Gas-exchange and sap flow measurements of willow trees in short-rotation forest. I. Transpiration and sap flow

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Summary

Simultaneous measurements of transpiration and sap flow were performed on short-rotation willow trees (two-year-old sprouts on 8-year-old stumps) in the field. Transpiration was measured by an infrared gas analyser (IRGA) using an open-top ventilated chamber enclosing the whole foliage of a tree. Sap flow was measured using a tree-trunk heat balance (THB) technique with a constant temperature difference and variable heat input. Both the instantaneous and daily values of water flux measured by these two absolute techniques agreed well with a difference of up to about 5 %. The THB response to abrupt flux change when inducing emboli by cutting-off the stem was very rapid: the registered signal dropped by 85 % within 10 minutes for a specimen with a projected leaf area of 2 m^2. For the *Salix* trees, transpiration was linearly correlated with stem cross-sectional area and with leaf area.

Key words

sap flow, transpiration, open-top chamber, THB method, easily available water, tree size, leaf area, climate, rain

Introduction

Short-rotation forests, mainly consisting of different *Salix* species, are increasingly being introduced in Sweden today in order to produce wood for fuel. The plantations require ample water supply to obtain high biomass production which is the key to profitable cultivation. Knowledge of the water use of *Salix* trees under different conditions is thus essential for, e.g., choice of land suitable for plantations, management practices, etc.

Several studies on evaporation of short-rotation *Salix* stands show high evaporative rates, even exceeding those estimated for open water surfaces according to the Penman (1948) formula (e.g., Grip et al. 1989; Persson and Lindroth 1994). These studies were based on determinations of evaporation by water balance and micrometeorological methods, thus giving total evaporation including soil evaporation. However, in order to obtain data easily related to a certain dendrometric size and to facilitate a link between physiological and meteorological approaches, it is also desirable to analyse the processes at the level of individual specimens (shoot or trees).

In this study, the measurements of water fluxes by two independent methods are presented: the open top chamber technique to measure fluxes of water vapour and CO_2 (CO_2 fluxes not shown here) and the stem tissue heat balance (THB) method to measure sap flow in stems. The chamber is a top-down ventilated unit with a infrared gas analyser (IRGA) measuring differences of gas concentrations. The THB method used for sap flow measurements is a modification of the approach developed during the 1960s and 1970s for large-sized trees (Daum 1967; Cermák et al. 1973; Kucera et al. 1977). The THB method has also been used for short-term measurement on small diameter stems by Rychnovska et al. (1980) and by Cermák et al. (1984) and for long-term measurements on the same species, as done in this study by Lindroth et al. (1994). The THB method used here uses external heating and internal sensing of temperature and it is the improved version of the system used by Lindroth et al. (1994). There are other modifications of THB method used for herbaceous plants or tree stems (e.g. Sakuratani 1981; Baker and Van Bavel 1987; Granier 1987; Steinberg et al. 1989), but these are not adapted in a similar way to a long-term application on smal-size fast-growing stems. Moreover, the set-up using external sensing of temperature gradients, that is used in some commercially available products, was found inappropriate for the studied material (unpublished results by the authors).

The aim of this study was to compare the fluxes as measured in the chamber by IRGA and by the THB technique, to evaluate the application of the two methods and to estimate some fundamental relations between water flux and dendrometric characteristics of the *Salix* trees.

Materials and methods

Site and material description

The stand of *Salix viminalis* L. was established in 1984 using cuttings at a spacing of 0.7 m by 0.7 m, i.e., $20.4*10^3$ cuttings ha^{-1} (Verwijst 1991) on a site in Ultuna, Uppsala (Lat. 59°49'N, Long. 17°40'E, Alt. 5 m above sea level). The stand was coppiced at 5-10 cm above the soil surface in the winters of 1986/1987 and 1990/1991. Thus the measurement were performed on two-year-old trees - sprouts of the 8-year-old stumps/stools. Note: in this study, the term "tree" (one individual specimen of a cormic body) will be used instead of "shoot". In May 1992, when the experiment started, there were 18-19 living trees per stool and at the end of the growing season there was only 12-13 living specimens per stool. A typical tree height was about 2 m at the beginning of the experiment (May), and up to 4 m at the end of the growing season (October). The clay soil had pH values around 7.4 and a high nutrient status (Olsson and Samils 1984). The stand was irrigated and fertilised by a drip tubing system; the fertiliser included all essential macro- and microelements except Ca, Mg and S which were already in sufficient amounts in the soil (Rytter and Ericsson 1993).

