RATE OF PHOTOSYNTHESIS OF SOME FOREST MOSSES AS A FUNCTION OF TEMPERATURE AND LIGHT INTENSITY AND EFFECT OF WATER CONTENT OF MOSS CUSHION ON PHOTOSYNTHETIC RATE

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SELOSTE:

ERÄIDEN METSÄSAMMALIEN FOTOSYNTEESINOPEUS LÄMPÖTILAN JA VALON FUNKTIONA SEKÄ KASVUSTON KOSTEUDEN VAIKUTUS FOTOSYNTEESINOPEUTEEN

The photosynthetic rate of *Pleurozium schreberi* (Willd.), *Hylocomium splendens* (Hedw.) and *Dicranum polysetum* (Sw.) grown in plastic containers was monitored with an infrared gas analysor in the open air under natural weather conditions. It proved that the photosynthetic rate of wet moss cushions was satisfactorily predicted by temperature and light intensity. In dry moss cushions this kind of model gave too high an estimate for photosynthetic rate. Water requirements of each moss species were found to be moderate, and water content of moss cushions limited photosynthetic rate only under serious water deficiency.

INTRODUCTION

In the boreal zone, lichens and mosses are major producers of ground vegetation as shown by MÄLKÖNEN (1974). Their production of structural dry matter, especially in closed stands, may rise to 10—20 per cent of that of the aerial parts of trees. In the northernmost parts of the boreal zone this share increases, and in tundra areas lichens and mosses play a more pronounced role in dry matter production on mineral soils. Thus, the ecology of the photosynhesis and production of structural dry matter by lichens and mosses

is of primary importance in investigations concerning boreal and arctic ecosystems.

TAMM (1953) has shown the importance of rainfall in the dry matter production of forest mosses and their distribution in a stand. The water consumption of lichens and mosses has been studied in detail by ANDERSON and BOURDEAU (1955), KAPPEN et al. (1975) and PETERSON and MAYO (1975). All of them mention the modest water requirements of lichens and mosses, and pay attention to the importance of rainfall and dew formation in the photosynthesis and dry matter production of bryophyta. In addition, BLISS and HADLEY (1964), HARRIS (1971 a, b) and DILKS and PROCTOR (1974) have carried out investigations on the water economy of lichens and mosses and its physiological and ecological effects on the photosynthetic and productive functions.

RASTORFER and HIGINBOTHAM (1968) have demonstrated, that light saturation levels of photosynthesis in some mosses are of the same magnitude as those of the shade leaves of vascular plants. Furthermore BAZZAZ et al. (1970) and PETERSON and MAYO (1975) have reported similar results concerning the light requirements of lichens and mosses compared to vascular plants. According to BLISS and HARLEY (1964) the adaptation of lichens and mosses to moderate light intensity conditions gives these plant species a considerably higher survival value, since the most favourable conditions for their photosynthetic functions are found under moist period with moderate light and temperature.

The temperature requirements of lichens and mosses are, in general, moderate. DILKS and PROCTOR (1975) have reported that photosynthesis of many bryophyta commences at temperatures below 0° C (cf. also KALLIO and HEINONEN 1971). On the other hand, the photosynthesis of lichens and mosses seems to cease at temperature of —5 — —10° C. According to STÅLFELT (1937) optimum photosynthesis of *Hylocomium squarrosum* occurs at 14—15° C. However, great variations can be found in this respect, because the temperature tolerance for *Bryum sandbergii* ranges from —15 to 41° C with the optimum between 24—30° C. PAOLILLO and BAZZAZ (1968) mention the general stability of photosynthesis and respiration between 0—20° C in *Polytrichum* and *Funaria* sporophytes and gametophytes.

The aim of this paper is to study the photosynthetic rate of *Pleurozium schreberi* (Willd.), *Hylocomium splendens* (Hedw.) and *Dicranum polysetum* (Sw.) as a function of light and temperature, and the effect of the moisture content of moss cushions on the photosynthetic rate.

