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ANNUAL GROWTH LEVEL OF SOME PLANT SPECIES AS A FUNCTION OF LIGHT AVAILABLE FOR PHOTOSYNTHESIS

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SELOSTE:

ERÄIDEN METSÄKASVILAJIEN VUOTUISEN KASVUN JA FOTOSYNTEESISSÄ KÄYTTÖKELPOISEN VALON SUHDE

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A quantitative method for determining the annual growth level of plant species has been presented. In particular, attention is paid to the dependence of the growth level on the amount of light available for photosynthesis. A mathematical model for the dependence of structural matter production on photosynthetic production has been presented for some plant species.

INTRODUCTION

Recongnition of the relationship between environmental factors and plant growth is of prime importance in the manipulation of ecological systems. HARI *et al.* (1977) have applied the following model to the analysis of this interaction

$$(1) \qquad B_j = f(s_j) \cdot k_j \cdot a,$$

where B_j denotes daily production of structural matter, $f(s_j)$ self regulation of the plant species, k_j the direct effect of environment and a the level of growth (cf. also KELLOMÄKI *et al.* 1977a, LEHTONEN *et al.* 1977).

During the formation of structural matter temperature plays a role of prime importance in determining the self regulation of the plant species and the effect of environment, as demonstrated by HARI *et al.* (1977), and hence temperature is the only environmental factor included in the above model. The effect of other factors on growth takes place through the level parameter a, which determines the limits for daily variation of growth. It includes for example the effect of stand density, site fertility, light conditions and other factors having an effect on growth (cf. HARI *et al.* 1977, KELLOMÄKI *et al.* 1977b).

Carbon assimilation is basic to primary production, and hence the factors affecting it are of primary importance when considering the role of different factors in determining the level of daily growth (cf. EMMINGHAM and WARING 1977). In particular, the total amount of annual photosynthesis is of great importance in determining the relationship between photosynthetic production and structural matter production, as demonstrated for example by LEDIG (1969, 1976).

As light is the basic factor controlling the rate of photosynthesis, the light conditions set limits for the maximum annual production which a plant species is capable of attaining (cf. HORN 1971). In other words, light conditions determine the basic limits, within which the annual variation of growth is dependent upon other environmental factors and the self regulation of the plant species in question (cf. HARI *et al.* 1977).

The aim of the present study is to describe a quantitative method for determining the annual growth level of plant species by means of their photosynthetic production, and to develop further the model for daily growth rate of plant species presented by HARI *et al.* (1977). Special attention is paid to the role of light available for photosynthesis as a limiting factor in the production of structural dry matter. Only production by the above ground parts of plant species has been considered.

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STUDY APPROACH

The study approach is the same as that used in our earlier study concerning the annual production of structural matter of some forest mosses (KELLOMÄKI *et al.* 1977 b). Thus the study is based on the assumption that the total amount of annual net photosynthesis plays a role of primary importance in determining the relationship between photosynthetic production and structural matter production. Let P(t) denote the amount of CO_2 fixed up to the moment t during the photosynthetically active period of a year. The photosynthetic rate, p, is defined as a time derivative of P

$$p = \frac{dP}{dt}. \tag{1}$$

The basic environmental factors determining the photosynthetic rate are light and temperature, if the water and nutrient supply is adequate (cf. for example EMMINGHAM and WARING 1977). Both factors can be expressed as functions of time. Let x denote temperature and y light intensity, then

$$p(t) = p(x(t), y(t)). \tag{2}$$

Let t_i be the initial and t_{i+1} the final instant of a certain time period. The amount of fixed CO_2 during the period $[t_i, t_{i+1}]$ can be approximated by integrals as follows

$$P(t_{i+1}) - P(t_i) = \int_{t_i}^{t_{i+1}} p(x(t), y(t))dt \quad \text{(cf. HARI 1976).} \tag{3}$$

The concept of photosynthetic light ratio, PLR, presented by KELLOMÄKI *et al.* (1977 b), was utilized in quantifying the principle presented in Eq. (3). Photosynthetic light ratio is defined as the ratio between the total amount of CO_2 fixed in an actual environment divided by the total amount of CO_2 fixed in the reference environment. The value of PLR can be approximated through light and temperature measurements. Let y_{ae} denote light intensity in the actual environment and y_{re} in the reference environment. Then the photosynthetic light ratio is

$$PLR = \frac{\int_{t_i}^{t_{i+1}} p(x(t), y_{ae}(t))dt}{\int_{t_i}^{t_{i+1}} p(x(t), y_{re}(t))dt}. \tag{4}$$

Thus, the ratio PLR indicates how much photosynthetic products a plant species has available for growth processes, accumulated during the period $[t_i, t_{i+1}]$, compared with the situation in the reference environment. Since the photosynthetic response of a plant species to light and temperature is specific for each plant species, the plant specific functions for the photosynthetic rate must be taken into consideration. Thus, the photosynthetic light ratio can be easily extended to cover a great variety of plant species. Since carbon assimilation is basic to primary production, the estimates of photosynthetic light ratio should bear a close relationship to the productivity of plant species (cf. also EMMINGHAM and WARING 1977).

