

## Canopy transpiration from a boreal forest in Sweden during a dry year

E. Cienciala<sup>a,\*</sup>, J. Kučera<sup>b</sup>, A. Lindroth<sup>c</sup>, J. Čermák<sup>d</sup>, A. Grelle<sup>c</sup>, S. Halldin<sup>e</sup>

<sup>a</sup> Department of Soil Sciences, Swedish University of Agricultural Sciences, Box 7014, 750 07 Uppsala, Sweden

<sup>b</sup> Ecological Measuring Systems, CZ-621 00 Brno, Czech Republic

<sup>c</sup> Department for Production Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

<sup>d</sup> Institute of Forest Ecology, Mendel's Agricultural and Forest University, CZ-613 00 Brno, Czech Republic

<sup>e</sup> Institute of Earth Sciences / Hydrology, Uppsala University, Norbyvägen 18B, S-752 36 Uppsala, Sweden

Received 7 May 1996; revised 18 February 1997; accepted 3 March 1997

### Abstract

Estimation of areal evapotranspiration is crucial for the parameterization of the soil–vegetation–atmosphere interface in climate models and for the assessment of land-use changes on water resources. Present knowledge on how areal forest evapotranspiration depends on forest species composition and age is insufficient. In this study, transpiration of 50- and 100-year-old coniferous stands was estimated on the basis of sap-flow measurements on 24 trees, 12 in each stand. The measured samples represented the size distribution of *Pinus sylvestris* and *Picea abies* trees. Daily canopy transpiration ( $E_Q$ ) was scaled from individual tree flow rates using the quotients of stem circumferences of the sample trees to those of the stands.  $E_Q$  was used in a rearranged Penman equation to deduce a potential canopy conductance, valid for non-limiting soil–water conditions, from a period when soil–water storage was not limiting transpiration. This enabled quantification of the seasonal transpiration deficit, which in both stands reached at least one fifth of the total potential transpiration over the growth season. The estimated fluxes of  $E_Q$  were low with a maximum daily value of about 2.8 mm in the 50-year-old stand. For dry-weather days,  $E_Q$  was well correlated to daily sums of stand evapotranspiration estimated from eddy-correlation measurements. Responses to drought were species specific. Transpiration in pines from the 50-year-old stand was less affected by drought relative to spruce or older pine trees, which was also reflected by stem increment during the season. © 1997 Elsevier Science B.V.

**Keywords:** Transpiration deficit; Drought; Pine; Spruce; *Pinus sylvestris*; *Picea abies*

### 1. Introduction

Transpiration flux from coniferous forests in the boreal region is largely controlled by canopy conductance ( $g_c$ ). This is because boreal-forest canopies are

aerodynamically rough and well ventilated, which minimizes the effect of aerodynamic conductance (Jarvis and McNaughton, 1986). The influx of carbon dioxide will be similarly constrained by  $g_c$ , since both water vapour and CO<sub>2</sub> pass through the stomata. Hence, stomatal control is not only the key for assessment of transpiration and water balance, but it is also important for estimation of carbon

\* Corresponding author. Fax: +46-18-672795. E-mail: Emil.Cienciala@mv.slu.se.

assimilation and net primary production of trees and stands. Under given concentrations of nitrogen in the soil,  $g_c$  is mostly limited by a high vapour-pressure deficit, by soil-water deficit or by a combination of those factors. In these cases, stomata will close and  $g_c$  will decrease. In many evaporation models, conductance sub-models of various complexities are usually included in a Penman-type equation. Known determining factors such as radiation, vapour-pressure deficit, soil-water deficit or water potential, are commonly expressed as individual multiplicative members which determine the actual  $g_c$  (c.g. Jarvis, 1976). Such models do not provide any information about mechanisms of the limitations, but they can mimic the actual rates well for most modelling purposes.

The forest in the region has a rich mosaic of stands with a specific pine/spruce share and age. Comparing studies on water fluxes from monospecific stands of either pine (e.g. Lindroth and Halldin, 1986) or spruce (e.g. Cienciala et al., 1994) in Sweden indicates that the importance of age and species for the site water budget is large. It is therefore desirable to compare the actual water use for the individual species and age classes. This will help to clarify the importance of species composition and age for averaging fluxes on larger spatial scales.

Another important aspect of forest functioning is response to drought. This has become important especially in recent years: there is growing evidence of a higher frequency of climatic extremes as a result of global climate change (e.g. Karl et al., 1995). Even in the regions without climatic extremes, the annual variability of precipitation may be high and distribution of rainfall during a growth season very uneven. This may affect both growth and stability of forest ecosystems. As drought limits both water and carbon fluxes, quantification of the effects of drought on forest transpiration is therefore also important for assessment of a potential loss of production. To assess drought effect on transpiration, we estimated transpiration deficit, defined as the difference between the stand transpiration for non-limiting soil-water conditions and the actual transpiration. We quantified transpiration deficit on daily basis for two stands of different ages and assessed the performance of species under water deficit conditions during a particularly dry growth season. Canopy con-

ductance was obtained from a rearranged Penman-type equation with actual transpiration as an input variable. It was parameterized on a short moist period and then used to compute transpiration, not limited by soil-water, for the whole growth season. This enabled quantification of the seasonal transpiration deficit and its variation with tree age and species, which was the aim of this paper.

## 2. Material and methods

### 2.1. Site and stands

The NOPEX (Northern Hemisphere Climate-Processes Land-Surface Experiment; Halldin et al., 1995) Central Tower Site (60°5'N, 17°29'E, altitude 45 m) is located in the Norunda Common about 30 km north of Uppsala. Forests in the area are mixtures of Norway spruce and Scots pine which have been managed by forestry practices for over 200 years. Stands are distinguished by different spruce–pine proportions and age classes; the stands are harvested at 100- to 120-year intervals. The soil is a deep boulder-rich sandy loam of glacial origin. At the site, the soil was podzolized and classified as Dystric Regosols (Stähli et al., 1995). Ground water was very variable—it was observed at depths of 40–90 cm in May 1994. Rooting depth is mostly up to 50 cm, but occasional roots were found up to a 1-m depth. In Uppsala, the 1961–1990 average air temperature was 5.5°C, the average annual precipitation 527 mm and the average Penman (1948) reference evaporation 454 mm. Measurements used in this paper were performed during the 1994 growth season. This season was warm and dry relative to the average climatic conditions; the cumulative precipitation reached only 271 mm for the growth period (Fig. 1), which is about 16% lower than the long-term average in Uppsala.

