 1982. The daily values of the internal state decreased in the dry period from 9 July to 8 August. The time development of the internal state was rather similar in each of the measured shoots. The decrease in the dry period was slightly stronger in the tree on the upper slope than in the tree on the lower slope. There were rainfalls on 6 August and on 9 August. Daily precipitation was 5.7 mm and 24.4 mm respectively. In August the monthly precipitation was 156 mm. The average precipitation measured for August at the Forestry Field Station from 1931 to 1960 is 79 mm. The water deficit was soon reco-

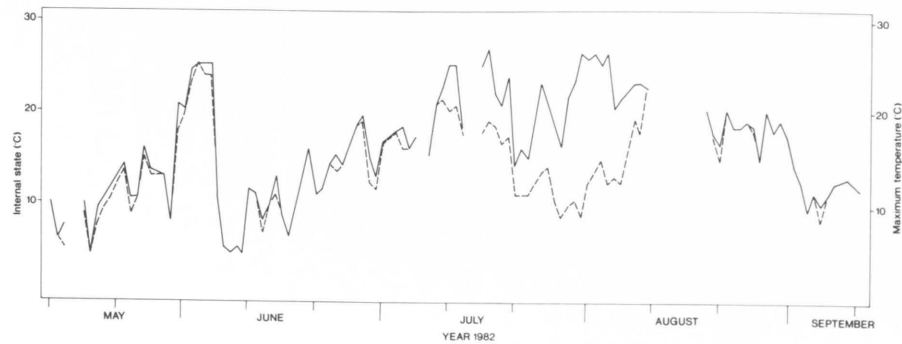


Figure 18. Estimated daily values of the internal state (broken line) and the daily maximum temperature (solid line) in 1982. Estimation of the internal state was not possible, if the ambient temperature was not high enough to call for the stomatal regulation. The internal state was possible to estimate confidently from the field data, if difference between the ambient temperature and the internal state was a few degrees, i.e. on 1 June, 2 June, 5 June, 6 June and from 9 July to 8 August (Korpilahti and Hari 1988 b).

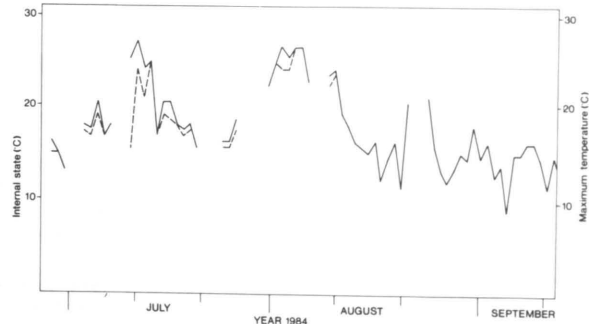


Figure 19. Estimated daily values of the internal state (broken line) and the daily maximum temperature (solid line) in 1984. The internal state was possible to estimate from 10 to 12 July, on 2 August and 3 August.

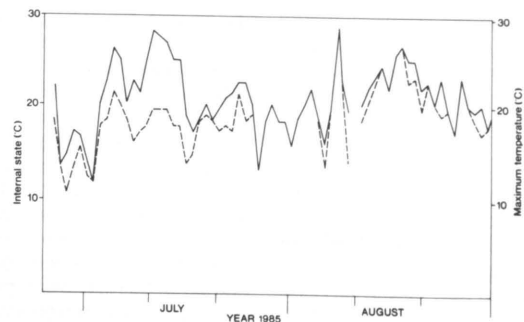


Figure 20. Estimated daily values of the internal state (broken line) and daily maximum temperature (solid line) in 1985. The internal state was possible to estimate on 28 June, 30 June, and from 4 July to 24 July.

vered by the rainfalls. The internal state could not be estimated after the rainfalls (Korpilahti and Hari 1988 b).

No decrease was observed in the rate of the CO_2 exchange in late August and September. The rate of the photosynthesis followed the dependence on irradiance and temperature as shown in Fig. 10.

The weather was cloudier and rainier in summer 1984 than in 1982. In June, the monthly precipitation was 96 mm, in July 129 mm and in August 31 mm. The daily value of the internal state was estimated from the measurements of the CO_2 exchange in the period from 28 June to 12 September (Fig. 19). The estimation of the internal state was possible on a few days, i. e. 10 to 12 July, 2 August and 3 August. The temperature was high enough to call for a regulation of the photosynthesis on a few warm days in July and in early August. The monthly precipitation indicated no water deficit in the soil. There was a slight decrease in the measured rate of the CO_2 exchange at midday and in the early afternoon of those days. The regulation of the photosynthesis seemed to operate also in the conditions where no water deficit was obvious in the soil, but the temperature of the air was high and there was a high deficit of the water vapour in the air.

The weather was rather sunny in June and July 1985. In June, the monthly precipitation was 44 mm, in July 55 mm and in August 80 mm. In June and July, the monthly precipitation was lower than the average precipitation over the years 1931 to 1960. In August it was close to the average precipitation. The daily values of the internal state were estimated for the period from 26 June to 31 August. The internal state was clearly discovered on 28 June, 30 June and 4 through 24 July (Fig. 20). The internal state showed a descending trend in the period from 4 July to 17 July. There was a decrease in the measured rate of the CO_2 exchange at midday and in the afternoon hours on those days.

The validity of the model for the CO_2 exchange with the regulation was studied by the data from the summers 1984 and 1985. The validity of the model seemed approximately the same in the summers of 1982, 1984 and 1985.

The regulation of the photosynthesis operated similarly in the different years and in

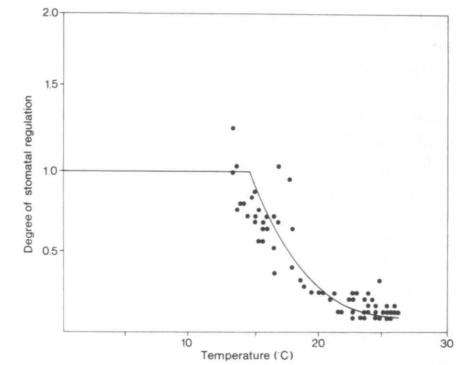


Figure 21. Degree of the stomatal regulation according to the Eq. (20) as function of the temperature on 1 August 1982 (solid line). The measured rate of the CO_2 exchange divided by the Eqs. (4) and (16) predicted rate of the CO_2 exchange (points) on 1 August 1982. (Korpilahti and Hari 1988 b).

the different shoots. A threshold temperature was discovered above which the stomatal regulation began to operate and below which the stomatal regulation of photosynthesis did not operate. The threshold temperature decreased with the soil water deficit and increased with rainfalls after the dry period. The degree of the stomatal regulation was dependent on the threshold temperature and on the ambient temperature. In a severe water deficit, the values of the degree of the stomatal regulation fell from 1.0 to 0.5 within a small increase in the ambient temperature. There was a severe water deficit on 1 August 1982, when the threshold temperature was $+15^\circ\text{C}$. The degree of regulation dropped from 1.0 to 0.5 when the ambient temperature increased by $+2.5^\circ\text{C}$ (Fig. 21).

4.2.2. Optimal control of the gas exchange

An optimization theory has been introduced as an instrument to study the control of the gas exchange in plants (Cowan 1977, Cowan and Farquhar 1977, Cowan 1982 and Hari et al. 1986). The approach is based on the assumption that the control of the gas

exchange operates to form the maximal amount of carbohydrates per unit of water transpired under the prevailing conditions.

The study by Hari et al. (1986) gives the mathematical formulation of the optimization problem. Photosynthetic carbon assimilation is handled as a two-step process: the diffusion of the atmospheric CO₂ into the intercellular space of the leaf and the biochemical process of carbon fixation. The inflow of carbon per unit leaf area is determined by the stomatal conductance, the intercellular concentration of CO₂ and the ambient concentration of CO₂. The rate of the photosynthetic carbon assimilation is proportional to the intercellular concentration of CO₂ in the leaf and it depends on irradiance. The dynamics of the intercellular concentration of carbon dioxide is described by the inflow of carbon dioxide and by the consumption of carbon dioxide in the assimilation of carbon. The flow of water vapour is determined by the ambient concentration of water vapour and by the intercellular concentration of water vapour and by the stomatal conductance. The primary regulation of the gas exchange is assumed to involve stomatal conductance. The stomatal conductance is determined by the conductance when the stomata are fully open and by a control signal which is termed the degree of the stomatal opening. The degree of the stomatal opening varies between 0 and 1. It is assumed that the movement of the stomata and the changes in the environmental factors are slow compared to the changes in the internal concentration of CO₂. The optimization problem yields the solution (Eq. 21, Hari et al. 1986), the optimal degree of the stomatal opening, denoted by u^* . The Equation (21) can be used only if $0 \leq u^* \leq 1$. Otherwise the solution equals either zero or unity corresponding to fully closed or fully open stomata.

$$(21) \quad u^* = \left(\sqrt{\frac{C_a}{\lambda B(c_e - c_a)}} - 1 \right) \frac{c(I)}{g_0}$$

where C_a denotes the ambient concentration of CO₂, c_a denotes the ambient concentration of water vapour, c_e the intercellular concentration of water vapour, g_0 the stomatal conductance when the stomata are fully open, $c(I)$ denotes the net rate of CO₂ assimilation per unit leaf area and per unit of carbon

dioxide concentration. The symbol B is a constant with the value of 1.6. The symbol λ is a parameter for the cost of transpiration, measured as the amount of carbon required per unit amount of water transpired.

The stomatal optimization hypothesis can be applied only to short intervals because of the diurnal rhythm of irradiance and temperature and the water content of the soil is required to be constant (Cowan 1982, Hari et al. 1986). The 24-hour period is analysed further. It is assumed that the water content of the soil and the concentration of water vapour in the air are constant in each optimization period. This allows the assumption that the cost of transpiration, λ , is constant in the optimization period. The optimal degree of stomatal opening depends on irradiance and on the intercellular concentration of water vapour in each optimization period. The intercellular concentration of water vapour is assumed to be saturated, which is determined by the temperature of the leaf. Thus, if the amount of water in the ambient air is constant, the difference between ambient and intercellular concentration of water vapour is determined by the temperature. Assuming that the temperature of the leaf is approximately the same as that of the air, the temperature of the air determines the difference in the concentration of water vapour between intercellular and ambient air spaces.

The optimal degree of stomatal opening has the value 1 close to the dew point temperature of the air. When the temperature rises from the dew point temperature, the intercellular concentration of water vapour increases and there is a threshold temperature at which the optimal degree of stomatal opening becomes smaller than the unity. The properties of the solution to the optimization problem are summarized in the following hypotheses (Hari et al. 1986). The hypotheses are formulated by using the threshold temperature and the response of the degree of the stomatal opening to temperature.

1. There is a threshold temperature above which the stomata begin to close.
2. The threshold temperature rises with an increasing partial pressure of the atmospheric water vapour.
3. The threshold temperature increases with increasing irradiance.

4. The threshold temperature decreases with an increasing soil water deficit.
5. The temperature range within which the optimal degree of the stomatal opening decreases from one to zero becomes narrower when the water deficit becomes more severe.
6. The optimal degree of the stomatal opening drops from 1.0 to 0.5 when there is a severe water deficit within 2.5 °C of the temperature increase. It is assumed that the dew point temperature of the air is +5 °C, the threshold temperature +15 °C, and irradiance does not limit the photosynthesis.

Due to the similarity of the previously applied model for the degree of stomatal regulation, f_3 (Eq. 20), and the optimal degree of the stomatal opening (Eq. 21), the above six hypotheses can be studied from the field data by analysing the estimated values of the internal state and the parameter k in the Eq. (20).

The daily values of the internal state decreased in the dry period of 1982 as presented earlier (Fig. 18). The pattern of the time development in the daily values of the internal state was rather similar in each of the measured shoots. The analysis of the field measurements of the CO₂ exchange supported the hypotheses 1 and 4.

The values of the internal state showed a descending trend with the increasing water deficit and there was a variation of the internal state around the descending trend (Fig. 18, 20). The water content of the air bulk and the ambient temperature determine the ambient deficit of water vapour. The water content of the air bulk changes slowly and it can be assumed to be constant during the day. The deviation of the internal state from the descending trend of the internal state showed a dependence on the dew point temperature of the day (Fig. 22). The same feature was observed in each measured shoot. Thus the behaviour deduced in the 2nd hypothesis was found in the field data.

The fitness of the predicted rate values of the CO₂ exchange to the measured rate values of the CO₂ exchange were studied by giving different values to the parameter k in the Eq. (20). The value of the parameter k ranged from 0.10 to 0.40. With a moderate water deficit, no clear difference could be observed in the fitness when the values of the parameter k were in the range of 0.20 and

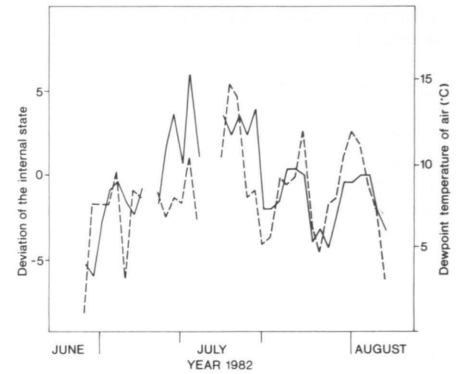


Figure 22. Dewpoint temperature of the air (solid line) and the deviation of the internal state around the decreasing trend in the dry period in July and at the beginning of August 1982. (Korpilähti and Hari 1988 b).

0.30. The fitness improved with a severe water deficit to the value of 0.30 for the parameter k . With a severe water deficit the value 0.30 gave the best fitness in each shoot. The value of the parameter k and the value of the internal state proved to be interrelated, which disturbed the estimation. Due to this interrelation it was not possible to estimate the best value for the parameter k with a moderate water deficit. With a moderate water deficit the model gave the best fitness to the field data in the range of 0.20 to 0.30 of the parameter k . The 5th hypothesis was not clearly detected from the field data, although some properties of the field data indicated support to the hypothesis.

The hypothesis that the threshold temperature depends on irradiance was studied by estimating the daily values of the internal state from two sets of data. The data was divided according to irradiance:

1. irradiance below 400 Wm⁻²
2. irradiance above 400 Wm⁻².

The results supported the hypothesis with a moderate water deficit. With a severe water deficit no dependence on the internal state was observed. When studying this hypothesis there were problems with the measuring

techniques and the analysis. The values for the degree of regulation are close to zero with a severe water deficit, when the irradiance is high. This disturbs the estimation of the internal state.

The water deficit was severe in Finnish weather conditions at the end of July and at the beginning of August in 1982. The 6th hypothesis was studied during that period. The degree of regulation fell from 1.0 to 0.5 with an increase of a few degrees in the temperature. The estimated value of the internal state was +15 °C on 1 August. The degree of regulation fell from 1.0 to 0.5 with an increase of 2.5 °C in the temperature. This feature was uniform with the result of the optimal degree of the stomatal opening. The field data supported the property deduced in the 6th hypothesis. With a severe water deficit the optimal degree of the stomatal opening and the degree of the regulation are uniform within a range of 1.0 to 0.3. Below 0.3 the optimal degree of the stomatal opening results in smaller values and drops to zero earlier than the degree of the stomatal regulation. The field data seemed to fit the degree of the stomatal regulation (Eq. 20) better than the optimal degree of the stomatal opening (Eq. 21) in a range below 0.3 (Fig. 18). The qualitative properties of the optimal degree of the stomatal opening are also presented in the study by Korpilahti and Hari (1988 b).

The solution to the optimization problem and the model used previously to study the CO₂ exchange in field conditions behave similarly. Both of them have a threshold temperature below which the water deficit has no effect on the gas exchange and above which the gas exchange gets strongly depressed.

4.3. The effect of the annual cycle on the rate of the photosynthesis

The range of the environmental factors changes during the year. Irradiance and temperature show a decreasing trend in autumn and an increasing trend in spring. Irradiance is low in winter and the temperature drops down to -20°C . . . -30 °C. Irradiance is high in summer and the temperature can

rise to +20 . . . +35°C. Seasonal variations of the rate of the photosynthesis are obvious in the Scots pine. The photosynthesis of the Scots pine is in principle exhausted in the winter. It recovers gradually in the spring to reach full activity. Autumn is a transition phase from summer activities to winter conditions. In winter the needles are exposed to extremely low temperatures.

The specific photosynthetic rate of Scots pine has appeared to recover gradually in the spring (Pelkonen 1980, and Linder and Troeng 1980). Long-term effects of the temperature have been observed in the specific photosynthetic rate in the spring time in addition to the direct effects of the temperature (Pelkonen and Hari 1980). On account of that, it is presumable that the specific photosynthetic rate ceases gradually in the autumn and the environment has long-term effects on the specific photosynthetic rate. Let us assume that the control process of the annual cycle works through a long-term impact of the environment on the photosynthesis. It changes the response of the rate of the photosynthesis to the environmental factors. The effect of the annual cycle on the photosynthesis is analysed with the state of the photosynthetic activity, $(S(t))$, (Eqs. 5 and 6). The state of the photosynthetic activity affects the rate of the photosynthesis to result in the gradual recovery of the rate of the photosynthesis in the spring. Early in spring, the state of the photosynthetic activity is low and the rate of the photosynthesis is strongly reduced in the prevailing environment compared to the respective conditions in full activity. The state of the photosynthetic activity reaches full activity (the summer state) in spring; after that the control effect on the rate of the photosynthesis is not operational. The state of the photosynthetic activity is determined by the function $f_4(S(t))$ in the Eqs. (5) and (6). The function $f_4(S(t))$ is determined as follows:

$$(22) \quad f_4(S(t)) = \begin{cases} S(t)/d_1 & \text{when } 0 \leq S(t) \leq d_1 \\ 1 & \text{when } S(t) > d_1 \end{cases}$$

where d_1 is a parameter.

