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TION, PHOTOSYNTHESIS, AND HEIGHT INCREMENT OF
SCOTS PINE SEEDLINGS

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TRANSPIRAATIOON, FOTOSYNTEESIIN JA PITUUS-
KASVUUN*

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Suomen Metsätieteellisen Seuran julkaisusarjat

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EFFECT OF PLANTING SHOCK ON THE TRANSPIRATION, PHOTOSYNTHESIS, AND HEIGHT INCREMENT OF SCOTS PINE SEEDLINGS

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SELOSTE:

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TIOON, FOTOSYNTEESIIN JA PITUUSKASVUUN*

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INTRODUCTION

Planting stock is subjected to a rapid change in environmental conditions when it is planted out in the regeneration area. The previous optimal conditions of the nursery are replaced by the field environment. In addition, during transportation and planting many types of physiological stress occur. The development of water stress is commonly considered to be the most harmful (cf. KOZLOWSKI 1966).

The damage to the seedling caused by these types of stress is visible as a decreased height increment, loss of the terminal shoot and in the worst cases as the dying off of the seedling. Many roots are cut off when the seedling is taken up from the nursery bed. The root tips are destroyed to a great extent during transportation. In addition, the roots dry out during planting and often the fine rootlets fail to make good contact with the soil particles after planting. All these factors produce a water deficit in the plant after planting, as it is impossible for the seedling to take up water in sufficient amounts. The water deficit will not cease until new root tips have grown (TRANQUIL-LINI 1973). Stored carbohydrates are consumed during handling and transportation. Mechanical damage also occurs during transportation. This interference in the development of planted seedlings is called planting shock. It clearly has a harmful effect on the subsequent development of the seedling stand. Less severe planting shock may decrease the resistance to disease and produce serious complications later on. If the planting shock is moderate, growth of the seedlings is reduced and uneven, thus causing a subsequent reduction in the yield of the stand. The effect of planting shock on the development of the seedlings has been frequently studied through field experiments. Small plants seems to be more sensitive to drying out and the development of Norway spruce after planting is more reduced than that of Scots pine. Mortality and the decrease in growth can only be studied through field experiments. The fact that such experiments last for several years produces additional variance in the results. The effects of planting shock are often hidden by this additional variance. Destructive methods are also available for studies of planting shock. These methods have, however, the disadvantage that the continuous monitoring of the same seedling is impossible. Thus the measurements have to be carried out by sampling, which generates excess variance. The results are much more reliable, however, if the same seedling is monitored before and after planting in such a way, that the measurements do not have any adverse affect on the seedlings. This is very difficult to do with the conventional methods applied in forest regeneration studies. Thus new methods are very desirable.

Studies concerning the gas metabolism and height growth of plants in the field, especially those concentrated on water deficit stresses have enabled our research group to adapt the achieved measurement and data analysis technique to planting shock studies. The aim has been to study the self regulation of transpiration, photosynthesis and height increment of Scots pine seedlings stressed by planting. The difference in the degree of self regulation has been assumed to reflect planting shock accurately.

MATERIAL AND METHODS

All the measurements made in this investigation were carried out near the Forestry Field Station of Helsinki University in Central Finland. The experimental site was at the edge of a clear-cut area of about one hectar next to a young stand of Scots pine (*Pinus silvestris* L.). The potted seedlings used as experimental material were placed on a 1.2 meter high table.

The experimental material consisted of eleven five-year-old Scots pine seedlings of local genetical origin. The plants were grown for the first three years in the nursery in the same way as plant material used in reforestation work. At the beginning of their third growing season they were transplanted into the open at the nursery. One year later they were again transplanted for the present experiment into 7″ clay pots, one in each, using sandy soil taken from a field.

In the present experiment the plants had been growing for sith growing season. In early spring their mean height was 56 cm. They were divided into three treatment groups. The first one (4 plants) served as a control group. The plants in it were allowed to grow for the whole season untouched in their pots. The plants belonging to the two other treatments were dug out from their pots and then replanted into the same pots and soil on May 15 1975. This operation can be considered to correspond to normal transplanting in a nursery. The second treatment group (3 plants) was transplanted immediately after classifying and photographing the bared roots, which took altogether 1.5—2 minutes. In the third treatment (4 plants) the plants were kept in the sun with uncovered roots for 20 minutes before planting. During that time the plants lost about 18 % of their fresh weight.

The gas exchange, growth and environmental factor measurements made in this investigation can in principle be divided into two categories. In the first the measurements of transpiration and photosynthetic rates and the environmental factors were
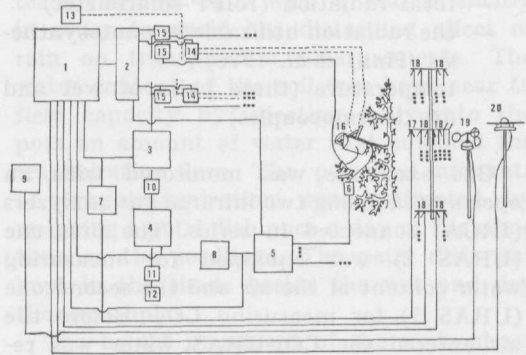

Fig. 1. A block diagram of the measuring system. Control signal (thick line), measurement signal (medium line) and gas conduction tubing (thin line). The numbers refer to the following pieces of equipment: 1. data-logging unit, 2. relay-unit, 3. IRGA-apparatus for H_2O, 4. IRGA-apparatus for CO_2, 5. central unit of ELP, 6. summing amplifier, 7. millivolt recorder for the output of URAS (H_2O) and for the difference between dry and wet temperatures, 8. millivolt recorder for the output of URAS (CO_2) and that for one ELP, 9. potentiometer for temperature measurements, 10. ice bath, 11. flow meter, 12. membrane pump, 13. compressor, 14. magnetic switch for compressed air, 15. magnetic switch for gas to be analysed, 16. cuvette, 17. two pairs of thermocouples for measuring the difference between dry and wet temperatures, 18. thermocouples for measuring dry and wet temperatures, 19. apparatus for measuring wind velocity, 20. KIPP-solarimeter.

monitored with an automatic system. The second category included the measurements of daily amounts of transpiration, potential evaporation and height increment. The data for the second category was collected manually.

The automatic measuring system consisted of several devices which are illustrated in a block diagram in Fig. 1. The central unit of the automatic system was a data logger supplied by Nokia Oy, Finland. It controlled the system, collected the data and punched it out on paper tape.

The following parameters were continuously (every 100 seconds) monitored:

- photosynthesis (URAS 1)
- transpiration (URAS 2)
- total radiation (KIPP-solarimeter)
- the radiation utilizable in photosynthesis (HARI et al. 1976)
- temperature (three pairs of wet and dry thermocouples)

Gas exchange was monitored with an open system using two infrared gas analyzers (IRGA) connected in series. The first one (URAS 2) was equipped for measuring water content of the air and the second one (URAS 1) for measuring CO_2. Before the air entered the CO_2-URAS, water was removed from the gas flow because of its disturbing effect on CO_2-measurements. The seedlings were sequentially enclosed in trap-type pneumatically operated chambers or cuvettes for 100 seconds (Fig. 2). During that time an air pump sucked air (60 l/h) from the cuvette through the two URAS-apparatuses.
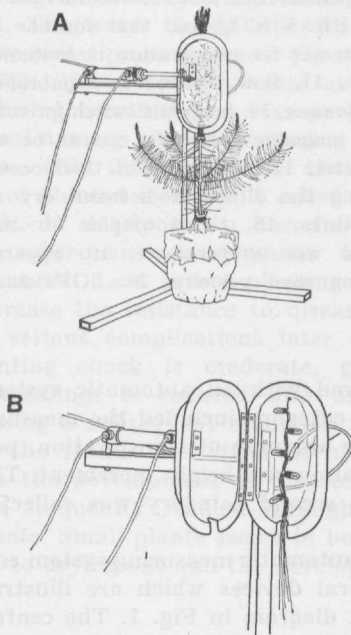

Fig. 2. A. A closed cuvette.
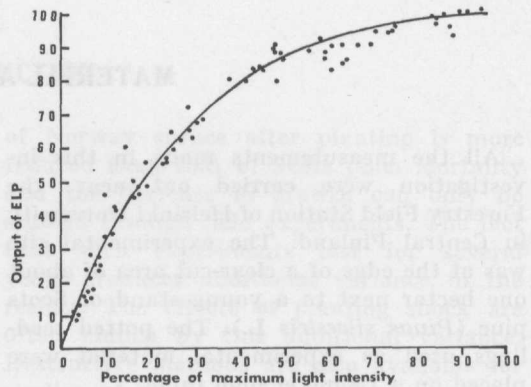B. An open cuvette in which five silicon diodes of the ELP are visible.

Fig. 3. Relationship between output of ELP and total radiation.

The gas exchange measurements were based on differences in CO_2 and H_2O concentrations inside the closed chamber and in the ambient air. Altogether 11 cuvettes were used in the present experiment. In addition, two channels of the circulating system were used in monitoring the CO_2 and H_2O concentrations of the air around the cuvettes. The aim of this study was not to study absolute values of photosynthesis and transpiration. In order to increase the accuracy of the relative values each seedling was kept in the same cuvette throughout the whole measuring period.