The studied stands were 50 and 100 years old. The basal area was 29.3 m<sup>2</sup> ha<sup>-1</sup> and maximum stand height was 23 m for the 50-year-old stand. The corresponding values for the 100-year-old stand were 34.7 m<sup>2</sup> ha<sup>-1</sup> and 28 m. The canopy of the 50-year-old stand was closed with occasional openings. The projected leaf-area index (LAI) was about 4–5. The stand was composed of Norway spruce (*Picea abies*

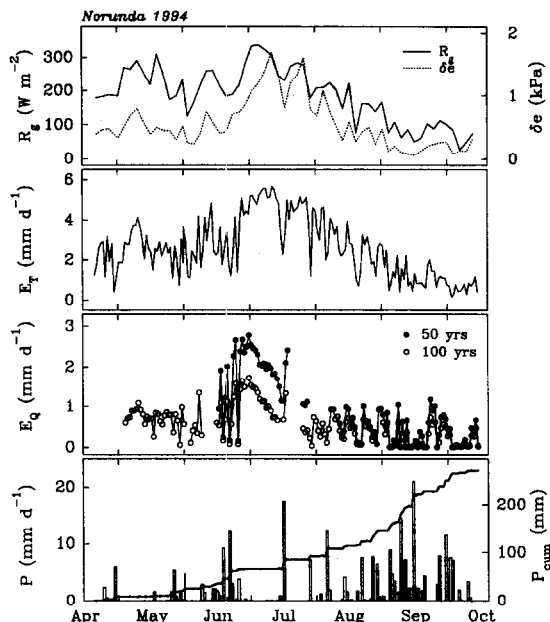


Fig. 1. Weather conditions and soil–vegetation–atmosphere fluxes during the 1994 growth season: 3-day average values of short-wave radiation ( $R_g$ ) and vapour-pressure deficit ( $\delta e$ ); daily sums of evaporation according to Turc ( $E_T$ ) and transpiration ( $E_Q$ ) for the 50- and 100-year-old stands; daily and cumulative precipitation ( $P$ ,  $P_{cum}$ ).

(L.); 66% of the stand basal area) and Scots pine (*Pinus sylvestris* (L.); 33%) with a few specimens of birch (*Betula alba* (L.)). The 100-year-old stand was more open with an emerging small understory of Norway spruce. LAI of this stand was about 3–4. The main canopy was composed of pine (80% of the stand basal area), spruce (19%) and birch (1%). There was a sparse vegetation in the older stand that consisted of many small young spruces and acidophilous vegetation (*Vaccinium myrtillus*).

## 2.2. Measurements

Tree sap flow was measured by the heat-balance method (Čermák et al., 1973, Kučera et al., 1977) with instruments from EMS, Brno, Czech Republic. Twelve trees in each of the stands were measured from two sides (24 channels per stand), distributed equally between pine and spruce. The logistics of the tree sample selection and scaling of tree fluxes into stand flux was similar to that described by Čermák et

al. (1995). The measurements started in May, about 2 weeks after the initiation of the growth period. In the younger stand, sap flow was not measured in both species simultaneously until mid-June and consequently the canopy transpiration data are not available for this earlier period (Fig. 1). There are also some shorter periods during the summer when the sap-flow equipment was not in operation due to lightning. Sap flow from individual trees was scaled into canopy transpiration ( $E_Q$ ) on the basis of stem circumference quotients. This type of scaling was required due to the large variability of the measured sap flow among trees on the site (Čermák et al., 1995).

Dry-weather situations were used to compare stand evapotranspiration ( $E_{35}$ ) with canopy transpiration ( $E_Q$ ).  $E_{35}$  was measured with an eddy-correlation system on a 100-m tower at 35 m height. The tower was located 150 m from the 100-year-old stand and about 600 m from the 50-year-old stand. The eddy-correlation system consisted of a sonic anemometer (Solent) and an infrared gas analyser (LI-COR LI-6262) which measured the fluctuating components with a frequency of 10 Hz (Grelle and Lindroth, 1994, 1996). The forests surrounding the mast is relatively homogeneous with a fetch of 1 to tens of kilometres. A detailed footprint analysis for the measurements on the tower was not available for this study.

Stem diameter increment was measured with dendrometer bands made of a thin metal sheet. They were placed at a height of about 1.5–2 m on those trees where sap flow was measured. Readings were taken at 2- to 3-week intervals.

Weather data were taken from the System of Information in NOPEX (SINOP).

## 2.3. Calculations

The following analysis with a daily time step was performed. Daytime average canopy conductance ( $g_c$ ) was obtained by inversion of the Penman–Monteith equation using  $E_Q$  as an input variable. This permitted analysis of  $g_c$  as a function of short-wave radiation ( $R_g$ ) and vapour-pressure deficit ( $\delta e$ ). The parameterization of the individual functions was performed using data from June 1994, the period

with several rain showers. During this period transpiration was assumed to be unaffected by soil-moisture scarcity. This assumption was based on the observed good correlation of  $E_Q$  with the potential evaporation ( $E_T$ ) according to Turc (1961), in sharp contrast with the situation in July, when  $E_Q$  rapidly decreased relative to  $E_T$  (Fig. 2).  $E_T$  is calculated from daily means of short-wave radiation ( $R_g$ ;  $\text{kJ day}^{-1}$ ) and air temperature ( $T_a$ ;  $^{\circ}\text{C}$ ) as

$$E_T = (R_g/41.868 + 50) \times 0.013 \times T_a / (T_a + 15) \quad (1)$$

$E_T$  mimics well the rates of potential evapotranspiration (e.g. Cienciala et al., 1992, Federer et al., 1996). Since it does not use atmospheric humidity that would interact with stand evapotranspiration, it was used as a truly independent index of evaporative conditions in this study.