The wind speed, global radiation and temperature were measured at a height of 2 m above the canopy by standard equipment. The precipitation was measured by a weighing rain gauge (IS200W Rain Gauge, In Situ, Ockelbo, Sweden), which has an accuracy better than 0.1 mm and resolution of 0.02 mm. The gauge was located about 60 m from the measured trees in an opening. All climatic data were registered as 10-minute mean values using CR-10 or CR-21X dataloggers (Campbell Scientific Ltd, England).

Biometric measurements

Diameters at 50 cm height (d_{50}) of about 200 trees were measured at 2-3 week intervals during the growing season. On these occasions, the leaf area of a sub-sample of trees (3-4 specimens) was measured destructively using a leaf area meter (LI-3000, LI-Cor, Inc., USA). All leaves were ripped off from the sample trees and leaf area to dry weight ratios were determined for sub-samples. Total leaf area was then determined from the total leaf dry weight per tree. Dry weights were determined after drying for one week at 80°C.

Open-top chamber

The transpiration (the simultaneously measured CO_2 fluxes are shown in Cienciala and Lindroth (1994)) of whole trees was measured in a ventilated open-top chamber, enclosing completely the crown of one tree (Fig. 1).

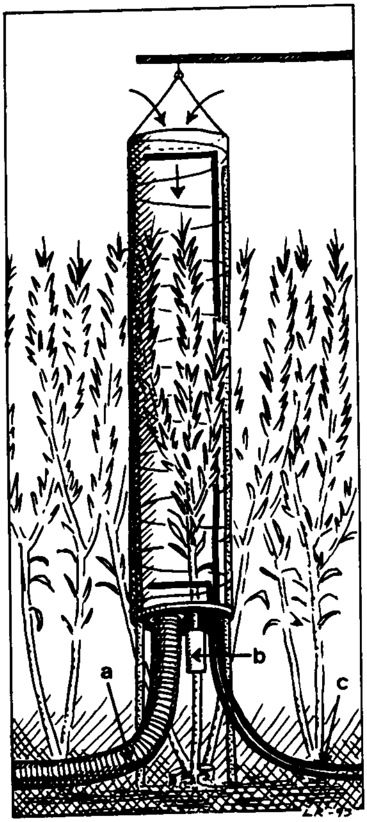

Fig. 1: The design of the chamber and set-up of the measurements: a - tube leading to a ventilator and propeller anemometer; b - THB-device measuring sap flow; c - polyethylene tubes leading to IRGA - air is taken in at the top and bottom of the chamber via perforated segments placed horizontally across the chamber.

The circular chamber, 4 m long and 40 cm in diameter, had a spiral supporting "net" consisting of a single-strand 3 mm stainless steel wire and covered by a transparent polyethylene foil. A supporting arm, attached to the top of the chamber, and extending from a nearby tower was used to keep the chamber in a vertical position. At the bottom of the chamber the polyethylene foil was sealed airtight to a 40 cm disc. The disc also had a muff below where a flexible, 20 cm diameter tube leading to a ventilator was attached. The stem of the tree could pass through an opening in the centre of the disc. The opening was made large enough to permit growth of the tree without risk of strangulation. Polyurethane foam was used to seal the space between the stem and the disc. The disc was made in two halves to enable mounting on a leafed tree. The disc was supported from below by two steel tubes extending about 30-40 cm down into the soil.

The air was ventilated top-down through the chamber at a constant rate of 0.063 m^3 s^{-1} corresponding to an average wind speed of 0.5

m s^{-1} within the chamber. Typical wind speeds at daytime at 1 m above the stand was 2 m s^{-1}. and considering the decreasing wind speed down through the canopy (e.g., Perrier, 1979) it was judged that the ventilation chosen was fairly representative of average conditions. At the outlet of the ventilator, a 2 m long 20 cm diameter steel tube was attached. A propeller anemometer (Young Co., USA) was mounted inside the tube about 50 cm from the end. This anemometer was used to measure the volume flow of air through the chamber. The anemometer was calibrated in a wind tunnel and the error of the flow measurement was estimated to be less than 5%.

The climatic conditions of a tree enclosed in a chamber of this type will always somewhat differ compared to those of freely growing trees. The main effects will be on the radiation and temperature regimes. To check this, global radiation was measured, for a shorter period, inside and outside an empty chamber using a solarimeter (Kipp & Zonen CM-5, the Netherlands). Diffuse radiation was estimated by shading the sensor. The temperature increase from when the air entered until it left the chamber was measured by a differentially connected fine wire thermocouple. In the latter case, a tree with a fully leafed crown was placed within the chamber to obtain realistic radiation absorption conditions.

