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ANNUAL PRODUCTION OF SOME FOREST MOSSES AS A FUNCTION OF LIGHT AVAILABLE FOR PHOTOSYNTHESIS

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SELOSTE:

ERÄIDEN METSÄSAMMALIEN VUOTUINEN TUOTOS FOTOSYNTEESISSÄ KÄYTTÖKELPOISEN VALON FUNKTIONA

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The aim of the present paper is to study the annual production of *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) B.S.G. and *Dicranum polysetum* Sw. as a function of light available for photosynthesis. The productivity of the above moss species is studied using the harvested quadrats method in spruce stands of the *Myrtillus* site type representing different stand density classes. The annual production of each species in different stands was correlated with the amount of light available for photosynthesis, i.e. with the photosynthetic production. Functions for the dependence of productivity on light conditions were produced for each species. The individual functions and their ecological significance are dicsussed.

INTRODUCTION

TAMM (1953) has demonstrated the importance of light in the distribution of a moss population within a stand. In addition, the role of throughfall is evident in dry matter production of forest mosses. KELLOMÄKI and HARI (1976) have reported the small water requirements of *Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum polysetum* (cf. also ANDERSON and BOURDEAU 1955, PETERSON and MAYO 1975) for photosynthesis. According to KAPPEN et al. (1975) dew formation and air humidity satisfy the photosynthetic requirements of bryophytes in desert conditions. Evidently, the small water requirements of bryophytes allow them to perform their photosynthetic functions in the boreal zone throughout the whole growth period except during long and extremely dry periods. Thus, light seems to play the main role in the environmental control of structural dry matter production of moss cushions as far as the normal range of temperature variation is concerned.

The aim of the present paper is to study the production of structural dry matter by *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium* splendens (Hedw.) B.S.G. and *Dicranum polysetum* Sw. as a function of light available for photosynthesis.

Professor Paavo Yli-Vakkuri, Head of Department of Silviculture of University of Helsinki, is acknowledged for his supporting attitude to the present study. The financial support from Academy of Finland is acknowledged.

STUDY APPROACH

The total amount of annual net photosynthesis is considered to be of primary importance in determining the relationship between photosynthetic production and structural matter production (cf. Horn 1971). Let P(t) denote the amount of CO_2 fixed up to the moment t during the photsynthetically active period of a year. The photosynthetic rate, p, is defined as the time derivative of P

$$(1) \qquad p = \frac{dP}{dt}.$$

The photosynthetic rate is determined to a great extent by light and temperature, if there is no water stress. Let x denote temperature and y light intensity (cf. Hari et al. 1976) then

$$(2) \qquad p = p(x, y).$$

The light intensity and temperature are easily monitored in the field and can be expressed as a function of time, i.e. x = x(t) and y = y(t). The photosynthetic rate also varies as a function of time, p = p(t). The variation in photosynthetic rate is caused by variation in the environmental factors. If there is no water stress, the photosynthetic rate is determined by light and temperature as follows

$$(3) \qquad p(t) = p(x(t), y(t)).$$

If the function p is known and if temperature and light intensity are known as a function of time, then the total amount of CO_2 fixed during the photosynthetically active period can be approximated by intergration

$$(4) \qquad P(t) = \int_{t_0}^{t} p(x(t), y(t))\, dt \text{ (cf. Hari 1976)}$$

where t_0 is the beginning instant of the photosynthetically active period.

The approximation of P(t) by Eq. (4) can be carried out if the photosynthetic response of a plant species to different light intensities and the light available for photosynthesis is known (cf. Horn 1971).

In order to obtain a quantitative measure for varying photosynthetic response a concept called photosynthetic light ratio, PLR, is defined as the ratio between the total amount of CO_2 fixed in a shaded place divided by the total amount of CO_2 fixed if there was no shading.