Analysis of canopy conductance  $g_c$  was based on a type of Lohammar (Lohammar et al., 1980) equation. This phenomenological function has proven to be one of the most efficient to explain how measured conductance data depend on weather conditions (e.g. Massman and Kaufmann, 1989). The Lohammar equation is commonly expressed as:

$$g_c = g_{\max} \times R_g / (a + R_g) / (1 + b \times \delta e) \quad (2)$$

where  $R_g$  is incoming short-wave radiation and  $\delta e$  vapour-pressure deficit. Eq. (2) contains three pa-

rameters ( $g_{\max}$ ,  $a$ ,  $b$ ) whose values must be estimated on the basis of available data. In our case, the total set of data was rather limited for situations where soil-water was apparently not a limiting factor. Instead of trying to estimate parameter values for a three-parameter function with an insufficient data set, we modified the original form of the equation and estimated parameter values in two steps. The influence of radiation on  $g_c$  ( $\text{m s}^{-1}$ ) was first evaluated for values of  $\delta e$  below 1 kPa. The following function was used:

$$g_c = aR_g / (b + R_g) \quad (3)$$

Days with precipitation and the first day after a precipitation event were excluded from the data set used to estimate parameter values. The influence of vapour-pressure deficit on  $g_c$  was subsequently evaluated with  $R_g$ -values constrained to those above  $300 \text{ W m}^{-2}$ . The following function was used:

$$g_c = c \exp(-d\delta e) \quad (4)$$

Values for parameters  $a$  ( $9.32 \times 10^{-3}$ ;  $8.03 \times 10^{-3}$ ),  $b$  (281; 152),  $c$  ( $8.03 \times 10^{-3}$ ;  $3.62 \times 10^{-3}$ ) and  $d$  (0.569; 0.331) were estimated from a least-squares regression fitting procedure for the respective stands (50 years; 100 years) using the independent variables  $R_g$  ( $\text{W m}^{-2}$ ) and  $\delta e$  (kPa). Actual canopy conductance was finally taken as the minimum value as given by Eqs. (3) and (4). Stand transpiration for non-limiting soil-water conditions ( $E_N$ ) for the whole growth season was calculated with these parameterized conductance functions in the Penman–Monteith equation.

Transpiration deficit can then be quantified as the difference between  $E_N$  and  $E_Q$ . This way, transpiration deficit represents the amount of water required by trees, but not available from the soil or accessible to trees. Note also, that  $E_N$  does not directly relate to the potential evapotranspiration estimate  $E_T$ .  $E_N$  represents a function for maximum transpiration flux that was parameterized for a given stand(s) through the canopy conductance functions.

To assess the importance of differences in species composition and age for pine and spruce in the 50- and 100-year-old stands, we expressed  $E_Q$  for each of the species by weighting the species' contribution to  $E_Q$  ( $E_{QP}$  and  $E_{QS}$  for pine and spruce, respec-

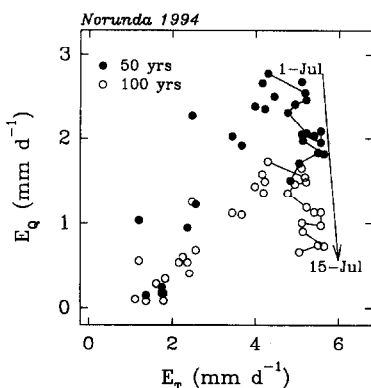


Fig. 2. Daily transpiration ( $E_Q$ ) of the two stands against evapotranspiration by Turc ( $E_T$ ) for the period of 1 June–15 July. The sharp decline of  $E_Q$  relative to  $E_T$  reflecting the progression of water deficit during 1–15 July 1994 is marked by connecting lines.

tively) by the quotient of the total stand basal area to the basal area of the particular species ( $A_P$ ,  $A_S$ ;  $m^2$ ). This way, the stand was represented by a hypothetical monoculture of either pine or spruce. The transpiration flux for such a monospecific stand of, for example, pine can be written as

$$E_Q = E_{QP}(A_P + A_S)/A_P \quad (5)$$

where the fluxes  $E_Q$  and  $E_{QP}$ , are given in  $mm\ day^{-1}$ . For these calculations, we included all the cases where pine and spruce trees were simultaneously measured in both stands ( $n = 95$  days). The species-specific transpiration rates were then used to derive species-specific  $g_c$ .

### 3. Results

#### 3.1. Canopy transpiration and stand evapotranspiration

The daily values of canopy transpiration ( $E_Q$ ) reached maxima of 2.8 mm for the 50- and 1.7 mm for the 100-year-old stands (Fig. 1). The seasonal daily average, including all cases for which  $E_Q$  was estimated in both stands, was  $0.9\ mm\ day^{-1}$  and  $0.5\ mm\ day^{-1}$ , i.e. transpiration rates in the older stand were about 60% of those in the younger stand. The correlation between  $E_Q$  of the 50- and 100-year-old stands was strong ( $r = 0.98$ ), but the relation of the absolute values changed during the season. This indicated slightly different drought responses of these two stands.

The maximum values of transpiration were reached in the beginning of July, just before the start of the dry period (Fig. 1). The transpiration rates then decreased continuously while the evaporative demand continuously increased until mid-July when the dry spell was interrupted by two thunderstorms giving 19 mm of rain. After these showers, there was again a dry spell about 10 days when transpiration rates continued to decrease. In contrast, the reference evaporation estimated from empirical equations by Penman (1948) and Turc (1961) showed increasing rates during these two sub-periods, following the trends of the driving variables (radiation, air temperature, vapour-pressure deficit). These two estimates of evaporation had similar seasonal sums, namely 468 mm and 462 mm.