The chamber was used on three trees, two of which were of the dominate size class group and one was representative of the small-to-intermediate sizes on the interface of the two groups as described below.

Measurement of water vapour concentration

To measure the water concentration of the air before and after it had passed the crown, air was drawn continuously through two 1/4" polyethylene tubes to a LI-6262 gas analyser (Li-Cor Inc., USA). The air is taken in at the top and bottom of the chamber via 40 cm long polyethylene segments placed horizontally across the chamber and perforated with small holes in order to sample the entire profile of the airstream in the chamber. The flow rate in the sample tubes was 1 l min^{-1} and it took 15 s for the air to reach the gas analyser. The air pumps were placed before the gas analyser to minimise the effect of pressure differences in reference and sample channels, respectively, due to possible differences in air flow.

A complete measurement of the water concentration difference was performed over a time period of 10 minutes. During this period the sample air was switched after 5 minutes, so that air previously leading to the sample channel now was directed to the reference channel and vice versa. Switching was done by solenoids controlled by the datalogger. In this way, errors caused by an offset in the calibration of the gas analyser were substantially reduced. The values collected during the first half-minute after channel switching were discarded in the calculation of averages in order to allow the gas analyser to adapt to the new concentrations. Sampling of the output from the gas analyser was done every 2 seconds. In order to estimate the concentration differences accurately, the ambient concentration in one of the channels had to be known. A relationship between ambient vapour pressure (e) and concentration in the reference cell was therefore determined by scrubbing the sample cell during a range of e-values. Ambient vapour pressure was then used to calculated the concentration in the reference cell when the analyser was used in differential mode. The gas analyser was calibrated against known water vapour concentrations before the measurements began and it was verified with good results afterwards.

Calculation of transpiration

The transpiration of a tree in the chamber was calculated as:

$$E = \Delta \mathrm{w} \mathrm{v} \qquad (1)$$

where Δw is the water vapour concentration difference (g m^{-3}) and v is the air flow ($m^3 s^{-1}$). The air flow was calculated as the wind speed as measured by the propeller anemometer times the cross section area of the tube where the anemometer was placed. The concentration difference was calculated as:

$$\Delta w = ((a_1V'+a_2V'^2+a_3V'^3)(T/T_0))-C_r)(M_w/M_a)k\rho \qquad (2)$$

where a_1, a_2 and a_3 are instrument-specific coefficients for linearizing voltage output, T is the temperature of gas analyser (K), T_0 is a instrument-specific constant (K) (the gas analyser temperature at factory calibration), M_w and M_a are the molecular weights of water and air weighted for water vapour content (g mol^{-1}), respectively, C_r is the concentration in the reference cell of the analyser (mmol mol^{-1}), k is a coefficient (=1000; to convert the unit of the concentration given by the polynomial from mmol mol^{-1} to mol mol^{-1}), ρ is the air density (g m^{-3}) and V' is the computed voltage calculated as:

$$V' = (V(1-V_r/K)+V_r)P_0/P \qquad (3)$$

where V is the measured differential voltage (mV), K an instrument specific constant, P_0 is an instrument-specific air pressure (kPa), P is ambient air pressure and V_r is the voltage of the reference cell obtained as:

$$V_r = -V_{sc}/(1-V_r/K) \qquad (4)$$

where V_{sc} is the voltage output when the sample cell is scrubbed. The scrubbing was only made occasionally and therefore V_{sc} was obtained from a correlation between ambient air humidity, which was measured continuously, and V_{sc}. The concentration in the reference cell was calculated as:

$$C_r = (a_1(V_rP_0/P) + a_2(V_rP_0/P)^2 + a_3(V_rP_0/P)^3)(T/T_0) \qquad (5)$$

Measurements of sap-flow

Sap flow (Q_{wt})was measured by the tissue heat balance (THB) method with external heating and internally sensed temperature gradient. The system, designed for measurements on small diameter trees (1.5 to 4.5 cm), was originally developed at the Institute of Forest Ecology, Agricultural University, Brno, Czech Republic[1] and described in detail for a previous *Salix* application by Lindroth et al. (1994). The system used in this study was, however, improved compared with that described by Lindroth et al. (1994). Here, the power to the heater was regulated to keep the temperature of the heated and non-heated part of the stem at a constant difference of 4 K instead of having a constant power and a variable temperature difference. The voltage output from the measurement device was made proportional to the power utilised by the heater. This modification made the sap flow measurements less sensitive to ambient temperature gradients in the stem, which were the source of error in the measurements by Lindroth et al (1994). The other modification was the length of the heater, which was shortened to 6 cm. The sap flow, Q_{wt}, is estimated as

