A NEW APPROACH FOR MEASURING LIGHT INSIDE THE CANOPY IN PHOTOSYNTHESIS STUDIES

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SELOSTE:
UUSI MAASTOKELPOINEN VALONMITTAUSMENETELMÄ YHTEYTTÄMIS-TUTKIMUKSIA VARTEN

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Light intensity inside the canopy varies considerably both in space and time. To avoid this difficulty, we have developed an apparatus which is disturbed as little as possible by the above-mentioned variation. The construction is based on the linear relationship between light intensity (measured using silicon diodes) and photosynthesis. This procedure permits linear operations (summing and integration) to be carried out on the output of the diodes without any loss of accuracy. There are five diodes in each assimilation chamber. Let \( V_i(t) \) denote the output of the \( i \)th diode at the moment \( t \), \( t_i \) the beginning instant of the \( i \)th photosynthesis measurement, and \( t_{i+1} \) the moment when the \( i \)th measurement is completed. Our equipment is constructed so that summing and integration takes place according to the following formula:

\[
\int_{t_i}^{t_{i+1}} \sum_{j=1}^{5} V_j(t) \, dt.
\]

A model, in which the independent variables include light, measured with the present equipment, and temperature, fits the photosynthetic rates well even inside the canopy.

INTRODUCTION

Although there are no serious technical problems involved in the monitoring of photosynthetic rate under field conditions, interpretation of the data obtained is rather complicated. This is due to the difficulties involved in measuring the light intensity. Light intensity, however, is the most important environmental factor affecting photosynthesis in the humid conditions of the temperate zone (cf. NEUWIRTH 1963, SCHULZE 1976, 1972, EVANS 1973). The great temporal fluctuations in light intensity (cf. KORNNER & RODSKJER 1967, RODSKJER 1972, HARI & LUKKANEN 1974), especially inside the canopy (cf. REINSYDER 1962, SETLIC 1968) make it difficult to obtain reliable measurements of the light intensity which can be utilized in photosynthesis. The aim of the present paper is to describe some new equipment which we have designed for measuring light intensity in photosynthetic studies. The apparatus is not disturbed by the great temporal and spatial variations in light intensity inside the canopy.

THE EQUIPMENT

General setup of the field station

The light measuring equipment forms part of an automatic system for measuring gas exchange, growth and environmental factors in the field. Net photosynthesis and transpiration within the canopy and ground vegetation are monitored continuously during the growing season in a young stand of Scots pine (Pinus silvestris L.) with a few scattered Norway spruce at the University of Helsinki Forestry Field Station in Central Finland. The system includes two infrared gas analyzers (URAS, Hartmann & Braun AG, BRD) and 20 trap-type pneumatically operated assimilation chambers or cuvettes. One analyzer is used for monitoring CO₂ levels and the other for H₂O levels. The cuvettes are closed in a pre-arranged sequence for 100 seconds. The CO₂ concentration of the air in the cuvette is measured before the cuvette opens. Photosynthetic rate is determined on the basis of the difference between the CO₂ concentration inside and outside the cuvettes. A data-logging unit, supplied by Nokia Oy, Finland, is used to control the system and to collect the data for photosynthetic rate, transpiration rate, temperature and light.

Requirements for a System to Measure Light Intensity

The output voltage of a photo-voltaic cell (Siemens BPY 11) is almost a linear function of the light intensity at low illumination in an electrical circuit as shown in Fig. 1 (cf. Optoelectronics semiconductors 1974). When the light intensity increases the output reaches a saturation level and the cell generates a constant voltage. The threshold value of the saturation level is greatly dependent on the value of resistance \( R_C \). The relationship between the light intensity and the output of the photo cell is rather similar to the relationship between photosynthesis and the light intensity at constant temperature. Thus it is possible to construct a linear relationship between the photosynthetic rate and the output of the photo cell by including a suitable resistance in the circuit, which furthermore, makes it possible to construct a piece of equipment for measuring light intensity in photosynthetic studies. This apparatus is not disturbed by the great spatial and temporal variations in light intensity inside the canopy.