MATERIAL AND METHODS

The study was carried out at the Forest Training Station of the University of Helsinki in late summer 1974. The photosynthetic rate of the study material grown in plastic containers was monitored with an infrared gas analyser (Uras 2T) in semi-laboratory conditions, i.e. in the open air under natural weather conditions. The moss cushions were 15 × 20 cm in size. Dead parts of the mosses were cut off before the moss cushions were placed in containers with a plastic gauge bottom. Density and structure of the moss cushions were arranged so far as possible natural conditions were replicated. During measurement the moss cushions were placed in trap type cuvettes. The photosynthetic rate of the mosses was measured at half hour intervals for 100 seconds. The technical details and general layout of the measuring systems are described in detail by PELKONEN et al. (1975).

During the measurement, temperature was monitored by data logger (model Nokia)

using wet and dry thermocouples. The light conditions were monitored with equipment for measuring light in photosynthetic stu
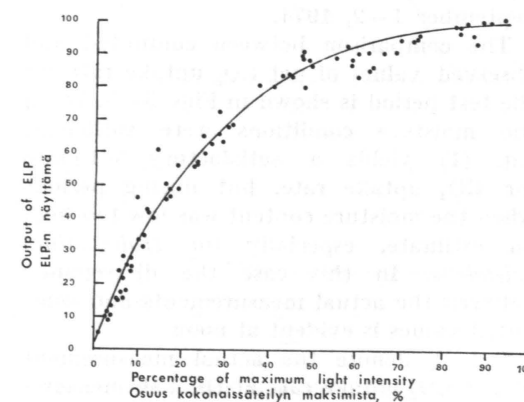

Fig. 1. The output of ELP as a function of maximum light intensity.

Kuva 1. ELP:n näyttämä kokonaissäteilyn maksimin funktiona.

dies (ELP) (Fig. 1) described by HARI et al. (1976). The moisture content of the moss cushions was controlled gravimetrically to an accuracy of 0.1 g at intervals of 0.5—4.0 hours. The dried moss cushions were rewetted once a day if there was no rainfall.

RESULTS

Let f denote the CO_2 uptake rate of the moss cushions at conditions of sufficient moisture. The CO_2 exchange rate is mainly determined by temperature x and light intensity y analogously with vascular plants (cf. HARI and LUUKKANEN 1974), thus

(1) $f = f(x, y)$.

Let $x_1 = 0$, $x_2 = 5$, $x_3 = 10 \ldots$, $x_7 = 30$ denote temperature of defined levels. The net uptake rate of CO_2 can be presented as a function of light intensity y at temperatures x_i (i = 1, 2, 3 ..., 7) from measurements carried out on the wet moss cushions. The results based on measurements during the period September 6—15, 1974 are presented in Fig. 2. For the small variation in temperature which occured during the measuring period only four functions for each moss are depicted. The functions $f(x_i, y)$ can be used for predicting CO_2 uptake rate. The mathematical methods needed to compute values for net CO_2 uptake rate with light intensity and temperature are described in detail by HARI and LUUKKANEN (1974).

The reliability of prediction was studied by making independent measurements of the wet and dry moss cushions during the period September 1—2, 1974.

The comparison between computed and observed values of net CO_2 uptake rate for the test period is shown in Figs. 3—5. When the moisture conditions were sufficient, Eq. (1) yields a satisfactory estimate for CO_2 uptake rate, but during periods when the moisture content was low too high an estimate, especially for *Hylocomium splendens*. In this case the discrepancy between the actual measurements and computed values is evident at noon.

Let P_i denote the actual measurement of net CO_2 uptake rate at the i th measurement. The degree of control of photosynthesis, CP, is defined as a ratio between the actual measurements and those computed from the light and temperature values of net CO_2 uptake.
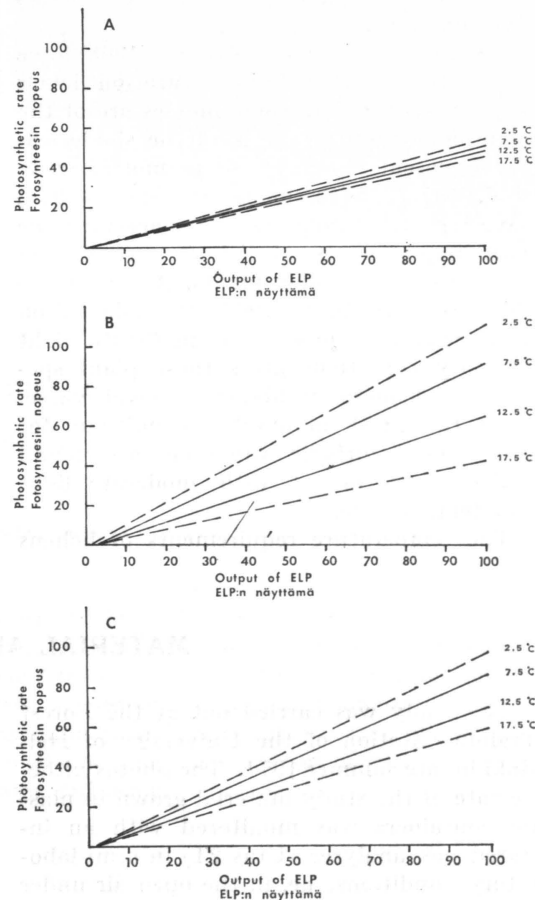