$$Q_{wt} = P/(\Delta T c_w) - \lambda/c_w \qquad (6)$$

where P (W) the heat-effect, ΔT the temperature difference, c_w the specific heat of water and λ the mean heat loss coefficient that accounts for total heat loss from the measuring point. This second term is usually regarded as a "fictitious" flow (Kucera et al. 1977) and it is usually estimated during zero-flow conditions (rainy weather or nights with relative humidity close to 100 %). The gauge is flexible and permits a long-term use (months); the flexible heater with the insulation is usually replaced by a larger one when the diameter has increased more than 1 cm from its initial value. The output from the gauge was recorded by a datalogger and averaged over 10 minutes. Altogether 12 trees were measured by the THB method, eight of them at the same time, including the tree within the chamber.

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[1] *Now commercially available from Ecological Measuring Systems, Inc., Brno, Czech Republic.*

Results & Discussion

Plant development during the measurement period

At the beginning of the measurement period, a distinct bimodal distribution of diameters was observed, showing a minor group of suppressed and subsequently dying specimens, and a major group of dominating and fast-growing trees (Fig. 2). The bimodal distribution successively turned into a unimodal one which was clearly seen at the end of the period studied.

The diameters, d_{50}, of dominant trees increased typically from about 15 mm to 30 mm from early May to early October (the period of the growing season) and the average stand height reached 4 m at the end of the season. Leaf area (LA) of trees was linearly correlated to the corresponding tree cross-sectional area (A_{50}; Fig. 3).

Water flux, plant size and chamber effect on growth

The chamber's effect on the trees was an increased LA and height growth as compared with the other trees. Thus the trees that were enclosed in the chamber did not follow as closely the general relationship of LA to A_{50}. It was estimated, that during one month, the LA of the tree inside the chamber increased by 22 % as compared to a tree of the same size growing free. A similar figure is anticipated for the height growth.

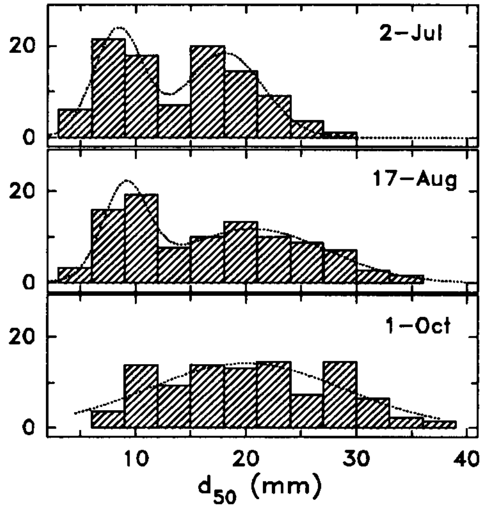

Fig. 2: The example of rapid growth of willow trees during the growing season: the distributions of diameters (measured at 50 cm) in the stand during three months of growing period. A distinct bimodal pattern of the distribution (dotted line), which became successively normal (P=0.024 for Oct 1). Measurements were performed repeatedly on same stools with 202 living specimens (2nd July).

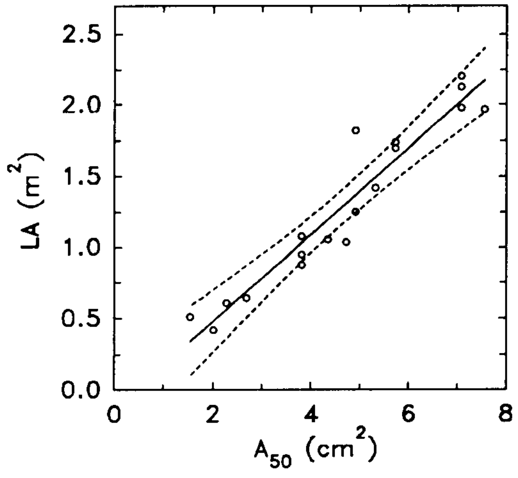

Fig. 3: The leaf area (LA) of individual trees (symbols) related to the cross-sectional area - the regression (r^2=0.92; a=-0.130, b=0.305) and 99 % confidence intervals are shown.

Daily Q_{wt} weighted by the vapour pressure deficit of the ambient air (outside of the chamber) increased linearly with leaf area (Fig. 4). For freely growing trees, sap flow is also linearly related to A_{50} due to the relationship to LA shown above. It is obvious from Fig. 4 that for the period of July until early October there is no change of the relationship between Q_{wt} and LA, or between Q_{wt} and A_{50}, respectively. It should, however, be pointed out that this period does not cover the phases of leaf development and desiccation at the beginning and end of the growing season, respectively.

