Partitioning of forest evapotranspiration: The impact of edge effects and canopy structure

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ABSTRACT

The magnitude of small scale variability in tree transpiration was explored in a structurally heterogeneous Norway spruce (Picea abies (L.) H. Karst.) plantation in western Denmark. The trees are arranged in a distinctive small scale mosaic (0.25 ha) of young open-canopy stands interspaced with older mature closed-canopy stands. Tree transpiration was measured in the open and closed canopy stands using Granier type thermal dissipation probes; forest floor evapotranspiration (ET) was estimated by monitoring the weight of cut out sections of forest floor; and total ET was estimated using the eddy covariance (EC) method. We show that (a) canopy structure had a major impact on transpiration rate allowing the open-canopy stands to transpire at approximately 30% higher rate than the closed-canopy stands; (b) within the open-canopy stand there was a significant relation between tree size and sap-flux density; and (c) within the closed-canopy stands there was an edge effect with trees next to access roads and aisles being responsible for a disproportionately large part of the stand transpiration. Through careful scaling, taking into account the observed variability, it was possible to get good agreement on dry days between independent measures of transpiration plus forest floor ET and the EC estimate of total forest ET. On average transpiration and forest floor ET amounted to 86% of the EC estimate on dry days.

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1. Introduction

The eddy-covariance method (EC) provides an integrated measure of the water vapor flux at the scale of a few hectares, but no information on the variability of the flux within this area. Partitioning the evapotranspiration (ET) can provide both knowledge of the magnitude of the variability and insight into the processes that govern the variability. This knowledge is important for modern process-based land surface models such as JULES (Best et al., 2011) or CLM (Oleson et al., 2010), which treat the components of ET separately. Information on the partitioning and spatial variability of water and carbon fluxes is also important in the context of afforestation – whether to accurately predict the water balance for forests established to protect groundwater resources or to accurately predict the CO₂ sink strength of forest established to counteract global warming. Using a combination of EC-ET measurements, sap-flux tree transpiration measurements and forest floor evaporation measurements we aim to add to the knowledge of within-stand and inter-stand variability by means of a case study in a medium sized Norway spruce plantation.

Norway spruce stands have been studied intensively in Europe (e.g., Alsheimer et al., 1998; Pedersen and Bille-Hansen, 1999; Köstner et al., 2002; Lehtonen et al., 2004; Gartner et al., 2009). Large variations in transpiration have been observed between stands. This is ascribed in part to a differentiation in development due to climate and soil conditions (Pretzsch, 1996) and in part to an age effect (Ryan et al., 1997) where stands experience a decline in transpiration after 80–100 years due primarily to decreased hydraulic conductance and decreased leaf area index. Management practices such as thinning (Mäkinen and Isomäki, 2004; Skovsgaard and Vancay, 2008) or fertilization and liming (Ingerslev, 1997; Ewers et al., 2001) have been found to have only limited effect on stand transpiration. Within stand variability has been ascribed to increased transpiration rates near the edge of the wood (Herbst et al., 2007) and to situations where a subset of trees differs from the general canopy structure – e.g., small trees below a closed canopy (Köstner et al., 1998b; Köstner et al., 2002; Staudt et al., 2011). At the single tree scale large variations are often observed, but no significant correlation has been found between biometric factors such as stem diameter or projected crown area and sap-flux density (e.g., Alsheimer et al., 1998; Köstner et al., 1998a; Gartner et al., 2009). However, Lagergren and Lindroth (2004) noticed a potential...
influence of the distance between individual trees on tree transpiration in a mixed spruce and pine stand.

The forest in this study features a distinctive small-scale (0.25 ha) mosaic of stands aged 20–40 years. The young stands still have an open-canopy structure, while the older stands have a mature closed canopy. By employing separate measurements of transpiration in both stand types we aimed to confirm or reject the following hypotheses:

1. Transpiration rates of Norway spruce in a strip plantation style management differ significantly within the stand with variations being related to the structure and age characteristics of the stand.
2. Models which include structural differences in their parameterization are well suited for evaluating stand structure effects on evapotranspiration.
3. Up scaled transpiration rates can be effectively validated at the stand scale by independent EC measurements and soil lysimeters.