Fig. 2. Photosynthetic rate of study material as a function of light and temperature.

A: *Pleurozium schreberi*
B: *Hylocomium splendens*
C: *Dicranum polysetum*

Dotted lines are approximations of the photosynthetic functions based on the limited material.

Kuva 2. Tutkittujen sammalten fotosynteesin nopeus valon ja lämpötilan funktiona.

A: Pleurozium schreberi
B: Hylocomium splendens
C: Dicranum polysetum

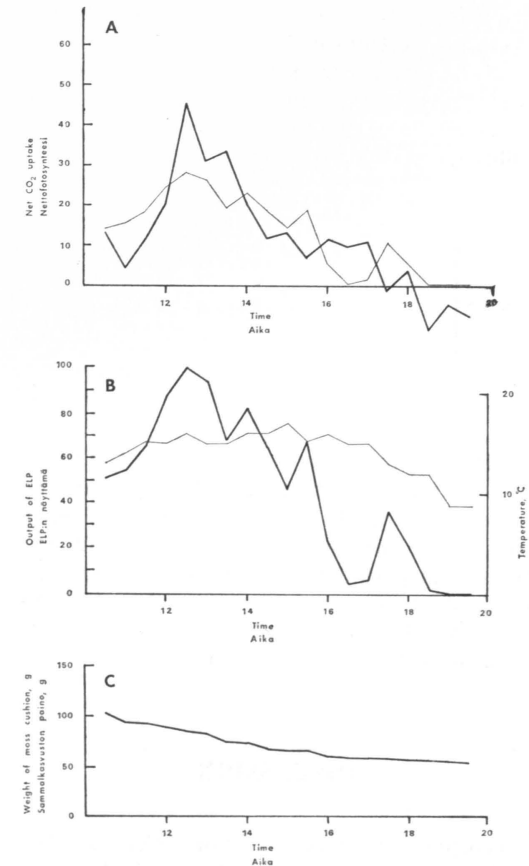*Katkoviivat ovat suppeaan aineistoon perustuvia fotosynteesinopeuden approksimaatioita.*

Fig. 3. Prediction of photosynthetic rate of *Pleurozium schreberi*.

A: thick line is observed values of photosynthetic rate, thin line is computed values of photosynthetic rate
B: thick line is light intensity during study period thin line is temperature during study period
C: weight of moss cushion during study period

Kuva 3. Pleurozium schreberin fotosynteesinopeuden ennuste.

A: paksu viiva merkitsee fotosynteesinopeuden todettuja arvoja, ohut viiva merkitsee ennustettuja fotosynteesinopeuden arvoja
B: paksu viiva merkitsee valaistuksen arvoja tutkimusjaksossa, ohut viiva merkitsee lämpötilan arvoja tutkimusjaksossa
C: sammalkasvuston paino tutkimusjaksona

(2) $$CP_i = \frac{P_i}{f(x_i, y_i)}$$

By definition, $CP \approx 1$ when there is no degree of photosynthetic control and $CP < 1$ when some degree of control is present. Thus CP measures the degree of the effect of water deficit on photosynthetic rate.