Let us assume that the progress of the state of the photosynthetic activity depends on the temperature and on the state of the photo-

synthetic activity itself during an annual cycle. Then,

$$(23) \quad dS/dt = g_2(T(t), S(t))$$

where g_2 denotes a function. Pelkonen and Hari (1980), and Pelkonen (1981) have studied different types of models for the progress of the state of the photosynthetic activity in the spring. The following model has best fitted the field measurements of the Scots pine in spring.

$$(24) \quad g_2(T(t), S(t)) = \frac{100}{1+100d_2^{-(T(t)-(S(t))/d_3)}} - \frac{100}{1+100d_2^{(T(t)-(S(t))/d_3)}}$$

where d_2 and d_3 are parameters. The values of these parameters were $d_2=2$, $d_3=600$ and in the Eq. (22) $d_1 = 6500$.

The analysis was begun by studying the importance of the function $f_4(S(t))$ in the photosynthesis in autumn. P_i denotes the daily amount of photosynthesis per needle area and Y_i^p the integral of the product of f_1 , f_2 and f_4 during the i th day. Parameters determined in the first part of the summer were used for the functions f_1 and f_2 . The ratio P_i/Y_i^p measures the importance of the function f_4 in the analysis of the photosynthesis. To test the importance of the function f_4 , the ratio P_i/Y_i^p was calculated from the measurements of the CO₂ exchange, the temperature and the irradiance. The function f_4 was given the value 1.0 in autumn. The ratio was calculated in time periods, when the irradiance exceeded 80 Wm⁻². Late in autumn, in October and November, the irradiance did not exceed this limit on several days. The daytime becomes shorter in autumn and in the second part of October the daytime is less than 10 hours. The ratio P_i/Y_i^p varied around unity till mid-November 1982 and late October 1985 (Fig. 23). In result, the role of the state of the photosynthetic activity is of minimal importance in the autumn (Korpilahti 1988 a).

The Eqs. (22), (23) and (24) allow to determine the time development of the function $f_4(S(t))$ using the temperature measurements. The time development of the function f_4 differed from the ratio P_i/Y_i^p (Fig. 23). The model overestimated the effect of the annual

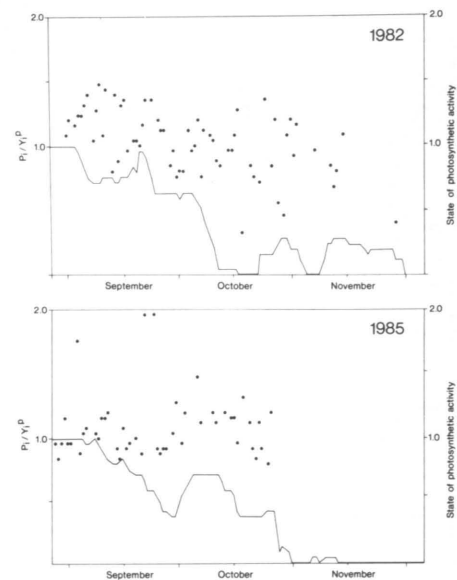


Figure 23. Time development of the daily values of the state of the photosynthetic activity (according to Eqs. 22, 23 and 24) in autumn 1982 and in autumn 1985 (solid line) and daily values of P_i/Y_i^p (points). (Korpilahti 1988 a).

cycle on the rate of the photosynthesis in autumn. Yet, the model has predicted the recovery of the rate of the photosynthesis in spring (Pelkonen and Hari 1980).

The rate of the CO₂ exchange was predicted from the temperature and irradiance measurements in autumn periods. In the model for the rate of the CO₂ exchange (Eq. 4) only the functions f_1 and f_2 were used for the photosynthetic rate and the values of the parameters were fixed at the beginning of summer. The rate of the CO₂ exchange was predictable on most days through the autumn, for example on 31 October 1982 (Fig. 24).

The photosynthesis ceased in autumn due to a decrease in irradiance, shorter day and a decrease in temperature. In central Finland cloudy weather stays on in autumn. The sun elevation becomes lower in autumn. The maximum sun elevation is below 26 degrees in October and below 16 degrees in

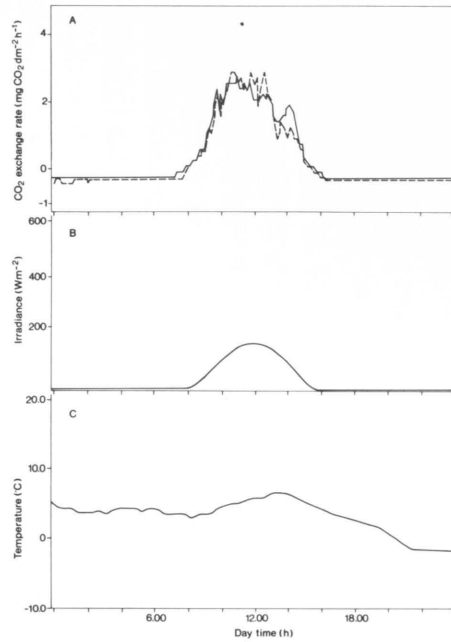


Figure 24. A. Measured rate of the CO₂ exchange (solid line) and, according to the Eqs. (4) and (16) predicted rate of the CO₂ exchange (broken line) on a clear day, i.e. on 31 October 1982. B. Irradiance and C. temperature on 31 October 1982. (Korpilahti 1988 a).

November. The irradiance remains under 200 Wm⁻² even when the sky is clear in October (Fig. 24) and under 120 Wm⁻² in November. Low irradiance therefore becomes dominant on late autumn days. The rate of the CO₂ exchange is then very low, as it was for example on 15 October in 1982 (Fig. 25).

There were some days when the predicted rate of the CO₂ exchange did not fit the measured rate of the CO₂ exchange. Those days were characterized by an extremely low temperature in the previous night. On such days the rate of the CO₂ exchange decreased and seemed to respond with a delay to an increase in the air temperature in the daytime. The CO₂ exchange ceased when the air temperature dropped below -5 °C.

Let us assume that there are two internal

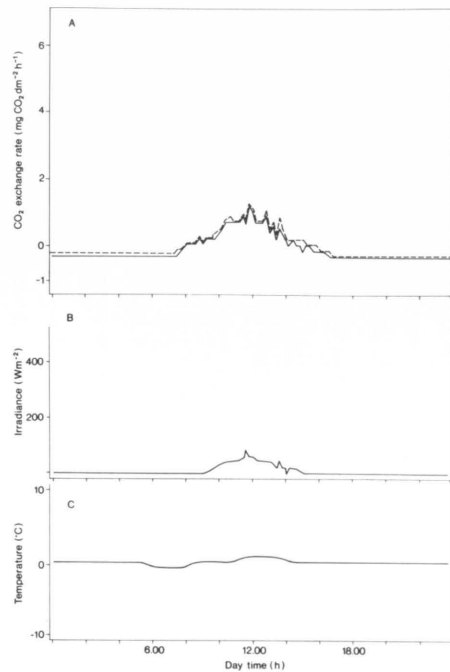


Figure 25. A. Measured rate of the CO₂ exchange (solid line) and, according to the Eqs. (4) and (16) predicted rate of the CO₂ exchange (broken line) on a cloudy day, i.e. on 15 October 1982. B. Irradiance and C. temperature on 15 October 1982. (Korpilahti 1988 a).

control processes of the photosynthesis associated with the effect of the annual cycle. The dominating process operates slowly in the winter period affecting the recovery of the photosynthesis in the spring. The second process operates in sudden cold periods inhibiting the photosynthesis. It is characterized by a rather rapid response to the cold and is analysed with the state of chilling, $f_3(\Gamma(t))$. The model for the rate of the photosynthesis is modified as follows:

$$(25) \quad f(x, t) = f_1(I(x, t)) f_2(T(t)) f_3(\Gamma(t))$$

Let us assume that the progress of the state of chilling depends on the difference of the air temperature and on the state of chilling as follows:

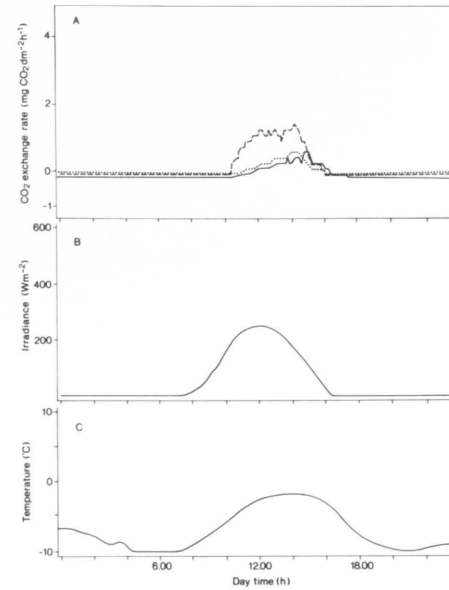


Figure 26. A. Measured rate of the CO₂ exchange (solid line), according to the Eqs. (4) and (16) predicted rate of the CO₂ exchange (broken line), and according to the Eqs. (5) and (25) predicted rate of the CO₂ exchange (dotted line) on 19 October 1982. B. Irradiance and C. temperature on 19 October 1982. (Korpilahti 1988 a).

$$(26) \quad d\Gamma/dt = m_1 (T - \Gamma)$$

where Γ denotes the state of chilling, T is the air temperature and m_1 is a parameter. The state of chilling is approximated by the following expression:

$$(27) \quad \Gamma(t) = \Gamma(t_0) + m_1 \sum_{i=0}^{t/\Delta t} (T_i - \Gamma_i) \Delta t$$

where T_i is the i :th measurement of temperature and Γ_i is respectively the state of chilling, t_0 is the initial moment, i runs from the initial moment to the moment denoted by t with the time step Δt .

If the increase in the air temperature is a transient increase to a constant temperature, T , then the equation (26) can be solved:

$$(28) \quad \Gamma(t) = (\Gamma_0 - T) \exp(-m_1 t) + T$$

where Γ_0 denotes the state of chilling at the initial moment and t denotes the time from the initial moment of the temperature input and m_1 is a parameter. The factor $1/m_1$ is the time constant of the system and it was given the value of 4 hours.

The dependence of the rate of the photosynthesis on the state of chilling, $f_3(\Gamma(t))$, was quite similar to the f_2 . The function f_3 was determined as follows:

$$(29) \quad f_3(\Gamma(t)) = \begin{cases} 0 & \text{if } \Gamma \leq a_2 \\ 1 - \exp(-a_1(\Gamma(t) - a_2)) & \text{if } \Gamma > a_2 \end{cases}$$

where a_1 and a_2 are parameters with values equal to the Eq.(18), $a_1 = 0.32$ and $a_2 = -5^\circ\text{C}$. The function f_3 was given the value of unity, if $\Gamma \geq T$.

The rate of the photosynthesis was calculated using the Eq. (25) and irradiance and temperature measurements. The predicted rate of the CO₂ exchange was consistent with the measured rate of the CO₂ exchange during the days following a low night temperature, for example on 19 October in 1982 (Fig. 26). The diurnal pattern of the state of chilling and the air temperature is shown in Fig. (27) for 19 October 1982. The state of chilling conformed with a delay to the increase in the air temperature (Fig. 27). The effect of the state of chilling was observed in late autumn on few days when the air temperature dropped in the preceding night to -10 °C. The rate of the photosynthesis was again predictable by the model with the functions f_1 and f_2 on a few days following such cold spells if the temperature rose and the irradiance was high enough, like on 22 October 1982 (Fig. 28). The control processes of the photosynthesis seemed to respond in a shorter time to the environment in autumn than in spring (Korpilahti 1988 a).

The CO₂ exchange was also observable on a few days in November 1982. The diurnal course of the predicted rate of the CO₂ exchange followed the diurnal course of the measured rate of the CO₂ exchange in November, for example on 12 November 1982 (Fig. 29). The rate of the CO₂ exchange was predicted using the functions f_1 and f_2 in the model for the gas exchange, irradiance and temperature measurements.

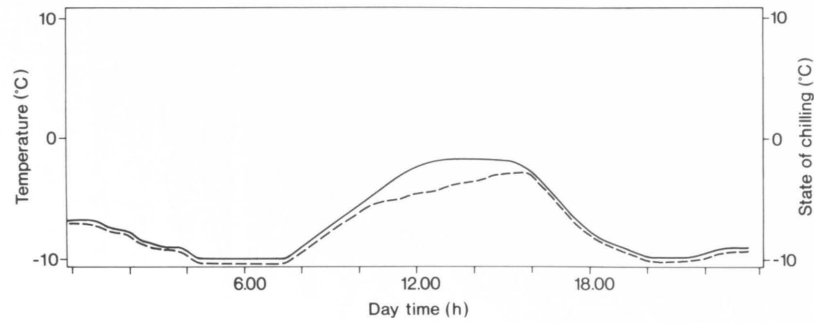


Figure 27. Temperature (solid line) and the state of chilling according to the Eq. (27) (broken line) on 19 October 1982. (Korpilahti 1988 a).

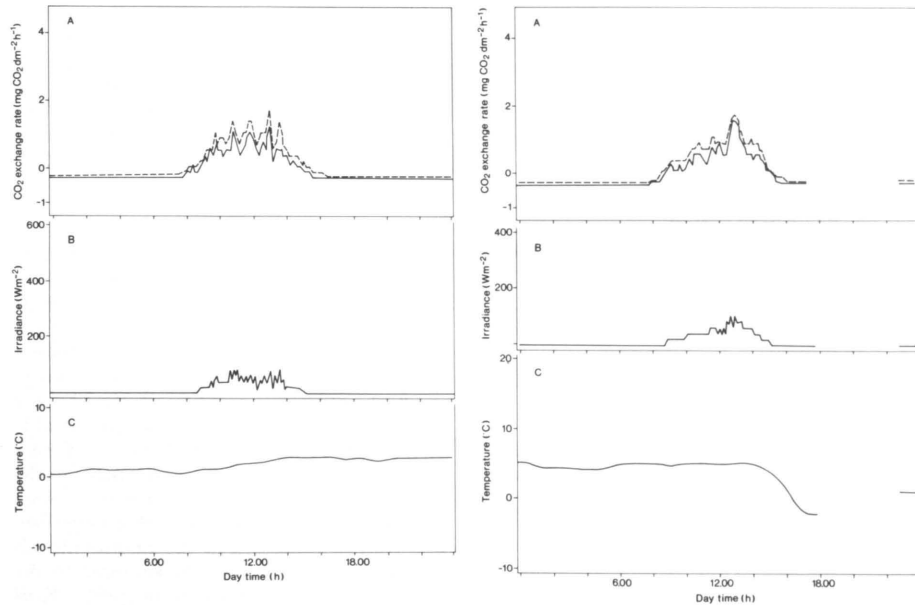


Figure 28. A. Measured rate of the CO_2 exchange (solid line) and, according to the Eqs. (4) and (16), predicted rate of the CO_2 exchange (broken line) on 22 October 1982. The weather had turned cloudy and warmer after the cold period. B. Irradiance and C. temperature on 22 October 1982.

Figure 29. A. Measured rate of the CO_2 exchange (solid line) and, according to the Eqs. (4) and (16), predicted rate of the CO_2 exchange (broken line) on 12 November 1982. The weather had remained cloudy and rather mild in a two-week period. B. Irradiance and C. temperature on 12 November 1982.

5. INTERACTIONS OF TRANSPIRATION AND WATER CONDITIONS

5.1. The water regime in a pine stand

A model of the dynamic soil-plant-atmosphere system was developed to estimate the soil water conditions. The movement of the water in the soil-plant-atmosphere system was described as the mass flow of water. The schematic representation of the model is given in Fig. 30. The throughfall part of the precipitation is the source of soil water. The soil water is a reservoir with a limited capaci-

ty and a source for the transpiration flow from the plants into the atmosphere. The intercepted water is the source of the evaporation flow. The soil profile was assumed homogeneous. The water movement in the soil and the spatial variation of soil moisture were not treated in this study.