The value of PLR can be approximated through light and temperature measurements. Let y denote light intensity above the canopy and y_s under the canopy. Then the photosynthetic light ratio is approximately (cf. Eq. 4)

$$(5) \qquad PLR = \frac{\int_{t_0}^{t_1} p\,(x(t), y_s(t))\, dt}{\int_{t_0}^{t_1} p((t), y(t))\, dt}.$$

In other words, the photosynthetic production in an actual environment is related to the photosynthetic production above the canopy (cf. Horn 1971). Correlating the photosynthetic light ratio to annual production of structural matter should provide the regression demanded by the study problem.

MATERIAL

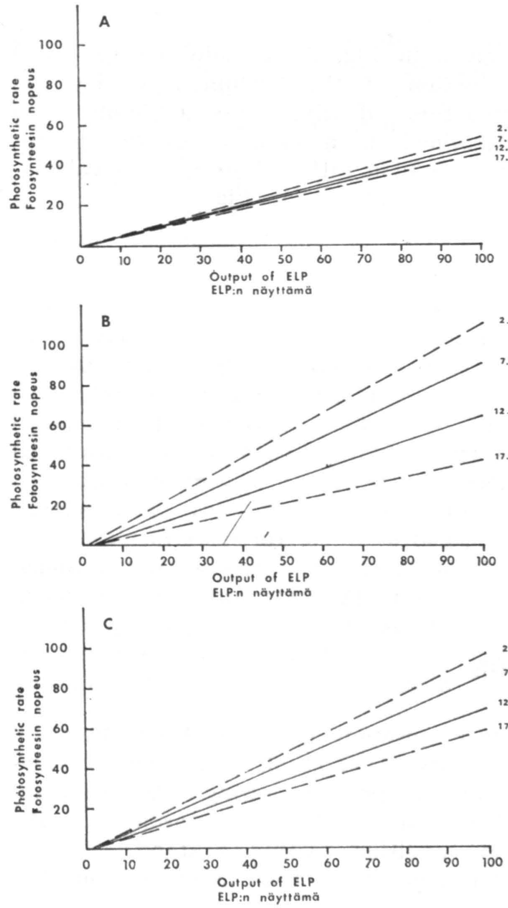
The study areas include several stands representing different density classes situated near the Forest Field Station of the University of Helsinki (60° 50' N, 24° 20' E, 150 m a.s.l.) in central Finland. All the stands were of the *Myrtillus* site type according to classification of Cajander (1949). Stand density classes from open to a basal area of 34 m^2/ha were included in the material. The tree stratum of each stand was dominated by Norway spruce *(Picea abies* L. Karst).

A sample area 10 × 10 m in size was selected from each stand. A sample consisting of five replications (400 cm^2 per

replication) was taken from each moss species. The total biomass of each plant species under study was determined gravimetrically in the laboratory (105° C, 24 h) (cf. Newbould 1967). One third of the total biomass of each species was considered as annual production (cf. Mälkönen 1974). The result for the five samples were pooled and expressed as g/m^2.

A photosynthetic simulator (ELP) described by Hari et al. (1976) was used to monitor the light conditions in which the plant communities under study existed (cf. also Kellomäki and Hari 1976). The light sensors were placed at the center of the sample area. The measuring equipment took into account only the light available for photosynthesis, i.e. it imitated the quantitative response of photosynthesis to different light intensities and rejected the excess light intensities (cf. Horn 1971). In order to eliminate random variation in the light pattern caused by clouds tree strata, the integrals covering a period of one daylight period were used in the calculations. In addition, the photosynthetic rates as determined by light conditions and temperature for the plant species under study, presented earlies by Kellomäki and Hari (1976), were utilized in the calculations.