$E_Q$  was well correlated to daily sums of eddy-correlation measurements of actual evapotranspiration ( $E_{35}$ ) during periods of dry weather (Fig. 3).

The linear regression between  $E_Q$  and  $E_{35}$  had a slope of 1.12 and a correlation coefficient  $r = 0.93$  for the 50-year-old stand, whereas the 100-year-old stand had slope of 0.54 and a lower correlation ( $r = 0.80$ ). For all dry-weather situations when soil-water was assumed to be non-limiting, the average value of  $E_Q$  reached 85% of  $E_{35}$  for the young stand and 45% of  $E_{35}$  for the old stand.

Accumulated species-specific transpiration was 69.8 mm for pine and 85.8 mm for spruce in the 50-year-old stand. This gives the relative rates of the two species: pine transpiration rate reached 81% of the rate for spruce. The corresponding pine values were 38.0 mm and spruce values 80.0 mm in the 100-year-old stand, i.e. pine transpiration reached 47% of the rate for spruce. This analysis is biased by the species-different responses to drought. If data from the drought in July–August 1994 were excluded, the pine–spruce transpiration-rate quotient reached 61% in the 50-year-old stand and 52% in the 100-year-old stand. The within-species comparison with respect to tree age showed that specific transpiration was lower for 100-year-old trees than for younger ones. The difference was moderate for spruce, about 7% (16%), whereas it was large for pine, about 46% (28%), with the values in parenthesis based on the estimates excluding data from July–August 1994.

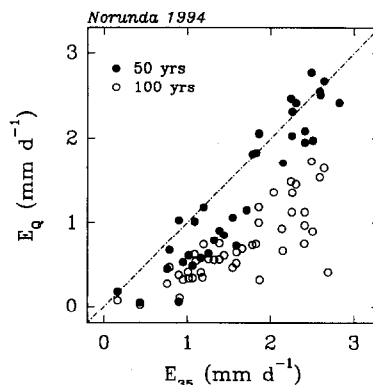


Fig. 3. Daily values of canopy transpiration ( $E_Q$ ) for the 50- and 100-year-old stands (only dry-weather days included) versus actual stand evapotranspiration ( $E_{35}$ ) estimated from measurements at 35 m by eddy-correlation equipment.

### 3.2. Canopy conductance

The parameterization of the canopy-conductance functions (Eqs. (3) and (4)) with the given constraints was complicated by a large scatter, giving low regression coefficients ( $r^2$ ). For the radiation ( $R_g$ ) function (Eq. (3)),  $r^2$  was 0.27 for the 50-year-old stand and 0.26 for the 100-year-old stand (Fig. 4). Also the dependence of  $g_c$  on vapour-pressure deficit ( $\delta e$ ; Eq. (4)) was relatively weak: using the constrained  $g_c$  from June, the corresponding  $r^2$  values were 0.53 and 0.31 for the 50- and 100-year-old stands, respectively (Fig. 4).

The average actual  $g_c$  for all times with simulta-

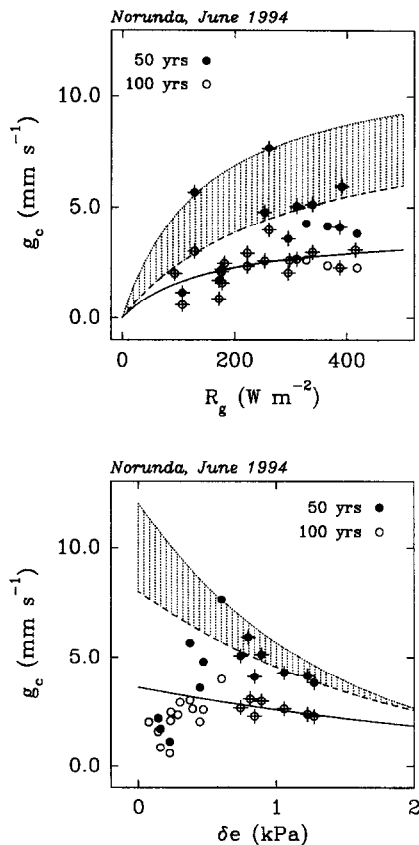


Fig. 4. Parameterization of canopy conductance ( $g_c$ ) as a function of radiation ( $R_g$ , top) and vapour-pressure deficit ( $\delta e$ , bottom) for the 50- and 100-year-old stands, with the constrained values used for fitting marked by '+'. A possible range of underestimation, provided the assumption of saturated soil in June was not fulfilled, is shown by shading for the 50-year-old stand.

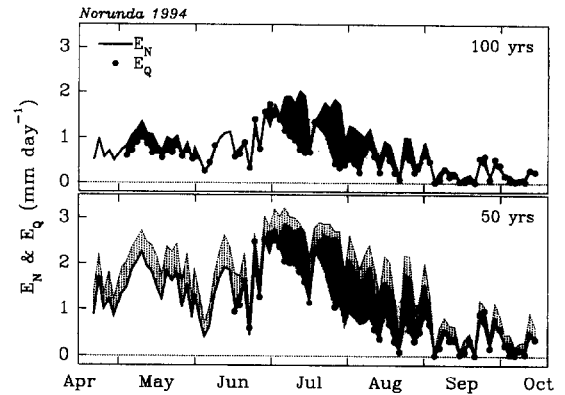


Fig. 5. Seasonal course of 2-day-average actual canopy transpiration ( $E_Q$ , dots) and potential (non-limiting soil water) transpiration ( $E_N$ ). Transpiration deficit, given by the difference  $E_N - E_Q$ , is shown by dark shading. A possible range of underestimation, based on the assumption of saturated soil in June was not fulfilled, is shown by light shading for the 50-year-old stand.

neous measurements in both stands were 2.60 mm s<sup>-1</sup> for the 50- and 1.52 mm s<sup>-1</sup> for the 100-year-old stands. The corresponding average values estimated by the parameterized functions representing non-limiting soil-water conditions were 3.55 mm s<sup>-1</sup> and 2.13 mm s<sup>-1</sup>. The maximum actual values of  $g_c$  reached about 7 mm s<sup>-1</sup> and 4 mm s<sup>-1</sup> for the two stands in the studied growth season.