The stand was assumed horizontally homogeneous. Variables are therefore treated in the stand as a function of height. The precipitation rate is divided into two parts,

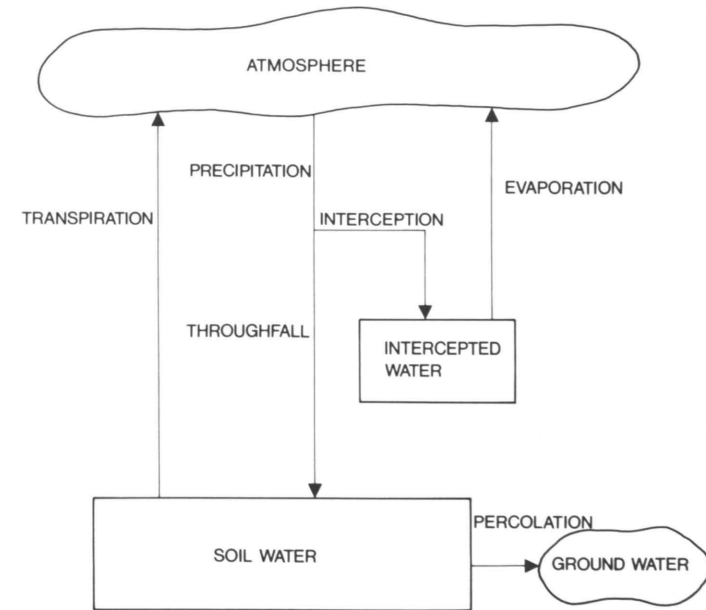


Figure 30. Mass flow of water in the model for the water regime in a pine stand. From the beginning of a rainfall water is intercepted by needles according to the interception rate. The throughfall rate is determined by the precipitation rate and the interception rate. After the rainfall the intercepted water is evaporated first and transpiration begins when the needles become dry of intercepted water. (Korpilahti 1988 b).

the throughfall rate and the interception rate. The height in the stand is denoted by z , the interception rate by $i(z,t)$, the precipitation rate by $s_0(t)$, and the throughfall rate by $s_t(z,t)$. The throughfall rate at the height of z is obtained

$$(30) \quad s_t(z,t) = s_0(t) - \int_z^{z_{\max}} i(z,t) dz$$

The density of the needle area at the height of z is denoted by $q(z)$, the amount of water intercepted per unit of the needle area in the canopy at the height of z by $R_a(z,t)$, and the maximum interception per unit of the needle area by R_{\max} . The interception rate is in the stand at the height of z

$$(31) \quad i(z,t) = \begin{cases} 0 & \text{if } R_a(z,t) \geq R_{\max} \\ A \frac{R_{\max} - R_a(z,t)}{R_{\max}} s_t(z,t) q(z) & \text{if } R_a(z,t) < R_{\max} \end{cases}$$

where A is a parameter. The value of the parameter A was 1.0 m^{-2} .

The maximum interception was determined empirically as the maximum amount of water held per unit area of needles for a branch of Scots pine. The value of R_{\max} was 1.0 g dm^{-2} .

The intercepted water per unit needle area during a time interval, $t_0 - t_1$, in the canopy at the height of z from the beginning of rain, t_0 , is (cf. Massman 1983)

$$(32) \quad R_a(z,t) = \int_{t_0}^t i(z,t) dt$$

The needle temperature was assumed to equal the air temperature (Gates 1980). The intercellular concentration of water vapour is considered saturated (Gaastra 1959). The specific transpiration rate Eq. (7) can be written as a function of the saturation pressure deficit of water vapour in the air, i.e.

$$(33) \quad h(x,t) = h_1(D(z,t)) f_3(W(t),T(t))$$

After the rainfall the intercepted water evaporates from the surface of the vegetation into the atmosphere. The specific evaporation rate of the intercepted water, $e(z,t)$, was defined as a function of the saturation pressure deficit of water vapour as follows:

$$(34) \quad e(z,t) = h_2(D(z,t))$$

$$(35) \quad h_2(D(z,t)) = e_1 D(z,t)$$

where e_1 is an empirically determined parameter. It was given the value $e_1 = 5.56 \text{ cm s}^{-1}$. Evaporation operated in the model, if there was water on the needles, whereas transpiration operated if the needles were dry.

The saturation pressure deficit in the air has a vertical gradient within the stand. The saturation pressure deficit was defined within the canopy as a function of the saturation pressure deficit on the top level of the canopy. The saturation pressure deficit at the top level of the canopy is denoted by D_0 . The saturation pressure deficit is at the height of z

$$(36) \quad D(z,t) = (l_1 + l_2 z) D_0(t)$$

The symbols l_1 and l_2 are parameters. The equation (36) was determined by Piche evaporimeters. The values of the parameters were in the studied pine stand $l_1 = 0.451$ and $l_2 = 0.084$.

The amount of transpiration of the canopy during the time interval (t_1, t_2), (H_c), is obtained by the integral of the specific transpiration rate and the density of the needle area. The amount of transpiration of the canopy is

$$(37) \quad H_c(t_1, t_2) = \int_{t_1}^{t_2} \int_z^{z_{\max}} q(z) h_1(D(z,t)) f_3(W(t), T(t)) dz dt$$

Determination of the functions in the Eq. (37) allows to determine the integral.

Let us assume that, after the snow has melted in the spring, there is a water reservoir in the soil. The amount of soil water, $M(t)$, at the time instant t can be obtained by integrating the throughfall rate over the time interval, the transpiration rate and the density of the needle area over the canopy height and time, and the percolation rate over time.

$$(38) \quad M(t) = M(t_1) + \int_{t_1}^{t_2} s_t(t) dt -$$

$$\int_{t_1}^{t_2} \int_z^{z_{\max}} q(z) h_1(D(z,t)) f_3(W(t), T(t)) dz dt - \int_{t_1}^{t_2} q(t) dt$$

where $M(t_1)$ denotes the water reservoir in the soil at the beginning instant t_1 , s_t denotes the throughfall rate to soil and q stands for the percolation rate.

The components of the Eq. (37) had to be determined. The specific transpiration rate was defined by Eq. (33). The dependence of the specific transpiration rate on the saturation pressure deficit in the air was determined when the stomatal regulation was not operating. The assumptions of the needle temperature and saturation of the intercellular content of water vapour are retained. Let us assume

$$(39) \quad h_1(D(x,t)) = e_2 D(x,t)$$

where e_2 is a parameter.

$q(x)$ denotes the density of the needle area in a canopy of a tree and V_t the volume of a tree canopy. The amount of needles in a canopy of a tree, N , is obtained from

$$(40) \quad N = \int V_t q(x) dV$$

The transpiration rate of a tree, $h_t(t)$, at a moment t is obtained

$$(41) \quad h_t(t) = e_2 \int V_t q(x) D(x,t) dV$$

$H_t(t_1, t_2)$ denotes the amount of water transpired by a tree during the interval (t_1, t_2). Then

$$(42) \quad H_t(t_1, t_2) = \int_{t_1}^{t_2} h_t(t) dt = e_2 \int_{t_1}^{t_2} \int V_t q(x) D(x,t) dV dt$$

Let us consider a situation in which the saturation pressure deficit is not dependent on x . This is achieved for example when potted seedlings are grown in an open place or at the top level of a canopy. Then $D(x,t) = D(x_0,t)$, where x_0 is a point within the crown of a

seedling. Now Eq. (42) is simplified as follows:

$$(43) \quad H_t(t_1, t_2) = e_2 \int_{t_1}^{t_2} D(x_0,t) \int V_t q(x) dV dt = e_2 \int_{t_1}^{t_2} D(x_0,t) dt N$$

The Eq. (43) allowed us to determine the parameter e_2 empirically. The value of the parameter e_2 was 0.24 cm s^{-1} .

The function f_3 described the stomatal regulation in the photosynthesis. The stomatal regulation in the transpiration, function f_3 , was determined by the Eq. (20).

5.2. Simulation of transpiration and soil water

The water regime was simulated in 1982 by the model Eq. (38) for the pine stand in which the measurements of the gas exchange were made. The needle area was 5.8 m^2 (needle) m^{-2} (ground). The simulated transpiration varied up to 7.8 mm per day. The potential transpiration was simulated with the assumption that the stomatal regulation was not operating. The simulated potential transpiration varied up to 10.9 mm per day. The daily transpiration was quite close to the potential transpiration on those days when transpiration remained low and in late summer (Fig. 31). The transpiration was lower than the potential transpiration on days when the potential transpiration was high. The potential transpiration was high in the warm and dry period in July and in the early part of August. Transpiration was clearly lower than the potential transpiration in that dry period.

In the period from 12 May to 9 September the cumulative transpiration was 340 mm, whereas the cumulative potential transpiration was 509 mm (Fig. 32). In the same period precipitation was 259 mm. The cumulative potential transpiration was about twice the amount of precipitation, whereas the cumulative transpiration was 31 % higher than precipitation. The slope of the

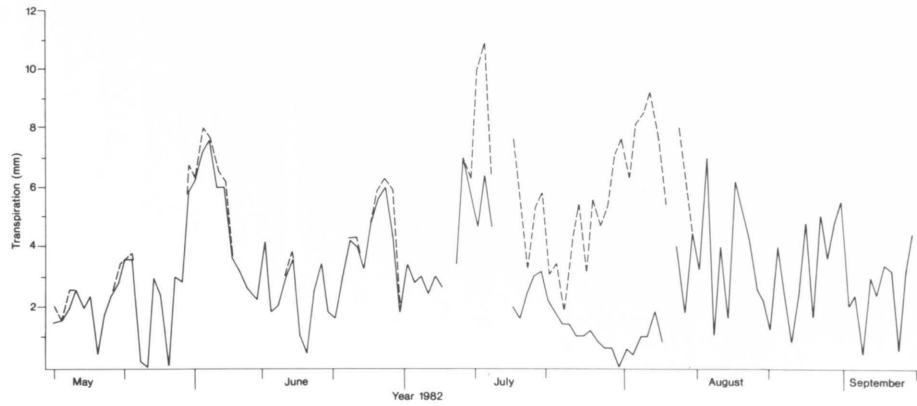


Figure 31. Daily amounts of simulated transpiration from a pine stand with the stomatal regulation (solid line) and daily amounts of potential transpiration simulated without the stomatal regulation (broken line) in summer 1982. (Korpilahti 1988 b).

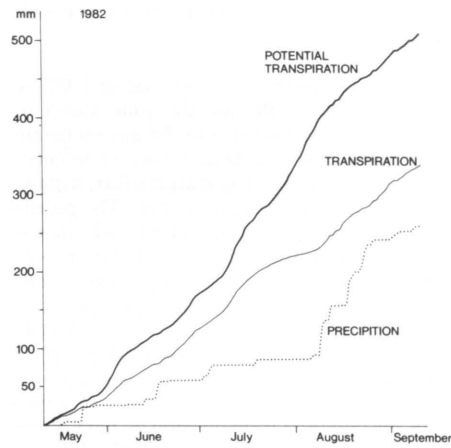


Figure 32. Time development of the cumulative potential transpiration (thick line), the cumulative transpiration with the stomatal regulation from a pine stand (thin line), and the cumulative precipitation (dotted line) in 1982. (Korpilahti 1988 b).

cumulative potential transpiration and the cumulative transpiration differed clearly in the dry period. At other times the slopes of the cumulative potential transpiration and the cumulative transpiration were parallel.

The amount of soil water was simulated for the tree on the upper slope and for the tree on the lower slope. The average soil depth was 0.5 m on the upper slope and 0.7 m on the lower slope. The depth of the soil was surveyed around both sample trees on a square of 36 m². The trees were situated in the center of the square. The content of the soil water was assumed to equal the field capacity at the beginning of the simulation period. Figures 33 and 34 illustrate the time development of the simulated soil water in both areas from 12 May to 10 September 1982. Soil water decreased in May, June and July in both areas. Simulation results of soil water without the stomatal regulation and with the stomatal regulation showed the extent of the stomatal regulation in the content of water in the soil. The reservoirs of soil water were exhausted without the stomatal regulation of the gas exchange in mid-July on the upper slope and at the end of July on the lower slope. The model with the stomatal regulation of the gas exchange produced a decrease in the soil water down to 100 mm at the beginning of August. The measurements of the gas exchange showed a deep decrease at that time. Yellowing of the older needles started in July. The water reservoirs were also exhausted on the upper slope in the simulations of the model with the stomatal regulation of the gas exchange. The tree on the upper slope obvi-

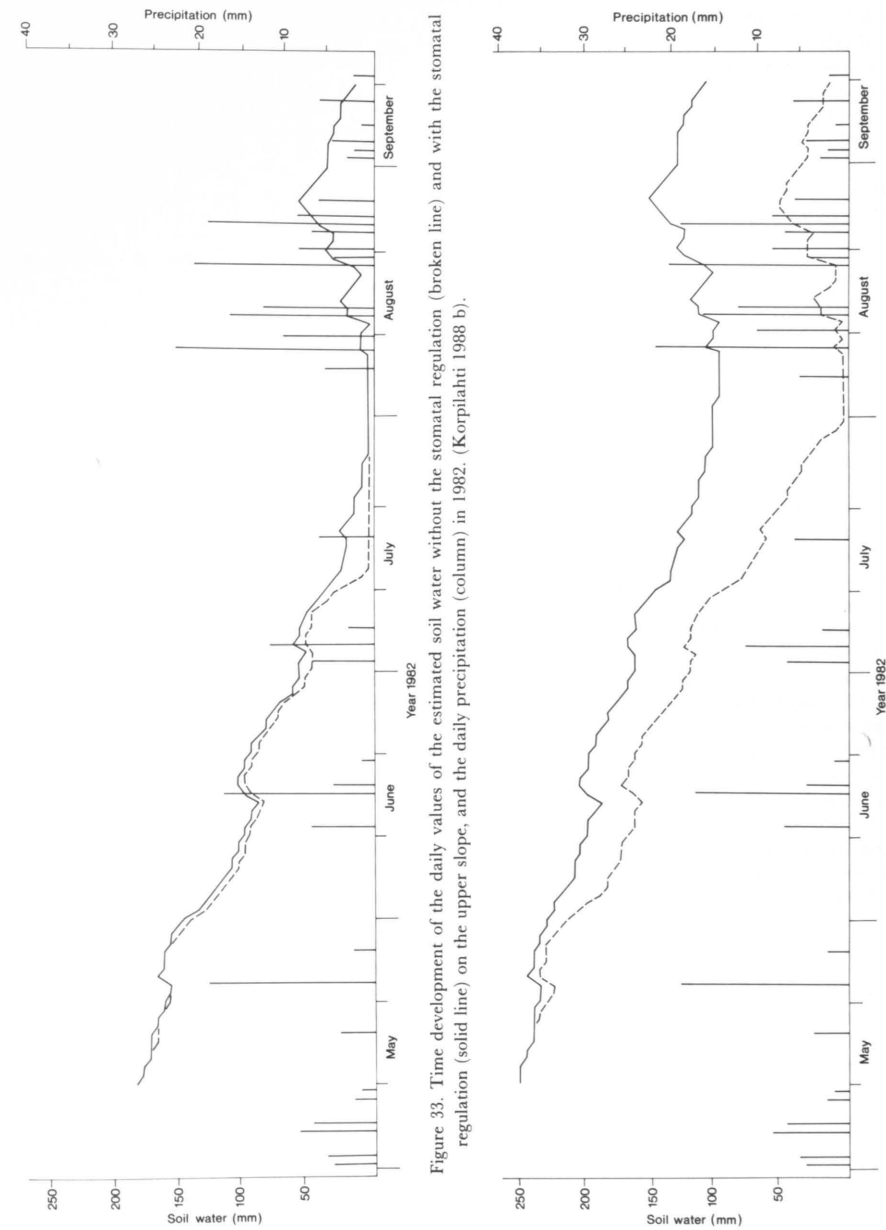


Figure 33. Time development of the daily values of the estimated soil water without the stomatal regulation (broken line) and with the stomatal regulation (solid line) on the upper slope, and the daily precipitation (column) in 1982. (Korpilahti 1988 b).

Figure 34. Time development of the daily values of the estimated soil water without the stomatal regulation (broken line) and with the stomatal regulation (solid line) on the lower slope, and the daily precipitation (column) in 1982. (Korpilahti 1988 b).

ously had a source of water, which could not be evaluated in this study. The initial reservoir of soil water is also difficult to evaluate.

The weather turned rainier in August. The amount of soil water increased with the rainfalls. Transpiration and soil water conditions of the pine stand are reported and discussed in greater detail in another paper by Korpilahti (1988 b).

5.3. Dependence of the internal state on the soil water conditions

The internal state values estimated from the measurements of the CO_2 exchange were plotted against the simulated amounts of soil water. The internal state was possible to estimate on some days in early June, when the temperature and the saturation deficit of water vapour in the air was high, i.e. on 1 June. Simulated amounts of soil water were rather close to the initial amount of the soil water on those days. No dependence of the internal state on the soil water was found in the range of the soil water above 200 mm. Estimation of the internal state was not possible in a certain quantity range of soil water (from 200 mm to 150 mm). The ambient temperature was not high enough to provoke the stomatal regulation to operate. The internal state was possible to estimate in a range of clearly decreased amounts of soil water. A linear dependence of the internal state on the amount of soil water was discovered with a water

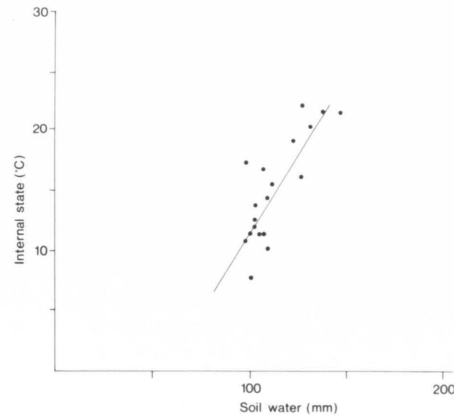


Figure 35. The daily values of the internal state as a function of the estimated soil water with a water deficit in the soil at the lower slope. (Korpilahti 1988 b).

deficit in the soil (Fig. 35). Determination of the relation of the internal state and the soil water allows to derive the internal state and further the stomatal regulation from the soil water conditions. The Eq. (8) can be determined by this relationship. The dependence of the internal state on the soil water allows the prediction of the stomatal regulation in the gas exchange with a feedback function from the soil water. The dependence links together the mean concentration of water in the soil, the transpiration rate and the rate of the photosynthesis (Korpilahti 1988 b).