2. Materials and methods

2.1. Site description

The experiment was carried out in Gludsted Plantation in the central part of Jutland, Denmark (56° 44’ N, 9° 20.1’ E). The plantation was established about 100 years ago, and is today one of the largest forest areas in Denmark (3500 ha). The climate can be characterized as maritime, with a mean annual temperature of 8 °C and an annual precipitation of 850 mm. The weather is dominated by cyclonic weather systems from the Atlantic Ocean and the accompanying prevailing westerlies. The site is located on an outwash plain from the last glaciation. The topography is flat throughout the plantation and there are no morphological features which might induce variability in the soil texture or soil water content. The soil texture is coarse sand with some large rock mixed in and a clay content of <1%. A 5-cm thick organic horizon with a C/N ratio of 27 overlies the mineral soil (Gundersen et al., 2009).

The plantation consists mainly of Norway spruce (Picea abies (L.) H. Karst.) arranged in a distinctive checkerboard pattern with the size of individual squares being approximately 0.25 ha (Fig. 1). The age of the stands ranges between 12 and 45 years, but a general grouping of “young” stands aged approximately 20 years and “mature” stands aged approximately 40 years can be identified. The young and mature stands are arranged in strips oriented east–west with a typical repeated north–south pattern of young–mature–young–mature or young–mature–young. The mature stands are bound on their northern edge by a single row of Grand fir (Abies grandis (Douglas ex D. Don) Lindl.).

The young Norway spruce stands have an open canopy structure. Green needles extend all the way down to the forest floor in many places, and small patches of forest floor are visible from the sky. The mature Norway spruce stands have a closed-canopy structure. The live crowns only make up one-third to half the height of the trees, and the forest floor is completely shaded. The typical tree heights are 15 m for the young Norway spruce stands, 20 m for the mature Norway spruce stands and 25 m for the Grand fir rows. Tree density is 30% higher in the young stands than in the mature stands while at the same time the sapwood area per ground area is 30% less in the young stands due to a smaller average tree size (Table 1). Sapwood area was determined by examining 9 cut trees. Heartwood and sapwood can easily be distinguished by color in Norway spruce, and a simple relation between sapwood area and breast height circumference was established.

Each mature stand is made up of 20–22 rows of trees arranged in subgroups of 4–5 rows (Fig. 1, top right). Inside the subgroups the rows are spaced 1.8 m apart, while the distance between subgroups is 5 m and between adjacent stands 8 m. Three classes of Norway spruce trees can be identified based on the space
available for canopy development. “Internal” trees which have 1.8 m to the next row on both sides, “internal edge” trees which have 1.8 m to the next row on one side but 5 m on the other side and “south edge” trees which have 1.8 m on one side but 8 m on the other side. There is a marked difference in average tree size between the three classes. Table 2 shows that the average sapwood area per tree in the “south edge” class is about double that of the “internal” class, while the “internal edge” class is in between.

The undergrowth is comprised predominantly of different mosses, though some grasses are present along access roads. The access roads make up less than 5% of the total area. Moss ground coverage is about 90% with the remaining area being either bare soil or dense needle cover (Lind and Madsen, 2011). Five species of moss can be identified in the forest: Hypnum jutlandicum, Pleurozia schreberi, Dicranum spp., which are found throughout the forest, and Rhytidium reuteri. Plagiocoma undulatum, which are only found under the mature, closed-canopy stands. Of the five, H. jutlandicum is the most common, followed by P. schreberi and Dicranum spp. R. reuteri and P. undulatum both make up less than 5% of the moss cover.

2.2. Sap flow measurements

Sap flow measurements were made using Granier-type (Granier, 1985, 1987) Thermal Dissipation Probe (TDP) sets (Dynmax Inc., Houston, TX). The two probes for each sensor were installed 5 cm apart at breast height, covering the outer 3 cm of sapwood. The upper probe was heated constantly, and the temperature difference was measured every 10 s with averages stored every 30 min to a datalogger (Model 21X, Campbell Scientific Ltd., Shepshed, UK). The probes were insulated by means of quarter foam eggs and wrapped in reflective bubble wrap to dampen the effect of ambient temperature variations. Sap-flux density (mm s⁻¹) was calculated using the original calibration coefficients of Granier (1985). For the smallest trees the correction established by Clearwater et al. (1999) was used to account for the fraction of the probes not in contact with conducting sapwood. At no point did the correction reach a value of more than +15%.

Sap flow was measured from March through to September 2010. Two sensors were installed per tree – one set of probes on the north side and one set on the south side. No significant differences were observed between the north and south facing sensors. At any time five trees in a “young” stand, five trees in a “mature” stand and two Grand fir trees were sampled. To increase the number of sampled trees, half of the sensors were moved to new trees in a bimonthly cycle, making the total number of trees sampled 15 for the “young” and “mature” Norway spruce stands and 6 for the Grand fir row. No bias or significant trends were observed between “moved” and “non-moving” sensors. This is in agreement with the literature, where sensors have been installed for a growing season or longer, without any loss in sensitivity due to formation of stigmata tissue (Köstner et al., 1998a; Olivas and Llorens, 2001). For the “mature” stand the sampled trees were always three trees from the “internal” class and two trees from the “internal edge class” (Fig. 1).