The absolute differences of actual  $g_c$  values for the 50- and 100-year-old stands reflect the observations of species- and age-specific transpiration. The average value of  $g_c$  for a period of 95 days, when simultaneous measurements were performed on all the trees, were 2.85 mm s<sup>-1</sup> for the hypothetical monospecific stand of 50-year-old spruce, 2.09 mm s<sup>-1</sup> for 50-year-old pine, 2.64 mm s<sup>-1</sup> for 100-year-old spruce and 1.25 mm s<sup>-1</sup> for 100-year-old pine. The canopy conductance (per ground area) was lower for the older stand by 7% (17%) in spruce and by about 40% (31%) in pine trees (values in parenthesis calculated without data from the dry period of July–August).

### 3.3. Transpiration deficit and stem-diameter increment

The seasonal integral of potential canopy transpiration ( $E_N$ ) reached 237 mm for the 50- and 144 mm

for the 100-year-old stands, whereas the actual canopy transpiration ( $E_Q$ ) was 193 mm and 112 mm, respectively. Transpiration deficit, i.e. the difference between  $E_Q$  and  $E_N$ , reached 19% of the seasonal integral of  $E_N$  for the 50-year-old stand and 22% for the 100-year-old stand (Fig. 5).

The responses of trees to the water shortage in July and August were species-specific. In the 100-year-old stand, both species lowered transpiration in similar ways relative to the potential evaporation. In the 50-year-old stand, pine trees partly compensated for the water shortage in the upper soil layers and maintained their transpiration rate well correlated to the evaporative demand for most of that period. This can be demonstrated with data from 1 June to 15 July, indicating onset of water shortage around 1 July (Fig. 2). For the individual species, the relation of  $E_Q$  to  $E_T$  was similar to that shown for the total canopy transpiration, with the exception of the 50-year-old pine trees, whose  $E_Q$  remained highly correlated to  $E_T$  (Fig. 6). This species/age-specific response to drought was also reflected in the independent measurements of stem-diameter increment. The increment for the pine trees in the 50-year-old stand was less reduced during the drought period of

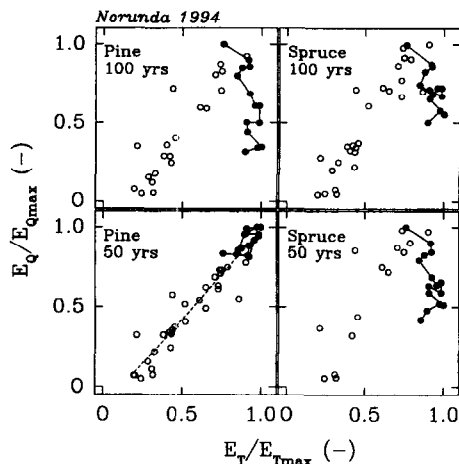


Fig. 6. Canopy transpiration ( $E_Q$ ) for the individual species relative to the potential evaporation by Turc ( $E_T$ ) for the period of 1 June–15 July;  $E_Q$  and  $E_T$  are normalized by the maximum values ( $E_{Qmax}$  and  $E_{Tmax}$ , respectively) for the categories shown. The progression of water deficit during 1–15 July, which had no obvious effect on  $E_Q$  of the 50-year-old pine trees at that period, is shown by connecting lines and filled symbols.

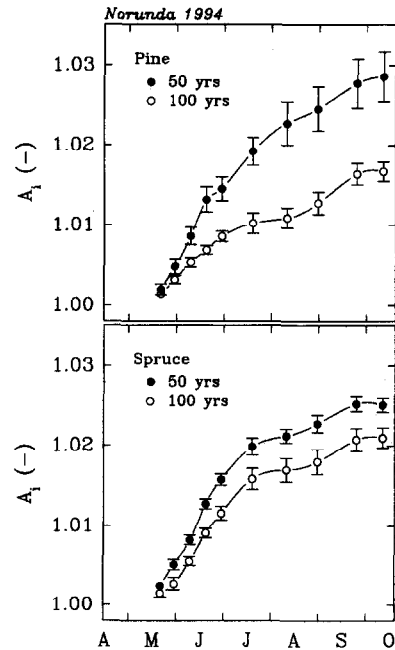


Fig. 7. Seasonal basal-area increment of trees ( $A_i$ ) from the 50- and 100-year-old stands (averages and standard errors of six trees per species and stand) where also sap flow was measured.

July–August while the reduction was distinct for spruce trees in both stands and for pine trees in the 100-year-old stand (Fig. 7).

#### 4. Discussion

The absolute values of transpiration found here are lower than most of the values reported for conifers. The quantitative comparison of the measured fluxes with literature is difficult, because most of the published measurements have been made over younger, shorter and denser plantations (e.g. McNaughton and Black, 1973, Jarvis et al., 1976, Milne, 1979, Tajchman et al., 1979) and they also include understory evapotranspiration. The range of literature values for conifers is high: Lindroth (1985) and Gash et al. (1989), who measured evapotranspiration over mature pine forests with low tree density and leaf-area index (LAI) found maximum daily evaporation rates of 4.5 and 4.8 mm. On the other hand, the measurements of Stewart (1988) over the 35-year-old Thet-

ford pine forest revealed evapotranspiration rate maxima similar to the values found here. Investigations in boreal coniferous forests in Canada revealed daily transpiration rates less than 2 mm, much less than normally found for temperate forests (Sellers et al., 1995). It is thus obvious, that for a single category of coniferous forests a wide range of actual flux rates is reported, which depends on many factors like structure, age, species composition, climatic and soil-water conditions etc.