6. WEATHER-INDUCED VARIATION IN THE ENVIRONMENT

6.1. The environment of plants

The sun sends the high-energy quanta of radiation which are essential for the formation of molecules in the primary production. All solar radiation absorbed by the earth's surface not utilized in the photochemical processes of photosynthesis is converted into heat. The radiation absorbed by the earth's surface is eventually returned into space as heat. The electromagnetic radiation of the sun warms the earth. The atmosphere screens off the ultraviolet radiation from the sun and shields the earth's surface from a heat loss into space.

Plants are rooted in their environment. They are coupled to the physical environment by the flow of energy, the gas exchange, the water and the nutrients. The coupling of the plants to the physical environment depends on the permeability of the organism's surface, on the concentration of the compound in the interior of the organism, and on the concentration of the compound in the environment.

The physical environment of the plants is implicated by the geometrical relations of the location on the earth's surface, the sun and the atmospheric conditions. These impose the climatic tolerance on the physical environment. Weather induces variations in the physical environment, which change from one moment to another. The weather factors are the solar radiation (cloudiness), the temperature, the content of water vapour in the air, the rain and the wind. These factors change the physical environment of plants and influence the physical environment simultaneously.

Two components of the variation in the physical environment can be detected, i.e. a spatial variation and a temporal variation. The range of both the spatial and the temporal variation is the environmental factor specific. Monitoring of the environmental factors in a fixed place provides data for an analysis of the temporal variation. Weather

data was used to analyse the temporal variation of the environmental factors over a long period.

6.2. Solar radiation

The earth travels in an elliptical orbit around the sun, while spinning about its polar axis. The distance of the earth from the sun varies with the time of the year. The amount of solar radiation incident on a point just outside the atmosphere is a function of the time of the year, the time of the day, and the latitude. The earth's atmosphere attenuates the solar radiation passing to the surface of the earth. The amount of solar radiation incident on a point on the earth's surface depends on the atmospheric conditions in addition to the geometrical relations of the sun and the earth. The atmospheric factors involved are the extinction of the solar radiation in clear sky conditions, the content of water and dust in the atmosphere. The extinction of solar radiation in clear sky conditions depends on the water and dust content of the atmosphere and on the elevation above the sea level. A flux of solar radiation passing across the surface of the earth is termed irradiance (Gates 1980).

The altitude of the sun and the atmospheric conditions cause a variation in incident irradiance on the top of the canopy. The variation of incident irradiance is caused also by the cloud cover. The distribution of clouds, thickness of clouds and movement of clouds affect the irradiance. The crown structure and the movement of the branches and stems introduce an additional variation in the irradiance within the canopy.

When traversing through the atmosphere, part of the electromagnetic radiation is scattered and absorbed. The absorbed photons are either emitted in photons of changed energy or the energy of photons is stored in the internal energy of the atmosphere. The non-scattered

part of the electromagnetic radiation gets attenuated while traversing through the atmosphere. The total incoming radiation is divided into direct solar radiation and diffuse sky radiation. The direct solar radiation consists of the transmitted unscattered part of the radiation. The diffuse sky radiation consists of the scattered part of the radiation that reaches the surface of the earth from all directions of the hemisphere. The incident total irradiance (I_t) was determined in clear sky conditions by means of the direct solar irradiance (I_r) and the diffuse sky irradiance (I_d) (Eq. 44).

$$(44) \quad I_t(t) = I_r(t) + I_d(t)$$

The attenuation of the direct solar radiation in the atmosphere is dependent on the optical thickness of the absorbing material and on the path length of the solar beam characterized by the air mass (m). The attenuation of the direct solar radiation is spectrum-selective. The fraction of the direct solar beam of the monochromatic radiation reaching the ground is expressed by Beer's law (Gates 1980). Derived from Beer's law the fraction of the direct solar irradiance reaching the ground is also expressed by the solar constant (S_0) and the mean transmittance of the atmosphere (τ^m) averaged over the solar spectrum wave lengths (Gates 1980).

The incident direct solar irradiance received on a horizontal surface was determined by the Eq. (45) (Gates 1980 and Ross 1981)

$$(45) \quad I_r(t) = S_0(\sin \Omega \sin \delta + \cos \Omega \cos \delta \cos \Phi) \tau^m,$$

where S_0 is the solar constant at the mean distance from the sun (1360 Wm^{-2}), the symbol Ω denotes the latitude of the observer, δ denotes the declination of the sun, Φ denotes the hour angle of the sun, τ^m denotes the mean transmittance of the atmosphere (cf. Spitters et al. 1986), m denotes the air mass. The air mass, m , is approximated by $m \approx 1/\cos \gamma$ plus a refraction correction for long slant paths through the atmosphere. γ denotes the zenith angle of the sun. The declination of the sun is an angular distance of the sun north or south of the equatorial plane. Declination is a function of a day of the year.

The hour angle is the angle through which the earth must turn to bring the meridian of the observer directly under the sun. The hour angle is a function of the time of the day. Spherical trigonometry gives the following relationships among the angles for the solar altitude, β , as seen from the observer (Gates 1980).

$$(46) \quad \sin \beta = \sin \Omega \sin \delta + \cos \Omega \cos \delta \cos \Phi$$

The values of the direct solar transmittance vary considerably with the geographical location. The transmittance of the direct solar radiance was estimated from the monitored total irradiance and diffuse sky irradiance at the Forestry Field Station in clear sky conditions. The direct solar transmittance at the direction of the zenith was given the value $\tau = 0.715$.

Air molecules, dust and pollution particles scatter the solar irradiance in the atmosphere. Scattering increases with decreasing wave lengths. A pure molecular sky without dust particles is known as Rayleigh scattering and gives the sky its blue colour. The blue wave lengths of solar radiance are scattered more strongly than the red wave lengths. In the dusty and cloudy sky, scattering also occurs in larger particles known as Mie scattering giving the sky a whitish appearance. The spectrum of the scattered radiation in larger particles is nearly the spectrum of the direct radiance. The irradiance of the incident diffuse sky radiation depends on the solar elevation. In clear sky conditions, the sky is brightest in a small region near the sun and darkest in a zone approximately 90° from the sun in the plane of the sun and the observer. The sky just above the horizon is brighter than the regions higher up in the sky, except for the regions near the sun.

The incident diffuse sky irradiance under clear sky conditions was determined as an integral over the hemisphere by the Eq. (47) (Ducray 1975)

$$(47) \quad I_d(t) = \mu \int_0^{2\pi} \int_0^{\pi/2} I_r(\beta) L_r(\beta, \alpha, \Theta) \sin \Theta \cos \Theta d\Theta d\Phi$$

where I_z denotes the irradiance at the zenith as the function of the sun altitude (β), L_r

denotes the relative luminance of the sky at the line of sight, Θ denotes the elevation angle of the line of sight, φ denotes the azimuth angle of the line of sight, β denotes the altitude angle of the sun, α denotes the angle between the sun and the line of sight and μ is the local empirical constant. The irradiance at the zenith (I_z) was calculated using the formula presented by Ducray (1975). The relative luminance at the line of sight over the hemisphere was calculated according to the standardized distribution of luminance in clear sky conditions (C.I.E. 1973 according to Ducray 1975). The formula presented by Ducray systematically produced higher values for the diffuse sky irradiance than the values of the diffuse sky irradiance measured at the Forestry Field Station. The empirical constant was applied to the Eq. (47) for modification in local conditions. The value used for the empirical constant was $\mu = 0.59$. Clear sky conditions during a whole day are quite seldom in Finnish weather in summer. The estimated values of the direct solar irradiance and diffuse sky irradiance were consistent with the measured values in really clear sky conditions. The diurnal course of the estimated irradiance followed the measured values, but the level of the measured values was quite sensitive to the brightness of the sky (Fig. 36).

The irradiance of the diffuse sky radiation is different in the presence of clouds compared to cloudless conditions. The irradiance of the diffuse sky radiation depends on the amount of clouds, the thickness of the clouds, and the distribution of the clouds in the sky. When the sky is heavily overcast, the irradiance of the diffuse sky radiation is low. The irradiance of the diffuse sky radiation is high, when there is a thin deck of clouds in the sky. Clouds affect the irradiance of the direct solar radiation whether the direction of the sun is covered with clouds or not. The attenuation of the direct solar radiance depends on the transmittance of the clouds in the direction of the sun.

The monthly averages of the diurnal courses of the total irradiance in clear sky conditions were calculated from the estimated total irradiance (Eqs. 44, 45 and 47) at the Jokioinen Observatory. The irradiance in clear sky conditions was highest in June and declined in August due to the elevation of the

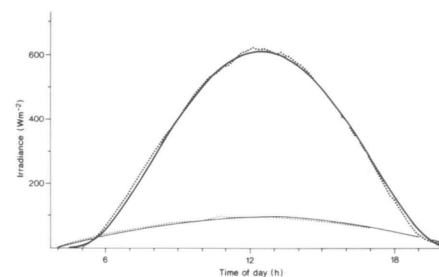


Figure 36. Measured direct solar radiation (thick dotted line), estimated direct solar radiation according to the Eq. (45) (thick solid line) in clear sky conditions at the Forestry Field Station on 1 August 1984. Measured diffuse sky radiation (thin dotted line) and estimated diffuse sky radiation according to the Eq. (47) (thin solid line) in clear sky conditions at the Forestry Field Station on 1 August 1984. (Korpilahti and Hari 1988 c).

sun (Fig. 37). The monthly averages of the total irradiance monitored at the Jokioinen Observatory over the years 1958–1977 were calculated respectively. The diurnal course of the monthly averages of the monitored total irradiance was lower compared to the averages in the clear sky conditions (Fig. 37). The differences between the diurnal courses of the averaged irradiance indicate the mean reduction of cloud cover to incident irradiance. The reduction of irradiance due to cloud cover seemed to be slightly stronger in the afternoon than in the late morning hours.

The frequency distribution of irradiance was established for June, July and August in the years 1958–1977. The irradiance values were classified in classes of 25 Wm^{-2} . The average frequency distributions over the years 1958–1977 were similar in form in June, July and August (Fig. 38). The distributions reached the maximum in the irradiance class 0 Wm^{-2} . A strongly positive skewness was characteristic of the distributions. The frequencies decreased towards the higher irradiance classes but a small maximum appeared in the high irradiance classes. The maximum frequency at high irradiance was in the range of the maximum irradiance val-

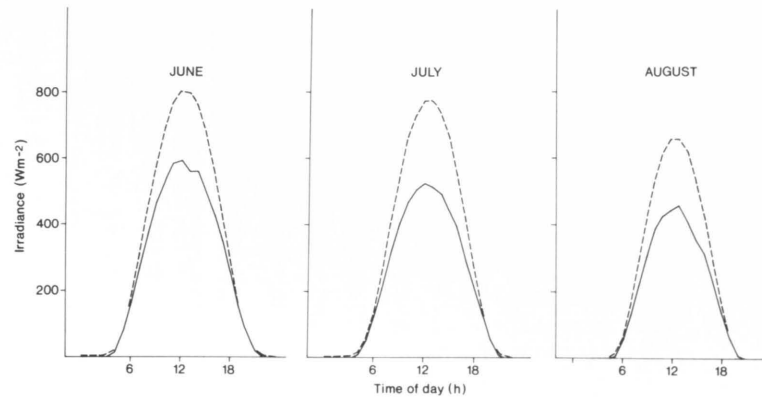


Figure 37. Monthly average of the diurnal course of the estimated irradiance in clear sky conditions (Eqs. 44, 45 and 47) at Jokioinen (broken line) and monthly average of the diurnal course of the measured irradiance; the measurement made at the Jokioinen Observatory in 1958–1977 (solid line). (Korpilahti and Hari 1988 c).

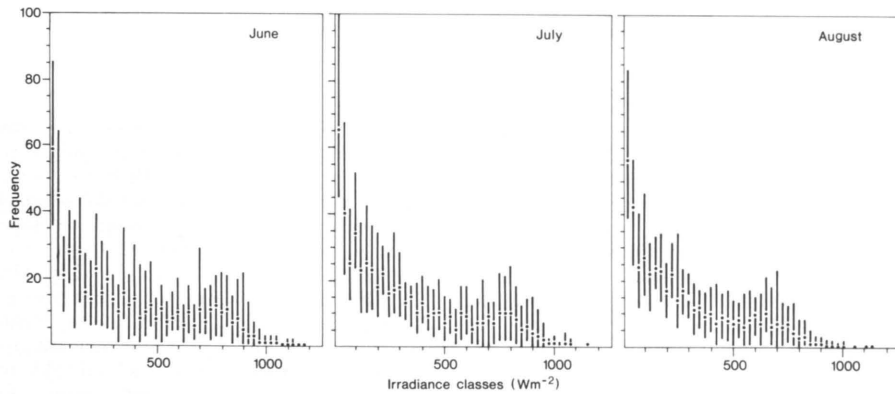


Figure 38. Frequency distributions of the irradiance in June, July and August 1958–1977. The mean of the frequencies in the years 1958–1977 in an irradiance class (points) and a range of variation of the frequency in an irradiance class (column). The mean of the frequency of the observations in the irradiance class 0 Wm^{-2} was 171 in June, 200 in July, and 277 in August (not shown in the figure). (Korpilahti and Hari 1988 c).

ues in clear sky conditions. The range of the frequency distribution in August was narrower at high irradiance compared to the frequency distribution in June and July. The frequencies of irradiance classes 0 Wm^{-2} and $1\text{--}25 \text{ Wm}^{-2}$ were bigger in August than in June and July. These features are due to the elevation of the sun. The standard deviation of the frequency was of the same magnitude in June, July and August. The range of varia-

tion in the distributions was large, which indicated differences between years. The frequency distributions of irradiance involved differences between the years and differences between the months of the same year (Korpilahti and Hari 1988 c).

The gain in solar radiation energy was estimated by integrating the solar irradiance over a time period (Fig. 39). The average of the radiation energy in the years 1958–1977

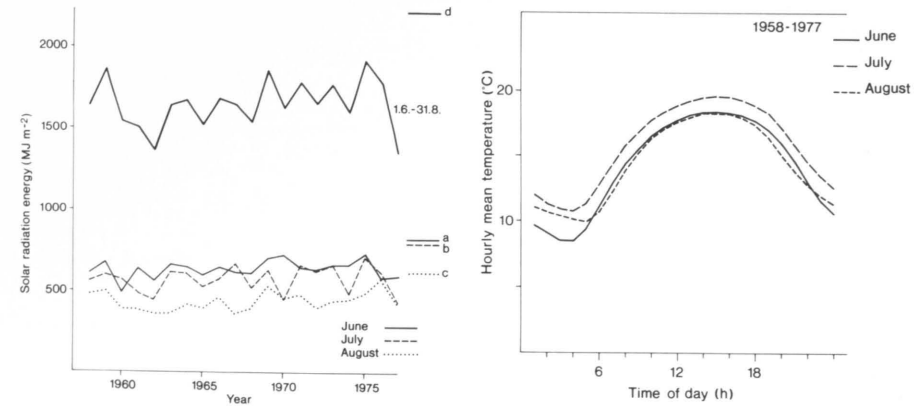


Figure 39. Solar radiation energy reached on a horizontal plane at Jokioinen in June (thin line), in July (broken line), in August (dotted line), and in the period 1 June – 31 August (thick line) in the years 1958–1977. Solar radiation energy calculated for clear sky conditions was 828 MJm^{-2} (a) in June, 805 MJm^{-2} (b) in July, 613 MJm^{-2} (c) in August, and 2246 MJm^{-2} (d) in the period from 1 June to 31 August, as shown in the right margin of the figure. (Korpilahti and Hari 1988 c).

was 644 MJm^{-2} in June, 579 MJm^{-2} in July and 442 MJm^{-2} in August. The hypothetical radiation energy, integrated from the estimated irradiance in clear sky conditions, was 828 MJm^{-2} in June, 805 MJm^{-2} in July and 613 MJm^{-2} in August. The solar radiation energy varied in the years 1958–1977 from 72 % to 89 % of the hypothetical solar radiation energy in June, in July respectively from 54 % to 88 %, and in August from 59 % to 96 %.