METHODS AND RESULTS



The dependence of photosynthetic rate on temperature and light conditions for each moss species are given in Fig. 1. Using these regeressions the photosynthetic light ratio for each stand was determined by integrating the photosynthetic rate over the growth period and relating the estimate of total photosynthesis to that of the reference area, i.e. that of the clear cut area. In order to determine the role of light in structural matter production in moss cushions the annual production of each moss species in each stand was related to the photosynthetic light ratio respectively. The annual production of each moss species as a function of the photosynthetic light ratio

Fig. 1. Photosynthetic rate of study material as a function of light and temperature according to Kellomäki and Hari (1976).
A: *Pleurozium schreberi*
B: *Hylocomium splendens*
C: *Dicranum polysetum*

Kuva 1. Tutkittujen sammallajien fotosynteesinopeus valon ja lämpötilan funktiona Kellomäen *ja* Harin *(1976) mukaan.*
A: Pleurozium schreberi
B: Hylocomium splendens
C: Dicranum polysetum

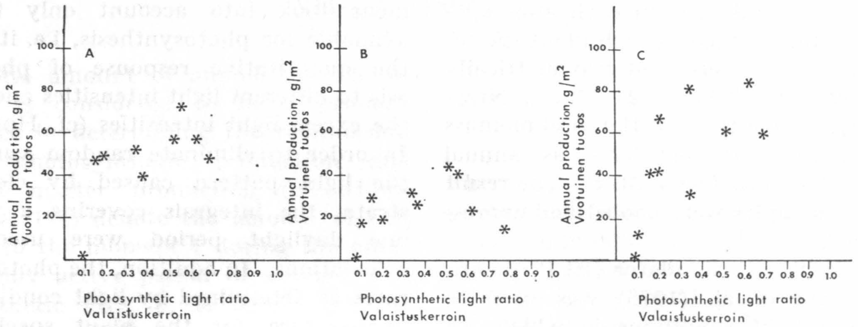


Fig. 2. Structural matter production of study material as a function of photosynthetic light ratio.
A: *Pleurozium schreberi*
B *Hylocomium splendens*
C: *Dicranum polysetum*

Kuva 2. Tutkittujen sammallajien kuiva-ainetuotanto valaistuskertoimen funktiona.
A: Pleurozium schreberi
B: Hylocomium splendens
C: Dicranum polysetum

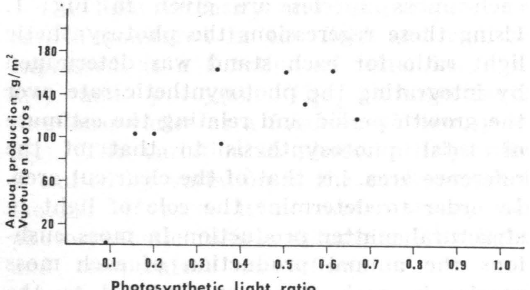


Fig. 3. Total production of moss cushions as a function of photosynthetic light ratio. Only the sample plots with all the species have been considered.

Kuva 3. Sammalkasvustojen kokonaistuotos valaistuskertoimen funktiona. Vain kaikki lajit sisältävät koealat on otettu huomioon.

is given in Fig. 2. In addition the total production of the bottom layer i.e. the production of the moss cushions, was determined as a function of the photosynthetic light ratio. Results of the calculations are presented in Fig. 3.

DISCUSSION

Determination of the photosynthetic light ratios is affected by the reliablity of the equipment used to monitor the light climate and the photosynthetic rate. The latter problem has earlier been discussed in detail by KELLOMÄKI and HARI (1976). The former question has also been discussed earlier by HARI et al. (1976) but it gives rise to some problems owing to the pronounced spatial and temporal variation in the light conditions within a stand.

An attempt has been made to avoid the temporal variation in light conditions by integrating the output of the electronic measuring system over the monitoring period. This procedure is based on the linear relationship between the output of the photosynthetic simulator and the photosynthetic rate. This facilitates the monitoring of the response of moss species to the environmental conditions in terms of photosynthesis, i.e. simulation of photosynthetic production (cf. HORN 1971).

Furthermore the spatial fluctuations in the light conditions give rise to many problems in carrying out light measurements within a stand. Reliable sampling of incoming radiation under the forest canopy would evidently require more sensors than used in the study (SCHOMAKER 1968). On the other hand, pooling the output from different sensors tends to average out the variation in the light conditions under the forest canopy. The measuring accuracy is, however, considered sufficient due to the utilizing values of photosynthetic light ratio, in further calculations instead of pure outputs from the sensors. Readers who are interested in obtaining more detailed information about the measuring of light conditions under a forest canopy should turn to more advanced discussions such as that by ANDERSON (1964) or HARI et al. (1976).