Due to the limited maximum cable length between sensors and data logger, the “south edge” trees could not be measured at the same time as the other classes. Therefore, a second experiment was performed in 2011 to examine the heterogeneity and the edge effect in the “mature” stand. Six sensors were installed in three trees in each of the three classes: “internal”, “internal edge” and “south edge”. By comparing average sap-flux densities from the three classes and taking into account the sapwood distribution (Table 2), it was possible to estimate the contribution from each class to the stand transpiration, and to develop a correction for the 2010 sap-flux density estimates when the distribution of the sensors among the classes did not represent their relative sapwood area.

Calculation of sap-flux density requires accurate determination of the maximum temperature difference ΔTmax (i.e., the ΔT at zero sap flow). Granier (1987) and Lu et al. (2004) suggest using a 7–10-day window in periods with no drift in ΔTmax to avoid underestimation of the flux during days where the predawn flux does not reach zero. Periods with drift in ΔTmax – e.g., due to changes in sapwood water content in response to drought – should be treated separately. In practice we found that using a 3-day moving window was sufficient to avoid underestimation of the true flux while being short enough to handle periods of drift in ΔTmax.

Scaling of sensor sap-flux density to tree level transpiration requires assumptions about the azimuthal and radial variations of flux density. In this study we found no systematic differences between north and south facing sensors, or between multiple sensors in the same tree. This is in agreement with other observations, e.g., Olivas and Llorens (2001) and Köstner et al. (2002). Čermák et al. (1992) found a symmetric radial sap velocity pattern in Norway spruce with the highest flow rates in the center of the sapwood and lower rates near the cambium and heartwood. Most of the sapwood had relatively high velocities, and Köstner et al. (2002) found no significant differences in observed sap-flux densities when using probes that integrated over either the outer part or the inner part of the sapwood. The average sapwood depth of the trees used in the experiment was 3.6 cm. Compared with the sensor length of 3 cm the probes integrated over most of the sapwood, and the observed sap-flux densities were assumed to represent the average flux density of the entire sapwood depth. Thus, tree level transpiration was calculated as the average sap-flux density of all sensors in a tree, multiplied by the tree’s sapwood area.

2.3. Eddy-covariance measurements and meteorological data

Forest ET was measured using the eddy-covariance (EC) technique. The instrumentation consisted of a sonic anemometer (R3–50, Gill Instruments Ltd., Lymington, UK) and an open-path CO₂/H₂O gas analyzer (LI-7500, LI-COR, Lincoln, NE). The instruments were mounted atop a 38 m high mast near the center of

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### Table 1

<table>
<thead>
<tr>
<th></th>
<th>Young Norway spruce</th>
<th>Mature Norway spruce</th>
<th>Grand fir</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree density (number ha⁻¹)</td>
<td>2520</td>
<td>1808</td>
<td>500</td>
</tr>
<tr>
<td>Breast height area (m² ha⁻¹)</td>
<td>29</td>
<td>40</td>
<td>43</td>
</tr>
<tr>
<td>Sapwood area (m² ha⁻¹)</td>
<td>19</td>
<td>26</td>
<td>25</td>
</tr>
</tbody>
</table>

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### Table 2

<table>
<thead>
<tr>
<th>% of rows in stand</th>
<th>Avg. tree circumference (cm) (±SD)</th>
<th>Avg. tree sapwood area (cm²)</th>
<th>% of sapwood in stand</th>
</tr>
</thead>
<tbody>
<tr>
<td>Internal</td>
<td>55</td>
<td>46.7 (±12.8)</td>
<td>118</td>
</tr>
<tr>
<td>Internal edge</td>
<td>40</td>
<td>57.1 (±12.9)</td>
<td>170</td>
</tr>
<tr>
<td>South edge</td>
<td>5</td>
<td>70.5 (±11.7)</td>
<td>250</td>
</tr>
</tbody>
</table>
the plantation (Fig. 1). Fluxes were calculated as 30-min averages using the AltEddy Software Package Version 3.5 (Alterra, University of Wageningen, The Netherlands). The data were gap-filled according to Moffat et al. (2007) based on the quality classes proposed by Foken et al. (2004). For more information about the instrument setup and data processing see Ringgaard et al. (2011). Using the model by Schuepp et al. (1990) with a typical Monin–Obukhov length of $L = 40 \text{ m}$, 80% of the flux originated from a distance < 750 m. Within the 750 m footprint, the distribution of stand types was digitized from orthophotos (Fig. 2). Gravel access roads and clearings comprise less than 5% of the footprint and were not treated separately.