Light was monitored with equipment for measuring light in photosynthetic studies, called ELP. Photo-voltaic cells (Siemens BPY 11) were used as light sensors. They were fixed inside the cuvettes, five in each. The output voltage in the circuit applied simulates the response of photosynthetic rate on light (see Fig. 3). The output voltages were first summed together in a summing amplifier. These summed signals, one coming from each cuvette, were transferred to the central unit of the ELP. The central unit selected the signal from the correct cuvette and integrated it during the time the cuvette was closed. Just before the cuvette was opened the output of the integrator was read by the data logger. This light measuring system has been especially designed for photosynthetic studies. It has been thoroughly described and discussed by HARI et al. (1976).

Besides the ELP, light was also monitored with a KIPP-solarimeter, which recorded total radiation. Copper-constantan thermocouples were used for measuring wet and dry temperature. One of these was placed in the shade next to the seedlings of the present experiment. The difference between readings of the wet and dry thermocouples was used for estimation of the potential evapotranspiration rate (HARI *et al.* 1975).

In summary the automatic measuring system operated as follows. Each cuvette in turn was closed for one hundred seconds. During that time the ELP was simulating the dependence of the photosynthetic rate on light inside the closed cuvette and the air pump sucked air from the cuvette through the two infrared gas analyzers. At the end of the period of one hundred seconds the data was recorded on paper tape and the next cuvette was closed. The automatically collected data consisted of wet and dry thermocouple readings, total radiation, the output of the ELP and the output of the two URAS-apparatuses.

Of the measurements carried out manually the daily amounts of transpiration were measured by weighing the potted seedlings once a day to an accuracy of 0.1 g. To prevent evaporation from the surface of the pots each pot was enclosed in a plastic bag which was tightly sealed around the stem of the seedlings. The seedlings were protected against rain with a plastic shelter in order to avoid the disturbing effect of rain on transpiration measurements. The water content of the soil was kept near to field capacity by injecting daily into the pots an amount of water that equalled the transpiration loss. The potential amounts of evapotranspiration were estimated by weighing a petri dish once a day at the same time as the seedlings. The petri dish was kept in the shade beside the wet and dry thermocouples.

The height increment of the main shoot of each seedling was measured every day at 8.00 a.m. to an accuracy of 0.1 mm. In order to improve the accuracy, the measurements were carried out by the same person during the whole experiment. The temperature readings used in the analysis of the height increment data were monitored with a thermohygrograph placed in the shade.

MODELS FOR TRANSPIRATION, PHOTOSYNTHESIS AND HEIGHT INCREMENT

The analysis of the measurements is based on the hypothesis that the metabolic activities of the plants can be divided into two different types: 1. plant reactions to changes in the environment 2. the effect of self regulation on the reactions of plants, *i.e.* the internal control of gas metabolism and growth. An attempt is made to separate the two effects from each other in the analysis of the data. Planting affects the degree of the self regulation of the plant. The magnitude of the change in the degree of the self regulation is a measure of the planting shock.

Metabolic rates (photosynthesis and transpiration) and the daily values of integrals of metabolic rates (daily amounts of transpirated water and daily height increments) can be monitored in field conditions. Despite the differences between these two types of measurement, the data can be analyzed with very similar models.

Transpiration

Let x_i denote the temperature in the i:th measurement, v_i the wet temperature, y_i light intensity and h_{mi} the transpiration rate of the m:th seedling correspondingly. According to HARI *et al.* (1975) the difference between the readings of the wet and dry thermocouples gives quite an accurate estimate of the evaporation rate. The temperature inside the cuvette rises when it is closed. This is caused by solar radiation. The transpiration rate is analyzed with the following model in nonstressed conditions

$$(1) \qquad h_{mi} = a_m \cdot (x_i - v_i) + b_m y_i + c_m,$$

where a, b and c are plant specific parameters, the values of which have to be estimated. If the plant is stressed by the environment, the degree of the effect of this stress on transpiration can be estimated using the degree of the control of transpiration rate, ct, which is defined as follows

$$(2) \qquad ct_{mi} = \frac{h_{mi}}{a_m \cdot (x_i - v_i) + b_m y_i + c_m},$$

where the values of parameters a, b and c are estimated in nonstressed conditions (cf. HARI *et al.* 1975). The degree of control is measured transpiration rate divided by the predicted value if no stresses were present according to the definition.

The daily amounts of transpired water can be treated with quite similar methods as the transpiration rate. Let H_{mj} denote the amount of water transpired by the m:th seedling during the j:th day and PH_j the amount of potential transpiration during the j:th day. In nonstressed conditions H_{mj} can be predicted quite well with the following model

$$(3) \qquad H_{mj} = k_m \cdot PH_j.$$

The daily degree of control of transpiration, CT, is defined analogously to the control of transpiration rate

$$(4) \qquad CT_{jm} = \frac{H_{mj}}{k_m PH_j},$$

where the value of parameter k_m is determined in nonstressed conditions (cf. SMOLANDER *et al.* 1975).

Photosynthesis

Let p_{mi} be the photosynthetic rate in the i:th IRGA-measurement and y_i the value of the i:th light measurement. The photosynthetic rate p_{mi} is determined in nonstressed conditions by light and temperature, thus

$$(5) \qquad p_{mi} = p_m(x_i, y_i),$$

where p_m is a function to be estimated (cf. HARI *et al.* 1973 and 1976, SALO 1974 and REED *et al.* 1976).

The photosynthetic rate decreases in stress conditions. This is measured by the degree of the control of photosynthetic rate cp_{mi}

which is defined as follows (cf. HARI *et al.* 1975)

(6) $cp_{mi} = \dfrac{p_{mi}}{p_m(x_i, y_i)}$.

The daily integrals of photosynthetic rate are not available, but they can be approximated from the daily sums of the photosynthetic rate. The daily degree of photosynthetic control, CP, is defined

(7) $CP_{mi} = \dfrac{\displaystyle\sum_{i=i_j}^{i_{j+1}} p_{mi}}{\displaystyle\sum_{i=i_j}^{i_{j+1}} p_m(x_i, y_i)}$,

where i_j is the number of the first measurement of the photosynthetic rate during the j:th day.

Daily height increments

The self regulation of plants has a very pronounced effect on height growth. It is an essential feature of growth taking place in the absence of stress. During the phase of maximal height growth the height growth rate is primarily determined by temperature. Let h denote the dependence of height growth rate on temperature presented in Fig. 4 according to HARI *et al.* 1977. During the phase of maximal growth the daily height increment G_{mj} (m:th seedling, j:th day) can be analysed with the following model

(8) $G_{mj} = a_m \displaystyle\int_{t_j}^{t_{j+1}} h(x(t - \tfrac{6}{24})) \, dt = a_m k_j,$

where t_j is the beginning instant of the j:th day (cf. HARI 1976). The model defined by Eq. (8) gives satisfactory results only during the phase of maximal growth. It gives too large values for daily height increments at the beginning and at the end of the growing period (cf. HARI and LEIKOLA 1974). For this reason the model has to be developed
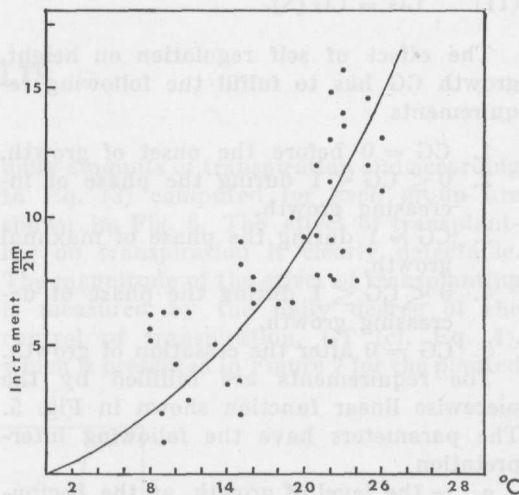

Fig. 4. The length increment of *Rubus saxatilis* runners as a function of temperature with a time lag of six hours.

further. In the early summer the rate of maturation is mainly determined by temperature. During cold days there is hardly any development at all, but during warm days the progress is very rapid. This effect is taken into consideration by means of the rate of maturation.

Let m denote the rate of maturation. Let us suppose that m depends on temperature only

(9) $m = m(x)$.

A new concept, physiological stage of development, S, is now defined which describes the stage of development of the plant using the rate of maturation

(10) $S(t) = \displaystyle\int_{t_0}^{t} m(x(t)) dt$ (HARI 1968 and 1972, ROBERTSON 1972, SARVAS 1976).

The self regulation of the height growth of plants can now be introduced into the model. Let CG denote the effect of self regulation on height growth. Assume that CG depends on the physiological stage of development

(11) $CG = CG(S)$.