Also the correlation between the actual transpiration via sap-flow measurements and evapotranspiration by eddy-correlation system revealed difficulties of quantitative comparisons. Logically, canopy transpiration was mostly lower than stand evapotranspiration. In addition to tree transpiration, stand fluxes incorporate soil and dew evaporation and transpiration from understory vegetation, especially for the less dense 100-year stand. The sporadic cases when tree transpiration was slightly higher than the evapotranspiration measured by eddy-correlation system are likely to be explained by a footprint analysis. This is necessary because the tower where eddy correlation was measured, was at a distance of about 150 and 600 m from the two investigated stands. There was also a large directional variability observed for the measured fluxes of stand evapotranspiration by eddy correlation on the tower (Grelle et al., 1997). This reflects the patchy structure of the forest in the area with many relatively small stands of different ages and densities. A detailed footprint analysis of the eddy-correlation flux measurements will likely improve the relationships of transpiration and evapotranspiration fluxes for the studied stands.

The  $g_c$  found here for the 50-year-old stand was about half of that found for a dense 24-year-old spruce monoculture in south Sweden (Cienciala et al., 1994). The latter forest had roughly twice as much needle area per unit of ground area compared with the present stand. The comparison of  $g_c$  with other literature values was hampered by the fact that most conductance values found in the literature refer to whole stands and not to a tree canopy, i.e. understory evaporation contributes to the stand conductances. Understory evapotranspiration can contribute considerably to stand evapotranspiration. For a 4-year-old *Pinus radiata* stand with a height of 2.5 m and LAI of about 3, Kelliher et al. (1990) reported

an understory contribution to the total evapotranspiration of up to 50%. Spittlehouse and Black (1982) found that the understory of a Douglas-fir forest with a leaf-area index of 4.5 transpired 35% of the canopy transpiration whereas Ovhed (1995) found similar values for a birch forest with an LAI of 2. For our site, the contributions from the forest floor was later estimated as 15% in the 50-year-old stand for the growth period of 1995 (Grelle et al., 1997). However, this contribution was estimated for a markedly more moist period in 1995 relative to the unusually dry year of 1994 investigated here.

The pronounced differences in species-specific canopy transpiration could explain much of the differences in canopy fluxes for the two stands. The much lower transpiration of the old pine trees together with their dominant representation makes the flux smaller in the 100-year-old stand. The absolute difference in transpiration observed between the two stands is partly biased by a slightly smaller leaf area index (by about one) for the older stand; this, however, did not explain the observed differences in transpiration fluxes. This supports the hypothesis of a lower hydraulic conductance in the vascular system of older trees as a primary reason for greater stomatal closure and lower transpiration (Hinckley and Ceulemans, 1989, Yoder et al., 1994). The increased tree hydraulic resistance in older and taller trees may also limit tree height and tree growth and herewith explain the decline of production in older trees (e.g. Yoder et al., 1994, Ryan and Yoder, 1997). We briefly checked this for pines, where major differences in canopy transpiration for the two age classes were observed, expressing the transpiration fluxes per leaf area on a tree basis. The biomass functions of Marklund (1988) were applied to calculate the needle mass for individual trees. Using a specific leaf area of  $20 \text{ m}^2 \text{ kg}^{-1}$ , we obtained the leaf area for individual trees. Also on a tree leaf area basis, transpiration was generally about 10–30% lower for the older pine trees relative to the younger ones (data not shown here).

The omega factor ( $\Omega$ ) was mostly below 0.1 for both stands. These are typical values for coniferous stands with good canopy ventilation (Jarvis and McNaughton, 1986).  $\Omega$  is an index of decoupling between plant cover and atmosphere (McNaughton and Jarvis, 1983). It reflects the importance of canopy



conductance ( $g_c$ ) as a factor controlling transpiration.

The uncertainty in assessing the impact of soil-water scarcity on canopy transpiration was primarily related to the low correlation between potential  $g_c$  and weather conditions. There are several reasons for the weak correlation of  $g_c$  to  $R_g$  and  $\delta e$ : (1) the limited set of data for which parameter values were estimated. The data set was limited on purpose to avoid seasonal averaging and to include only non-limiting soil-water conditions; (2) simplifications by reducing the complex 3-D nature of canopy gas exchange and interacting microclimatic variables into the 'big-leaf' surface transfer implicit in the Penman–Monteith equation—neglecting the species-specific radiation regime (light-sensitive pine versus less light-demanding spruce, which competes well as an understory species); (3) the uncertainty about soil-water conditions. The measurements of soil-water status were not available for this study and therefore the assumption of a fully saturated soil in June may not have been fully met. This would also contribute to the large variations of  $g_c$  in relation to  $R_g$  and  $\delta e$  (Fig. 4). Nevertheless, previous good results with similar forms of  $g_c$  in the Penman–Monteith equation (e.g. Lindroth and Halldin, 1986, Stewart, 1988, Cienciala et al., 1992, Granier and Loustau, 1994) still makes it reasonable to base an analysis on the functions. But there is a need to re-investigate the response of  $g_c$  to vapour pressure deficit, which might be only a mimicking factor of other likely limitation mechanisms such as hydraulic resistance and transpiration rate. The sole effect of humidity on  $g_c$  was recently questioned by Monteith (1995).

Since the soil-water measurements were not available at the site in 1994, our assumption about soil-water deficit might have underestimated the real conditions at the site. It is possible that the soil was not fully recharged in June (the period used for parameter-value estimation) even if this was indicated by the relation of  $E_Q$  to  $E_T$  (Fig. 2). The years 1993 and 1994 were dry relative to the long-term average and the soil may have been unsaturated at the beginning of 1994. If this were the case, the  $g_c$  functions (Eqs. (3) and (4)) should be determined by the maximum  $g_c$  values rather than by their average in order to mimic the non-limiting conditions (Fig.