6.3. Temperature

A plant leaf absorbs a certain fraction of the incident radiation and partitions this energy into three outgoing streams: reradiation, convective heat exchange with air and evaporation of water or transpiration. Leaves and needles have small masses and generally a low heat capacity. The radiation flux of the environment is coupled to the energy status of the plant by means of the plant's absorption

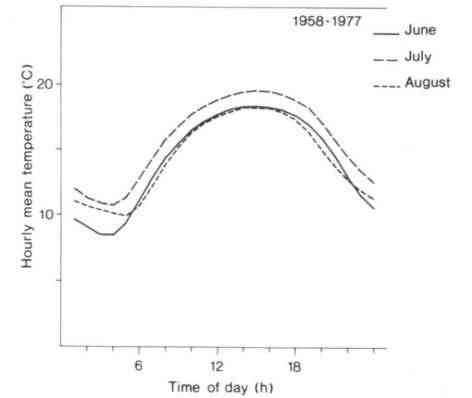


Figure 40. The diurnal course of the hourly mean temperature in June, July and August in the years 1958–1977. (Korpilahti and Hari 1988 c).

of radiation. The needles of conifers generally have a low reflectance and a high absorption through the ultraviolet, visible, and near-infrared bands of the spectrum. The energy status of the leaves and the air temperature are coupled through the convection of energy. Because the leaves and needles are relatively small with a low heat capacity, the convection tends to be large and the leaf temperature is strongly coupled to the air temperature (Gates 1980).

A diurnal variation is characteristic of the air temperature. The diurnal course of the average temperature in the years 1958–1977 was highest in July (Fig. 40). The nighttime was coldest in June. The diurnal course of the average temperature was rather equal in June and in August. In the daytime the average temperature was 1 to 2 °C lower in June and August than in July.

The frequency distributions of the temperature were formed hourly in June, July and August in the years 1958–1977 (Fig. 41). Temperature observations were grouped in classes of 1 °C. The forms of the frequency distributions of temperature were different from the frequency distributions of irradiance. The forms of the temperature distributions were close to the Gauss curve. The range of the temperature distributions was about 20 °C. The range of the temperature distributions in July was a few Celsius de-

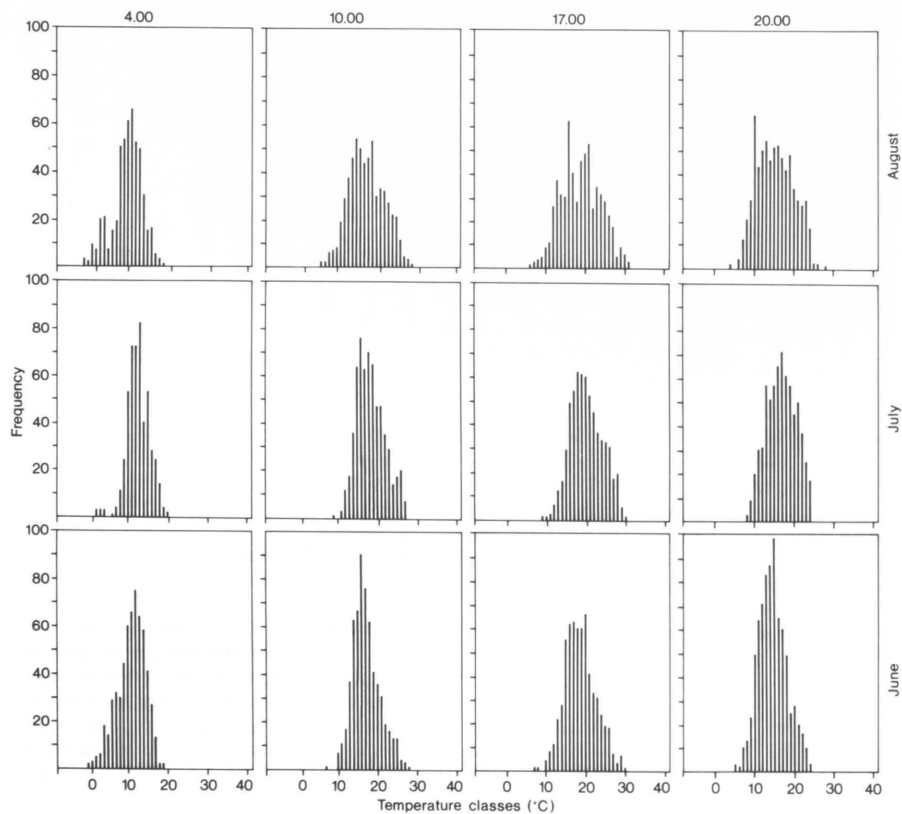


Figure 41. Frequency distribution of temperature at 4 a.m., 10 a.m., 5 p.m., and 8 p.m. in June, July, and August in the years 1958–1977. Temperature class is 1 °C. (Korpilahti and Hari 1988 c).

grees at warmer temperatures than the distributions in June and August. The temperature distributions were at warmer temperatures from the morning hours to the afternoon hours. The distributions were at colder temperatures from the afternoon hours towards daybreak (Korpilahti and Hari 1988 c).

The range of dominating temperature was calculated for every hour in a month-period from the cumulative frequencies (percentage) by dividing into three fractions. The range of temperature between the fractiles of 10 % and 90 % of the cumulative frequency was considered as the range of dominating temperature. The range of dominating tempera-

ture grew wider from the daybreak towards the afternoon (Fig. 42). From sunrise to sunset the range of the dominating temperature was in June from +3 °C to +25 °C, in July from +8 °C to +25 °C, and in August from +7 °C to +23 °C. At midday and in the afternoon the range of the dominating temperature was in June between +10 °C and +25 °C, in July between +13 °C and +25 °C and in August between +12 °C and +23 °C.

The thermal hour degree unit with the threshold temperature 0 °C was used in the cumulative temperature sum (Fig. 43). In the years 1958–1977 the mean of the cumulative temperature sum was in June 10274 h.d.u., in

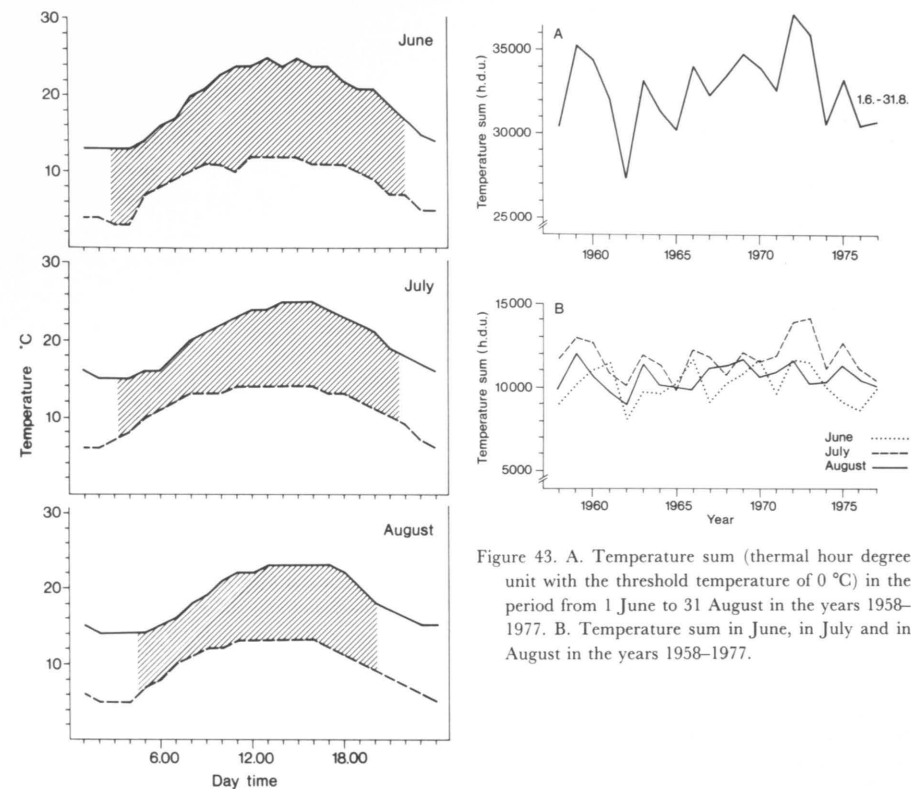


Figure 42. The diurnal course of the temperature between the fractile of 10 % (broken line) and the fractile of 90 % (solid line) of the cumulative frequencies (percentage) in June, July, and August in the years 1958–1977. The range of temperature is screened from sunrise to sunset. (Korpilahti and Hari 1988 c). (Korpilahti and Hari 1988 c).

Figure 43. A. Temperature sum (thermal hour degree unit with the threshold temperature of 0 °C) in the period from 1 June to 31 August in the years 1958–1977. B. Temperature sum in June, in July and in August in the years 1958–1977.

6.4. Precipitation

Energy is coupled into the change of the phases of water between liquid and vapour in the hydrological cycle. Precipitation replenishes the water reservoirs in the soil and is a source for the transpiration and the evaporation flow in the hydrological cycle.

The monthly precipitation data was available from the years 1883–1984 at the Tampere Observatory. The average of the monthly precipitation was 40 mm in May, 54 mm in June, 69 mm in July, and 72 mm in August. The monthly precipitation increases towards late summer. The relative frequency distributions of the monthly precipitation were in the same range in June, July and August (Fig. 44). The frequencies in the classes of the small precipitation were higher in June and July than in August. The median of the rela-

July 11760 h.d.u., and in August 10760 h.d.u. The range of the annual variation in the cumulative temperature sum was of the same magnitude in June, July and August. The accumulation of the temperature sum was generally highest in July and slightly lower in June and in August (Korpilahti and Hari 1988 c).

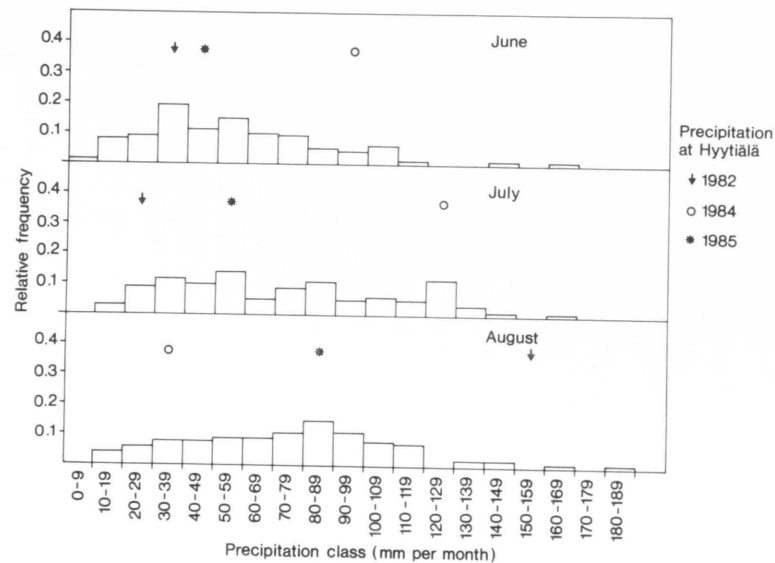


Figure 44. Relative frequency distribution of the monthly precipitation at Tampere in June, in July, and in August 1883-1984. The monthly precipitation at the Forestry Field Station in 1982 is marked by (↓), in 1984 by (○) and in 1985 by (*).

tive frequency distribution was in the class of 50-59 mm in June, 60-69 mm in July and 70-79 mm in August.

The monthly precipitation at the Forestry Field Station was in June and in July 1982 in the range of the classes of low precipitation at the frequency distribution (Fig. 44). In August 1982 the precipitation was in the range of the classes of high precipitation at the

frequency distribution. In June and in July 1984 the precipitation at the Forestry Field Station was in the classes of high precipitation in the frequency distribution. In August 1984 the precipitation was in the class of low precipitation. In June, July and August 1985 the precipitation was in each month in the range of the average precipitation.

7. PHOTOSYNTHETIC PRODUCTION

7.1. The consequences of irradiance and temperature in the photosynthetic production in summer

Photosynthetic production is an accumulation of carbon assimilated by the needles in a time interval. Photosynthetic production per unit of needle area is imposed by the time development of the rate of the photosynthesis. This rate is determined by the irradiance and temperature in the majority of days in the summer period. Weather conditions generate variation from one moment to another in the irradiance and temperature. Cloudiness reduces the incoming irradiance.

The photosynthetic production per unit of the needle area in unshaded conditions in a period was determined by the integral of the rate of the photosynthesis (Eq. 12). This rate was calculated by the Eq. (16) submitted by the Eqs. (17) and (18). Photosynthetic production in clear sky conditions is the hypothetical photosynthetic production. The hypothetical photosynthetic production ($F_h(t_1, t_2)$) per unit of the needle area in a time interval is obtained by

$$(48) \quad F_h(t_1, t_2) = \int_{t_1}^{t_2} f_1(I(x, t)) f_2(T(t)) dt$$

where I_t is the incident total irradiance in clear sky conditions. It was calculated by the Eqs. (44, 45 and 47). The function f_1 was determined by the Eq. (17) and the function f_2 was determined by the Eq. (18). The parameters in the Eq. (17) were given $P_m = 6.0 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ and $b = 170 \text{ W m}^{-2}$. The hypothetical photosynthetic production was calculated for the period from 1 June to 31 August. The hypothetical photosynthetic production was $1.28 \text{ g CO}_2 \text{ dm}^{-2}$ in June, $1.27 \text{ g CO}_2 \text{ dm}^{-2}$ in July and $1.06 \text{ g CO}_2 \text{ dm}^{-2}$ in August.

The photosynthetic production per unit of the needle area in the summer phase was determined by

$$(49) \quad F_p(t_1, t_2) = \int_{t_1}^{t_2} f_1(I(x, t)) f_2(T(t)) dt$$

where $F_p(t_1, t_2)$ denotes the photosynthetic production. The function f_1 was determined by the Eq. (17) and the function f_2 by the Eq. (18). The same values of the parameters were used in the Eq. (17) as in the hypothetical photosynthetic production. The photosynthetic production was calculated for the period from 1 June to 31 August using the irradiance and temperature measurements made at the Jokioinen Observatory in the years 1958-1977. In the years 1958-1977 the photosynthetic production per unit of the needle area was of the same magnitude in June and July, but slightly lower in August (Fig. 45). The mean of the photosynthetic production was $1.09 \text{ g CO}_2 \text{ dm}^{-2}$ in June, $1.06 \text{ g CO}_2 \text{ dm}^{-2}$ in July and $0.88 \text{ g CO}_2 \text{ dm}^{-2}$ in August. The range of variation in the photosynthetic production was $0.92 - 1.18 \text{ g CO}_2 \text{ dm}^{-2}$ in June, $0.89 - 1.19 \text{ g CO}_2 \text{ dm}^{-2}$ in July and $0.74 - 1.04 \text{ g CO}_2 \text{ dm}^{-2}$ in August.

The hypothetical photosynthetic production was calculated to evaluate the magnitude of the reduction in the photosynthetic production caused by the variation in the weather conditions. In the years 1958-1977, the photosynthetic production varied in June from 72 % to 93 % of the hypothetical photosynthetic production, in July respectively from 71 % to 94 %, and in August from 62 % to 98 % (Korpilahti and Hari 1988 c).

In the years 1958-1977, the photosynthetic production varied in June, July and August from 71 % to 90 % of the hypothetical photosynthetic production. The mean of the photosynthetic production was $3.02 \text{ g CO}_2 \text{ dm}^{-2}$ in June, July and August over the years 1958-1977. The range of the variation in the photosynthetic production was $2.57 - 3.25 \text{ g CO}_2 \text{ dm}^{-2}$ in three-month period. During the years 1958-1977, the received radiance energy varied in June, July and August from 61 % to 86 % of the radiation energy in clear sky conditions. The reduction in the photosynthetic production due to cloudiness was smaller compared to the reduction in the received radiation energy brought by cloudiness.

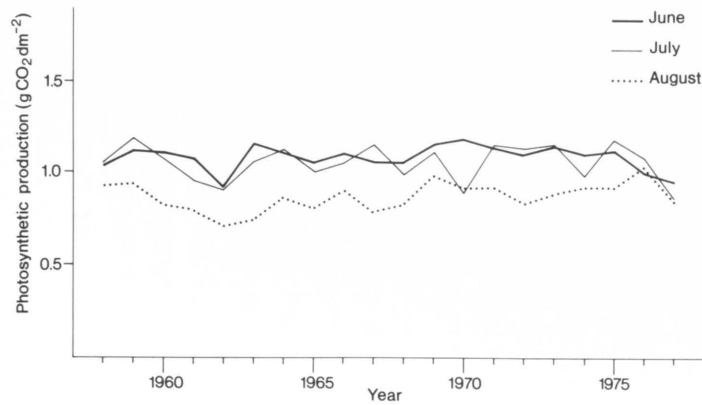


Figure 45. Photosynthetic production per unit of the needle area in June (thick line), in July (thin line) and in August (dotted line) in the years 1958–1977. The hypothetical photosynthetic production per unit of the needle area in clear sky conditions was $1.28 \text{ g CO}_2 \text{ dm}^{-2}$ in June, $1.27 \text{ g CO}_2 \text{ dm}^{-2}$ in July, and $1.06 \text{ g CO}_2 \text{ dm}^{-2}$ in August. (Korpilahti and Hari 1988 c).