The effect of self regulation on height, growth CG has to fulfill the following requirements

1. $CG = 0$ before the onset of growth,
2. $0 \leq CG \leq 1$ during the phase of increasing growth,
3. $CG \approx 1$ during the phase of maximal growth,
4. $0 \leq CG \leq 1$ during the phase of decreasing growth,
5. $CG = 0$ after the cessation of growth.

The requirements are fulfilled by the piecewise linear function shown in Fig. 5. The parameters have the following interpretation

a_1 = the level of growth, at the beginning of the daily height increments,

S_1 = the physiological stage of development in which maximum growth is attained,

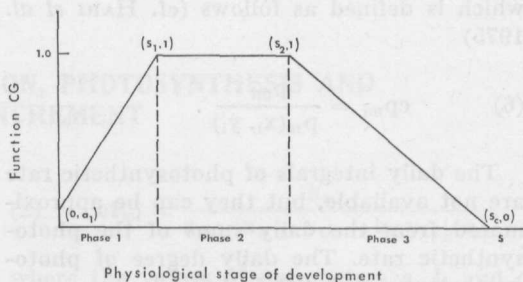S_2 = the physiological stage of development in which growth starts to decrease,

Fig. 5. The function CG used in the model.

S_c = the physiological stage of development in which growth ceases.

The daily height increments can now be analysed with the following model

(12) $Gmj = CG(S_j) \ a_m \ k_j$,

where $S_j = S(t_j)$ (cf. HARI *et al.* 1977 and VUOKKO *et al.* 1977) and k_j is defined in Eq. (8).

RESULTS

Transpiration

Effect of transplanting on the daily amounts of transpiration

The seedlings were weighed and watered once a day in order to control the amount of water in the pot and to measure the daily amounts of transpired water. The

Fig. 7. The daily degrees of control of transpiration, CT: A. planted group. B. exposed group.

daily amounts of transpiration and according to Eq. (3) computed for each group are shown in Fig. 6. The effect of transplanting on transpiration is clearly detectable. The magnitude of the effect of transplanting is measured by the daily degree of the control of transpiration, CT (cf. Eq. 4), which is presented in Figure 7 for the planted
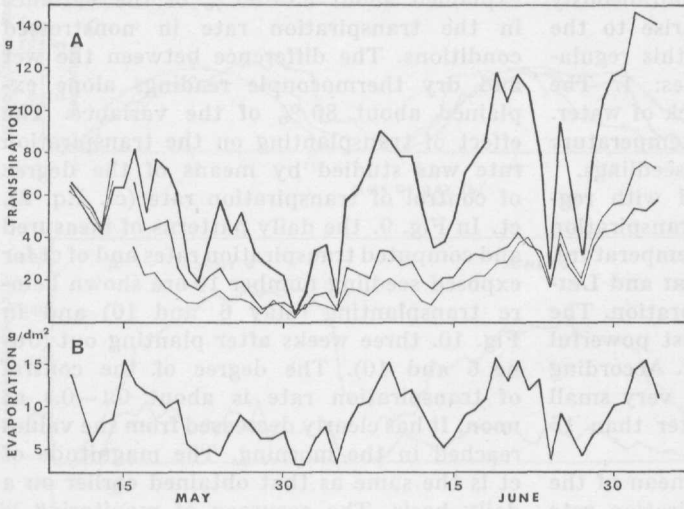
Fig. 6. A. The daily amounts of transpiration scaled according to Eq. (3) for control (thick line), planted (medium line) and exposed group (thin line).
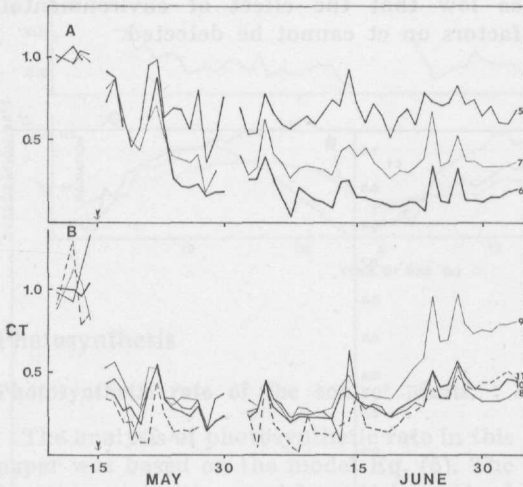B. The daily amounts of evaporation from petri dish.

and exposed seedlings for the whole measuring period.

Planting caused a very clear decrease in the gross level of transpiration. The effect lasted throughout the whole measuring period. The variation between seedlings is, however, quite pronounced. The degree of the control of transpiration for seedling number 5 is about 0.6−0.4 at the end of the monitoring period and for seedling number 7 about 0.3−0.5. For seedling number 6 the control of transpiration was increasing throughout the whole period and CT equalled 0.1−0.2 at the end of the period.

The effect of transplanting and exposure on transpiration is very clear and regular. The decrease in the value of CT is more pronounced and more rapid than that of the planted seedlings. The stressed seedlings transpired only 10−30 % of the potential

amount. Subsequently there is some recovery in transpiration. This effect is most pronounced in seedling number 9. Its CT increases from 0.4 to 0.8. There is also some recovery in the transpiration of other seedlings. Their CT values were about 0.5 by the end of the monitoring period.

The effect of environmental factors on CT

The pattern followed by CT is very similar in each treatment group. There is, however, some systematic effect causing the variation. The peaks in CT occur simultaneously in each plant. This fact gives rise to the question: what factor produces this regularity. There are two possibilities: 1. The stomata are closed due to the lack of water. 2. There is interaction between temperature and the self regulation of the seedlings.

These hypotheses were tested with regression analysis. The control of transpiration was explained with daily mean temperature, daily theoretical respiration (HARI and LEIKOLA 1974) and with daily evaporation. The last factor proved to be the most powerful in explaining the variance in CT. According to Fig. 8 the variation in CT is very small when daily evaporation is greater than 15 g dm^{-2}day^{-1}.

The daily value of CT is the mean of the degree of control of the transpiration rate weighted with the evaporation rate. For this reason a much more effective way of studying the effect of environmental factors on the control of transpiration is to study the relationship between ct and the environment.

Effect of transplanting on transpiration rate

Transpiration rate was monitored with an URAS-gas analyzer. However, this is rather difficult since water easily condenses in the tubing. Monitoring is reliable only during periods of fine weather and during the day time. The model defined by Eq. (1) explained about 85—90 % of the variance in the transpiration rate in nonstressed conditions. The difference between the wet and dry thermocouple readings alone explained about 80 % of the variance. The effect of transplanting on the transpiration rate was studied by means of the degree of control of transpiration rate (cf. Eq. 2), ct. In Fig. 9. the daily patterns of measured and computed transpiration rates and of ct for exposed seedling number 10 are shown before transplanting (May 6 and 10) and in Fig. 10. three weeks after planting out (June 6 and 10). The degree of the control of transpiration rate is about 0.1—0.3 at noon. It has clearly decreased from the values reached in the morning. The magnitude of ct is the same as that obtained earlier on a daily basis. The accuracy of monitoring is so low that the effect of environmental factors on ct cannot be detected.

