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RISTO SIEVÄNEN

A PRELIMINARY SIMULATION
MODEL FOR ANNUAL PHOTO-
SYNTHETIC PRODUCTION AND
GROWTH IN A SHORT ROTATION
PLANTATION

ALUSTAVA LYHYTKIERTO-
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KASVUN SIMULOINTIMALLI

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Risto Sievänen

A PRELIMINARY SIMULATION MODEL FOR ANNUAL
PHOTOSYNTHETIC PRODUCTION AND GROWTH IN A SHORT
ROTATION PLANTATION

Alustava lyhytkiertoviljelmän vuotuisen fotosynteesin
tuotoksen ja kasvun simulointimalli

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A simple simulation model for photosynthesis and growth in a short rotation plantation is presented. The plantation is described in terms of dry weight and carbohydrate concentration of plants. Photosynthesis, growth and seasonal changes of the plant's activity throughout the growing period are considered as separate processes. Two versions of the model are fitted to the measurements with simulation technique. No unique set of parameters can be obtained. The implications of the fitting for the model development are discussed.

Lyhytkiertoviljelmän fotosynteesille ja kasvulle esitetään yksinkertainen simulointimalli. Viljelmä kuvataan kasvien kuivapainon ja hiilihydraattipitoisuuden avulla. Fotosynteesiä, kasvua ja kasvien aktiviteetin vuodenaikaisvaihtelua kasvukauden aikana tarkastellaan mallissa erillisinä prosesseina. Mallin kaksi eri versiota sovitetaan mittaustuloksiin, mutta parametreille ei saada yksikäsitteisiä arvoja. Sovituksen tuloksia tarkastellaan mallin kehittämisen kannalta.

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1. INTRODUCTION

A short rotation plantation has many interesting special features. It can be subjected to intensive cultivation and the yield can be affected by controlling the environment. The same methods as are employed in improving the yield of cereal crops can be used to increase the production of a short rotation plantation by optimizing all the factors which have an effect on the yield. It is believed that a dynamic model is of great help in such work (cf. de Wit et al. 1978). By using dynamic model, the influence of relevant factors can be ef-

fectively analysed and the related empirical research guided. Furthermore, a dynamic model can reduce the time needed to achieve results in comparison to the traditional methods since simulations can substitute for time consuming experiments.

The aim of the present study is to establish a basic simulation model which can later be enlarged and made more complicated. Two different versions of the model are presented. Both versions are tested using data collected during summer 1978.

2. OUTLINE OF THE MODEL AND THE RELATED MEASUREMENTS

2.1. Structure of the model

The model was built to describe a *Salix* cv. 'Aquatika' plantation. The density of the plantation was 16 cuttings per square meter and its age two years. The shoots had been cut during the winter 1977—1978. Irrigation and the nutrient status of the plantation were kept at a satisfactory level.

The model assumes that the plantation is homogenous and describes it in amounts per unit ground area. In the model the plantation has two compartments: the dry weight of the shoots (DW) and the carbohydrate pool (C) (which is supposed to be evenly distributed throughout the plant). The roots are not included in the model and the leaf area (LA) is computed as a measured function of DW for calculation of the photosynthetic rate. The daily mean temperatures and the daily totals of irradiance (measured with a Bellani pyranometer) were used as the environmental variables in the simulation.

The basic structure of the model is adopted from de Wit et al. (1970) and the energy flows in the model are depicted in Figure 1.

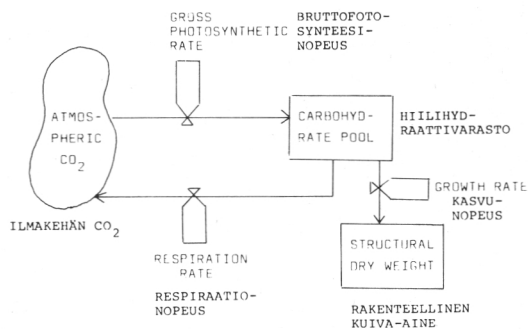


Figure 1. The energy flows in the model.
Kuva 1. Mallin energiavirrat

The formulae for the dependencies of process rates on the environmental variables were either derived from the measurements carried out during summer 1978 in the *Salix* 'Aquatika' plantation or taken from the literature.