Let z denote the moisture content of a moss cushions. Assume that the degree of photosynthetic control depends on the moisture content, thus

(3) $$CP = CP(z)$$

The moisture contents of the moss cushions was measured several times a day. Denote
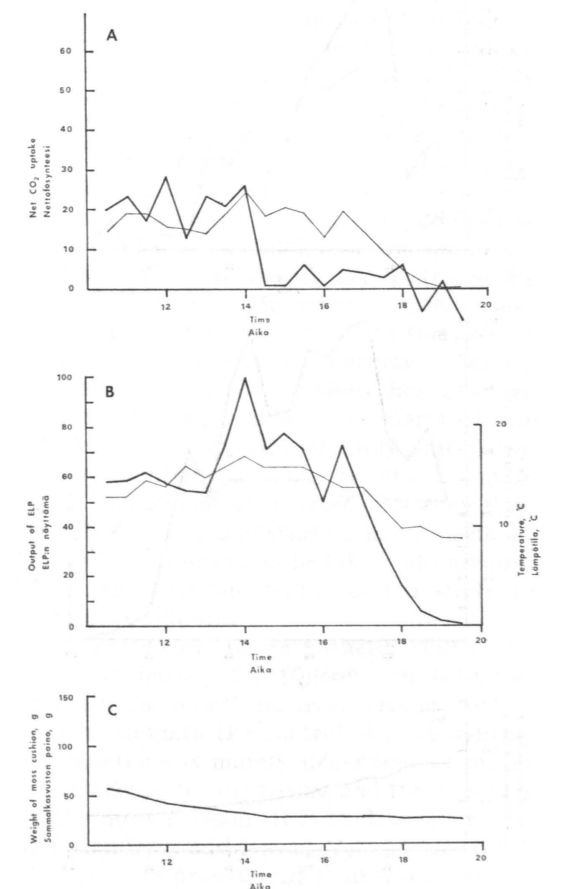

Fig. 4. Prediction of photosynthetic rate of *Hylocomium splendens*. For legend see Fig. 3.

Kuva 4. Hylocomium splendensin fotosynteesinopeuden ennuste. Merkintöjen selitys on annettu kuvassa 3.

t_j the time of j:th measurement of moisture content. Let us assume that the evaporation rate from the moss cushions is linearly correlated with the temperature deviation between the dry and wet thermocouples (cf. HARI et al. 1975), then the moisture content of the moss cushions $z(t)$ at time t can be estimated from temperature deviation between dry $x(t)$ and wet $v(t)$ thermocouples and from measured moisture contents $z(t_j)$ during time interval (t_j, t_{j+i}) as follows:

$$(4) \qquad z(t) = z(t_j) + \frac{\int_{t_j}^{t}(x(t) - v(t))\,dt}{\int_{t_j}^{t_{j+1}}(x(t) - v(t))\,dt}\left[z(t_{j+1}) - z(t_j) \right]$$

The correlation between CP and the moisture content of the moss cushions computed according Eq. (4) are shown in the Fig. 6. Owing to the moist weather during the measuring period there was no dry material available to carry out tests concerning the latest version of the photosynthetic model for mosses including water factor.