MATERIAL

The material was collected during 1975 and 1976 at the Forest Field Station of the University of Helsinki (60° 50'N, 24° 20'E, 150 m a.s.l.), in Central Finland. Several stands representing density classes from open to a basal area of 34 m² per hectare were included in the material. All the stands were of the *Myrtillus* site type according to the classification of CAJANDER (1949), *i.e.* of intermediate fertility. Tree covered stands were dominated by Norway spruce (*Picea abies* (L.) Karst.). The following members of the ground cover communities were selected for study: *Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L. and *Avenella flexuosa* (L.) Parl. In order to determine the annual yield of these species a sample area 10 m × 10 m in size was marked out in each stand. Five sample plots, each one meter square, were selected from each sample area (cf. Fig. 1). The total biomass of the shoots and their share of the structural matter produced during the course of the study period, *i.e.* May 1 — July 31, were determined gravimetrically (105° C, 24 h) (cf. NEWBOULD 1967). The results for the five sample plots were pooled and expressed as g/m².

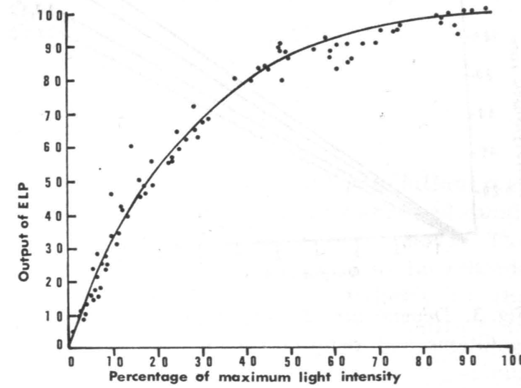

Fig. 2. The output of ELP as a function of percentage of maximum light intensity during summer.

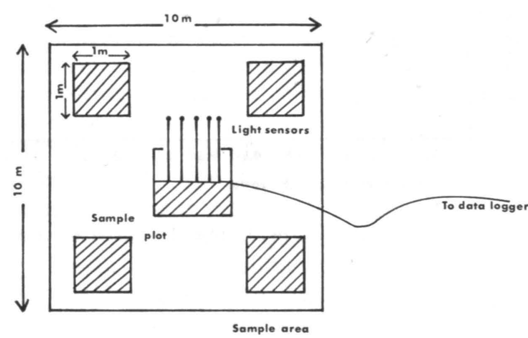

Fig. 1. Experimental layout for sampling the productivity of ground cover and monitoring light conditions in sample area.

The light conditions just above the canopy of the field layer and in the clear cut area were monitored using equipment which simulated photosynthetic production (ELP). The equipment is descriped in detail by HARI *et al.* (1976) (cf. Fig. 2). The positioning of the sensors in each sample area are presented in Fig. 1. The output from each sensor were pooled in the calculations, as presented by HARI *et al.* (1976). The dependence of photosynthetic rate on light conditions and temperature, needed for estimation of total photosynthesis was determined using an infrared gas analyser (model URAS 2T). Measurements were carried out in the open measuring system described by PELKONEN *et al.* (1975) utilizing natural plant populations in the study area.

RESULTS

The dependence of photosynthesis on light conditions and temperature for each species are given in Figs. 3—5. For the small variation in temperature during the measuring periods only a limited number of functions for each species are depicted. The mathematical methods used in computing the values for net CO_2 uptake rate with light

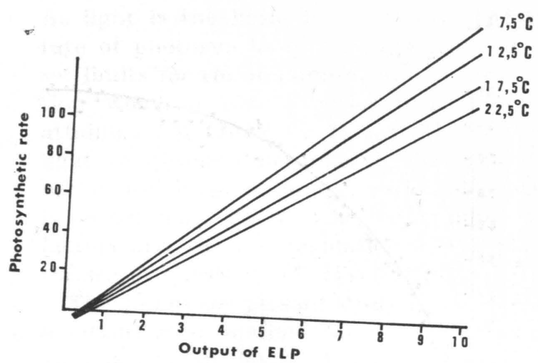

Fig. 3. Dependence of photosynthetic rate on light conditions and temperature for *Vaccinium myrtillus*.