The equipment has been designed on the basis of the following mathematical analysis of photosynthesis. Let \( P(t) \) denote the total amount of CO₂ fixed in photosynthesis at the moment \( t \) during the growing season. The photosynthetic rate \( f \) is defined as the time derivative of \( P(t) \), thus

![Fig. 1. The test circuit for the photo-voltaic cell BPY 11.](image-url)
If there is sufficient water available in the soil for the plant, then the photosynthetic rate is determined primarily by the temperature \( \text{x} \) and by the light intensity \( y \) (cf. HARI & LUUKKANEN 1974) thus

\[
f = f(x, y).
\]

The photosynthetic rate is most frequently measured in the field by the so-called open measurement system. A living branch is placed in a chamber. The cuvette is closed for between 60 and 120 seconds before the CO\(_2\) concentration in the cuvette is measured. It is then compared with the CO\(_2\) concentration of the air outside. The cuvette is opened after the measurements have been made. Let \( t_i \) be the moment at which the cuvette is closed for the \( i \)th measurement and \( t_f \) the moment when the cuvette is opened. When Eq. (1) is integrated from \( t_i \) to \( t_f \), Eq. (3) is arrived at

\[
\int_{t_i}^{t_f} f(x(t), y(t)) \, dt = \int_{t_i}^{t_f} f_1(x(t), y(t)) \, dt.
\]

The left hand side of Eq. (3) represents the amount of CO\(_2\) fixed in photosynthesis during the time when the cuvette was closed at the \( i \)th measurement obtained directly with IRGA measurement. The right hand side of Eq. (3) can be simplified by supposing that the effect of temperature and light intensity on photosynthesis is multiplicative, i.e.

\[
f(x, y) = f_1(x) f_2(y),
\]

where \( f_1 \) is the effect of temperature and \( f_2 \) the effect of light intensity. Without introducing any large inaccuracy it can be assumed that temperature is constant during the period when the cuvette is closed. The right hand side of Eq. (3) can now be evaluated as follows.

\[
\int_{t_i}^{t_f} f(x(t), y(t)) \, dt = \int_{t_i}^{t_f} f_1(x(t)) f_2(y(t)) \, dt.
\]

There are great spatial fluctuations in light intensity in the cuvette caused by shading of the branches. The disturbing effect of shade can be to a great extent reduced by using several cells in the cuvette. If there is linear relationship between the output of the cells and photosynthetic rate at constant temperature, then there is no loss of accuracy in the linear operations, summing and integration.

The requirements put on the light measuring equipment discussed above can be summarised as follows:

1. There are \( n \) cells in a cuvette.

2. Let \( V_{ij} \) denote the output voltage of the cell \( j \). The relationship between output \( V_{ij} \) and photosynthetic rate must be linear at constant temperature, i.e.

\[
f(x, y) = a_j f_1(x) (V_{ij}(y) + b), \text{ when } j = 1, 2, \ldots, n.
\]

3. The apparatus has to be able to compute the following integral (cf. KUHN 1971).

\[
V_i = \sum_{j=1}^{n} V_{ij}(y) \, dt.
\]

The apparatus is built to simulate the dependence of photosynthesis on light. It takes into consideration the nonlinearity of this phenomenon (cf. Ross 1970). Changes in the spectral composition of light are considered as having little importance in field studies. The justification of the assumptions on which the equipment is based have to be tested with empirical data.

The construction of the equipment

A piece of equipment was constructed which fulfills the above requirements. We have called this apparatus, equipment for measuring light in photosynthetic studies (ELP). The block diagramme for the ELP is shown in Fig. 2. According to requirement 1, there are \( n \) photo-voltaic cells in each cuvette, the output voltages of all the cells being summed together. The signal corresponding to light intensity which can be utilized in photosynthesis is transferred from the cuvette to the central unit (CU), consisting of an integrator and a multiplexer. The multiplexer selects which signal is to be passed to the integrator. The data logger reads the output of the integrator two seconds before the cuvette is opened. When the cuvette is opened and the next one is closed the integrator is reset and the multiplexer selects the signal from the cuvette which has just closed.

A photo-voltaic cell (Siemens BPY 11) was used as the light sensor. The electrical properties of the photo-voltaic cell are characterized by the following Eq. (cf. SZE, S.M. 1969).

\[
V_i = \frac{m k T}{q} \ln \left( \frac{T_i}{T} + 1 \right)
\]

Where

\[
V_i = \text{the output voltage of the photo cell}
\]

\[
T = \text{absolute temperature}
\]

\[
T_i = \text{photo current}
\]

\[
I_0 = \text{constant}
\]

\[
m = \text{constant}
\]

\[
k = \text{Boltzmann constant}
\]

\[
q = \text{Electronic charge}
\]

The photo current depends on the illumination and the load resistance \( R_L \) (c.f. Fig. 1). The relationship between \( V_i \) and \( L \) is shown in Fig. 3, using the resistance values \( 1 \, \Omega \), \( 2 \, \Omega \), and \( 3 \, \Omega \).

The dependence of photosynthetic rate on light intensity in constant temperature is rather similar to the photo current — illumination relationship — of the photo cell by including a suitable resistance \( R_L \) in the circuit. This enables the dependence of photosynthetic rate on light intensity to be simulated by means of a photo cell.