2.2. Related measurements

The dependency of the photosynthetic rate on the environmental variables in the field was studied. The measuring facilities included: an IRGA-device with trap-type

pneumatically operated assimilation chambers, equipment for measuring light in photosynthetic studies (H a r i et al. 1976), temperature sensors and a data logging unit to control the system and to collect the data.

The following results were got for the model: The dependence of the net photosynthetic rate on irradiance is depicted in Figure 2. The respiration rate was approximately 10 % of the net photosynthetic rate. The shape of the curve depicted in Figure 2 remained constant during the measuring period whereas the level of the maximum net photosynthetic rate, P_m , showed pronounced variation. P_m is depicted in Figure 3 as a function of both time and daily mean temperature. Any dependence of the photosynthetic rate on the temperature during the day could not be found. It may be supposed that the photosynthetic rate in natural conditions is insensitive to small fluctuations in temperature around the average, and the effect of it is outside the resolution capacity of the equipment.

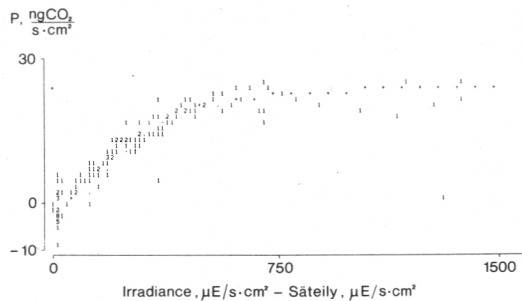


Figure 2. The relationship between the net photosynthetic rate and irradiance.
Kuva 2. Nettofotosynteesinopeuden riippuvuus säteilystä.

3. MATHEMATICAL DESCRIPTION OF THE MODEL

3.1. Stage of development

A plant exercises inner regulation of the rates of its different processes especially in the beginning and at the end of the active period (cf. H a r i 1972, S a r v a s 1972). The rates are not as high as in the middle or the growing period under the same environmental conditions. Such a

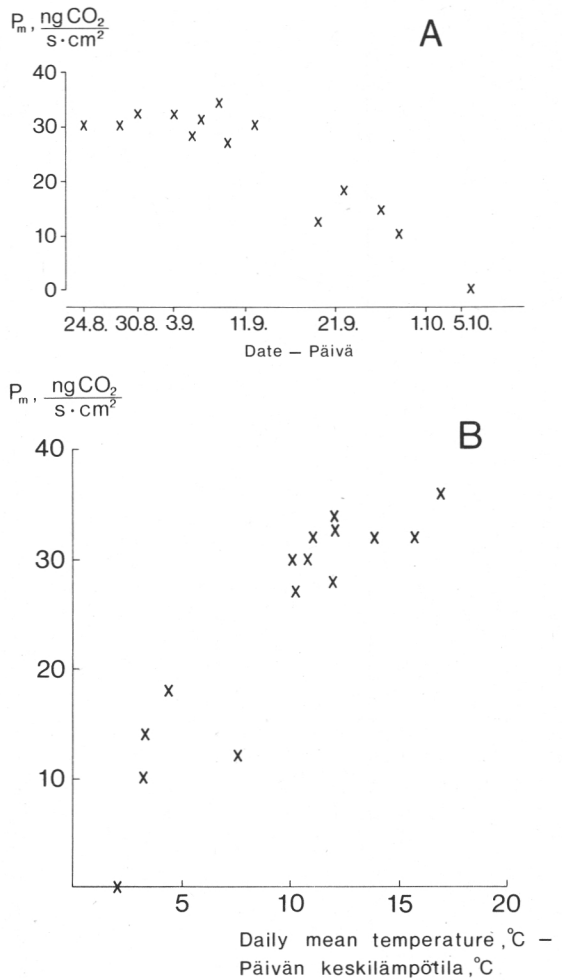


Figure 3. (A) The maximum net photosynthetic rate, P_m , during the measuring period, (B) P_m in relation to daily mean temperature.
Kuva 3. (A) Maksimaalinen nettofotosynteesinopeus, P_m (B) P_m päivän keskilämpötilan funktiona.