The forest canopy is selective as far as the penetration of radiation is concerend (cf. KNUCHELL 1914, COOMBE 1957). In particular, the share of the red and blue regions in the spectrun are reduced. This fact has, however, been omitted in carrying out measurements of the light conditions. Furthermore, the sensors used in the monitoring systems are sensitive to the red region of the spectrum. According to DAUBENMIRE (1959, pp. 218–221), the changes in the quality of the light as it passes through the canopy are, however, of little ecological importance, because each plant process is somewhat sensitive to all wavelengths of light.

The adaptation of each species to low light intensity is evident since no meaningful addition to production takes place when the photosynthetic light ratio reaches values greater than 0.3–0.4. In other words, the level of photosynthesis which is 30–40 per cent of that possible in the open, provides a sufficient supply of carbohydrates for the basic functions of the moss species studied. In particular, the adaption of *Hylocomium splendends* to low light intensity is evident and decreasing productivity at high light intensities seems to be possible. The productivity of *Pleurozium schreberi* and *Dicranum polysetum* increase with increases in the photosynthetic light ratio. These species seem to have greater light requirements than *Hylocomium splendens*. As a result of insufficient material the optimum light conditions for these species remain, however, undetermined but they seem to be higher for these species than for *Hylocomium splendens*. This kind of differentiation in adaptation was to be expected on the basis of the photosynthetic functions and earlier findings, for example, those of KUJALA (1926) and TAMM (1953).

The total production of the moss cushions was 150–180 g/m² at its maximum, depending on the light conditions. The result is of the same magnitude as that of TAMM (1953), MÄLKÖNEN (1974) and PERSSON (1976). Each moss species produces equal amounts and no clear differences exist, even though the annual production of *Hylocomium splendens* seems to be less than that of the other species. The differences in production levels may prove to meaningfull from the point of view of competition. Unfortunately, the present material does not facilitate evaluation of this difference in relation to the mutual successional ability of moss species and its effect on the structure of the ground cover community (cf. MONSI and SAEKI 1953).

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SELOSTE:

ERÄIDEN METSÄSAMMALIEN VUOTUINEN TUOTOS FOTOSYNTEESISSÄ KÄYTTÖKELPOISEN VALON FUNKTIONA

Työssä on tutkittu *Pleurozium schreberin* (Brid.) Mitt., *Hylocomium splendensin* (Hedw.) B.S.G. ja *Dicranum polysetumin* Sw. vuotuista kuiva-ainetuotantoa fotosynteesiin käytetyn valon funktiona. Tätä varten on tutkittu mainittujen sammallajien tuotosta satomenetelmällä mustikkatyypin metsiköissä, joiden puuston pohjapinta-ala vaihteli 00–34 m²/ha. Saatu tulos korreloitiin fotosynteesissä käyttökelpoiseen valoon, jonka arvojen perusteella on esitetty tuotosfunktiot kullekin lajille. Tuotosfunktioiden eroja on tarkasteltu ekologiselta kannalta.

ROITTO, YRJÖ — O.D.C. 378

1977. Finnish inland waterway fleet in 1975. An analysis with special reference to wood transporting vessels. — SILVA FENNICA Vol. 11, No. 1, 15 p. Helsinki.

The paper describes the Finnish inland waterway fleet in 1975. The number of inspected vessels was then 778. Of those 495 were tugs, 118 passanger boats, 71 warping boats with the others totalling 94. The average power of tugs was 65 kW and that of warping boats 16 kW. Other statistical data are presented in the tables.

Author's address: SF-57510 Savonlinna 51, Finland.