Fig. 8. Correlation between CT and daily evaporation: A. planted seedlings during the period May 2—June 20. B. exposed seedlings during the period May 2—June 30.
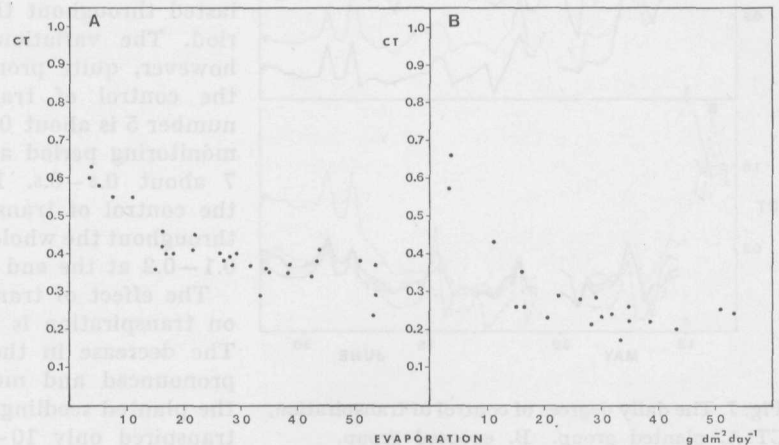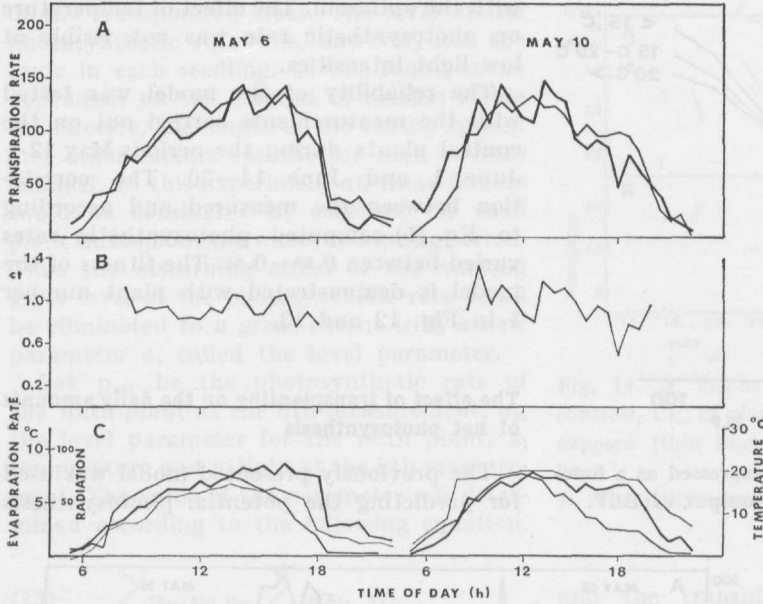
Fig. 9. A. Transpiration rates as measured by URAS (thick line) and computed according to Eq. (1) (thin line) for exposed seedling number 10 May 6 and 10.
B. The degree of control of transpiration rate.
C. Evaporation rate (difference between dry and wet thermocouple readings) (thick line), total radiation (medium line) and temperature (thin line).
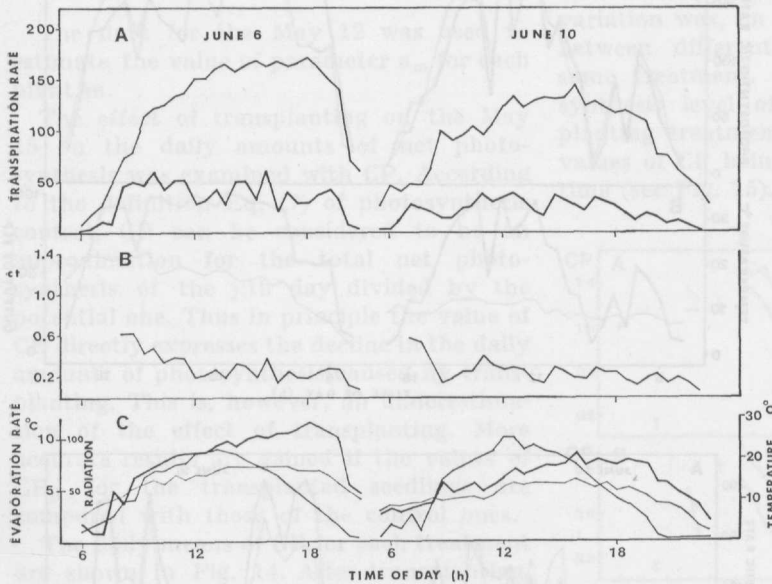

Fig. 10. Same as Fig. 9. June 6 and 10.

Photosynthesis

Photosynthetic rate of the control plants

The analysis of photosynthetic rate in this paper was based on the model Eq. (5). The function p in the model was determined using the measurements carried out with three control plants during the period June 2—13. During this period temperature varied between 15—25° C at high light intensities (output of ELP being 80—100) and between 3—20° C at low light intensities. The dependence of the photosynthetic rate on temperature and the output of the ELP is shown in Fig. 11. The optimum temperature near to the maximum output of the ELP was about 15° C. Photosynthetic rate was depressed by about 20 % at 25° C compared
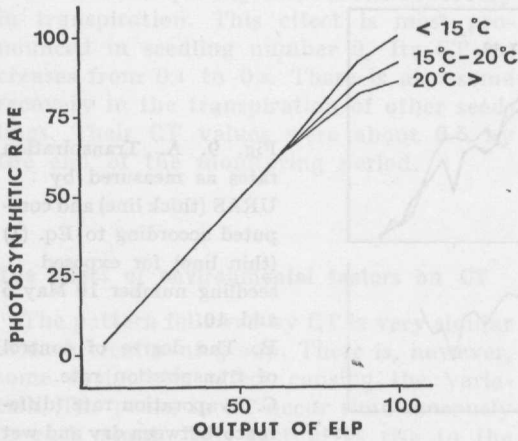
Fig. 11. Photosynthetic rate expressed as a function of temperature and the output of ELP.

with the optimum. The effect of temperature on photosynthetic rate was not visible at low light intensities.

The reliability of the model was tested with the measurements carried out on the control plants during the periods May 12— June 1 and June 14—20. The correlation between the measured and according to Eq. (5) computed photosynthetic rates varied between 0.90 — 0.95. The fitness of the model is demonstrated with plant number 1 in Fig. 12 and 13.

The effect of transplanting on the daily amounts of net photosynthesis

The previously presented model was used for predicting the potential photosynthesis

Fig. 12. A. Measured (thick line) and according to Eq. (5) (medium line) computed photosynthetic rates for control seedling number 1, during May 12 and 19. B. Output of ELP (thick line) and temperature (thin line).
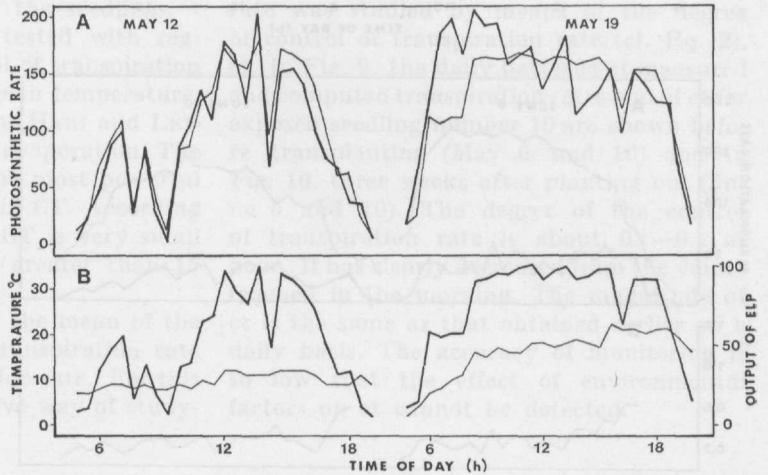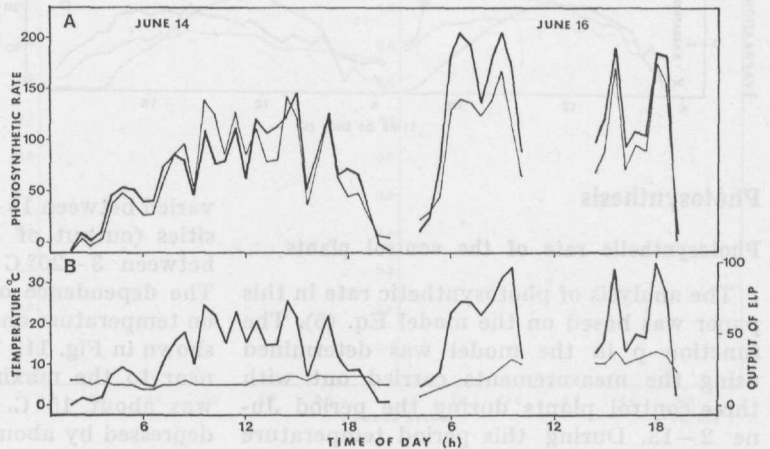

Fig. 13. Same as Fig. 12, June 14 and 16.

of the transplanted trees. The level of the photosynthetic rate was, however, not the same in each seedling. It was found to be dependent on the amount of needles inside the cuvette, the length of the tubing system and other factors specific for each cuvette channel. In this experiment all these factors could be considered as constant for each plant throughout the whole measuring period. Thus the disturbing effect of the varying gross level of the photosynthetic rate could be eliminated to a great extent with a new parameter a, called the level parameter.

Let p_{mi} be the photosynthetic rate of the m:th plant at the i:th measurement, a_m the level parameter for the m:th plant, x_i temperature and y_i light at the i:th measurement. The value of the parameter a is determined according to the following equation.

$$(13) \qquad \sum_i p_{mi} = a_m \sum_i p(x_i,\ y_i).$$

The data for the May 12 was used to estimate the value of parameter a_m for each plant m.

The effect of transplanting on the May 15 on the daily amounts of net photosynthesis was examined with CP. According to the definition Eq. (7) of photosynthetic control, CP can be considered to be an approximation for the total net photosynthesis of the j:th day divided by the potential one. Thus in principle the value of CP directly expresses the decline in the daily amounts of photosynthesis caused by transplanting. This is, however, an underestimation of the effect of transplanting. More accurate results are gained if the values of CP_{jl} for the transplanted seedlings are compared with those of the control ones.

The daily means of CP for each treatment are shown in Fig. 14. After transplanting, the CP values of the transplanted seedlings were about half those of the control plants. The only exceptions from this rule occurred on a few unusually cold days, for example on May 21 and June 13—14, when the decreases in the daily amount of photosynthesis were not so pronounced. Before June 20 it was not possible to detect any remarkable recovery from the shock caused by the transplanting as evaluated with CP.