phenomenon was also observed in this study. An attempt was made to take it into consideration in two ways: (the resulting models are called model A and model B)

A) P e l k o n e n and H a r i (1979) have used a model to describe the springtime recovery of the CO_2 uptake in Scots pine. It was employed with slight modifications in

the following way: The maximum net photosynthetic rate (P_m) depends on the temperature (T) via the physiological stage of development for photosynthesis (s_p) in the following way:

$$P_m = P_{m1}s_p$$

$$\frac{ds_p}{dt} = \frac{A_1}{1 + A_1 2^{-(T - \frac{s_p}{A_2} - A_3)}} -$$

$$\frac{A_1}{1 + A_1 2^{(T - \frac{s_p}{A_2} - A_3)}} = f_1(T, s_p)$$

$$s_p(t_b) = 0$$

where P_{m1} , A_1 , A_2 and A_3 are parameters and t_b is the beginning instant of the active period.

The function $f_1(T, s_p)$ has the following property: when T is constant (or oscillates around a constant value) over a long period of time, s_p (solved from the corresponding differential equation) is adjusted so that $f_1(T, s_p) = 0$ i.e. s_p and P_m do not change in constant environmental conditions.

B) A model for the regulation of growth rate was tested as an alternative. It was adopted from Hari et al. (1977). The growth rate of DW ($\frac{dDW}{dt}$) is regulated through the physiological stage of development for growth (s_g) by the formulae

$$\frac{dDW}{dt} = f_2(s_g) F$$

$$\frac{ds_g}{dt} = e^{kT}$$

$$s_g(t_b) = 0$$

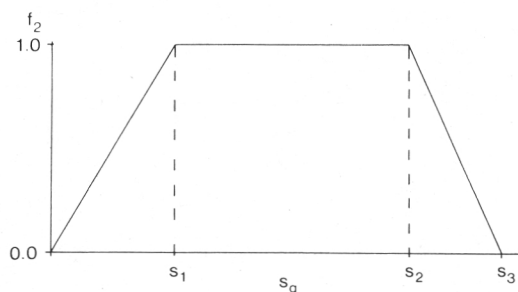


Figure 4. The relationship between function f_2 and s_g (see text for explanation).

Kuva 4. Kasvun fysiologisen kehitysvaiheen (s_g) vaikutus kasvunopeuteen.

where F is the effect of other factors on the growth rate (see 34.), k is a constant and f_2 has the form depicted in Figure 4, with parameters s_1 , s_2 and s_3 .

32. Net photosynthetic rate and respiration rate

The rate of net photosynthesis P was calculated using the formula

$$P = P_1 P_m LA f_3(i)$$

where P_1 is a constant which relates the photosynthesis and DW, i irradiance, f_3 is the effect of irradiance; because the daily totals of irradiance were used, the dependence depicted in Figure 2 could not be exploited; the relationship used (with parameter i_1), Figure 5, simulates the dependence.

LA was calculated as a function of DW. The relationship between LA and DW had been measured. P_m was related either on s_p (model A) or on T (model B). In the latter case the dependence was taken from measurements (Fig. 3b) and is depicted in Figure 6.

According to the measurements the respiration rate was approximately 10 % of the net photosynthetic rate. No measured data were available about maintenance respiration. For this reason the respiration rate was linearly related to the gross photosynthetic rate, and its effect is taken into consideration in the formula for net photosynthetic rate.