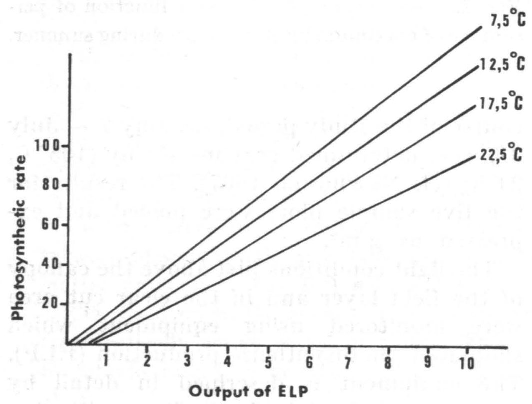

Fig. 4. Same as in Fig. 3. but *Vaccinium vitis-idaéa*.

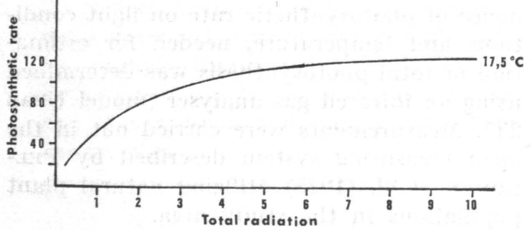

Fig. 5. Dependence of photosynthetic rate on light intensity for *Avenella flexuosa*.

conditions and temperature are described in detail by HARI and LUUKKANEN (1974).

Computation of the photosynthetic light ratio was carried out on a daily basis. The variation in the daily values was so small, however, that the value determined from measurements carried out during a seven day period was considered to give an accu-

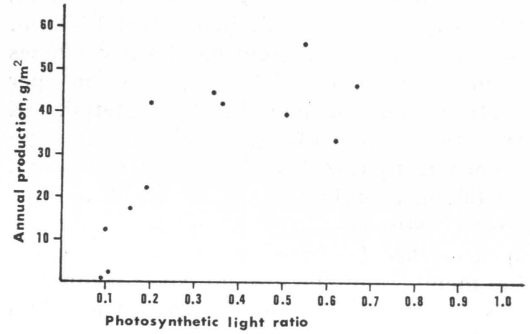

Fig. 6. Regression between photosynthetic light ratio and structural matter production for *Vaccinium myrtillus*.

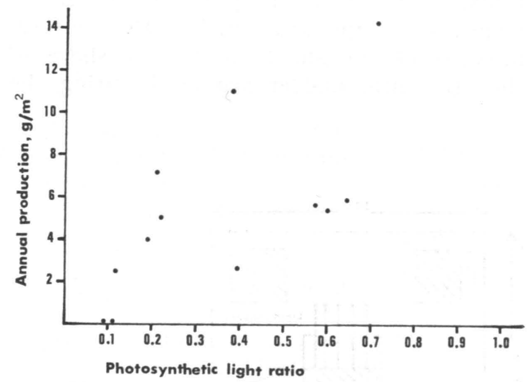

Fig. 7. Same as in Fig. 6 but *Vaccinium vitis-idaéa*.

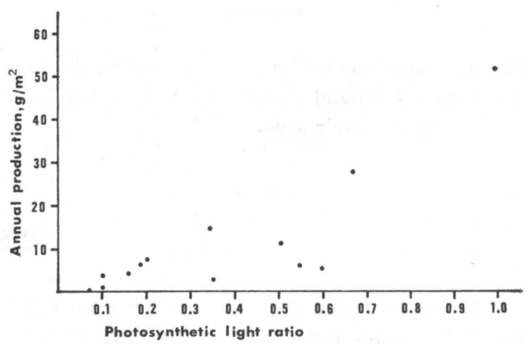

Fig. 8. Same as in Fig. 6 but *Avenella flexuosa*.

rate enough result. In computation, the photosynthetic production in the actual environment was related to the photosynthetic production in the clear cut area. The annual production of structural dry matter for each stand and species are shown in Figs. 6–8, as a function of the photosynthetic light ratio.

DISCUSSION

The dependence of photosynthetic rate on light and temperature was determined by monitoring the CO_2 uptake rate of natural plant populations with an infrared gas analyser. Comparisons between the photosynthetic levels of different plant species are not possible owing to the study approach, *i.e.* the measurements do not describe photosynthesis of the plant species in absolute terms. Since the ratio between estimates for photosynthesis in an actual environment and a reference environment is utilized in further calculations, the measuring approach used in this study for photosynthesis should give rise to no objections, because the conditions in the actual and the reference environment have been the same for each of the species except for the light conditions. A detailed description of the measuring system applied in the present study is given by PELKONEN *et al.* (1975).