Summing amplifier

The output signal of the photo cell is so low that it cannot be transferred more than a few meters. For this reason a summing amplifier is located near each cuvette. The circuit diagramme for amplifier is shown in Fig. 4. The output voltage of the circuit \( V_i \) depends on resistances \( R_P \) and \( R_L \) and, on the input voltage \( V_i \) as follows.

\[
V_i = \frac{R_P}{R_L} V_i
\]

The input resistance of the circuits is \( R_L \). Thus \( R_L \) can be used as the load resistance of the photo cell. The desired
degree of nonlinearity of the relationship between photo current and illumination can be obtained by adjusting the resistance of $R_L$. The gain can be determined by varying the value of resistance $R_P$. The circuit can be expanded into a summing amplifier according to the circuit shown in Fig. 5. The output of the summing amplifier number $l$ $V_{II}$ is

$$V_{II} = \sum_{j=1}^{n} \frac{E_P}{R_{Lj}} V_{IJ}$$

where $V_{IJ}$ is the output of photo cell number $j$ and summing amplifier $l$ and $R_{Lj}$ is the load resistance of photo cell number $j$.

Central unit

The central unit consists of a 20 channel multiplexer, and an integrator. The multiplexer selects the signal to be integrated. The circuit diagramme of the integrator is shown in Fig. 6. Let $t_{HI}$ be the closing instant of the $i^{th}$ measurement of the $j^{th}$ cuvette and $t_{LO}$ the opening instant, correspondingly and $V_{II}$ the output of the $i^{th}$ summing amplifier and $V_{HI}$ the output of the integrator in the $i^{th}$ measurement of the $j^{th}$ cuvette. The integrator computes the following integral

$$V_{HI} = \frac{1}{RC} \int_{t_{LO}}^{t_{HI}} V_{II}(t) \, dt.$$  

When Eqs (10) and (11) are combined, it can be seen that the output of ELP fulfills the earlier-mentioned requirements.

RESULTS

The value of resistance $R_L$ (cf. Fig. 1) was calibrated so that there is a linear relationship between the output voltage of the photo cell and photosynthesis at constant temperature. This was performed empirically and the value 3 kΩ was obtained. In Fig. 7 the IRGA measurements are shown as a function of the output of ELP in the temperature range $10^0 - 15^0$ C during the period 1974-06-06—06-23. It is clearly evident that the linear relationship between the IRGA measurements and the output of the ELP holds rather well.

The maximum output varies from one summing amplifier to another due to small differences in calibration. For this reason the output of each amplifier is normalized so that it has the value 100 in full sunlight during summertime.

Let $P_{HI}$ denote the results of the $i^{th}$

Fig. 7. The correlation between photosynthetic rate and the output of ELP in the temperature range $10^0$ C—$15^0$ C during the period 1974-06-06—06-23.

IRGA measurement, of the $i^{th}$ cuvette. When Eqs. (3), (6) and (7) are combined, the final model is obtained.

$$P_{HI} = f_1(s(t_{HI}))(V_{HI}b)$$

where $f_1$ is the effect of temperature, $V_{HI}$ is the output of the ELP, and $a$ and $b$ are parameters which have to be estimated. The function $f_1$ and parameters $a$ and $b$ were determined separately for pine and spruce. The estimation was based on data collected during the period 1974-06-21—06-25 for Scots pine and during the period 1974-07-31—08-04 for Norway spruce. The functions $f_1$ which were obtained are shown in Fig. 8. The measured photosynthetic rates and those computed from the model (Eq. (8)) for pine during the days 1974-06-06, 06-07 and 06-10 are depicted in Fig. 9, and for Norway spruce during the period 1974-07-21—07-25 in Fig. 10. The model explained 86% of the variance in photosynthetic rate for Scots pine and 89% for Norway spruce during the periods shown in Figs.

Fig. 8. The function $f_1$ for Scotch pine (thick line) and for Norway spruce (thin line).

Fig. 9. A. Measured (thick line) and according Eq. (12) computed photosynthetic rates during the period 1974-06-06, 06-07 and 06-10 for Scotch pine. B. The output of ELP (thick line) and temperature (thin line) during the period.
Measurements of photosynthetic rate have been analysed rather superficially in the literature. There are only a few papers available, in which some statistical analysis has been performed (cf. Reifsnyder, 1962). In particular, papers which consider photosynthesis inside the canopy are rare. This is most probably due to the great difficulties involved in measuring light intensity inside the canopy. Statistical analysis of photosynthetic rate is also rather complicated since the independent variables, temperature and light intensity, are strongly intercorrelated and also because water deficit and temperature have a pronounced interaction in photosynthesis (Hari and Luukkanen 1973). Thus it is difficult to use standard statistical methods in the analysis.