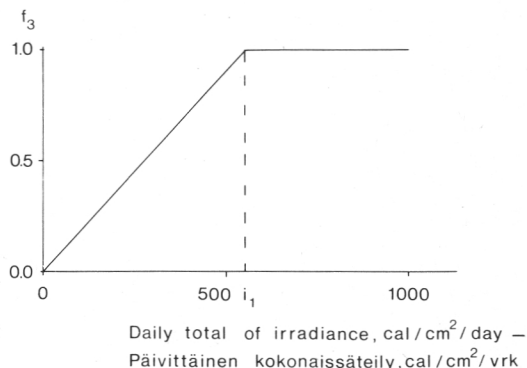


Figure 5. The relationship between function f_3 and daily totals of irradiance (see text for explanation).
Kuva 5. Päivittäisen kokonaissäteilyn vaikutus nettofotosynteesinopeuteen.

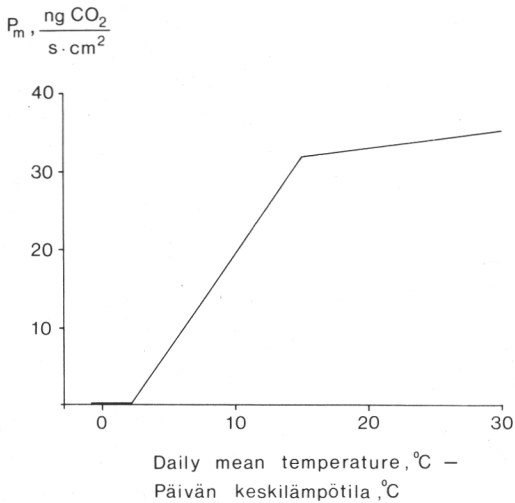


Figure 6. The relationship between the maximum photosynthetic rate, P_m , and the temperature, T (model B).

Kuva 6. Nettofotosynteesinopeuden maksimitason, P_m riippuvuus päivittäisestä keskilämpötilasta mallin B-versiossa.

33. Dynamics of the amount of carbohydrates

As a consequence of the structure of the model the amount of C is governed by

$$\frac{dC}{dt} = P - \frac{dDW}{dt}$$

The initial value of C was taken to be $\frac{DW}{5}$

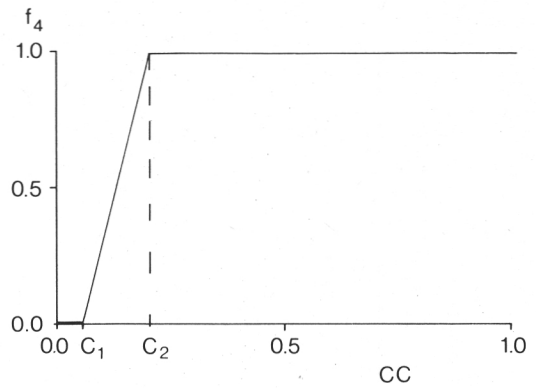


Figure 7. The relationship between function f_4 and CC (for explanation see text).

Kuva 7. Kasvunopeuden riippuvuus kasvin hiilihydraattipitoisuudesta CC .

34. Growth rate of dry weight

The growth rate of DW , $\frac{dDW}{dt}$, was assumed to depend on temperature, the carbohydrate content of the Plant (CC) and to be directly proportional to C :

$$\frac{dDW}{dt} = w f_4(CC) e^{hTC} \quad (\text{model A})$$

$$\frac{dDW}{dt} = w f_2(s_g) f_4(CC) e^{hTC} \quad (\text{model B})$$

where w and h are parameters, $CC = \frac{C}{C + DW}$. The dependence of f_4 on CC is depicted in Figure 7 (f_4 has parameters C_1 and C_2) and $f_2(s_g)$ is the effect of regulation (see 31.A.).