There are three probable reasons for the changes in growth of plants in the chamber as described above. One is a decreased demand

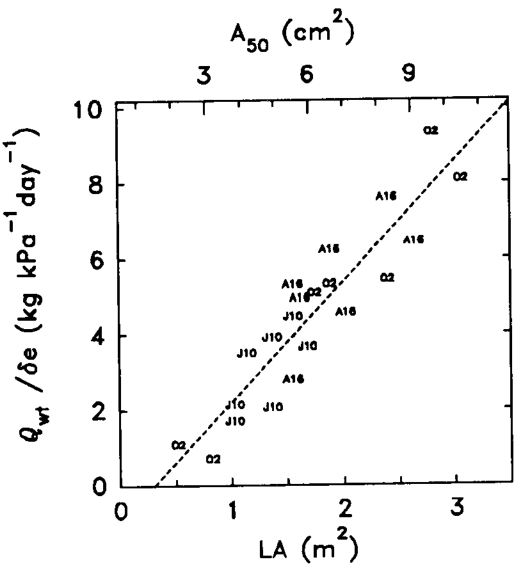

Fig. 4: Daily sap flow of simultaneously measured specimens for July 10 (J10), August 16 (A16) and October 2 (O2) normalised per unit of vapour pressure deficit (δe) in relation to tree cross-sectional area at 50 cm (A_{50}) or leaf area (LA).

for lignification of the stem to strengthen plant axis after it became protected against wind in the stable chamber frame (Valinger 1993).

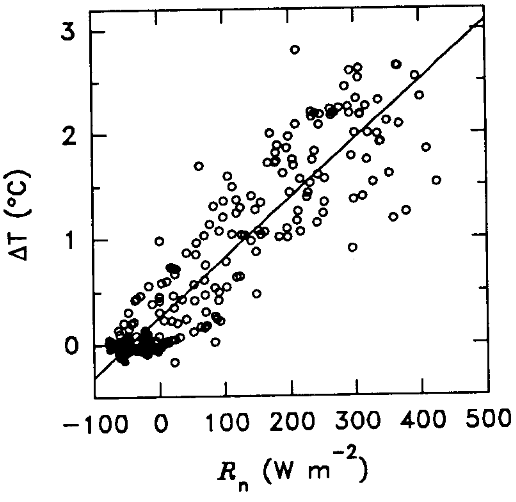

Fig. 5: The vertical temperature (ΔT) gradient in the chamber from the top sampling tube to the bottom-located sampling tube (distance 2.5 m) against net radiation (R_n) for light (open symbols) and dark (filled symbols) periods of a day.

Another reason could be a higher air temperature in the chamber. The temperature increase of air after passing through the chamber was highly correlated to net radiation above the canopy (Fig. 5).

The maximum net radiation in summer is in the order of 500 W m^{-2} (Lindroth and Iritz, 1993) implying a maximum temperature difference close to 3 °C. The average increase for the canopy as a whole is smaller than this value and since also the average net radiation is smaller, the mean temperature increase over longer periods is estimated to be less than 1 °C. This is, however, an effect large enough to increase growth significantly for plants growing in a climate where temperature is one of the limiting factors.

A third reason could be the change of radiation climate within the chamber. The measurements showed that the global radiation decreased by about 5 %, but on the other hand, the diffuse part of the short-wave radiation increased by about 11 %. Reduced intensity normally reduces photosynthesis but this might be compensated because of the increased fraction of diffuse light (Denmead et al. 1993).

It may be concluded that this type of chamber should not be used for periods longer than probably one week if the aim is to maintain the biometry of an enclosed tree similar to the other specimens. However, for the comparative measurement of water (and CO_2) fluxes on the same plant, the limitations described above do no matter at all.

Sap flow and transpiration

The maximum hourly values of sap flow (Q_{wt}) reached about 0.45 kg per specimen, or 0.2 kg per m^2 of leaf area and hour. Daily values of Q_{wt} reached a maximum of about 4 kg tree^{-1} at the end of July. Daily values of transpiration (E) and Q_{wt} for the small-to intermediate trees were typically 1/10 of those measured in dominant trees. The absolute rates of E and Q_{wt} showed very good agreement both for intermediate and low fluxes and for small trees,