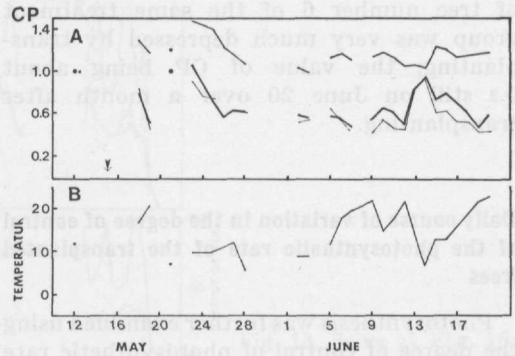The mean values of CP for the transplanted

Fig. 14. A. Means of the daily photosynthetic controls, CP, of plants in the planted (thick line), exposed (thin line) and control group (medium line).
B. The daily maximum temperatures.

and the transplanted and exposed trees differed only slightly from each other. The variation was, on the contrary, pronounced between different seedlings receiving the same treatment. For example the photosynthesis level of tree number 5 of the planting treatment was little affected; the values of CP being near to 1.0 most of the time (see Fig. 15). However, photosynthesis
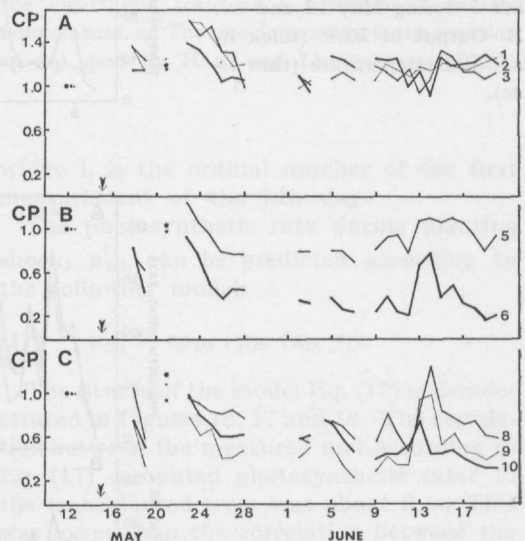

Fig. 15. The daily photosynthetic controls (CP).
A. The control seedlings B. The planted seedlings C. The exposed seedlings.

of tree number 6 of the same treatment group was very much depressed by transplanting; the value of CP being about 0.2 still on June 20 over a month after transplanting.

Daily course of variation in the degree of control of the photosynthetic rate of the transplanted trees

Photosynthesis was further examined using the degree of control of photosynthetic rate cp_{mi}, which expresses the relationship between the measured and according to Eq. (5) computed photosynthetic rate at the i:th IRGA-measurement (Eq. 6). The fitness between the measured and according to Eq. (5) computed photosynthetic rates was fairly satisfactory for the control plants as

demonstrated earlier in Fig. 10 and 11. Thus cp of the control plants during the whole day was about 1.0.

On the other hand, the photosynthetic control cp of the transplanted trees was less than 1.0 (see Figs 16, 17 and 18). However, the value of cp was not constant throughout the day. The typical pattern of the degree of photosynthetic control was: 1. In early morning $cp = 1$, 2. rapid decrease in the morning from about 7 to 10 a.m., 3. fairly constant value during the day, 4. increase in the evening. This pattern, however, changed during exceptionally cold days (for example June 14). Photosynthetic control on these days was near to 1.0 throughout the day (see Fig. 16).

In order to study the daily course of the variation in CP_i a new parameter was added to model Eq. (5). This parameter, called the

Fig. 16. A. Measured (thick line) and according to Eq.(5) (medium line) and (12) (thin line) computed photosynthetic rates for planted seedling number 5 during May 12 and 19. B. Output of ELP (thick line) and temperature (thin line).
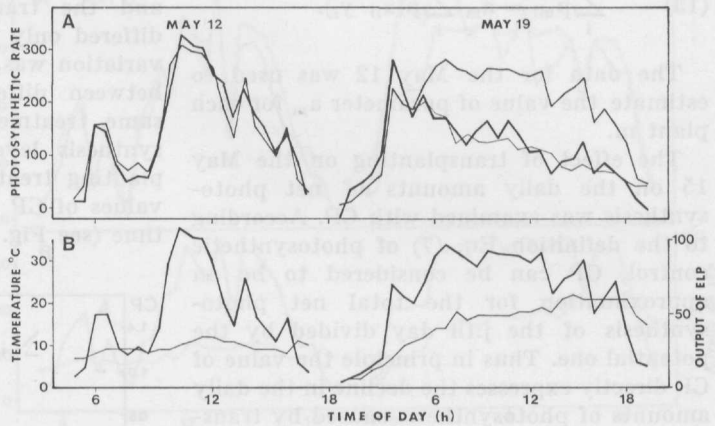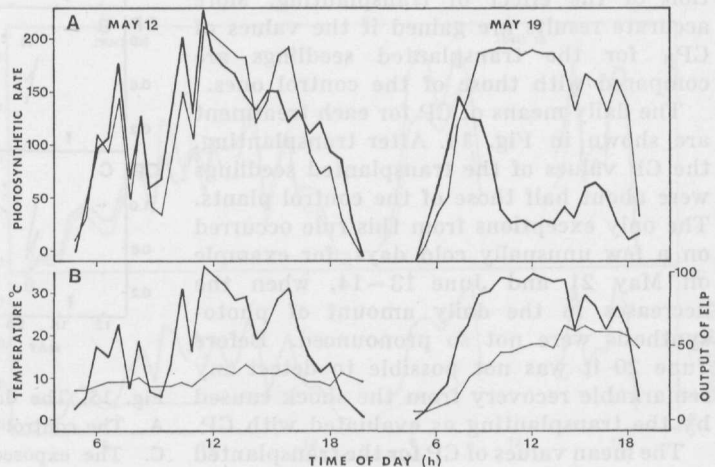

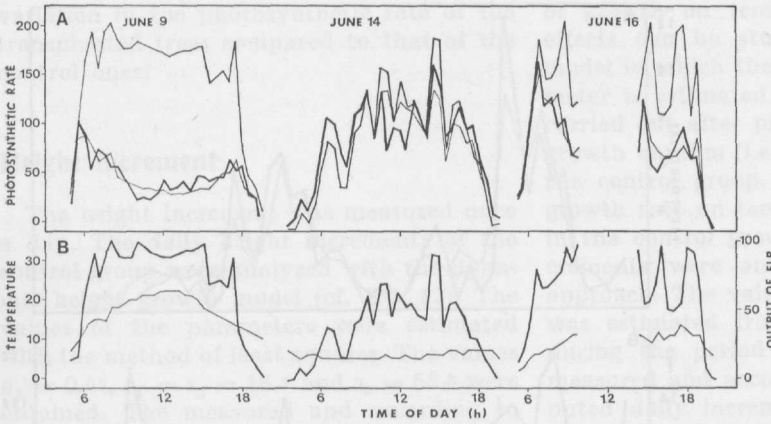Fig. 17. Same as Fig. 16. Exposed seedling number 9, May 12 and 19.

Fig. 18. Same as Fi g. 16, June 9, 14 and 16.

physiological water stress, w, has earlier been used by HARI and LUUKKANEN (1974) to explain the variation in the photosynthetic rate of birch trees under water stress. According to this study there is some interaction between water deficit and temperature.

Let cp_{mi} be, as earlier, the degree of control of the photosynthetic rate in the i:th measurement of the m:th plant, z_i the cuvette temperature at the i:th measurement and w_{mi} the physiological water stress of the m:th plant during the j:th day. The interaction between the water deficit and temperature can be introduced into the model by assuming that

(14) $cp_{mi} = cp (z_i, w_{mj})$.

The cuvette temperature was approximated with the temperature measured in the shade and the light intensity (HARI and LUUKKANEN 1973). In Fig. 19, cp_{mi} is plotted against cuvette temperature. The effect of temperature on cp seems to be exponential. Thus cp can be approximated as follows

$$(15)\ cp(z_i, w_{mj}) = \begin{cases} \exp[-0.10(z_i - 37 + w_{mj})], \\ \qquad \text{if } z_i \geq 37 - w_{mj}, \\ \\ 1, \text{ if } z_i \leq 37 - w_{mj}. \end{cases}$$

The value of parameter w_{mj} was estimated from the data for each day by minimizing the following residual sum of squares:

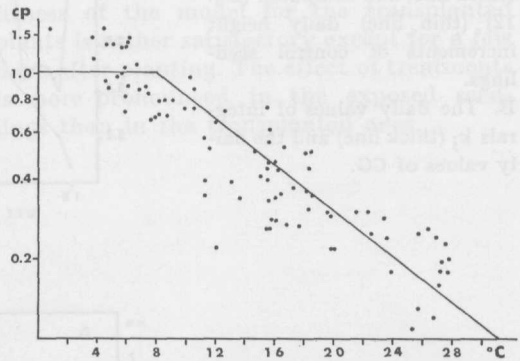$$(16)\quad \min_{w_{mj}} \left\{ \sum_{i=i_j}^{i_{j+1}} (cp_{mi} - cp(z_i, w_{mj}))^2 \right\},$$

Fig. 19. Photosynthetic control cp of plant number 9 on May 21 and June 9, 15 and 17 expressed in the logarthmic scale as a function of cuvette temperature, z_i. The line demonstrates the function cp (z_i) used by HARI and LUUKKANEN (1973).

where i_j is the ordinal number of the first measurement of the j:th day.