4. SIMULATION

Both models were tested with field data. The time courses of environmental variables are presented in Figure 8. The models were written in MIMIC language. The models were fitted to the data by simulating and using a computer terminal interactively. The best fit was obtained with the following values for the parameters:

Parameters common for models A and B

$$\begin{array}{ll} P_1 = 0.0011 & i_1 = 550 \\ C_1 = 0.05 & C_2 = 0.2 \\ w = 1.0 & h = 0.026 \end{array}$$

Parameters for model A

$$\begin{array}{ll} P_{m1} = 0.0013 & A_1 = 181 \\ A_2 = 79 & A_3 = 8 \end{array}$$

Parameters for model B

$$\begin{array}{ll} s_1 = 130 & s_2 = 385 \\ k = 0.1 & s_3 = 480 \end{array}$$

The obtained set of parameter values is not unique. When values for some parameters were chosen beforehand, values for others could be found to give a fairly good

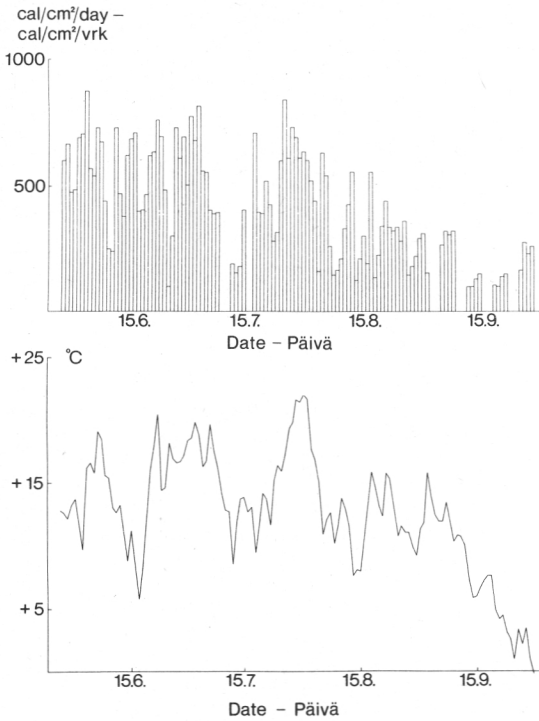


Figure 8. The time courses of daily mean temperature and daily totals of irradiation.
 Kuva 8. Päivittäinen keskilämpötila ja kokonais-
 säteily tutkimusjakson aikana.

fit. The reason for this is the small number of measured variables (= 1) in comparison to the large number of parameters.

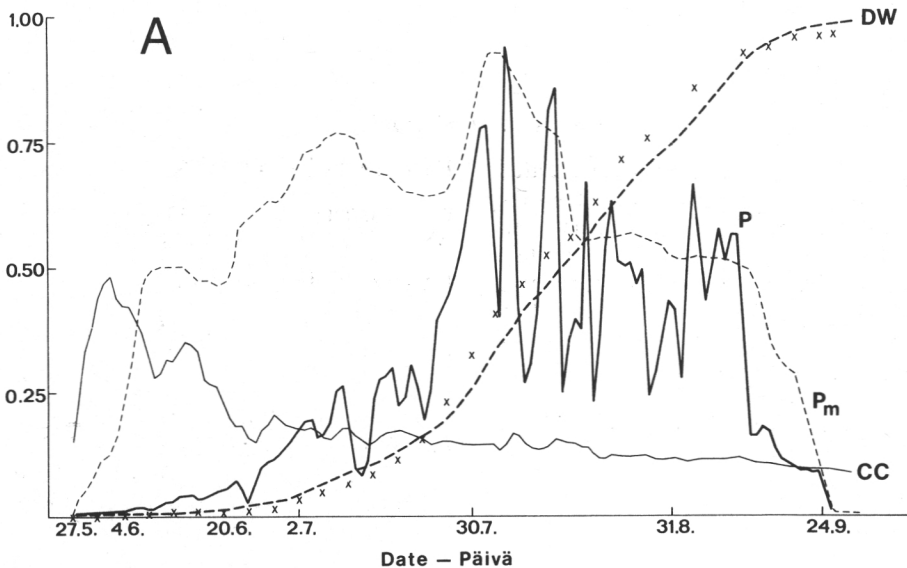
The results of simulation can be seen in Figure 9 for both models. The discrepancy

between the computed and measured values in the middle and at the end of the growing period of model A is due to the fact that regulation of P_m through s_p did not ensure a sufficiently rapid decrease of the growth rate of DW during the autumn. The simulated time course of P_m is qualitatively the same as the measured one (Fig. 3a).