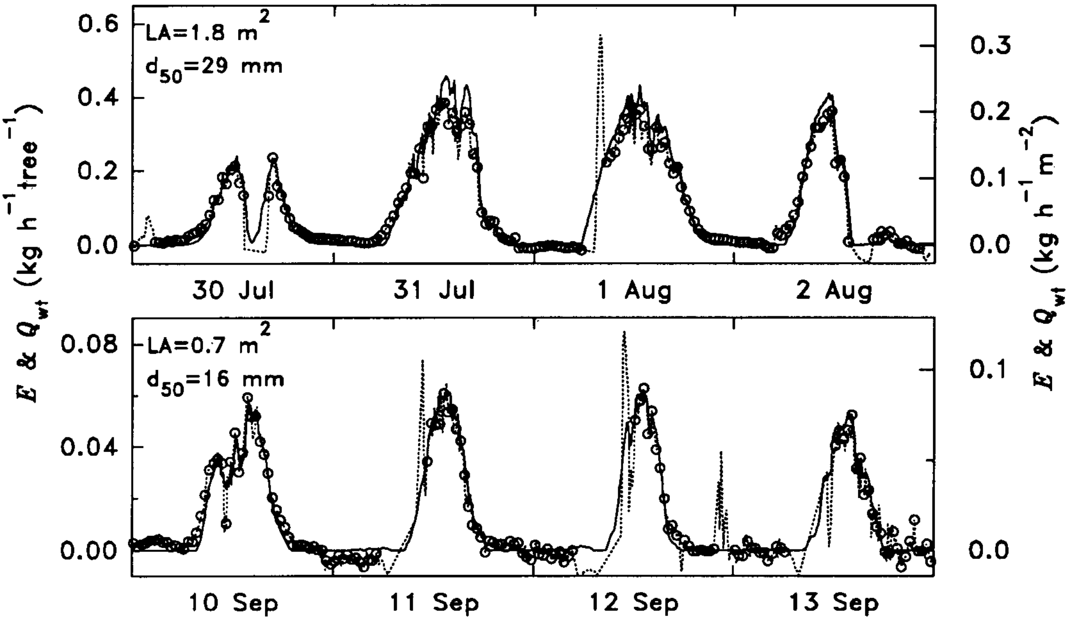

Fig. 6: Transpiration (E; open symbols) and sap flow (Q_{wt}; solid line) per tree (left axes) or per m^2 of one-sided leaf area (right axes) during 4-day example periods with dominant (top) or suppressed (bottom) specimen measured. Leaf area (LA) and diameter at 50 cm (d_{50}) are also given. The erroneous periods of E excluded from calculations of totals are shown by the dotted line without symbols.

whereas values of E were slightly lower than those of Q_{wt} during high evaporative conditions, usually by about 5 % (Fig. 6). E.g., for the period of 30th July to 2nd August with high water flux rates, the totals of E and Q_{wt} reached 8.91 and 9.48 kg, respectively, i.e., 6 % difference between E and Q_{wt}. Still better agreement was found for an example period of 10th to 13th September with lower flux rates, where totals of E and Q_{wt} were 0.99 and 0.98 kg, i.e., practically equal (1 % difference), which is also obvious from the diurnal courses of E and Q_{wt} rates (Fig. 6). The comparison of E and Q_{wt} is, however, restricted for the cases where E was not disturbed by condensation or rain (erroneous transpiration data caused by condensation within the chamber or in sampling tubes were excluded - see dashed line in Fig. 6).

We can only speculate about the reason for the 5% differences between accumulated values of E and Q_{wt} observed for period of high flux rate conditions. For THB-method, one possible explanation can be a beyond-optimum shifted position of the heat-field with respect to the position of inserted thermocouples (Jiri Kucera, personal communication 1993). The size of the error should, however, also be seen in relation to the uncertainty in the volume flow measurement in the open-top system. The estimated accuracy of the propeller anemometer used for this measurement was 5%, i.e., the value similar to the differences of measured fluxes found.

The instantaneous (10 minutes) values of E and Q_{wt} were usually highly correlated, e.g., with $r = 0.98$ for the two example periods. The time delay of Q_{wt} behind E was obvious only during the mornings (Fig. 6), whereas for the rest of a day the curves of E and Q_{wt} practically merged. A cross-correlation between the courses of E and Q_{wt} showed, however, a slightly better agreement for Q_{wt} shifted in time by minus one measuring time interval. This gives the average time shift of 10 minutes between the diurnal rates of E and Q_{wt}. The pool of easily available water, estimated from the time lag between E and Q_{wt} was found to be about 0.1 kg for a dominant tree (e.g., July 30 and 31). This is roughly only about 1/10 and 1/20 of the daily sum for these days. The pool for the small shoot was smaller and difficult to quantify, which is obvious from the rates of E and Q_{wt} during morning hours of, e.g., September 10 (Fig. 6).