7.2. The consequences of the water deficit in the photosynthetic production

The amount of the photosynthesis per unit of the needle area including the stomatal regulation was defined during the summer activity in a time interval, $t_1 - t_2$, by integrating the rate of the photosynthesis over a time interval as follows:

$$(50) F_w(t_1, t_2) = \int_{t_1}^{t_2} f_1(I(x, t)) f_2(T(t)) f_3(W(t), T(t)) dt$$

in which the photosynthetic production per unit of the needle area is denoted by $F_w(t_1, t_2)$. Functions f_1 , f_2 and f_3 were determined by the Eqs. (17), (18) and (20).

The potential photosynthetic production was estimated assuming that the stomatas stay open and the stomatal regulation of the gas exchange is not operational. The amount of the potential photosynthetic production per unit of the needle area was defined respectively by the Eq. (49). The potential photosynthetic production was denoted by $F_p(t_1, t_2)$.

The photosynthetic production was calculated by the model (Eq. 50) for the summers 1982, 1984 and 1985 using irradiance and

temperature measurements made at the Forestry Field Station. The parameters for the function f_1 were in the upper shoots $P_m = 4.0 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$, $b = 170 \text{ Wm}^{-2}$ in 1982, $P_m = 6.2 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$, $b = 180 \text{ Wm}^{-2}$ in 1984 and $P_m = 5.9 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$, $b = 170 \text{ Wm}^{-2}$ in 1985. The parameters in the function f_2 presented in the Chapter 4.1 were used for all summers. The estimated daily values of the internal state were used in the function f_3 (Figs. 18, 19 and 20, Chapter 4.2). The potential photosynthetic production was calculated respectively by the model (Eq. 49) using the irradiance and temperature measurements. The same parameter values were used for functions f_1 and f_2 in the calculations of the potential photosynthetic production as in the Eq. (50).

Figures 46, 47 and 48 show the time development of the estimated potential daily photosynthetic production and the estimated daily photosynthetic production in the summers 1982, 1984 and 1985. The potential daily photosynthetic production varied in a wide range. The amount of the potential photosynthetic production and the amount of the photosynthetic production were equal on many days. Every summer, the amount of the potential photosynthetic production was

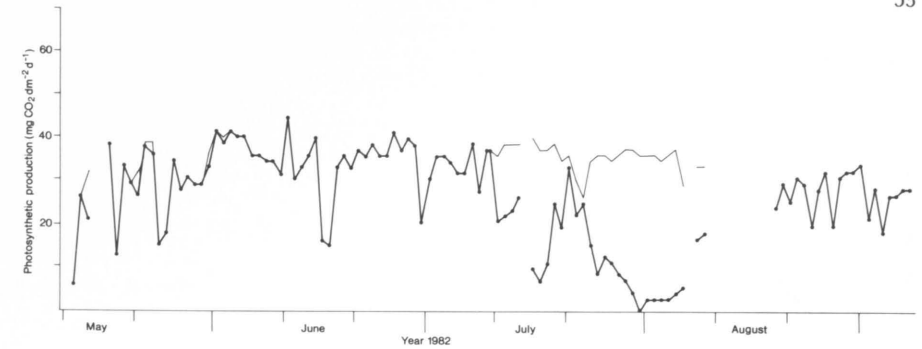


Figure 46. Daily photosynthetic production per unit of the needle area without the stomatal regulation (thin line) and with the stomatal regulation (thick line) in summer 1982.

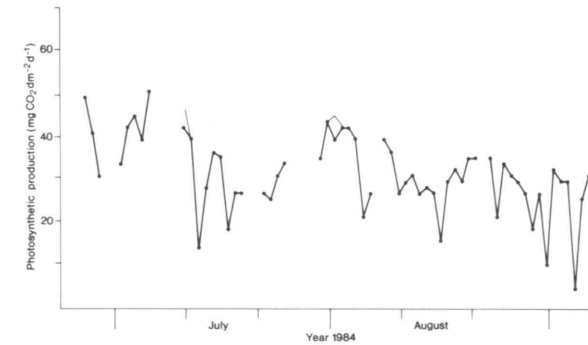


Figure 47. Daily photosynthetic production per unit of the needle area without the stomatal regulation (thin line) and with the stomatal regulation (thick line) in summer 1984.

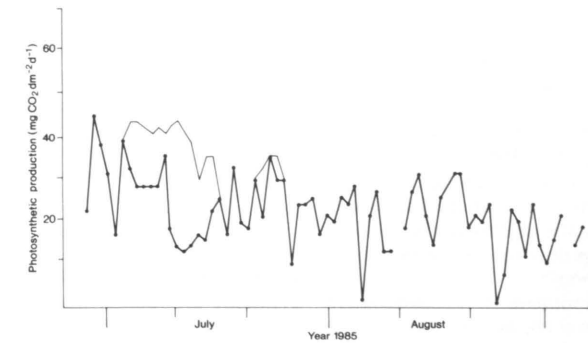


Figure 48. Daily photosynthetic production per unit of the needle area without the stomatal regulation (thin line) and with the stomatal regulation (thick line) in summer 1985.

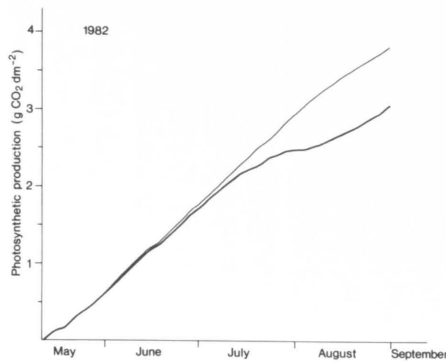


Figure 49. Time development of the cumulative photosynthetic production per unit of the needle area from May to August 1982 with the stomatal regulation (thick line) and without the stomatal regulation (thin line).

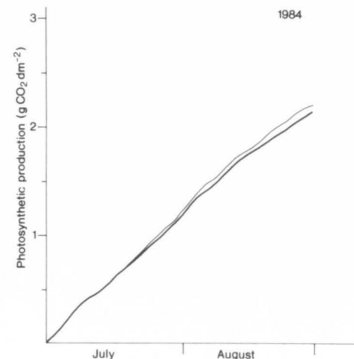


Figure 50. Time development of the cumulative photosynthetic production per unit of the needle area from July to August 1984 with the stomatal regulation (thick line) and without the stomatal regulation (thin line).

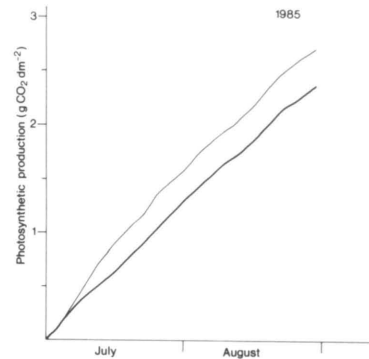


Figure 51. Time development of the cumulative photosynthetic production per unit of the needle area from July to August 1985 with the stomatal regulation (thick line) and without the stomatal regulation (thin line).

higher on certain days. A decrease in the measured rate of the CO_2 exchange at midday and in the early afternoon was characteristic of those days. The potential photosynthetic production was continuously higher than the photosynthetic production in the four-week period in July – August 1982 (Fig. 46) and in the two-week period in July 1985 (Fig. 48). Sunny and warm weather and low precipitation were characteristic of these periods. An increasing decrease in the measured rate of the CO_2 exchange occurred in these periods. The precipitation was 58 mm in the period from 15 June to 8 August 1982. The precipitation was 37.8 mm in the period from 21 June to 20 July 1985. There were 38 days without any rain in the dry period in 1982 and respectively 18 days without any rain in the dry period in 1985. The reduction which occurred in the photosynthetic production in the dry periods in field conditions was in agreement with Bengtson's results (1980), who exposed the pine trees to a water stress by isolating the roots.

The time development of the cumulative photosynthetic production per unit of the needle area and the cumulative potential photosynthetic production per unit of the needle area in the measuring periods of summers 1982, 1984 and 1985 are presented in

figures 49, 50 and 51. In 1982, the photosynthetic production was in June 3 % lower than the potential photosynthetic production, in July respectively 35 % and in August 33 % lower. The precipitation was low in June and July whereas it was high in August (Fig. 44). The first part of August was dry.

In July to August 1984 the photosynthetic production was nearly equal to the potential photosynthetic production (Fig. 50). In July the photosynthetic production was 2 % and in August 5 % lower than the potential photosynthetic production. The precipitation was high in June and July, but it was low in August (Fig. 44). In spite of the low precipitation in August, weather conditions did not generate a considerable reduction in the photosynthetic production.

In July 1985, the photosynthetic production was 19 % and in August 3 % lower than the potential photosynthetic production (Fig. 51). In June and July, the precipitation was rather low but in August it was quite normal.

In the period from July to August 1982, the photosynthetic production was 34 % lower than the potential photosynthetic production. The reduction in the photosynthetic production was respectively 4 % in 1984 and 13 % in 1985. In the three-month period from June to August 1982 the photosynthetic production was 23 % lower than the potential photosynthetic production. In the period from June to August, the precipitation was 216 mm in 1982, 256 mm in 1984 and 179 mm in 1985. The reduction in the photosynthetic production caused by the stomatal regulation and the water deficit in the soil could not be derived from the precipitation values of long periods. The dry period in 1982 may be considered to represent quite a long and severe drought in the Finnish weather conditions. We can evaluate the reduction of the photosynthetic production to be less than 25 % due to drought in the summer period. The relative frequency of the monthly precipitation respective to the precipitation in June 1982 was 0.19 and in July 1982 0.09. The reduction of the photosynthetic production is considerably lower in most summers.

7.3. Seasonal and annual photosynthetic production

The photosynthesis of the Scots pine has a dormant period in winter, when the photosynthesis is mainly exhausted. The photosynthesis of the pine recovers gradually in the

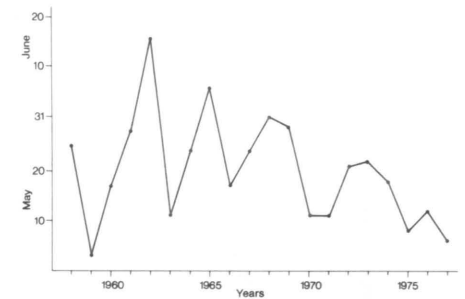


Figure 52. Dates in spring and in early summer when the state of the photosynthetic activity (according to the Eqs. (22), (23) and (24)) reached full activity in the years 1958–1977. (Korpilampi 1988 c).

spring, while irradiance and temperature increase (Pelkonen 1980, Linder and Troeng 1980). The active period of the photosynthesis continues until late autumn. The annual production of carbon is fixed in the spring, summer and autumn seasons. Weather conditions generate a variation in the timing of the photosynthetically active period and in the rate of the photosynthesis. In addition to the rate of the photosynthesis, the weather affects the length of the photosynthetically active period.

The variation in the spring recovery of the photosynthesis was studied by calculating the daily value of the state of the photosynthetic activity from the weather data of the years 1958–1977 using the Eqs (22), (23) and (24). The initial value of 0.1 was given to the state of the photosynthetic activity on 15 April. The progress of the photosynthetic activity varied in the springs. The full activity of the photosynthesis was reached in the period from 2 May to 16 June in the years 1958 – 1977 (Fig. 52).

The time development of the state of the photosynthetic activity varied considerably in the springs. A warm temperature in the spring induced the rapid progress of the state of the photosynthetic activity as for example in 1975 (Fig. 53). A cold temperature delayed the recovery of the photosynthetic activity. The state of the photosynthetic activity reached full activity on 6 June in 1965 and on 16 June in 1962 (Fig. 53). The progress of the

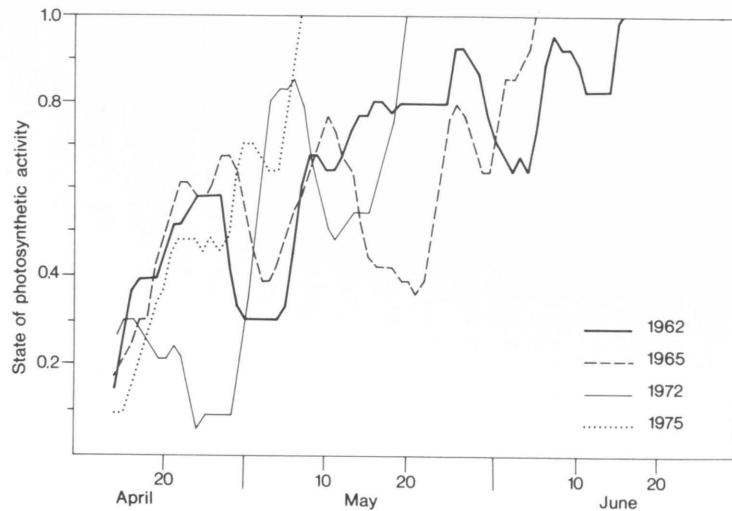


Figure 53. Time development of the daily values of the state of the photosynthetic activity (according to the Eqs. (22), (23) and (24)) in spring 1962, 1965, 1972 and 1975. (Korpilahti 1988 c).

state of the photosynthetic activity in 1972 illustrates the majority of springs, when the summer activity was reached from mid-May to the end of May (Fig. 53). The summer activity was reached on 21 May in 1972 (Korpilahti 1988 c).

The daily photosynthetic production per unit of the needle area in autumn was estimated by the Eq. (49) using the irradiance and temperature measurements made at the Forestry Field Station in 1982, 1984 and 1985. The parameters used in the Eq. (49) for functions f_1 and f_2 were the same as in the Eq. (50). The daily photosynthetic production varied in a wide range each autumn (Figs. 54, 55 and 56). The daily photosynthetic production decreased towards late autumn. The photosynthetic production was rather small in late October and in November. The photosynthetic production was small also on a number of days in September and in the early part of October. Those days were characterized by heavily clouded or cold weather.

The amount of the photosynthesis per unit of the needle area assimilated during the seasons was determined by the following integral (Eq. 51):

$$(51) F_s(t_1, t_2) = \int_{t_1}^{t_2} f_1(I(x, t)) f_2(T(t)) f_4(S(t), T(t)) dt$$

where $F_s(t_1, t_2)$ denotes the amount of the photosynthesis in a time interval of t_1, t_2 . The function f_4 was determined by the Eqs. (22), (23) and (24). The field data gave evidence that the control process of the photosynthesis does not operate in the autumn according to the function f_4 . Thus the function f_4 was given the value 1.0 in the autumn in the calculations of the photosynthetic production. The functions f_1 and f_2 were determined by the Eqs. (17) and (18). The parameters used in the function f_1 were $P_m = 6.0 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ and $b = 170 \text{ Wm}^{-2}$. The parameters in the function f_2 were $a_1 = 0.32 \text{ }^\circ\text{C}^{-1}$ and $a_2 = -5^\circ\text{C}$. The photosynthetic production per unit of the needle area was calculated for the years 1958–1977 using the irradiance and temperature measurements made at the Jokioinen Observatory from 15 April to 15 October each year.

The photosynthetic production in the different springs can be compared using the Eq. (51) to estimate the photosynthetic produc-

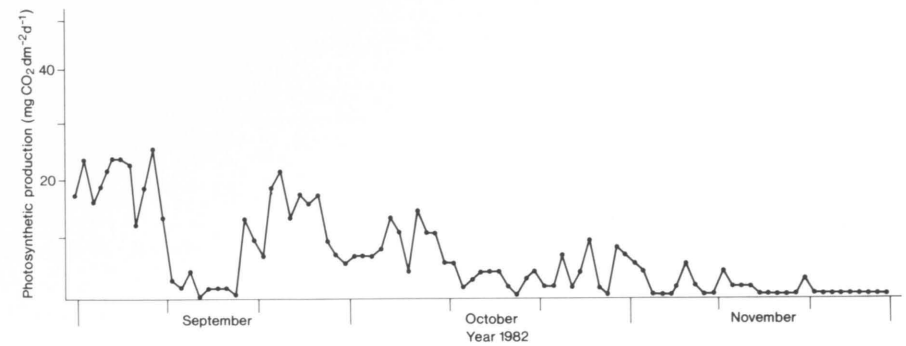


Figure 54. Daily photosynthetic production per unit of the needle area in autumn 1982.

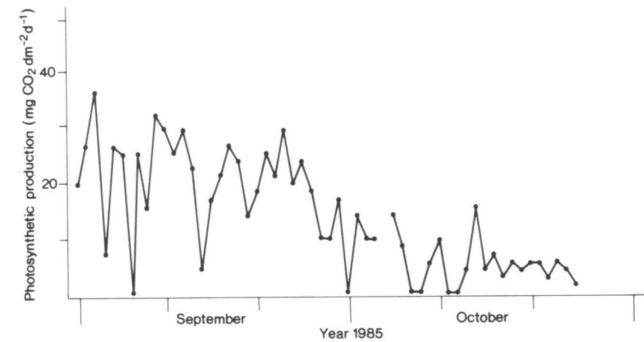


Figure 55. Daily photosynthetic production per unit of the needle area in autumn 1985.