Model B in turn gives too optimistic values for DW in the beginning of the growing period and has a better fit during the rest of the summer. The model predicts unrealistically large values for carbohydrate concentration at the beginning. During the autumn the time course of CC is more realistic than that of model A (cf. Axelsson and Ågren 1976). On the other hand the simulated sharp increase of CC in the beginning (with both models) may be artefactual because the models may give too crude a description for the plantation when the plants are very small.

The simulations revealed some interesting features of the models. The length of the active period has a pronounced effect on yield because the accumulation of DW mainly occurs during the rest of summer.

The net photosynthetic rate was linearly related to the leaf area. The difficulties involved in fitting models either in the beginning of at the end of the growing period may reflect the effect of the canopy architecture on photosynthesis. The linear approximation does not cover the whole growing period.



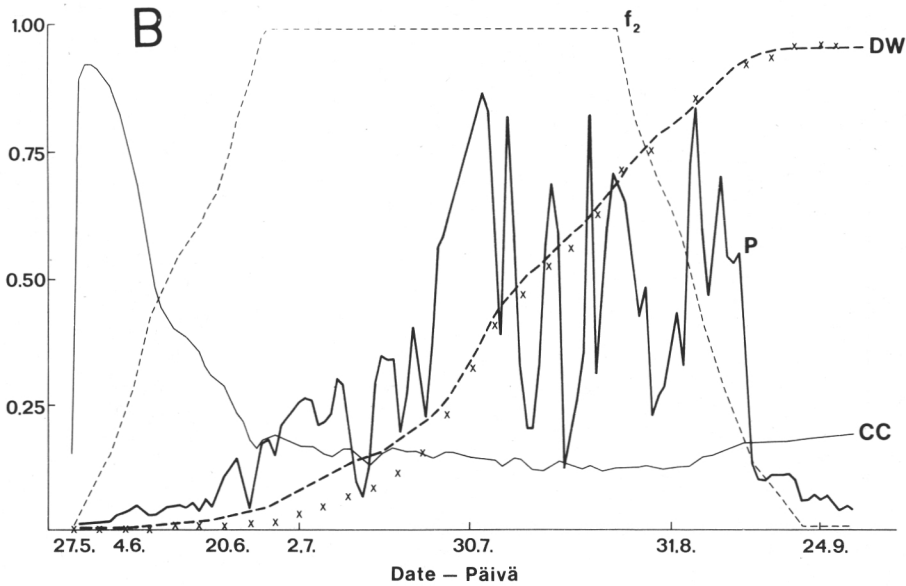


Figure 9. The simulated results for model A (A) and for model B (B). The crosses are measured values of DW. The ranges of values are following:

DW: 0...1 (kg/m²), CC: 0...1
 P_m : 0...32 (ng CO₂/s·cm²/m²) (model A),
 f_2 (s_g): 0...1 (model B),
 P : 0...3.5·10⁵ (ngCO₂/s/m²)

Kuva 9. Sovituksen tulos mallille A (A) ja mallille B (B). Ristit ovat mitattuja kuiva-aineen määriä. Eri suureiden vaihteluvälit ovat seuraavat:

DW (kuiva-aine): 0...1 (kg/m²),
 CC (hiilhydraattipitoisuus) 0...1,
 P_m (maksimi nettofotosynteesinopeus): 0...32 (ngCO₂/s·cm²/m²)
 (malli A), f_2 (s_g) (kehitysvaiheen vaikutus kasvunopeuteen): 0...1 (malli B),
 P (nettofotosynteesinopeus): 0...3.5·10⁵ (ngCO₂/s/m²)

5. DISCUSSION

The models presented are rather simple and involve many far-reaching assumptions. Some points may be mentioned.