The photosynthetic rate during planting shock, p^1_{mi}, can be predicted according to the following model:

(17) $p^1_{mi} = cp_{mi} \cdot p_m (x_i, y_i)$.

The fitness of the model Eq. (17) is demonstrated in Figures 16, 17 and 18. The correlation between the measured and according to Eq. (17) computed photosynthetic rates in the transplanted trees was about 0.85. This was lower than the correlation between the measured and according to Eq. (5) computed photosynthetic rates in the control plants. This fact was probably caused by smaller
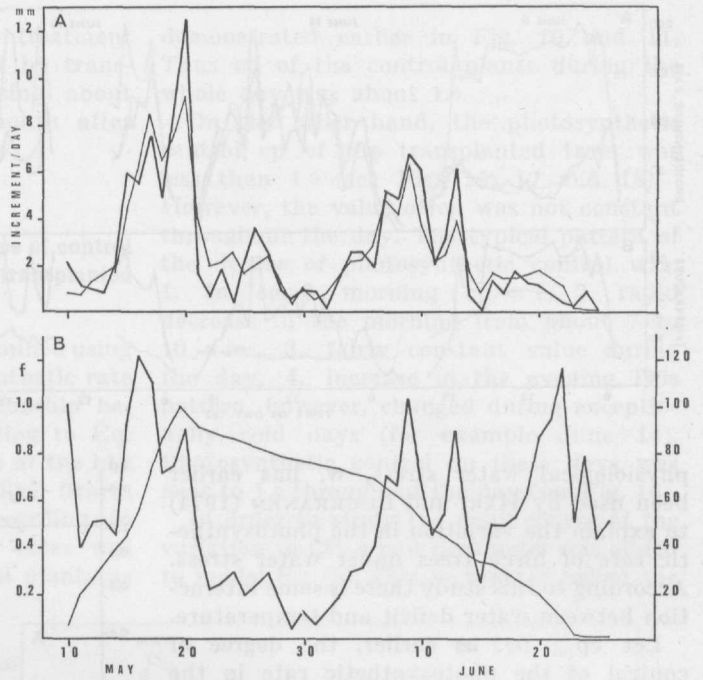
Fig. 20. A. The measured (thick line) and computed (Eq. 12) (thin line) daily height increments of control seedlings.
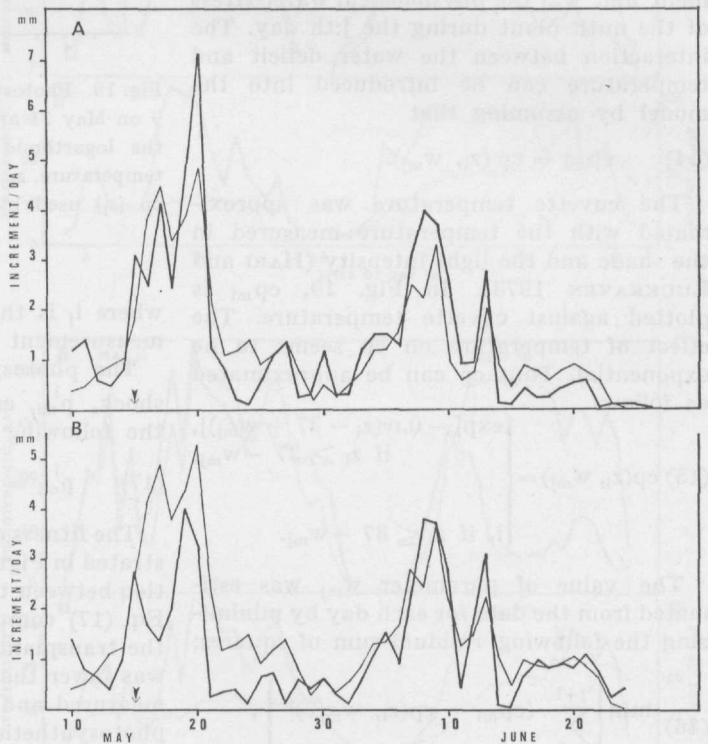B. The daily values of integrals k_j (thick line) and the daily values of CG.

Fig. 21. A. The measured (thick line) and computed (Eq. 12) (thin line) daily height increments of planted seedlings.
B. Same as A. for exposed seedlings.

variation in the photosynthetic rate of the transplanted trees compared to that of the control ones.

Height increment

The height increment was measured once a day. The daily height increments of the control group were analyzed with the dynamic height growth model (cf. Eq. 12). The values of the parameters were estimated with the method of least squares. The values $a_1 = 0.07$, $s_1 = s_2 = 16.3$ and $s_c = 58.6$ were obtained. The measured and according to the model computed daily height increments are shown in Fig. 20 for the control group. Transplanting may have three different effects on daily height increments: 1. The decrease in the gross level of height increment. 2. Change in the growth rhythm of the seedlings. 3. Change in the dependence of growth on temperature. The last two effects can be studied by constructing a model in which the value of the level parameter is estimated from the measurements carried out after planting and the effect of growth rhythm (i.e. CG) is the same as for the control group. The dependence of the growth rate on temperature is the same as in the control group. The daily height increments were analyzed using the above approach. The value of the level parameter was estimated from the increment values during the period June 1 — June 25. The measured and according to the model computed daily increments are shown in Fig. 21 for the whole measuring period. The fitness of the model for the transplanted plants is rather satisfactory except for a few days after planting. The effect of treatments is more pronounced in the exposed seedlings than in the transplanted ones.

DISCUSSION

The continuous monitoring of the principle metabolic processes, photosynthesis and transpiration, and height increment, under natural conditions offers an opportunity to study the nature of planting shock. The main principle involved in the measuring technique was the monitoring of the relevant external conditions and simultaneously the principal processes. The height increment of the leader shoot and the total transpiration were monitored daily, photosynthetic and transpiration rate every twenty minutes. As all these measurements were nondestructive they could be carried out with the same seedlings throughout the whole experimental period. This kind of measuring technique is well suited to the study of the metabolic processes, their dependence on environmental conditions and functional changes caused by transplanting. The measurements can be easily automated thus permitting continuous monitoring.

The present experiment was carried out under natural conditions. The plastic shelter protected the seedlings against rain and the seedlings were grown in clay pots covered with plastic bags. For these reasons the temperature of the air under the shelter was a few centigrades higher than that of the surrounding air on sunny days, and the soil inside the pots was clearly warmer than the soil in normal planting sites. To some extent the pot also restricted the growing space of the roots, and the plastic bag restricted the diffusion of oxygen into the soil.

The gas exchange measurements were carried out with an automatically operating measurement system, pneumatically operating cuvettes, tubing system, etc. Continuous checking of the operation of the system was essential for reliable measurements. Lightning constituted a potential danger for the electrical equipment. To avoid damage the equipment was switched off during thunderstorms. The measurement of the transpiration rate with H_2O-URAS was rather difficult owing to water condensation inside the cuvettes and the tubing system. This happened especially in the morning and on rainy days.

By replacing the nylon tubes with copper ones the disturbing effect of this phenomen could be diminished. However, when the transpiration rate was analyzed much of the data had to be rejected. It was thus impossible to carry out a thorough comparison of the daily patterns of the transpiration and photosynthetic rates. The daily total transpiration was monitored by weighing the pots every morning. At the same time the height increment was measured using a vernier scale. Both these methods are simple and do not require any additional equipment.

The analysis of photosynthesis was based on the dependence of the photosynthetic rate on light and temperature. This function (Eq. 5) was obtained from the measurements carried out with the control plants. The result illustrated in Fig. 11, is not complete because of the limited variation in light and temperature during the measuring period. It does show, however, the fairly small effect of temperature on photosynthetic rate compared to that of light. The effect of temperature on the photosynthetic rate was not visible at low light intensities. At high light intensities the optimum temperature was about $15°$ C. These results correspond fairly well with earlier observations on the dependence of photosynthetic rate on temperature and light in Scots pine (HAVAS 1971, ZELAWSKI *et al.* 1973, PELKONEN 1977). The correlation between the measured and according to Eq. (5) computed photosynthetic rates was about $0.90-0.95$.

The above model was used for analyzing the photosynthesis of the planted trees. This gave an estimate for the value of the level parameter for each plant. The measurements taken before transplanting had to be used for this estimation. The data available for this purpose was restricted to the measurements carried out on one day (May 12.) The reliability of the results was to a great extent dependent on the reliability of the data collected on May

12. During the day in question the photosynthetic rate of each plant was monitored about 30 times. This was enough to check the suitability of the above mentioned model (Eq. 5) and thus obtain information about the reliability of the data for the day. The correlation between measured and according to Eq. (5) computed photosynthetic rates were in each plant over 0.90. The estimation of the level parameter can thus be considered as satisfactory.