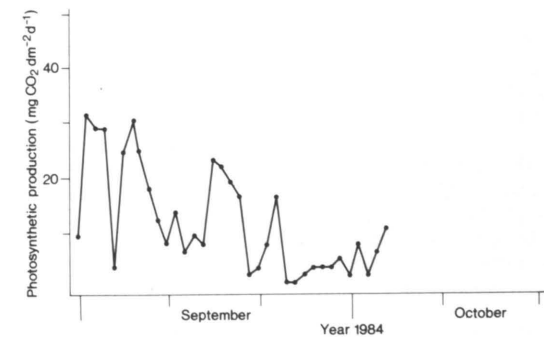


Figure 56. Daily photosynthetic production per unit of the needle area in September and in the first part of October in 1984.

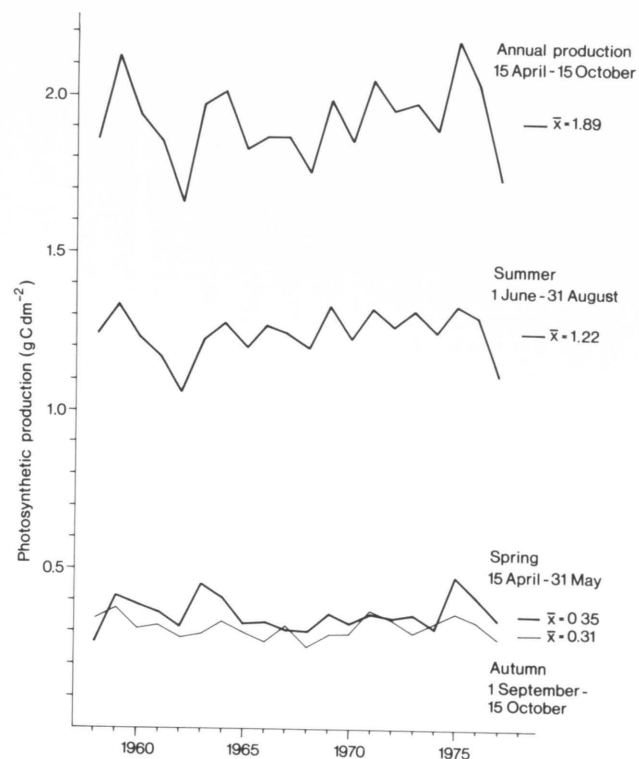


Figure 57. Photosynthetic production per unit of the needle area in spring (from 15 April to 31 May) (thick line), in autumn (from 1 September to 15 October) (thin line), in summer (from 1 June to 31 August), and the annual photosynthetic production per unit of the needle area (from 15 April to 15 October) in the years 1958–1977. (Korpilahti 1988 c).

tion. The progress of the spring recovery of the photosynthetic activity and the weather conditions affect the photosynthetic production in the spring phase of the annual cycle. In the years 1958–1977, the photosynthetic production varied in the period from 15 April to 31 May in the range of 0.26 to 0.47 g C dm⁻² (Fig. 57). The photosynthetic production was bigger in the spring periods, when the recovery of the photosynthetic activity was early and the temperature remained warm.

In the years 1958–1977, the photosynthetic production varied in the range of 1.03 to 1.31 g C dm⁻² in the summer period from 1 June

to 31 August. The photosynthetic production varied in the autumn period from 1 September to 15 October in the range of 0.25 to 0.37 g C dm⁻² (Fig. 57). The photosynthetic process continues to be active after 15 October, too. The daily photosynthetic production is small in late autumn due to the low irradiance or the low temperature. The photosynthetic production of late autumn plays a minor role in the annual photosynthetic production (Korpilahti 1988 c).

The relative range of the variation in the photosynthetic production was largest in the spring period and smallest in the summer period. In the spring period the relative range

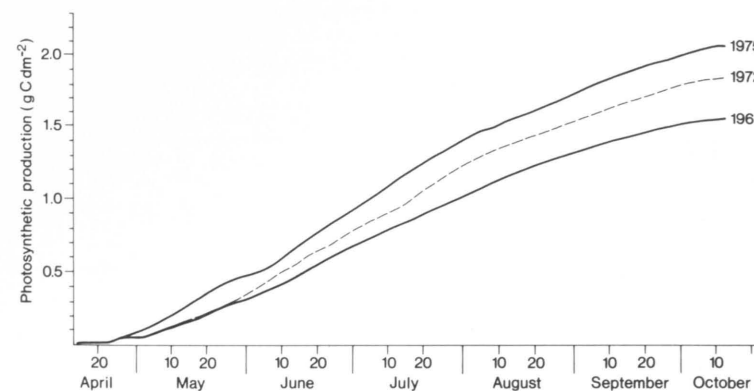


Figure 58. Time development of the cumulative photosynthetic production per unit of the needle area from 15 April to 15 October in 1962, 1972 and 1975. (Korpilahti 1988 c).

of the variation was 35 % below the mean and 34 % above the mean. In summer, the relative range of the variation was 15 % below the mean and 7 % above the mean, and in the autumn period respectively 18 % below the mean and 20 % above the mean.

A high annual photosynthetic production was obtained in 1959, 1971 and 1975. In those years the photosynthetic production was high in all the seasons, spring, summer and autumn. The annual photosynthetic production was lowest in 1962 and 1977. The low photosynthetic production in the summer period was essential to these years (Fig. 57).

In the years 1958–1977, the annual photosynthetic production varied from 1.63 g C dm⁻² to 2.13 g C dm⁻². The relative range of the variation in the annual photosynthetic production was 26 % of the average annual photosynthetic production. In the spring

period, the photosynthetic production was on an average 19 %, in the summer period 65 % and in the autumn period 16 % of the annual photosynthetic production. Figure (58) illustrates the time development of the annual photosynthetic production in 1962, 1972 and 1975. The annual photosynthetic production was low in 1962 and high in 1975. The year 1972 represents an average level of the annual photosynthetic production. The accumulation of the photosynthetic production was clearly higher in the spring of 1975 than in 1962 and 1972. The accumulation of the photosynthetic production was rather similar in the springs of 1962 and 1972. The accumulation of the photosynthetic production remained low in the summer period of 1962. The accumulation of the photosynthetic production is high in the summer period and becomes low in September.

8. DISCUSSION

8.1. Empirical measurements and the method of analysis

Measurements of the gas exchange in natural conditions require a complicated measuring system. Measuring in nature is involved with special technical difficulties compared to laboratory conditions. Such technical difficulties often affect the accuracy of the measurements. In consideration of the laboratory measurements careful attention should be paid to the time interval, within which the environmental factor is changed from one level to another, in order not to expose the plant to abnormally rapid changes of the environmental factors and to abnormal combinations of the environmental factors. When measuring in natural conditions, the environmental factors vary in the range in which the plant has grown and acclimated. The rate of the change in the environmental factors follows the natural variation and combination in field measurements.

The measurements of the gas exchange are based on a decrease in the CO₂ content of the air flowing through the measuring chamber. The CO₂ content of the air decreased in the chambers from about 340 ppm to 280 ppm. The CO₂ content of the air affects the rate of the photosynthesis. With a lower CO₂ content of the air, the rate of the photosynthesis saturates at a lower level of the maximum photosynthesis in the presence of high irradiance than with a higher concentration of CO₂ in the air in respective irradiance (Tolbert et al. 1983). The effect of the decrease in the CO₂ concentration of the air in the measuring chambers on the maximum rate of the photosynthesis was approximately 10 %.

The distribution of irradiance on the needle surface depends on the shoot geometry and on the directional distribution of the surrounding radiation field (Oker-Blom 1985, Oker-Blom 1986 a). The distribution of irradiance on the needle surface affects the rate of the photosynthesis of a shoot (Smolander et al. 1987). The shoots were chosen parallel to the axis of the earth in order to minimize the variation in the inclination an-

gle between the shoot and the sun. The measuring principle of the ELP equipment is to measure irradiance at five points among the needles and to integrate the output of the sensors over the measuring period. The output of the sensors relates the Michaels-Menten response to irradiance. Due to a variation in the distribution of irradiance on the needle surface and because of the close dependence of the rate of the photosynthesis on irradiance, irradiance should be measured at numerous points among the needles at dense recording intervals during the measuring interval of the gas exchange. The sensors of the measuring equipment ought to be extremely small. The present technical facilities make it possible to construct such equipment that fulfils the measuring principles better than the ELP equipment used now.

Measuring breaks occurred during long measuring periods due to the technical maintenance of the measuring system and thunder-storms. A rapid change in the CO₂ content of the outside air disturbed the measurements especially in the mornings and in the evenings. Observations were rejected when the standard deviation of the CO₂ content of the outside air was over 6 ppm per 30 minutes.

Quantitative studies on transpiration are associated with special problems. Measuring of the transpiration by weighing limits the experimental material on potted seedlings and only long-time integrals can be detected. Measuring of the transpiration by measuring the water content of a chamber includes problems, because the water content of the chamber changes during a measuring interval and it affects the transpiration rate. New technical facilities are therefore needed for the quantitative research of transpiration.

The information required of a biological phenomenon influences the premises of a mathematical model and the usefulness of the model as a tool for interpreting the phenomenon. A mathematical model provides a representation of the system. It should therefore resemble the system and, if the system is dynamic, it should be capable of simulating

its movements (Thornley 1976). Direct measuring of the variables is often emphasized in the ecophysiological models. Usually the requirement for direct measuring of variables encounters problems in the study of the operation of the biological system related to the environment, because a change may occur in the biological state during the time interval. Charles-Edwards (1981) has pointed out that the essential problem in the mathematical description of the control processes is how to set up the problem in a dynamic form in which the state of the system is obtained by integrating the rates over time from a given set of initial conditions. If part of the system becomes inaccessible for direct observations, the system presented by observable variables may develop properties, which become unpredictable. The observer may be able to restore the predictability by taking the system's past history into account, i.e. by assuming the existence of a "memory" (Ashby 1976). The "memory" is a concept that the observer invokes to fill in the gap caused when a part of the system is unobserved (Ashby 1976). In the analysis of the dynamic systems, the state variables, which are not directly observable, are usually required to map the observable output set (Luenberger 1979, and Spriet and Vansteenkiste 1982). A requirement for complete observability cannot often be stated. The unobservable variables used in the analysis of this study are the internal state, the state of the photosynthetic activity and the state of chilling. Models may be written at a number of levels of aggregation. The level chosen and the usefulness of a model is determined by the progress in the understanding of the operation of a system and the ability to predict its responses to a range of stimuli (Landsberg 1981).

The model for the CO₂ exchange predicted in the range of the measuring accuracy the measured CO₂ exchange in different conditions and in the summer and autumn seasons. The predictability of the model remained stable during the entire measuring period with the parameter values of the irradiance response estimated at the beginning of the measuring period. The parameters for the temperature response were estimated from the data set of the measurements made in 1982. The same parameter values were also used in the models of 1984 and 1985.

In the model for the CO₂ exchange, the daily value of the internal state was estimated from 40 to 100 measurements of the gas exchange per day.

The result of the model of the photosynthetic production is sensitive to the parameter P_m. An increase in the value of the parameter P_m induces linearly the same proportional increase in the photosynthetic production. The consequences of the parameter b in the photosynthetic production are dependent on the distribution of the irradiance during the period (Hari et al. 1984).

Information on the small time scale, i.e. at metabolic rates, is used to get information on the large time scale, i.e. photosynthetic production and transpiration. The model structure is constructed to include information hierarchically from the detailed time level to a grosser time level. The transition from the metabolic rates to the amounts produced during the prolonged periods is carried out by integration. This resulted in a model construction that permits to consider the effect of the different environmental conditions on the photosynthetic production in the different seasons of the annual cycle. The model construction also allows the use of weather data to get insight into the photosynthetic production on a large time scale.

8.2. Dynamics of the gas exchange

The response of the rate of the photosynthesis to irradiance remained stable in the growing season. The needles of the Scots pine live for about four years. The senescence of the needles had no effect on the rate of the photosynthesis in the growing season, although the effect of the needle senescence on the photosynthesis of the pine has been observed between four different year classes of needles by Linder and Troeng (1980).

Of the environmental factors, irradiance dominates the photosynthetic response. On the majority of the days, the model for the CO₂ exchange with irradiance and temperature response explained 80 – 95 % of the variation in the measured rate of the CO₂ exchange. The direct effect of the temperature on the photosynthesis at a moment has a

significance to the rate of the photosynthesis in a temperature range of -5°C to $+3^{\circ}\text{C}$. The direct effect of the temperature on the rate of the photosynthesis is of minor importance at higher temperatures in the temperature range from $+3^{\circ}\text{C}$ to about $+30^{\circ}\text{C}$, which is seldom exceeded in the field conditions. Respiration increases at higher temperatures and the stomatal regulation frequently affects the rate of the photosynthesis.

Water affects the gas exchange through the water content of the air and through the water content of the soil. The effect of the water on the photosynthesis is connected to the stomatal regulation. With a water deficit the control processes of the plant seem to cause slow changes in the state of the plant. A threshold temperature describes the state of the plant. The threshold temperature is a temperature above which the gas exchange becomes strongly depressed and below which the water deficit has no effect on the gas exchange. The stomatal regulation depends at a moment on the state of the plant and on the ambient temperature. The effect of the stomatal regulation on the rate of the photosynthesis becomes essential with a water deficit.

In literature, the effect of the water deficit on the CO_2 exchange has been quantified by the stomatal resistance and by mesophyll resistance according to the model for the gas exchange presented by Gaastra (1959) (Jarvis 1976 and 1981, Kaufmann 1976, Reed et al. 1976, Hellkvist et al. 1980, Charles-Edwards 1981, Jarvis and Mansfield 1981, Leverenz 1981, Schulze et al. 1985). Gaastra (1959) described a number of biochemical and biophysical variables which affect the CO_2 exchange by a mesophyll resistance. It has been difficult to apply the model to predict the gas exchange because this model does not involve any dependence of the resistances on the environmental factors with a changed water deficit (cf. Jarvis and Morrison 1981).

The study of the stomatal regulation and the gas exchange as an optimization problem introduced a new theoretical approach to the problem. The properties of the solution of the optimal stomatal control presented by Hari et al. (1986) were studied from field data by the threshold temperature and by the slope of the response of the stomatal control to the temperature. Four of the six hypotheses were

supported by the field data. A threshold temperature above which the stomatas begin to close was observed. The threshold temperature decreased with an increasing deficit of soil water. The variation of the threshold temperature followed the partial pressure of the atmospheric water vapour. The degree of the stomatal opening fell from 1.0 to 0.5 in the conditions with a severe water deficit after a small increase in temperature. The property predicted by the dependence of the threshold temperature on the irradiance could not be clearly detected from the field data. The statement that the temperature range within which the optimal degree of the stomatal opening drops to zero becomes narrower when the water deficit increases could not be clearly detected, either. The field data indicated some properties to support these statements, but they require further research. Quantitative testing of the characteristics of the optimal degree of the stomatal opening provides, in addition to the CO_2 exchange, irradiance and temperature measurements, monitoring of the transpiration and measuring of the amount of soil water.

A water deficit induces a slow response to the rate of the photosynthesis described by the threshold temperature. The stomatal regulation is dependent on the threshold temperature and on the ambient temperature.

The recovery of the photosynthesis is affected in the spring by the slow response of the rate of the photosynthesis to the temperature (Pelkonen and Hari 1980). A change in the response is detectable on the time scale of a day. Investigations of the rate of the photosynthesis in the autumn did not indicate a respective slow response to the temperature. The response of the temperature to the rate of the photosynthesis was detected on the time scale of a few hours in autumn. As regards the control of the annual cycle, the effect of the control on the rate of the photosynthesis seems to be slower in the spring causing a gradual recovery. The effect of the control is on the time scale of a few hours in the autumn giving quite a rapid response to weather conditions. This kind of a procedure seems favourable to the plant concerning the risk of cold damages due to the changing weather conditions. Linder and Troeng (1980) pointed out the effect of a limited water supply in the spring. But, the low rate of the

photosynthesis was not solely the result of a limited water supply. Water supply and transpiration conditions are evidently different in autumn and in spring.

The transpiration rate is known to depend on the difference of the content of water vapour in the ambient air and in the intercellular space and on the stomatal regulation (Gaastra 1959, Jarvis 1981, Hari et al. 1986). A water deficit affects the transpiration rate through the stomatal regulation. The dynamics of the transpiration rate deserves more quantitative research.

8.3. Environmental factors

A large variation of irradiance was observed in June, July and August between the different years. There were considerable differences also between the months of the same year. The effect of a cloud cover was more indicative in July and August than in June. As regards the response of the rate of the photosynthesis to the environmental factors, irradiance is the dominating environmental factor during the major part of the photosynthetically active period. The variation in irradiance therefore causes a large proportion of the variation in the rate of the photosynthesis. Differences in the distribution of irradiance over long periods indicate the effects on the rate of the photosynthesis and the differences in the photosynthetic production in the different months or summers.