4). If the functions of  $g_c$  for the 50-year-old stand are drawn through the maximum values, the predicted potential transpiration would increase to a maximum of about 3.3 mm and a seasonal sum of 308 mm (Figs. 4 and 5). This would mean a substantially larger transpiration deficit for the site (Fig. 5). To clarify this question, a detailed analysis of diurnal courses of water uptake could be used, preferably in combination with a high resolution SPAC model, like the one of Eckersten (1991a,b). Alternatively, new measurements at the site during a hydrologically different year or concurrent independent measurements of soil-water conditions might clarify this uncertainty.

Deep roots are one of the features which makes trees drought tolerant (e.g. Kramer, 1983, Kozłowski et al., 1991). Pine and spruce are expected to perform differently in drought conditions. Pine is characterized by a deep root system, whereas spruce is a shallow-rooted species. In 1993, when measurements were performed only in the 100-year-old stand, it was observed that the recovery of sap flow after a drought period was more rapid for spruce than for pine (Čermák et al., 1995). That observation was based on data from two short time intervals. Here the seasonal courses showed that pine trees reduced transpiration in a similar way to spruce trees in the 100-year-old stand during an extended drought period. We cannot say whether the older pine trees were just not able to operate under the same gradient of water potential as the younger ones or whether these gradients were higher in older trees. Additional measurements of water potential would help us to answer these questions.

Using measurements of stem increment to assess the effect of drought on production may be biased by several factors, e.g. by a varying allocation of carbon to different tree compartments, changing respiration components in a tree carbon budget etc. However, the age- and species-specific transpiration responses to drought (Fig. 6) agreed well with the stem increment for the studied categories (Fig. 7). We observed a similarly good correspondence of stem increment to infiltrated water in another study on 24-year-old Norway spruce trees (Cienciala et al., 1994). The parallel measurements of stem increment appear to be a simple and useful independent measure on how trees respond to drought.

## 5. Conclusions

1. For dry-weather days, daily canopy transpiration estimated on the basis of sap-flow measurement and stand evapotranspiration estimated from eddy-correlation measurements were highly correlated.
2. Seasonal transpiration deficit in the studied mixed spruce/pine boreal forest stands was at least one fifth of the seasonal potential (not limited by soil moisture) transpiration.
3. Canopy conductance and transpiration were lower for pine than for spruce at stand and tree level.
4. Canopy conductance was lower for 100-year-old trees than for 50-year-old ones approximately by one tenth for spruce and by a third for pine. A probable reason for this is a decreased hydraulic conductance in the sapwood of older trees.
5. In the 50-year-old stand, transpiration in pines was less affected by drought as compared with spruce or older pine trees.
6. Local-scale fluxes depend on species distribution and age, and this may affect regional fluxes. Distribution functions could be achieved by categorizing forests in the region into age classes and pine/spruce quotients. Future measurement programmes should be planned to cover these categories.

## Acknowledgements

This study was performed within the framework of the NOPEX project. The senior author acknowledges the support from the Swedish Natural Science Research Council in his postdoctoral stay at the National Center for Atmospheric Research, Boulder, Colorado, USA. The field investigations were funded by the Swedish Council for Forestry and Agricultural Research, the Swedish Natural Science Research Council and the Knut and Alice Wallenberg Foundation. Some climatic data were retrieved from the System for Information in NOPEX (SINOP). We thank Jan Seibert for giving access to precipitation data and Meelis Mölder for some other local-climate data.

## References

- Čermák, J., Deml, M., Penka, M., 1973. A new method of sap flow rate determination in trees. *Biol. Plant. (Praha)* 15, 171–178.
- Čermák, J., Cienciala, E., Kučera, J., Lindroth, A., Bednářová, E., 1995. Individual variation of the sap-flow rate in large pine and spruce trees and stand transpiration: a pilot study at the central NOPEX site. *J. Hydrol.* 168, 17–28.
- Cienciala, E., Lindroth, A., Čermák, J., Hällgren, J.-E., Kučera, J., 1992. Assessment of transpiration estimates for *Picea abies* trees during a growing season. *Trees Struct. Funct.* 6, 121–127.
- Cienciala, E., Lindroth, A., Čermák, J., Hällgren, J.-E., Kučera, J., 1994. The effects of water availability on transpiration, water potential and growth of *Picea abies* during a growing season. *J. Hydrol.* 155, 57–71.
- Eckersten, H., 1991. Simulation model for transpiration, evaporation and growth of plant communities. SPAC-GROWTH model description. Division of Agricultural Hydraulics, Report 164, Department of Soil Science, Swedish University of Agricultural Sciences, Uppsala, 36 pp.
- Eckersten, H., 1991. SPAC-GROWTH model, user's manual. Division of Agricultural Hydraulics, Communications 91:4, Department of Soil Science, Swedish University of Agricultural Sciences, Uppsala, 31 pp.
- Federer, C.A., Vorosmarty, C., Fekete, B., 1996. Intercomparison of methods for calculating potential evaporation in regional and global water balance models. *Water Resour. Res.* 32 (7), 2315–2321.
- Gash, J.H.C., Shuttleworth, W.J., Lloyd, C.R., André, J.C., Goutorbe, J.P., Gelpe, J., 1989. Micrometeorological measurements in les landes forest during Hapex-Mobilhy. *Agric. For. Meteorol.* 46, 131–147.
- Granier, A., Loustau, D., 1994. Measuring and modelling the transpiration of a maritime pine canopy from sap-flow data. *Agric. For. Meteorol.* 71, 61–81.
- Grelle, A., Lindroth, A., 1994. Flow distortion and solent sonic anemometer: wind tunnel calibration and its assessment for flux measurements over forest and field. *J. Atmos. Oceanic Technol.* 11, 1529–1542.
- Grelle, A., Lindroth, A., 1996. Eddy correlation system for long term monitoring of fluxes of heat, water vapour, and CO<sub>2</sub>. *Global Change Biol.* 2 (3), 297–307.
- Grelle, A., Lundberg, A., Lindroth, A., Morén, A.-S., Cienciala, E., 1997. Evaporation components of a boreal forest: variations during the growing season. *J. Hydrol.*, in press.
- Halldin, S., Gottschalk, L., van de Griend, A.A., Gryning, S.-E., Heikinheimo, M., Höglström, U., Jochum, A., Lundin, L.-C., 1995. Science plan for NOPEX. Technical Report No. 12, Uppsala University, Uppsala, 38 pp.
- Hinckley, T.M., Ceulemans, R., 1989. Current focuses in woody plant water relations and drought resistance. *Ann. Sci. For.* 46s, 317–324.
- Jarvis, P.G., 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Phil. Trans. R. Soc. Lond.* 273, 593–610.
- Jarvis, P.G., McNaughton, K.G., 1986. Stomatal control of tran-