The variation in transpiration, photosynthesis and growth is very pronounced from one measurement period to another. This is mainly caused by variations in environmental conditions. Especially in the spring the variation in the main environmental factors, temperature, light intensity and evaporation rate is great. This is reflected in the measurements (cf. Figs. 6, 12 and 20). The great variation makes the interpretation of the results difficult. When studying the photosynthesis and transpiration measurements, the question arises: to what extent are the metabolic processes reduced? In order to answer this the various degrees of control are defined. By definition CP, cp, CT, ct and CG are the proportions between the measured values and the expected ones computed from pure environmental factors. Ecological interpretation of the different types of degree of control is very clear. In addition they are quite easy to measure and compute. The effect of different kinds of stress on gas metabolism is as a rule studied using so called stomatal resistance. Its physiological background is clear but the ecological interpretation is difficult. The measurement of stomatal resistance is very difficult to automate. For this reason it is difficult to arrange a long monitoring period for the stomatal resistance of a seedling.

In practical forestry the planting shock is the sum effect caused by exposure during transportation and planting. The experimental seedlings were larger than those commonly used in regeneration work. For this reason planting could produce a stronger and longer-lasting planting shock. On the other hand, the nature of the shock should be rather independent of the size of the experimental plants. The measuring accuracy was improved by the large seedlings

especially in the weighing of daily amounts of transpiration. The limited number, only eleven, of seedlings makes it difficult to make generalizations about the results.

According to our observations, planting can have a very pronounced and long lasting effect on the metabolism of a seedling. The daily amounts of transpiration were reduced in a few days to 40 % of the potential transpiration. The daily total amounts of photosynthesis were decreased to 50 % of the potential value. The variation between the seedlings was, however, great in both transpiration and photosynthesis. One reason for this great variance may be the differences in the size and density of the root systems.

Exposure caused, especially a few days after treatment, a more rapid decrease in the daily amounts of transpiration than planting. Transpiration was then about 25 % of the potential amount. The decrease in photosynthesis was of the same magnitude. Exposure has to be considered as quite a severe treatment, since the seedlings lost about 18 % of their fresh weight during exposure. Many investigators, for example GÜRTH (1970) and v. LÜPKE (1972) have discovered that a 15 % loss of weight is dangerous to Norway spruce and LÅNGSTRÖM (1971) has noticed that a 12 % loss of weight resulted in a storage experiment decrease of 35 % in the survival rate of Scots pine. Despite this fact there were only slight differences in the mean values of CT and CP between the treatments. More replications are needed to obtain a reliable estimate of the effect of exposure on CT and CP, because the variance between the seedlings is so large.

The effect of planting shock proved to last for a longer time than expected. There was no sign of recovery in photosynthesis when the monitoring of the photosynthetic rate was finished on 20th June. However, there was some recovery in transpiration five weeks after planting. The degree of control of transpiration for the seedling which showed the most rapid recovery, rose in two weeks from 0.4 to 0.8. The recovery in other seedlings was not so clear and was not dectectable at all in the planted seedlings. Recovery occurs at the same time as the cessation of height increment and the maximal growth of needles. The rapid growth of roots starts

after the cessation of height increment according to HOFFMAN (1973), TRANQUIL-LINI (1973) and HAVRANEK (1975) have found that the recovery of water balance is connected with the degree of root regeneration. This connection between the different growth phenomen may possible affect the timing of the recovery. The continuous monitoring of root growth is necessary in order to obtain reliable results about the nature of the recovery of the seedlings. Occasionally there are many problems involved in the nondestructive monitoring of root growth (cf. SUTTON 1969, SAFFORD 1976). The recovery of water balance makes the recovery of photosynthesis possible. In the present experiment there was a drastic decrease in photosynthesis and no recovery after five weeks. The loss in the amount of fixed CO_2 is a natural explanation for the decrease in growth after planting. If the planting shock is decreased or if its duration can be shortened the possibilities for normal development of the seedling are essentially improved.

The daily values of CT and CP depend, besides on the planting shock, on the weather conditions. DENMEAD and SHAW (1962) have explained the variation in the daily relative transpiration, CT, during drought with the daily amounts of evaporation. It also proved to be the most powerful environmental factor in explaining the variance of CT. The variation in CT was quite small when the evaporation was over 15 g dm^{-2} day^{-1}. As there were only a few observations under this limit it is difficult to draw any clear conclusions about the nature of the mechanism behind the variation in CT. The effect of environment on self regulation is most effectively studied at the rate level. Thus the dependence of ct on environmental factors should be determined. As there are many problems involved in monitoring the transpiration rate in field conditions, the measurements of transpiration rate are often not reliable, especially during rainy periods and early in the morning. This generates complications in determining the dependence of ct on environmental factors. More representative data is needed for this purpose.

There is strong interaction between the effect of temperature and water deficit in photosynthesis (cf. HARI and LUUKKANEN 1975). This interaction makes accurate study of the dependence of CP on environmental factors quite complicated. This trouble is avoided if the dependence of cp on environmental factors is studied instead. HARI and LUUKKANEN (1975) have presented a model for the interaction between the effect of water stress and temperature on photosynthesis. The essential feature of this model is that photosynthesis becomes sensitive to elevated temperatures. The threshold value of temperature above which photosynthesis is depressed is quite a good estimate of the severeness of the water deficit. In the present study the same model was applied as that during drought by HARI and LUUKKANEN (1975). The fitness between the measured and observed values was quite satisfactory (cf. Figs. 16—18). The threshold temperature above which photosynthesis is depressed is quite a good estimate of the degree of planting shock, but for its estimation temperatures above the threshold are needed. The variation in temperature is so small during overcast weather that the estimation of the threshold value from the data is impossible for several days.

The daily degree of the control of photosynthesis, CP, gives the essential information about the changes in the amount of carbohydrates stored during the day. The interpretation of the results is, however, very difficult without knowing the change in the dependence of photosynthetic rate on temperature. This change may confuse the results in an experiment in a controlled environment with constant temperature. If the relationship between ct, cp and, on the other hand, environmental factors is known exactly, then the ecological importance of a particular treatment could be studied using daily amounts of transpired water. This enables a large number of treatments and replications to be used without increasing the work load.

The daily height increments of the control plants were determined to a great extent by temperature and self regulation. This result supports earlier results (cf. HARI and LEIKOLA 1974). The height increments of the planted and exposed seedlings also followed a very regular pattern after treatment. Despite the possible decrease in the

gross level there was no effect on the daily height increments. Thus in a few days the self regulation of the seedling could adjust to height increment within reduced limits. It can be concluded from Figs. 20 and 21 that the dependence of the height increment of temperature and self regulation is not essentially effected by planting.

In field experiments the height increment during a growing season is normally measured. It is the integral of height growth over the summer. From the methodological point of view it is more effective if the time derivatives, i.e. the rates of the corresponding processes are studied instead. Only at the level of the derivatives is it possible to divide the effects regulating the metabolic processes into two components: that dependent on the environmental conditions and that dependent on the self regulation. By studying these components simultaneously there is an opportunity to analyse in detail the effect of the planting shock and the environmental changes. The final results can be obtained by integration. The self regulation of plants can be taken into consideration in the integration with the different degrees of control.

The present study approach seems to be applicable to research into planting shock, if the number of the seedlings is rather limited and if the complex interactions which occur in practical planting are omitted. The whole complex of different stresses is under study using a further developed method on the guide lines of the present paper. It is evident that research can be extended to consider most of the essential features of planting such as genetical aspects, (LEDIG 1973), the state of seedling dormancy (PELKONEN 1977) and hardiness to match the season. On the basis of understanding the actions of plants the seedling material can be improved. The research should be extended in a more physiological direction in order to more deeply understand the mechanisms of the self regulation of transpiration, photosynthesis and growth.

SUMMARY

In the experiment pine seedlings were transplanted out in the field and, in addition, exposed. The effect of these treatments on gas metabolism and daily height increment were examined. The seedlings were 5-year old Scots pine plants growing in clay pots, covered with plastic bags. The transpiration and photosynthetic rates were monitored with the so-called open IRGA-measuring system for a few days before being subjected to the treatments and for one month after. In addition, the daily amounts of transpired water and daily height increments were measured.

In the first step of the data analysis a model for the potential rate of each metabolic process was constructed. The independent variables used in the model are the external factors specific to the various processes and self regulation of the seedling. The effect of the different treatments on self regulation is examined in the second step of the analysis.

Planting and additional exposure have a strong and rather permanent effect on the self regulation of each of the processes under study. This effect is very similar to that caused by water deficit. Exposure makes the disturbance more pronounced. Transpiration of the transplanted seedlings decreased in

a few days after planting to less than half of the potential value and that of the exposed ones decreased to a quarter of the potential value. The daily amounts of photosynthesis decreased to half of the potential value. There was no recovery in photosynthesis during the whole monitoring period, which lasted for four weeks. There was a slight recovery in transpiration about five weeks after transplanting. Thus the treatment probably generated stress conditions throughout the whole growing period, which is characterized by strong self regulation of photosynthesis and transpiration, thus causing an essential decrease in the total amount of CO_2 fixed. The effect of environment on the self regulation was very clearly evident in photosynthesis, which was depressed especially at elevated temperatures after planting, as during water deficit.