The temperature was in the range in which it has quite a small effect on the rate of the photosynthesis in the summer periods during the major part of the time when irradiance was available for the photosynthesis. The effect of the temperature on the rate of the photosynthesis becomes more dominant in spring and in autumn.

In 1982 the estimated transpiration in 1982 was around 85 mm per month. The estimated transpiration was higher than the average monthly precipitation, which was 40 mm in May, 54 mm in June, 70 mm in July, and 72 mm in August. In 1883–1984, the annual precipitation varied in the range of 450 mm to 790 mm. The initial reservoirs of soil water are needed for transpiration when the precipitation is not adequate to offset the tran-

spiration. The importance of a snowpack on the source of water for the trees has been pointed out by Running (1984) in Montana. Transpiration slowly diminishes the reservoirs of soil water in the growing season. Whether the diminishing of soil water causes a water deficit in trees or not is combined to precipitation, the frequency of rains, the meteorological conditions and the character of the growth site.

Derivation of the model for the water regime in a pine stand involved a simplification of the water relations in the soil and water transportation. The model should therefore be considered concerning these simplifications as a first attempt at constructing relations of the air humidity, the transpiration of a pine stand and the soil water. Estimates of the transpiration of a pine stand vary largely according to the estimating method as reported in the literature (Eriksson and Grip 1979, Gash et al. 1979, Jansson and Halldin 1979, Jensen 1979 and Keller 1979). The simulated cumulative transpiration of the stand was 340 mm in the period from 12 May to 9 September in 1982, and the cumulative potential transpiration was 502 mm. During that period the precipitation was 259 mm. The simulation results seemed reasonable in a frame of precipitation. Keller (1979) has reported the estimates of the cumulative transpiration to range from about 110 mm to 300 mm in a pine stand of the Jedraås forest from May to September 1977 according to the estimating method used.

The simulation results give an idea of the significance of the stomatal regulation in the estimates of the transpiration and the soil water. The numerical values of transpiration and soil water and the detailed construction of the model still require some research. The introduced dynamic model for water in the soil-plant-atmosphere allows a separation of evaporation and transpiration (Huillet and Lauga 1985). It involves the effect of the leaf area and the stomatal regulation. The dependence of the internal state on the conditions of soil water allows to predict the stomatal regulation of the gas exchange with a feedback function of the conditions of the soil water. As regards the dependence of the internal state on the soil water, it includes the impact of the severity of drought. It is possible to conclude from the simulation results

of soil water the significance of the dynamic water relations in the soil-plant-atmosphere continuum to evaluate the effects of a water deficit.

8.4. Photosynthetic production

The time derivative of the photosynthetic production is the rate of the photosynthesis. When the derivative and its dependence on the environment are known, the amount of the photosynthetic production is obtained by integrating over time.

In order to compare the results of the model for the photosynthetic production with the results presented in the literature, the amount of the daily photosynthetic production per unit of the needle area was calculated. The photosynthesis of the Scots pine trees is studied under field conditions in the Swedish Coniferous Forest Project (SWECON). The model of the photosynthesis (FAST-P) used in the Swedish project explains 83 % of the variance in the measured amount of the daily photosynthesis in the three-week period in July 1977 (Lohammar et al. 1980). The model explained 97 % of the variance in the measured daily photosynthesis in the period from 27 June to 3 August in 1984 (Fig. 59). If the desired information is to interpret the rate of the photosynthesis and the amount of the photosynthesis, the given dynamic model derives high predictability.

In the spring, the photosynthetic production composed 19 % of the annual photosynthetic production, in summer 65 % and in autumn 16 %. The variation in the annual photosynthetic production is caused mainly by the length of the photosynthetically active period, by irradiance and temperature. The relative range of variation in the annual photosynthetic production was 26 % of the average annual photosynthetic production. The effect of the temperature on the photosynthetic production is more significant in spring and in autumn than in summer. In summer, the variation in the photosynthetic production is dominantly caused by irradiance. The relative range of variation in the photosynthetic production was in summer 22 % of the average photosynthetic production.

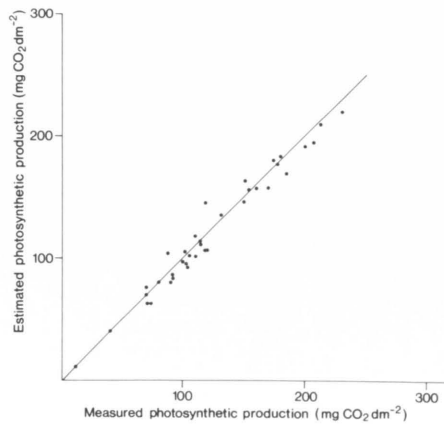


Figure 59. The predicted photosynthetic production per unit of the needle area (the Eqs. 17, 18, 20 and 50) on the days from 27 June to 3 August 1985 as a function of the measured photosynthetic production. Diagonal is the line $y=x$. The predicted photosynthetic production covered 97 % of the variation in the measured photosynthetic production. (Korpilahti and Hari 1988 a).

In 1958–1977, the mean of the annual photosynthetic production in unshaded conditions was 1.9 g C dm^{-2} . In the twenty-year period, the annual photosynthetic production varied from 1.6 g C dm^{-2} to 2.1 g C dm^{-2} . The amounts of the annual photosynthetic production per unit of the needle area are in agreement with the result of the annual net photosynthetic production of one-year-old shoots of Scots pine derived from the measurements of the CO_2 exchange made by Ågren et al. (1980), and Troeng and Linder (1982 a and b).

The water deficit caused a decrease in the photosynthetic production. The photosynthetic production was decreased on single days when the demand for transpiration was high, and in the dry periods. The reduction of the photosynthetic production was in agreement with Bengtson's results (1980) who exposed the pine trees to a water deficit by isolating the roots.

The reduction of the photosynthetic production is evaluated to be about 5 % or less in summer due to the stomatal regulation on

separate days when the demand for transpiration is high. The dry period in 1982 may be considered to represent quite a long and severe drought in the Finnish weather conditions. We can evaluate the reduction of the photosynthetic production due to a water deficit to be less than 25 % in the summer. The effect of the water deficit on the photosynthetic production is mostly rather small in Finnish weather conditions, but occasional dry periods in some years have a considerable effect on the photosynthetic production. The effect of the water deficit obviously varies on the growth sites due to a watershed and the hydrology of the soil.

The amount of the photosynthetic production of a tree or a stand is obtained by integrating the rate of the photosynthesis over the canopy volume in addition to the integration over time. The environmental factors in the different parts of the canopy are needed to estimate the photosynthetic production of a tree or a canopy. Within a canopy, the environmental factors embed the interaction of trees. The photosynthetic production is conceivable to estimate with a rather good accuracy, compared to other factors involved in the stand growth models, as for example allocation of carbohydrates, supply of nutrients and transpiration.

9. CONCLUSIONS

The present study investigated the dependence of the rate of the photosynthesis and the transpiration rate on the environmental factors and on the control of the plant metabolic processes in Scots pine in its natural environment, and the importance of the different environmental factors in the photosynthetic production. The main results of the study are:

1. The dependence of the rate of the photosynthesis on irradiance is stable in the growing season. Irradiance dominates the response of the rate of the photosynthesis to the environmental factors during most of the photosynthetically active period.
2. The effect of the temperature on the rate of the photosynthesis is significant in the temperature range of -5°C to $+3^{\circ}\text{C}$.
3. The importance of the water deficit on the photosynthesis is quite small in Finnish weather conditions, but in some dry periods the effect of the water deficit on the rate of the photosynthesis is clear.
4. Four qualitative properties of the optimal degree of the stomatal opening were supported by the field data. Two qualitative properties require more research.
5. The soil water constitutes a feedback between the gas exchange and the dynamic water relations of the soil, the plant and the atmosphere.
6. In Finnish weather conditions the annual photosynthetic production is mainly affected by

the length of the photosynthetically active period and by the irradiance in the summer months. Clouds cause a varying reduction in the photosynthetic production. The water deficit is significant in the photosynthetic production in some exceptionally dry summers.

7. In unshaded conditions the mean of the annual photosynthetic production per unit of the needle area was 1.9 g C dm^{-2} .
8. The model construction makes it possible to analyse the gas exchange in different environmental conditions and in different seasons.

The photosynthetic production and, in some cases, the transpiration are the basic elements of the models for stand growth (Hagihara and Hozumi 1977, 1986, Hari et al. 1982, Lohammar et al. 1980, Murphy et al. 1981, Running 1984, Mäkelä 1988). When the effects of the environmental factors and those of the control process on the rate of the photosynthesis and on the transpiration rate are known, photosynthetic production and transpiration can be used in causal, process-based models for stand growth. During the stand development, the interaction of trees impose changes in the environmental factors, especially in the light climate. Knowing the causal relations of the environmental factors and of the metabolic rates composes a good basis for studying and understanding the role of the photosynthesis in the interaction of the trees and in the stand development.

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SELOSTE

Männyn yhteyttämistuotos luontaisessa kasvuympäristössä

Yhteyttämisenä muodostuu auringon energian avulla hiilidioksidista ja vedestä hiilihydraatteja, joita kasvi käyttää kasvuun ja elintoimintojen energian lähteenä. Männyn fotosynteesinopeus neulasten pinta-alayksikköä kohti vaihtelee suuresti luonnonoloissa. Fotosynteesi ei ole suoraan mitattavissa, mutta lehden tai verson hiilidioksidin vaihtoa voidaan mitata. Hiilidioksidin vaihtonopeudesta ja respiraationopeudesta voidaan laskea fotosynteesinopeus.

Fotosynteesiä voidaan tarkastella kaksivaiheisena tapahtumana: ensiksi ilman hiilidioksidin diffuusio ilmarakojen kautta neulaseen solujen sisälle ja toiseksi hiilidioksidin biokemiallinen sitoutuminen hiilihydraateiksi. Ilman hiilidioksidin diffuusio neulaseen soluihin noudattaa diffuusion fysikaalisia lainalaisuuksia (Gaastra 1959). Hiilidioksidin biokemialliseen sitoutumiseen hiilihydraateiksi tarvitaan energiaa, joka sitoutuu auringon säteilystä fotosynteesin valoreaktioissa. Hiilihydraattien muodostuminen sisältää useita välivaiheita ja useiden entsyymien toimintaa. Solujen monissa reaktioissa tarvitaan energiaa. Sitä vapautuu hiilihydraateista respiraatioreaktioissa. Fotosynteesi- ja respiraatioreaktiot tapahtuvat neulassa samanaikaisesti. Ilman hiilidioksidin virratessa ilmarakojen kautta neulaseen sisään samanaikaisesti virtaa vesihöyryä neulaseen sisältä ulkoilmaan. Ulkoilman vesipitoisuus vaikuttaa haihduntaan. Fotosynteesi ja haihdunta kytkettyvät läheisesti toisiinsa ilmarakojen kautta. Avaamalla ja sulkemalla ilmarakojen kasvi voi säädellä haihduntaa. Ympäristötekijät vaikuttavat kasvien fotosynteesiin, respiraatioon ja haihduntaan. Tässä työssä tutkitaan männyn (*Pinus sylvestris*) fotosynteesi- ja haihduntanopeuden riippuvuutta ympäristötekijöistä ja aineenvaihduksen säätymisestä luontaisessa kasvuympäristössä. Työssä arvioidaan eri ympäristötekijöiden merkitystä männyn yhteyttämistuotokseen.

Hiilidioksidin vaihdon ja ympäristötekijöiden mittaukset suoritettiin n. 20 vuotiaassa männikössä, joka sijaitsee Helsingin yliopiston metsäaseman läheisyydessä (61°51'N, 24°17'E, 160 m m.p.y.). Hiilidioksidin vaihdon ja ympäristötekijöiden mittaukset tehtiin automaattisella mittausjärjestelmällä. Hiilidioksidin vaihtoa ja ympäristötekijöitä mitattiin 13:sta toukokuuta 30:nteen marraskuuta 1982, 26:sta kesäkuuta 6:nteen lokakuuta 1984 ja 1:stä heinäkuuta 26:nteen lokakuuta 1985. Hiilidioksidin vaihtoa mitattiin kahdesta puusta 1982 ja yhdestä puusta vuosina 1984 ja 1985. Koepuusta mittaukset tehtiin toisen ja neljännen oksakiehkuran yksi-vuotiaasta versosta. Hiilidioksidin vaihdon, auringon säteilyn ja lämpötilan mittaukset suoritettiin samanhetkeisesti. Tutkimuksen aineistona käytettiin automaattisella mittausjärjestelmällä samasta metsiköstä tehtyjä mikrometeorologisia havaintoja: ilman kuiva- ja märkälämpötila, sademäärä, sateen alku ja loppu. Tutkimuksessa käytettiin myös Ilmatieteen laitoksen lämpötilan ja auringon säteilyn havaintosarjoja. Jokioista vuosilta 1958-1977 sekä sadehavaintoja Tampereelta vuosilta 1883-1984.

Tässä työssä tutkittiin fotosynteesinopeuden riippuvuutta auringon säteilystä, lämpötilasta, vedestä (ilma-

rakojen säätelystä) ja vuosirytmistä sekä haihduntanopeuden riippuvuutta ilman kosteudesta ja ilmarakojen säätelystä. Fotosynteesi- ja haihduntanopeuden riippuvuudesta ympäristötekijöistä ja aineenvaihduksen säätymisestä laadittiin dynaaminen malli. Yhteyttämistuotos ja haihduntamäärä pitemmän ajan kuluessa saatiin integroimalla fotosynteesi- ja haihduntanopeus. Metsikön haihdunnan ja vesiolosuhteiden vuorovaikutuksesta laadittiin myös dynaaminen malli. Sen avulla simuloitiin metsikön haihduntaa ja maan vesimäärää. Mallin avulla tarkasteltiin maan vesipitoisuuden ja ilmarakojen säteilyn välistä riippuvuutta. Auringon säteilyn ja lämpötilan ajallista vaihtelua pitkän aikajakson kuluessa tarkasteltiin säähavaintosarjoista. Sademäärien jakautumista pitkänä aikajaksona tarkasteltiin samoin säähavaintosarjoista. Fotosynteesituotoksen mallilla laskettiin auringon säteilyn ja lämpötilan havaintosarjoja käyttäen fotosynteesituotos kevät-, kesä- ja syksyjaksolle sekä vuotuinen fotosynteesituotos vuosille 1958-1977. Näiden avulla arvioitiin auringon säteilyn, lämpötilan ja vuosirytmien vaihtelun merkitystä fotosynteesituotoksen vaihteluun. Ilmarakojen säätelyn ja vedenpuutteen merkitystä fotosynteesituotokseen arvioitiin vuosille 1982, 1984 ja 1985 lasketun fotosynteesituotoksen avulla.

Tutkimuksen päätulokset ovat seuraavat:

1. Fotosynteesinopeuden riippuvuus auringon säteilystä on stabiili kasvukauden aikana. Auringon säteily dominoi fotosynteesinopeuden riippuvuutta ympäristötekijöistä suurimman ajan fotosynteesin aktiivisena jaksena.
2. Lämpötilan vaikutus fotosynteesinopeuteen on merkittävä lämpötila-alueella $-5\text{ }^{\circ}\text{C} - +3\text{ }^{\circ}\text{C}$.
3. Veden puutteen vaikutus yhteyttämistuotokseen on useimmiten melko vähäistä Suomen ilmasto-oloissa, mutta joinakin poikkeuksellisen kuivina sääjaksoina on selvästi havaittavissa veden puutteen vaikutus fotosynteesinopeuteen. Tällaisina jaksoina veden puute vähentää yhteyttämistuotosta.
4. Metsiköstä mitattu aineisto tuki ilmarakojen optimaaliselle säädölle esitettyä neljää kvalitatiivista ominaisuutta. Kaksi esitettyä kvalitatiivista ominaisuutta vaatii lisätutkimusta.
5. Maan vesimäärä muodostaa takaisinkytkentä säädön kaasuaineenvaihduksen ja maan, kasvin ja ilman dynaamisten vesisuhteiden välillä.
6. Vuotuisen yhteyttämistuotoksen määrään vaikuttaa Suomen ilmasto-oloissa pääasissa fotosynteesin aktiivisen jakson pituus sekä kesäkuukausien auringon säteily. Pilvisyys vähentää yhteyttämistuotosta vaihtelevasti eri kesinä. Veden puute alentaa selvästi yhteyttämistuotosta harvoin esiintyvistä poikkeuksellisen kuivina kesinä.

7. Männyn vuotuinen yhteyttämistuotos on varjostamattomissa olosuhteissa keskimäärin 1.9 g C dm^{-2} .
8. Mallin rakenne teki mahdolliseksi kaasuaineenvaihduksen analysoinnin vaihtelevissa ympäristöoloissa ja eri vuoden aikoina.

Yhteyttämistuotos on aineenvaihduksen prosesseihin pohjautuvien metsikön kasvu- ja tuotosten mallien peruselementti. Aineenvaihduksen prosessien ja ympäristötekijöiden välisen kausaalisen riippuvuuden tunteminen muodostaa käyttökelpoisen perustan primäärituotoksen tutkimiseen ja arviointiin metsikön kehityksen eri ikävaiheissa ja vaihtelevassa tiheydessä.

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