The size of the pool of the easily exchangable water found here is smaller than that estimated by Lindroth et al (1994). They found the pool to be about 0.2 kg of water, which would correspond to 1/4 of the average transpiration during the studied period. This is the value close to those reported for larger trees of oak (Cermák et al. 1982), larch (Schulze et al. 1985) or spruce (Cienciala et al. 1994). The higher value found for *Salix* trees by Lindroth et al. (1994) might be due to the fact that they compared Q_{wt} rates with E estimated for stands using Bowen-ratio method. In this way, E may have incorporated advective fluxes of dominant trees more exposed to radiation than those with measured sap flow. Our results confirm that the pool is a function of a certain biometric parameter (Cermák 1992).

A typical pattern of water flux in both freely growing specimens and the one in the chamber is shown during a day with a rain shower and changing climatic conditions (Fig. 7). On 30 July 1.0 mm of rain fell during 30 minutes in the middle of the otherwise mostly sunny day. Before the rain-shower, when the leaves were dry, the variations in Q_{wt} and E were highly correlated with the variations in radiation (R_g) and vapour pressure deficit (δe), all in accordance with theory. Just before the rain started, Q_{wt} and E decreased rapidly as did R_g and δe. Q_{wt} continued during the rain and became zero for a short while about 30 minutes after the rain had stopped. This coincided with the minimum in δe. Immediately after the rain, Q_{wt} was much better correlated to δe than to R_g. For instance, R_g started to increase already during the rain and reached its daily maximum about 80 minutes after the rain had stopped. At that time, Q_{wt} had only increased a little, in the order of 15% of the maximum value. After the rain, Q_{wt} reached its maximum simultaneously with δe but then it seemed to decrease according to the radiation curve although δe stayed high all afternoon and night. According to the Penman-Monteith equation (e.g., Monteith, 1965) evaporation can be estimated as the sum of two terms; one being a function mainly of the vapour pressure deficit and the wind speed (ventilation term) and the other a function

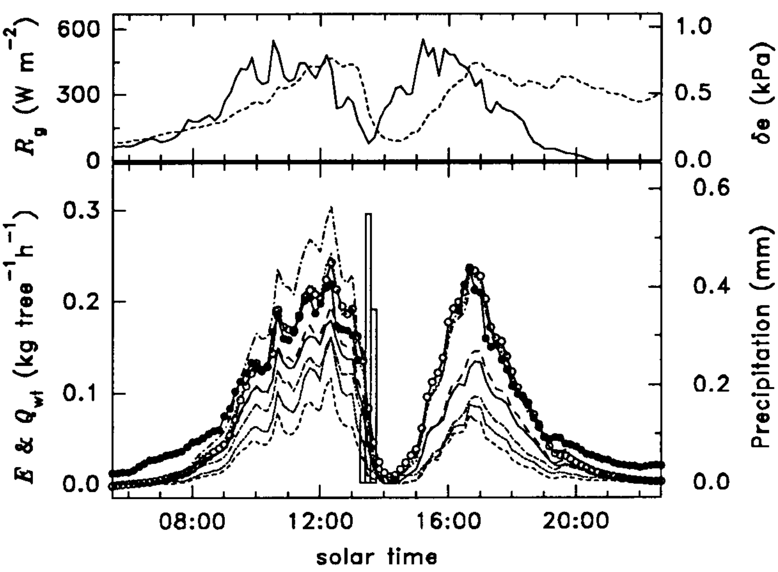

Fig. 7: Bottom: the diurnal dynamics of sap flow (Q_{wt}, open symbols) and transpiration (E, filled symbols) of a specimen in the chamber during a day with a rain shower (Precipitation, bars, 10-minute values). Q_{wt} for seven freely growing specimens is also shown (lines without symbols). Top: global radiation (R_g; solid line) and vapour pressure deficit (δe; dashed line).

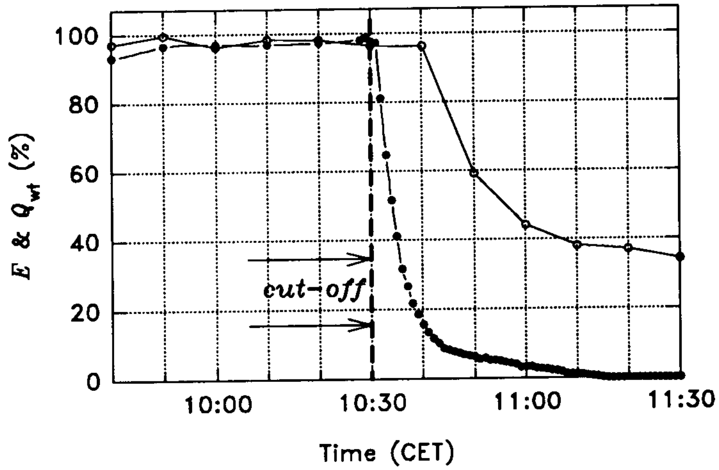

Fig. 8: The response of transpiration (E, open symbols, 10-minute values) and sap flow (Q_{wt}, filled symbols, 10- and 1-minute values) to cut-off.