DISCUSSION

Temperature has a minor effect on the photosynthesis of *Pleurozium schreberi*. As dicussed earlier the temperature adaptation of many lichen and moss species is not pronounced as reported by SCHOLANDER et al. (1952), BLISS and HADLEY (1964) and BAZZAZ et al. (1970). Especially, *Dicranum polysetum* seems to be quite sensitive to high temperature. Unfortunately, the present material is not very representative due to the small variation in the temperature during the study period. Therefore the optimum temperature of different moss species remains not to be determined. However, it seems evident, that *Pleurozium schreberi* prefers warmer habitats than *Hylocomium splendens* and *Dicranum polysetum* do (cf. KUJALA 1926). In particular, the distribution of *Hylocomium splendens* on the forest floor points to its preference for habitats with moderate light and temperature (TAMM 1953). It is evident that the photosynthetic activity of *Pleurozium schreberi* per unit area is lower than that of other moss species, independently on the light intensity of the habitat. Accord-
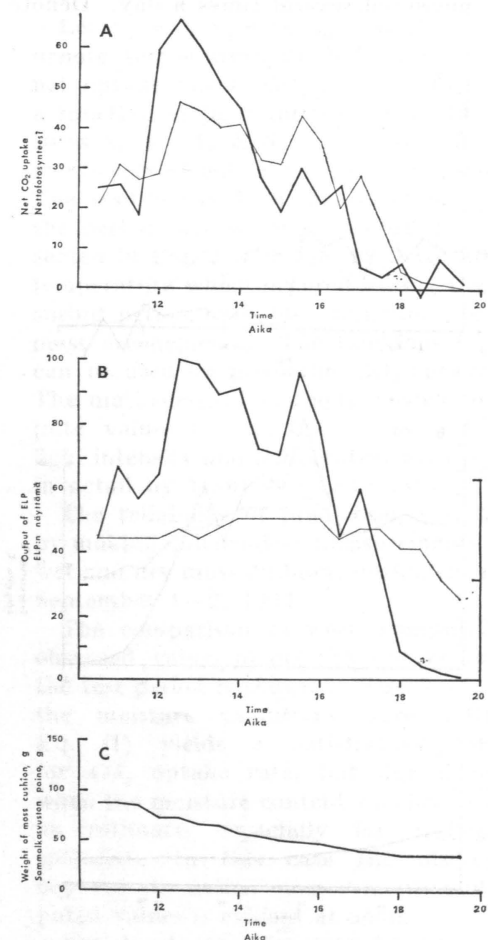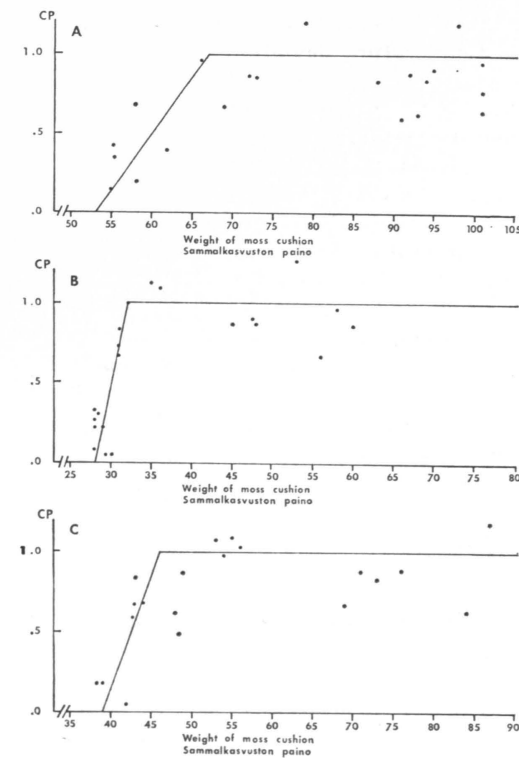
Figure 5. Prediction of photosynthetic rate of *Dicranum polysetum*. For legend see Fig. 3.

Kuva 5. Dicranum polysetumin fotosynteesinopeuden ennuste. Merkintòjen selitys on annettu kuvassa 3.

Fig. 6. Effect of moisture content of moss cushion on photosynthetic rate of study material.

A: control factor for *Pleurozium schreberi*
B: control factor for *Hylocomium splendens*
C: control factor for *Dicranum polysetum*

Kuva 6. Kasvuston kosteuden vaikutus fotosynteesinopeuteen.

A: Pleurozium schreberin fotosynteesin kontrolli

B: Hylocomium splendensin fotosynteesin kontrolli

C: Dicranum polysetumin fotosynteesin kontrolli

ing to MONSI and SAEKI (1953) the differences in the photosynthetic functions of plant species are of importance as far as the succession of plant community and its structure is concerned.

The result agree with earlier reports concerning the moderate water requirements of forest mosses and lichens (cf. MÄGDEFRAU 1937, ENSGRABER 1954, ANDERSON and BOURDEAU 1956, HOSOKAWA and KUBOTA