- spiration: scaling up from leaf to region. *Adv. Ecol. Res.* 15, 1–45.
- Jarvis, P.G., James, G.B., Landsberg, J.J., 1976. Coniferous forest. In: Monteith, J.L. (Ed.), *Vegetation and the Atmosphere*. Vol. 2. Case Studies. Academic Press, New York, pp. 171–240.
- Karl, T.R., Knight, R.W., Plummer, N., 1995. Trends in high frequency climate variability in the twentieth century. *Nature* 377, 217–220.
- Kelliher, F.M., Whitehead, D., McAneney, K.J., Judd, M.J., 1990. Partitioning evapotranspiration into tree and understorey components in two young *Pinus radiata* D. Don stands. *Agric. For. Meteorol.* 50, 211–227.
- Kozlowski, T.T., Kramer, P.J., Pallardy, S.G., 1991. *The Physiological Ecology of Woody Plants*. Academic Press, Inc., San Diego, 657 pp.
- Kramer, P.J., 1983. *Water Relations of Plants*. Academic Press, Inc., New York, 489 pp.
- Kučera, J., Čermák, J., Penka, M., 1977. Improved thermal method of continual recording the transpiration flow rate dynamics. *Biol. Plant. (Praha)* 19, 413–420.
- Lindroth, A., 1985. Canopy conductance of coniferous forests related to climate. *Water Resour. Res.* 21, 297–304.
- Lindroth, A., Halldin, S., 1986. Numerical analysis of pine forest evaporation and surface resistance. *Agric. For. Meteorol.* 38, 59–79.
- Lohammar, T., Larsson, S., Linder, S., Falk, S., 1980. FAST – simulation models of gaseous exchange in Scots pine. In: Persson, T. (Ed.), *Structure and Function of Northern Coniferous Forests – An Ecosystem Study*. *Ecol. Bull.* 32, 505–523.
- Marklund, L.G., 1988. Biomass functions for pine, spruce and birch in Sweden. Report 45, Dept. Forest Survey, Swedish University of Agricultural Sciences, Umeå, pp. 1–73.
- Massman, W.J., Kaufmann, M.R., 1989. Parameterizations of leaf stomatal conductance response functions. In: Price, J.C. (Ed.), *Proceedings of the Workshop on Stomatal Resistance Formulation and its Application to Modeling of Transpiration*. Pennsylvania State University, College of Earth and Mineral Sciences, pp. 101–103.
- McNaughton, K.G., Black, T.A., 1973. A study of evaporation from a Douglas-fir forest using the energy balance approach. *Water Resour. Res.* 9, 1579–1590.
- McNaughton, K.G., Jarvis, P.G., 1983. Predicting effects of vegetation changes on transpiration and evaporation. In: Kozlowski, T.T. (Ed.), *Water Deficits and Plant Growth*, vol. V. Academic Press, New York, pp. 1–48.
- Milne, R., 1979. Water loss and canopy resistance of a young Sitka spruce plantation. *Boundary-Layer Meteorol.* 16, 67–81.
- Monteith, J.L., 1995. A reinterpretation of stomatal responses to humidity. *Plant Cell Environ.* 18, 357–364.
- Ovhed, M., 1995. Evapotranspiration and energy exchange of a mountain birch forest, Abisko, Sweden. *Acta Universitatis Uppsaliensis, Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology*, 167, Uppsala, 38 pp.
- Penman, H.L., 1948. Natural evaporation from open water, bare soil and grass. *Proc. R. Soc. Ser. A* 193, 120–146.
- Ryan, M.G., Yoder, B.J., 1997. Hydraulic limits to height and tree growth. *Bioscience*, 47(4), 235–242.
- Sellers, P., Hall, F., Margolis, H., Kelly, B., Baldocchi, D., den Hartog, G., Cihlar, J., Ryan, M.G., Goodison, B., Crill, P., Ranson, K.J., Lettenmaier, D., Wickland, D.E., 1995. The boreal ecosystem–atmosphere study (BOREAS): an overview and early results from the 1994 field year. *Bull. Am. Meteorol. Soc.* 76, 1549–1577.
- Spittlehouse, D.L., Black, T.A., 1982. A growing season water balance model used to partition water use between trees and understorey. In: *Canadian Hydrology Symposium*, 14–15 June 1982, Fredericton, New Brunswick. National Research Council of Canada, Ottawa, Ont., pp. 195–214.
- Stähli, M., Hessel, K., Eriksson, J., Lindahl, A., 1995. Physical and chemical description of the soil at the NOPEX central tower site. NOPEX Technical Report No. 16, Department of Soil Sciences, Swedish Univ. Agric. Sci., Uppsala, Sweden, 19 pp.
- Stewart, J.B., 1988. Modelling surface conductance of pine forest. *Agric. For. Meteorol.* 43, 19–35.
- Turc, L., 1961. Évaluation des besoins en eau d'irrigation évapotranspiration potentielle. *Ann. Agron.* 12, 13–49.
- Tajchman, S.J., Hädrich, F., Lee, R., 1979. Energy budget evaluation of the transpiration–pF relationship in a young pine forest. *Water Resour. Res.* 15, 159–163.
- Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W., Kaufmann, M.R., 1994. Evidence of reduced photosynthetic rates in old trees. *For. Sci.* 3, 513–527.