The use of ELP and careful statistical analysis of the data make it possible to study photosynthesis in field conditions to an extent which has earlier only been possible in the laboratory. In this way, attention can be focused in the study on the ecologically important aspects of photosynthesis in the field.

**LITERATURE**


Ronskni, N. 1972. Experimental investigations into the alternation of Solar radiation in field crops with special regard to the 0.3–0.7 nm spectral band. Wäxholing Plant Husbandry 27. Publications from the department of plant husbandry at the agricultural college of Sweden, 1972.


**SELESTOE:**

**UUSI MAASTOKELPOINEN VALONMITTAMENETELMÄ YHTEYTTÄMIS- TUTKIMUKSIA VARTEN**

Nykykaisella mittausvälineistöllä voidaan kasvien fotosynteesiä seurata luotettavasti myös luomoon olosuhteissa. Maastomittauksissa kerätyn aineiston analysointi on ollut kuitenkin hankalaa, koska mittausaita aikana tapahtuva valon intensiteetin nopea vaihtelu ei ole pyystetty rekisteröi...
MÄNTYRUNKOJEN YDINSÄTEIDEN KORKEUS JA LEVEYS

MATTI KÄRKKÄINEN

SUMMARY:

HEIGHT AND WIDTH OF RAYS IN PINE STEMS

Saapunut toimitukselle 1976-02-19

Tutkimuksessa on mitattu 1888 pihkatiehyötöntä ja 454 pihkatiehyellistä yänsädetä tangentileikkauskista, jotka on otettu neljästä mäntyrungoasta eri korkeuksilta ja eri etäisyyksiltä ytimestä. Suurimmaksi ydensäteen leveydeksi saatiin keskimäärin 19,7 µm pihkatiehyettömille ydinsäteilteille ja 51,9 µm pihkatiehyelillise ydinsäteilille. Kesikorkeudet olivat vastaavasti 215,7 µm ja 406,2 µm. Korkeuden perusteella näyttää olevan mahdollisuuksia ydinsäteiden automaattiseen tunnistamiseen pihkatiehyettömiksi ja pihkatiehyelliksi ydensäteiksi. Kun rajaksi otetaan 300 µm, 90 % pihkatiehyettömistä ydensäteilistä olisi luettu virheellisesti pihkatiehyellisiä ydensäteisiin ja 65 % pihkatiehyellistä ydinsäteistä virheellisesti pihkatiehyettömäksi ydensäteisiin.

1. JOHDANTO

Yleisesti käytettyissä puuteknologian oppikirjoissa esitetty tiedot männyn ydinsäteiden mitoista ovat varsin vähäiset. Esim. TRENDLENBURGO ja MAYER-WEGELIN (1955, s. 133, 140) toteavat lyhyesti, että männyn ydinsädeparenkyymien leveys on 0,015 ... 0,035 mm ja että ydinsäteiden korkeus on 5 ... 15 soluriviä. Muissa puuteknologiassa oppikirjoissa esitetään yhtä vähäisiä tai vieläkin puutteellisempiä tietoja männyn ydinsäteiden dimensioista (esim. KNIGGE ja SCHULZ 1906, KOLLMAN ja CÔTE 1968, JANE 1970, PANSHIN ja DE ZEUV 1970, KOCH 1972, jne.).

Puuteknologisten oppikirjojen antaman tiedon vähäisyys selittää sillä, ettei puunamomisia tutkimuksia männyn ydinsäteiden mitoista ole juuri tehty. Pihkatiehyettömiä ja pihkatiehyettömäksi ydinsäteiden pinta-alasta ja osudesta koko rungon tilavuudesta on jonkin verran tietoa, joita aikaisemmassa tutkimuksessa on sitereaftta (KÄRKÄINEN 1973). Ydensäteiden leveydestä ja korkeudesta ei sen sijaan ole tiettävästi varsinaisia tutkimuksia. BACK (1958) sekä NYRÉN ja BACK (1959 a, b) tosin esittävät ydinsäteiden trakeidaalisien ja parenkyymmaisten solujen mitoista joitakin tuloksia, samoin mainittujen soluolautujen lumumäärästä ydensäteissä, mutta nämä lienevätkin ainoin raportoidut havainnot, juosta voidaan laskea keskimääräisiä männyn ydinsäteiden leveyksiä ja korkeuksia. Tässä tutkimuksessa tarkastellaan neljää runkoa koskevaa tulosta, jotka on laskettu aikaisemmin kuvattavilla aineistosta (KÄR-