Planting and additional exposure did not produce any detectable changes in the dependence of the growth rate on temperature or in the effect of self regulation on height growth. On the other hand the level of growth was decreased as a result of planting out. This effect will be subjected to a detailed analysis in later studies.

REFERENCES

DENMEAD, O. T. & SHAW, R. H. 1962. Availability of soil water to plants as affected by soil moisture content and meteorological conditions. Agron. J. 54: 385—390.

GÜRTH, P. 1970. Forstpflanzen und Kulturerfolg eine Literaturübersicht. Allg. Forst- u. Jagdztg. 141: 160—172.

HARI, P. 1968. A growth model for a biological population, applied to stand of pine. Commun. Inst. For. Fenn. 66.7.

— » — 1972. Physiological stage of development in biological models of growth and maturation. Ann. Bot. Fenn. 8: 107—115.

— » — 1976. An approach to the use of differential and integral calculus in plant autecology. University of Helsinki department of silviculture. Research notes no 13.

— » — & LEIKOLA, M. 1974. Further development of the dynamic growth model of plant height growth. Flora 63: 357—370.

— » — & LUUKKANEN, O. 1973. Effect of water stress, temperature and light on photosynthesis in alder seedlings. Physiol. Plant. 29: 45—53.

— » — & LUUKKANEN, O. 1975. Field studies of photosynthesis as affected by water stress, temperature and light in birch. Physiol. Plant. 32: 97—102.

— » — LUUKKANEN, P., PELKONEN, P. & SMOLANDER, H. 1975. Comparisons between photosynthesis and transpiration in birch. Physiol. Plant. 33: 13—17.

— » — SALMINEN, R., PELKONEN, P., HUHTAMAA, M. & POHJONEN, V. 1976. A new appoach for measuring light inside the canopy in photosynthesis studies. Silva Fenn. 10(2): 94—102.

— » — SMOLANDER, H. & LUUKKANEN, O. 1975. A field method for estimation of the potential evapotranspiration rate. J. Exp. Bot. 94: 675—678.

HAVAS, P. 1971. Injury to pines in the vicinity of a chemical processing plant in northern Finland. Acta For. Fenn. 121.

HAVRANEK, W. 1975. Wasserhaushalt und Zuwachs von Fichten nach versetzung zu vershiedenen Jahreszeiten. Cbl. Ges. Forstw. 92(1): 9—25.

HOFFMAN, G. 1973. Periodik des Substanzmassen Zuwachs von Wurzeln und Sprossorganen junger Forstgehölze. Flora 162: 126—133.

KOZLOWSKI, T. T. & DAVIES, W. J. 1975. Control of water balance in transplanted trees. Journal of Arboriculture 1(5): 1—10.

LEDIG, F. T. 1974. Photosynthetic capacity: developing a criterion for the early selection of rapidly growing trees. In: LEDIG, F. T. (ed). Toward the future forest: applying physiology and genetics to the domestication of trees. New Hawen: Yale University. pp 19—39.

LÜPKE, B. v. 1976. Wachstum junger Fichten in abhängigkeit von ihrem Frischezustand vor der Pflanzung — Allg. Forst- u. Jagdztog. 144: 141—146.

LÅNGSTRÖM, B. 1971. Viktförlust, vattenhalt och plantavgång hos kyllagrade tallplantor. Summary: Weight loss, water content and mortality of cold stored seedlings of Scots pine. Silva Fenn. 5(1): 20—31.

PELKONEN, P., HARI, P. & LUUKKANEN, O. 1977. Decrease of CO_2- exchange in Scots pine after naturally occuring or artificial low temperatures. Can. J. For. Res. 7: 462—468.

REED, K., HAMKLY, E., DINGER, B. & JARVIS, G. 1976. An analytic model for field measurement of photosynthesis. J. Appl. Ecol. 13: 925—942.

SAFFORD, L. O. 1976. Seasonal variation in the growth and nutrient content of yellowbirch replacement roots. Plant and Soil 44: 439—444.

SALO, D. 1974. Factors affecting photosynthesis in Douglas-Fir. University Washington. Ph. D. Thesis, Ann Arbor, Michigan.

SARVAS, J. 1977. Mathematical model for physiological clock and growth. Acta For. Fenn. 156.

SUTTON, R. F. 1969. Form and development of root system. Commonwealth Agricultural Bureaux. Oxford.

TRANQUILLINI, W. 1973. Der Wasserhaushalt junger Forstpflanzen nach dem Versetzen und seine Beeinflussbarkeit. — Cbl. Ges. Forstw. 90(1): 46—52.

ZELAWSKI, W. SZANIAWSKI, R., DYBCZYNSKI, W. & PIECHUROWSKI, A. 1973. Photosynthetic capacity of conifers in diffuse light of high illuminance. Photosynthetica. 7: 351—357.

VUOKKO, R., KELLOMÄKI, S. & HARI. P. 1977. The inherent growth rhythm and its effect on the daily height increment of plants. Oikos 29: 137—142.

Seloste:

ISTUTUSSHOKIN VAIKUTUS MÄNNYNTAIMIEN TRANSPIRAATIOON, FOTOSYNTEESIIN JA PITUUSKASVUUN

Tutkimuksessa tarkastellaan, miten istutus sekä sen yhteydessä tapahtuva juurten kuivuminen vaikuttavat paljasjuuristen männyntaimien elintoimintoihin: transpiraatioon, fotosynteesiin ja pituuskasvuun. Koemateriaalina käytettiin viisivuotiaita ruukkuun istutettuja männyntaimia, joiden fotosynteesi ja transpiraationopeutta seurattiin luonnonolosuhteissa avoimella IRGA-systeemillä ennen istutusta ja istutuksen jälkeen noin kuukauden ajan. Lisäksi taimista mitattiin päivittäiset pituuskasvut ja haihdunnat.

Aineiston analyysivaiheessa on ensin kehitetty kunkin elintoiminnon potentiaaliselle nopeudelle matemaattinen malli, jossa selittäjinä ovat kunkin prosessin kannalta olennaisimmat ympäristötekijät ja itsesäätely. Tämän jälkeen on tarkasteltu miten istutusshokki vaikuttaa itsesäätelyyn, eli ts. miten havaittu transpiraatio, fotosynteesi ja kasvu poikkeavat ennustemallin mukaan lasketusta.

Tutkimuksen tulokset osoittavat, että istutus aiheuttaa voimakkaan, ja hyvin pitkäaikaisen vedenvajauksen, ja että istutuksen yhteydessä tapahtuva juurten kuivuminen voimistaa tätä stressiä. Istutettujen taimien haihdunta aleni muutamassa päivässä istutuksen jälkeen alle puoleen potentiaalisesta, ja kuivatuskäsittelyn saaneiden taimien haihdunta puolestaan aleni noin neljänteen osaan potentiaalisesta. Fotosynteesi aleni molemmissa ryhmissä noin puoleen. Vasta viiden viikon päästä havaittiin kolmen taimen haihdunnassa elpymistä, joten istutusshokki aiheutti ilmeisesti taimille koko kasvukauden kestävän rasitustilan, jolle on tyypillistä voimakas transpiraation ja fotosynteesin itsesäätely. Tämä merkitsee kasvukauden kokonaisfotosynteesin huomattavaa vähentymistä.

Tutkimuksessa tarkastellaan myös ympäristötekijöiden vaikutusta transpiraatioon ja fotosynteesin itsesäätelyyn istutusshokin aikana. Erityisen selvästi tuli esille korkeiden lämpötilojen fotosynteesin itsesäätelyä lisäävä vaikutus istutusshokin aikana.

Pituuskasvun lämpötilariippuvuudessa ja kasvurytmissä ei havaittu istutusshokin aiheuttamia muutoksia, lukuunottamatta muutamaa istutuksen jälkeistä päivää. Sensijaan kasvun taso ilmeisesti laskee istutusshokin takia. Tätä kasvun tason alenemista tullaan käsittelemään projektin myöhemmissä töissä.

Seloste:

ISTUTUSSHOKIN VAIKUTUS MÄNNYNTAIMIEN TRANSPIRAATIOON, FOTOSYNTEE-SIIN JA PITUUSKASVUUN

HALLMAN, E., HARI, P., RÄSÄNEN, P. K. & SMOLANDER, H.
O.D.C. 232.412: 161.16/32

1978. Effect of planting shock on the transpiration, photosynthesis and height increment of Scots pine seedlings. — ACTA FORESTALIA FENNICA 161. 26 p. Helsinki.

The effect of transplanting and additional exposure on gas exchange and height increment was studied in Scots pine seedlings. Transplanting shock had a strong and rather permanent effect on transpiration and photosynthesis. Transplanting reduced transpiration to less than half of the potential level and the additional exposure to a quarter respectively. The daily amounts of net photosynthesis decreased to half of the potential value in both treatments. Planting shock made photosynthesis sensitive to elevated temperatures. Planting shock did not produce any detectable changes in the dependence of the growth rate on temperature or in the growth rhythm of height increment.

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ACTA FORESTALIA FENNICA

EDELLISIÄ NITEITÄ — PREVIOUS VOLUMES