KÄRKKÄINEN, MATTI — O.D.C. 812: 174.7 Araucaria angustifolia & Pinus silvestris

1977. Comparison of wood properties of Parana pine and Scots pine. — SILVA FENNICA Vol. 11, No. 1, 6 p. Helsinki.

According to the available literature, the appearance of Parana pine wood resembles that of Scots pine. The anatomy is quite different, however. There are no resin canals and fusiform rays with resin canals in Parana pine. They are abundant in Scots pine, however. The basic density of Parana pine is higher. In both tree species the density increases from the pith outwards, the maximum being reached at the age of one hundred years. Compression wood is more common in Parana pine than in Scots pine, and this makes the longitudinal shrinkage of Parana pine greater than that of Scots pine. Otherwise the shrinkage properties do not differ. The mechanical strength is of the same magnitude with the exception of hardness, where Parana pine is superior.

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LEHTONEN, IRJA, VÄISÄNEN, EERO, KELLOMÄKI, SEPPO and HARI, PERTTI — O.D.C. 18

1977. On control of daily structural matter production in population of *Avenella flexuosa* (L.) Parl. SILVA FENNICA Vol. 11, No. 1, 8 p. Helsinki.

The aim of the present study was to investigate the control of structural matter production in an *Avenella flexuosa* (L.) Parl. population. Special attention was paid to the role of temperature and radiation in addition to the self regulation of the plants themselves. Temperature and self regulation were found to explain over 90 percent of the daily variation of growth rate. Introduction of radiation into the analysis did not increase the explanatory power of the growth model based on temperature and self regulation.

Authors' address: University of Helsinki, Department of Silviculture, Unioninkatu 40 B, SF-00170 Helsinki 17, Finland.

SARASTO, JUHANI and SEPPÄLÄ, KUSTAA — O.D.C. 181.65

1977. The effect of dwarf-shrub vegetation supression on pine swamp tree stands. — SILVA FENNICA Vol. 11, No. 1, 12 p. Helsinki.

In most pine swamp stands on drained areas the dwarf-shrubs are rather important biomass producers. The aim of the experiment was to determine the effect of killing-off the dwarf-shrub vegetation on the subsequent development of the pine stand. The dwarf-shrub vegetation was killed-off by means of herbicides. The results show that by removing competition by the dwarf-shrub vegetation on drained pine swamps, it is possible to pass onto the trees at least some of the freed growth potential.

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KIRJOITUSTEN LAATIMISOHJEET

Silva Fennica-sarjassa julkaistaan lyhyitä metsätieteellisiä tutkimuksia ja kirjoituksia kotimaisilla kielillä tai jollakin suurella tieteellisellä kielellä. Julkaistavaksi tarkoitettu käsikirjoitus on jätettävä Seuran sihteerille painatuskelpoisessa asussa. Seuran hallitus ratkaisee asiantuntijoita kuultuaan, hyväksytäänkö kirjoitus painettavaksi.

Kirjoitusten laadinnassa noudatetaan Silva Fennican numerossa Vol. 4, 1970, N:o 3 painettuja kansainvälisiä ohjeita. Suureissa, yksiköissä sekä symbolien ja kaavojen merkinnöissä noudatetaan ohjeita, jotka ovat suomalaisissa standardeissa SFS 2300, 3100 ja 3101. Oikoluvussa noudatetaan standardia SFS 2324.

Kirjoituksen alkuun tulee julkaisun kielellä lyhyt yhdistelmä tutkimuksen tuloksista. Samoin laaditaan tutkimuksen yhteyteen lyhyt englanninkielinen tiivistelmä, jonka lisäksi kunkin Silvan numeron loppuun painetaan irti leikattavan kortin muotoon kustakin tutkimuksesta englanninkielinen esittely. Sisällysluetteloa ei käytetä. Mahdolliset kiitokset esitetään lyhyesti johdannon lopussa ja merkitään painettavaksi petiitillä.