Monitoring of light conditions in an actual and reference environment is needed for estimating the values of the photosynthetic light ratio. This was carried out using the photosynthetic simulator described by HARI *et al.* (1976). Simulation is made possible because a linear relationship exists between the output of the equipment and photosynthesis, as the nonlinearity of the photosynthetic response to light conditions (cf. ROSS 1970) has been taken into account in the design of the equipment. This facilitates the monitoring of the response of a plant species to the environment in terms of photosynthetic production. This fact can be utilized in estimating the carbon resources available for growth and reproduction by a plant species and hence its status in the plant community as indicated by the photosynthetic light ratio (cf. MONSI and SAEKI 1953, HORN 1971). A more detailed discussion of the present measuring system is given by HARI *et al.* (1976) and KELLOMÄKI *et al.* (1977b).

The productivity of plant populations was determined by applying the harvested quadrat method (cf. NEWBOULD 1967). The present method is considered to be reliable and preferable, since the validity of the results is easily controlled in contrast to many of the methods available for productivity measurement (cf. WOODWELL and BOURDEAU 1964). Obtaining a reliable estimate involves, however, sampling which should include sufficient replications. In addition, the size of the sample plots has to be determined in relation to parameters of the population under study. In comparison with sample sizes suggested by GREIG-SMITH (1964) and MUELLER-DOMBOIS and ELLENBERG (1974) the sampling procedure should produce reliable estimates for the plant populations under study. Evidently, an increased number of replications would, however, have increased the reliability of the estimates. In particular, the mosaic pattern of the horizontal layout of the ground vegetation increases the variance of the estimates (cf. GREIG-SMITH 1964, KELLOMÄKI 1974, 1975).

There are clear differences between species as regards the effect of light conditions on the annual growth level. In particular, the relationship for *Avenella flexuosa* differs from those of other species, since its productivity seems to be linearily correlated with the amount of photosynthesis. The productivity of *Vaccinium myrtillus* and *Vaccinium vitis-idaea* reaches its maximum values at a relatively low photosynthetic light ratio value, and nonlinear relationships between productivity and amount of photosynthesis seem to be characteristic for these species. There is, however, pronounced variation in each relationship due to factors other than light. The role of variation in soil fertility is especially apparent owing to the crude classification of the sites applied in the present study. In particular, this seems to be evident in conditions where the light climate is not a limiting factor in production (cf. also ZAVITKOVSKI 1976). Recognition of the effect of soil fertility on photosynthetic functions should facilitate the obtaining of estimates for the relationship between photosynthetic production and the production of structural matter which are more precise than those produced now. More advanced material than the present one, however, is needed for further study of this phenomenon.

The annual level of plant growth is dependent on the total carbon resources available for growth as argued earlier. Thus the level parameter of the model for daily growth presented by HARI *et al.* (1977) can be presented as a function of photosynthetic light ratio as follows

(5) $$a = a\ (PLR).$$

On integration of Eqs. (1) and (5), the following model for the daily growth will be yielded

(6) $$B_j = f(s_j) \cdot k_j \cdot a(PLR),$$

where B_j is daily production of structural matter, $f(s_j)$ is the effect of self regulation, k_j is effect of temperature and a (PLR) is the growth level determined by regressions presented in Figs. 6–8. Since the level parameter can be estimated from light data, the daily amount of primary production can be predicted from pure environmental data, *i.e.* from temperature, light and site types of a stand. In principle, this fact enables the evaluation of the mutual role of different factors in the formation of structural matter needed in evaluation management practices of ecological systems.

In the present study only the role of light conditions in determining the growth level was studied. As demonstrated by the variation in the relationships between photosynthetic production and structural matter production there are additional factors which are of importance in determining the annual growth level of plant species. In particular, the role of site fertility is important, as discussed above. The present approach provides, however, a more comprehensive consideration of factors affecting the annual growth level than carried out now. In further developing of the present method the effect of soil fertility on photosynthetic functions, for example, should be investigated. Other additional factors can also be taken into consideration through photosynthetic functions.

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SELOSTE:

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Työssä on tutkittu vuotuisen kasvun tason ja fotosynteesissä käyttökelpoisen valon välistä suhdetta. Työssä esitetään tarkoitukseen soveltuva matemaattinen malli, jonka käyttökelpoisuutta on testattu muutamilla tavallisilla metsäkasvilajeilla. Työssä on myös pohdittu mallin käyttöä ennusteisiin, joissa kasvu pyritään laskemaan pelkkiä ympäristötekijöitä hyväksi käyttäen.