The description of the plantation in terms of dry weight of shoots and carbohydrate pool neglects the separate active roles of the leaves, shoots and roots. The ratio between the shoots, roots and leaves is not likely to remain constant throughout the summer. The distribution of photosynthates is a very important factor for the development of a plant (cf. Monsi and Murata 1970, Axelsson and Ågren 1976). The net photosynthetic rate was linearly related to leaf area. It ignores the effect of the canopy architecture, which varies during the

summer, on photosynthesis. Respiration is an important process in the energy economy of a plant (McCree 1970). It is not only related to photosynthesis but it also contains the maintenance respiration component which may in some circumstances be important. The environment of the plantation had two components: daily total of irradiation and daily mean temperature. An accurate model should have smaller time steps for temperature and light. The use of daily mean temperature and daily total irradiance may give biased results because the dependencies of rates of the temperature and irradiance at a given moment are nonlinear. The CO₂ gradient in the canopy,

water and nutrient contents of the soil should be included in the environmental variables, too.

In the next stage of the modelling, work will be concentrated on improving the treatment of canopy photosynthesis, distribution of photosynthates during the growth period

and respiration. These research topics should also be the main points of related empirical research. The (net) photosynthetic efficiency is the most important factor affecting the yield. For this reason factors affecting the net photosynthesis of a canopy should be carefully analysed.

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SELOSTE

Lyhytkiertoviljelynä kasvatettava energiaviljelmä on uusi tutkimuskohde Suomessa. Sen tuottoon vaikuttavat monet tekijät. Voidaan olettaa, että lyhytkiertoviljelmää kuvaavalla simulointimallilla on mahdollista ohjata tehokkaasti viljelmän tuoton kohottamiseksi tapahtuvaa tutkimusta.

Laadittu malli on yksinkertainen, ja siinä kasvusto on kuvattu kasvien kuivapainon ja hiilihydraattipitoisuuden avulla. Kasvuston lehtipinta-ala lasketaan mittauksiin sovitettun regressioyhtälön avulla. Juuria mallissa ei tarkastella.

Mallin perusrakenne on otettu kirjallisuudesta, ja energiavirrat (massavirrat), joiden tuloksena kuiva-aine syntyy, on esitetty kuvassa 1. Toisiinsa vaikuttavina prosseina tarkastellaan fotosynteesiä, kasvua ja kasvien aktiiviteetin vuodenaikaista vaihtelua. Ympäristötekijöinä käytetään päivittäistä keskilämpötilaa ja kokonaissäteilyä.

Mallista käytetään kahta erilaista muunnosta. Ensimmäisessä vaihtoehdossa oletetaan maksimaalisen fotosynteesinopeuden (hetkellinen fotosynteesinopeus riippuu valon intensiteetistä ja lämpötilasta) riippuvan lämpötilan vaikutuksesta muuttuvasta kehitysvai-

heesta. Tällöin kasvunopeus riippuu vain lämpötilasta ja labiilien hiilihydraattien määrästä. Toisessa vaihtoehdossa asetetaan maksimaalinen fotosynteesinopeus vakioksi, ja oletetaan maksimaalisen kasvunopeuden riippuvan epälineaarisesti lämpötilan mukaan etenevästä kehitysvaiheesta. Myös tässä kasvunopeus riippuu hiilihydraattien määrästä ja lämpötilasta.

Molemmat versiot sovitettiin mittauksiin simulointitekniikalla. Mitattuja suureita oli vain yksi, kuiva-aineen määrä ja parametrejä mallissa useita, joten niille ei saada yksikäsitteisiä arvoja.

Simuloinneissa kävi ilmi, ettei kummallakaan versiolla pystytä täydellisesti kuvaamaan koko kasvukautta. Tämän voi arvella johtuvan siitä, että kasvit säätelevät sekä fotosynteesiä että kasvua. Kasvukauden alussa molemmat mallin versiot antoivat varsin suuria hiilihydraattipitoisuuksia, joita tuskin luonnossa tavataan.

Kokemuksien perusteella voidaan päätellä, että ensisijaisesti tarkennusta kaipaavia kohtia ovat kasvuston fotosynteesiprosessin ja fotosynteesituotteiden jakautumisen kuvaukset.

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