Kuvien ja piirrosten viivapaksuudet ja tekstikoko on valittava siten, että ne sallivat painatuksen vaatiman pienennyksen. Kuvien ja piirrosten painatuskoosta on syytä neuvotella etukäteen toimittajan kanssa, sillä tarpeettomia kustannuksia aiheuttavaa painatuskokoa ei sallita. Valokuvien tulee olla teknisesti moitteettomia ja kiiltävälle valkealle paperille suurennettuja. Värikuvia ei yleensä hyväksytä painettavaksi. Kuvat ja taulukot numeroidaan kummatkin erikseen juoksevasti, ja kuvien otsikoista laaditaan erillinen luettelo kirjapainoa varten.

Jos vieraskielisessä lyhennelmässä viitataan tiettyihin kuviin ja taulukoihin, on nämä varustettava vieraskielisin otsikoin ja selityksin. Muut kuvat ja taulukot voivat olla yksikielisiä.

Lähdeviittauksissa tekijännimet sijapäätteineen kirjoitetaan isoin kirjaimin, mikäli tekijännimen vartalo on muuttunut. Muutoin taivutuspääte kirjoitetaan pienaakkosin. Esimerkkejä: Koskisen (1972) tutkimus . . ., Yli-Vakkurin (1972) tutkimus . . . Milloin tekijöitä on kolme tai useampia, mainitaan tekstissä vain ensimmäinen (esim. Heikurainen ym. 1961). Vieraskielisessä tekstissä ym. korvataan merkinnällä et al. Jos julkaisulla on kaksi tekijää viitteessä, pannaan tekijöiden nimien väliin ja-sana painatuskielellä. Esimerkki: Keltikangas ja Seppälä (1973, s. 222) osoittivat . . .

Viitekirjallisuus luetteloidaan tekijännimien (kirjoitetaan isoin kirjaimin) mukaisessa aakkosjärjestyksessä. Jos tekijöitä on useampia, nimet erotetaan pilkulla, paitsi kaksi viimeistä, jotka erotetaan &-merkillä. Tekijän etunimistä suositellaan käytettäväksi vain alkukirjaimia. Tutkimusten nimet kirjoitetaan lyhentämättä. Julkaisusarjoista käytetään niitä lyhenteitä, jotka on painettu Silva Fennican numerossa Vol. 5, 1971, N:o 2. Täydellisempi luettelo on nähtävissä Seuran toimistossa. Kirjoituksen löytämisen helpottamiseksi mainitaan aikakauslehdistä myös sivunumerot. Suomenkielisistä tutkimuksista otetaan mukaan vieraskielisen lyhennelmän nimi. Volyymi merkitään julkaisusarjan nimen jälkeen. Jos kyseessä on aikakauslehti tai vastaava, numero merkitään volyymin jälkeen suluissa. Sivunumerot erotetaan kaksoispisteellä volyymistä tai suluissa olevasta numerosta. Jos samalla kertaa ilmestynyt volyymi sisältää useita tutkimuksia, merkinnässä sovelletaan ko. julkaisussa noudatettua tapaa. Esimerkkejä:

Ilvessalo, Y. 1952. Metsikön kasvun ja poistuman välisestä suhteesta. Summary: On the relation between growth and removal in forest stands. — Commun. Inst. For. Fenn. 40.1.

Wilcox, W. W., Pong, W. Y. & Parmeter, J. R. 1973. Effects of mistletoe and other defects on lumber quality in white fir. Wood & Fiber 4 (4): 272—277.

Englanninkielisen lyhennelmän ja mahdollisten kuva- ja taulukkotekstien käännättämisestä ja pätevän kieliasiantuntijan tekemästä tarkastamisesta huolehtii kirjoittaja. Seura voi maksaa kustannukset valtiovarainministeriön antamien ohjeiden mukaan. Jos kääntäjän lasku on ohjeiden edellyttämää tasoa korkeampi, kirjoittaja vastaa ylittävästä osuudesta.
Lähempiä tietoja antaa Seuran julkaisujen toimittaja.

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Hämeenlinna 1977, Arvi A. Karisto Osakeyhtiön kirjapaino