mainly of available energy, e.g., radiation minus storage (radiation term). Now, modelling Q_{wt} as a linear function of δe respectively as a combination of δe and R_g showed that three hours before the rain (10:00 to 13:00), 65% of the variation was explained by δe alone and adding R_g increased the explanation to 85%. Making the same exercise for a three hour period after the rain (14:00-17:00) showed that δe alone explained 99% of the variation and adding R_g made no difference. One possible explanation to the behaviour after the rain, could be the neglect of advective components in the radiation term. Higher evaporation rates at the wet spots compared to the dry ones will create differences in surface temperature and this might give rise to "microadvection", i.e., energy is transferred from the dry areas to the wet. If so, the magnitude of the radiation term would decrease and thus, the ventilation term would dominate. Similar results were found by Cienciala et al. (1994) when analysing water uptake from a young spruce stand using a soil-plant-atmosphere model. They had to introduce a redistribution of absorbed energy between dry and wet areas to make the model agree with the measured Q_{wt} during rain. The stand was probably dry again after the rain when δe reached its maximum value. The decrease in Q_{wt} after that time was then caused by decreasing stomatal conductance due to the decreasing light intensity.

The magnitude of Q_{wt} measured in the tree inside the chamber increased after the rain in relation to the other trees. Also, it started to increase earliest after the shower. This is according to expectations because it was more effectively ventilated and probably less wet than the freely-growing trees.

The response of E and Q_{wt} to cut-off

A test of the gauge's response to a rapid change in flux was performed by severing the stem of the experimental specimen (projected LA of 1.96 m^2) at the base (Fig. 8). Sap flow continued at the same rate up to one minute after cut-off. Then it decreased sharply during the second minute and continued to decrease down to 10 % of the initial value after 13 minutes (85% decrease of the registered signal within 10 minutes). Sap flow had stopped entirely 45 minutes after cut-off. Transpiration continued with unchanged intensity still 10 minutes after severing. Then it declined: first rapidly - to about 45 % of the original intensity within next 20 minutes and then more slowly. Still 4.5 hours after cut-off, the transpiration rate was 20 % of the initial value with leaves visibly wilting due to loss of turgor.

The sap flow response to abrupt change induced by severing or by other factors will always depend primarily on the conductive system of a tree. Thus, the most extreme changes - exceeding those found here - were reported for ring-porous species (Kucera et al. 1977; Cermák and Kucera 1991). The observed decrease in sap flow as measured by THB technique permits the following considerations: the cutting-off was performed by a large clipper and this procedure took 1 second. It is thus interesting to notice that it took one minute until the sap flow cessation was registered by the gauge. The distance between the cut-off surface and the gauge was 1 m and accordingly, the pressure signal propagated with a speed of 1 m min^{-1} within the stem. The time response of the gauge is practically instantaneous, which is obvious from the sharp sap flow decay registered for the second and following minutes. It is more complicated to interpret the decrease of transpiration, which could be measured in the chamber for 10 minutes intervals only. During the first 10 minutes after cut-off, water was apparently easily available for transpiration to continue at the initial rate. The relatively high rate of E at the end of the experiment indicates, that stomata did not close completely, because if water had only been lost through the cuticle, the rate could not have been particularly high.

Conclusions

The agreement of measured fluxes E and Q_{wt} by two independent absolute methods was very satisfactory and thus both techniques can be used with confidence. The transpiration measurement was occasionally erroneous due to condensation in the sample tubes, a problem severally occurring during morning hours. This problem might be minimised by heating and insulating the sample tubing. Measurements during rain will, however, still be problematic. The gauges measuring sap flow were reliable for all kinds of weather conditions; they do not alter the growth of a measured tree and the set-up of the gauges is easy.

Acknowledgements

We are obliged to Jerry Leverenz for his comments to the manuscript. We thank Achim Grelle for his kind and efficient help with the setting-up of IRGA and its accessories. This study was financed by the Swedish Natural Science Research Council under contracts S-FO 09382-319, G-GU 09382-321 and G-GU 09382-320.

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