1957, LECHOWICZ and ADAMS 1973, NÖRR 1974, KAPPEN et al. 1975). PETERSON and MAYO (1975) have demonstrated that photosynthesis in *Dicranum polysetum* ceased when the water potential of the leaves drops below $-21 - -23$ atm. The rainfall or dew held by the leaves has an important role in the photosynthetic functions of mosses because of the poor transportation of water from the base of the stem to its top (cf. VAIZEY 1887, MÜLLER 1909, BOWEN 1931, PATTERSON 1943, SMITH 1961, KLEPPER 1963). PETERSON and MAYO (1975) found differences in water potential of -15 atm between the leaf tips and stems of *Dicranum polysetum*. When the water caught by the leaves was used up, the photosynthetic functions ceased. However, it is evident, that this kind of situation takes place only under serious water deficit (e.g. HOSOKAWA and KUBOTA 1957. NÖRR 1974). It is probable, that in the boreal zone the complete cessation of photosynthetic functions of mosses is exceptional even in long dry periods due to dew and the humidity of the air layers within moss cushions as demonstrated by MÜLLER (1909), HEATWOLE (1966) and KERSHAW and FIELD (1975). In the present material, however, the natural humidity profile within moss cushions has changed due to the removal of dead parts of the shoots and the growing of study material in plastic containers. This results in more rapid and pronounced water deficiency than would occur in undisturbed moss cushions. These limitations must be taken into account when applying the results of the study to natural conditions.

In particular, photosynthetic control by water deficiency for *Hylocomium splendens* showed an on-off pattern. Owing to the lack of stomata the control of photosynthetic functions is mainly dependent on water conductivity by the tissues and the structure of the moss cushion. It is evident, that evaporation from cushions of *Hylocomium splendens* is more pronounced than from cushions of *Pleurozium schreberi* and *Dicranum polysetum*. The control of photosynthesis by water deficiency for *Hylocomium splendens* demonstrates adaptation to rapid and thorough depletion of the water resources available and efficient utilization of dew and air humidity.

According to the relevant literature, the recovery of photosynthetic functions of moss species after rewetting is a dramatic one. PETERSON and MAYO (1975) demonstrated that the photosynthesis of *Dicranum polysetum* reached the normal level within 30 minutes after serious water deficiency for eight days. HINSHIRI and PROCTOR (1971) have demonstrated that the time lag between rewetting and full recovery of photosynthetic activity of bryophyta is a function of the desiccation time. Physiological changes occured during desiccation and recovery of photosynthesis of different lichen and moss species are discussed in detail by ENSGRABER (1954), HARRIS (1971), SMITH and MOLESWORTH (1972), BEWLEY (1973) and NÖRR (1974).

In studying the effect of the water balance of moss cushions on photosynthetic functions, only a few measurements concerning the moisture content of moss cushions were available. In order to complete the material it was assumed that the evaporation rate of moss cushions is linearly correlated with the temperature deviation between the wet and dry thermocouples (HARI et al. 1975). This method gave, however, an enough accurate estimate for the water content of the moss cushions.

The photosynthetic rate of wet moss cushions could be predicted satisfactorily by temperature and light intensity, as was assumed. The discrepancy between the observed and computed values are mainly due to the measuring accuracy. Especially, the small biomass per unit area and low level of photosynthesis produce problems as far as the measuring accurary is concerned. According to LARSON and KERSHAW (1975) a careful balance between flow rate and amount of the study material must be maintained in order to obtain adequate measuring accuracy. In open systems, as in this study, these problems are more pronounced than in closed systems as reported by DENMEAD and McILROY (1971).

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SELOSTE:

ERÄIDEN METSÄSAMMALIEN FOTOSYNTEESINOPEUS LÄMPÖTILAN JA VALON FUNKTIONA SEKÄ KASVUSTON KOSTEUDEN VAIKUTUS FOTOSYNTEESINOPEUTEEN.

Työssä on tutkittu *Pleurozium schreberin* (Willd.), *Hylocomium splendensin* (Hedw.) ja *Dicranum polysetumin* (Sw.) fotosynteesinopeuden riippuvuutta lämpötilasta, valosta sekä kasvuston kosteuden vaikutusta fotosynteesinopeuteen. Tässä tarkoituksessa seurattiin muoviastioissa kasvatettujen sammalien fotosynteesinopeutta infrapunakaasuanalysaattorilla mahdollisimman luonnonmukaisissa sääolosuhteissa. Havaittiin, että kosteiden sammalkasvustojen fotosynteesinopeus voitiin ennustaa tyydyttävästi lämpötilaan ja valoon perustuvalla mallilla. Kuivissa sammalkasvustoissa tämä malli antoi fotosynteesin nopeudelle liian korkean estimaatin. Kaikkien sammallajien vaatimukset veden suhteen osoittautuivat vaatimattomiksi, ja kasvuston vesitalous rajoitti fotosynteesin nopeutta vasta voimakkaan kuivuuden vallitessa.