Ancillary meteorological data included short and long wave radiation (NR01, Hukseflux Thermal Sensors B.V., Delft, The Netherlands) measured 30 m above the forest floor, temperature and relative humidity (HMP 45 C, Vaisala Oyj, Helsinki, Finland) measured at 15 and 30 m above the surface and precipitation (Rimco 7499, McVan Instruments, Mulgrave, VIC, Australia) measured in the centre of a small clearing near the EC mast.

2.4. Moss evapotranspiration

Forest floor evapotranspiration or “moss ET” was measured during three 2-day campaigns in 2010. Five 210 mm × 297 mm sections of moss and the upper part of the organic soil layer were cut from the forest floor and placed in plastic trays with latticed sides and bottom to allow for drainage of excess precipitation. The trays were placed into the space left by the moss and soil, and moss ET was estimated by weighing the trays once every hour. Three trays were placed under a young Norway spruce stand and two trays under a mature Norway spruce stand. To estimate moss ET for the entire year, a model based on the Penman–Monteith (PM) equation (Monteith, 1965) was developed.

The model defines a “moss water store” from which water can be added through surplus precipitation, and removed through ET or drainage, if water content exceeds field capacity. The model works on two time scales – 24 h and 30 min. The water content is updated once every day at midnight, by adding surplus precipitation ($P_{EC}$-ET) and subtracting the cumulative 24 h calculated moss ET plus any drainage. Moss ET is calculated on a half-hour time scale using the PM equation, measured meteorological parameters and a resistance value based on the current water content. The resistance value is updated once every 24 h along with the water content.

To derive the water content versus resistance relationship the trays were brought back to the laboratory, wetted to field capacity, and then dried at ambient temperature until constant weight while moss temperature, air relative humidity at the moss surface and weight were recorded twice per day. The bulk resistance was calculated as:

$$R = \frac{VPD \cdot \rho_s \cdot c_p}{\gamma \lambda E}$$

where $R$ is the bulk resistance, VPD is the vapor pressure deficit, $\rho_s$ is the mean air density at constant pressure, $c_p$ is the specific heat of air, $\gamma$ is the psychrometric constant and $\lambda E$ is the latent heat flux (Monteith and Unsworth, 1990). Fig. 3 shows the obtained relationship between surface resistance and relative weight. With decreasing weight the resistance rose only gradually until a relative weight of about 0.5; below this value the resistance increased exponentially as the moss dried further. This is the same basic pattern observed by Bond-Lamberty et al. (2011) in a similar laboratory study using mosses collected in Canadian Black spruce stands.

Determination of the maximum water store (water content at field capacity) in the laboratory was not directly applicable to field conditions. Roots from the Norway spruce trees are present in the organic soil directly below the moss, and clear distinction between moss, organic soil without roots and organic soil with roots was impossible to establish for the tray samples. As a result the maximum size of the moss water store was found through calibration against field measurements, where the model was optimized to fit measured daily ET and measured water content. The calibrated maximum water store was 7 mm.

3. Results

3.1. Sapwood area

Sapwood area was determined from nine cut trees of both the young and mature Norway spruce stands. A simple power relationship was established between tree circumference at breast height and sapwood area (Fig. 4). This relationship is very close to the one reported by Alsheimer et al. (1998), for a 40 year old Norway spruce stand in southern Germany. Unfortunately no cut Grand fir was available for study. Transpiration estimates for the Grand fir stand were therefore based on the relation derived from Norway spruce. This will have only very limited effect on the total forest transpiration estimate given the small spatial extent of Grand fir.

3.2. Sap-flux density

The three stands had significantly different flux densities in 2010 (Fig. 5). The mean sap-flux density of the young Norway spruce was 0.008 (± 0.003) mm s⁻¹, the mean sap-flux density of the mature Norway spruce was 0.0034 (± 0.0015) mm s⁻¹ and the mean sap-flux density of the Grand fir was 0.0054 (± 0.0013) mm s⁻¹. Numbers in brackets indicate standard deviations. The young Norway spruce stand showed a significant positive correlation...
Black dotted: this study, \( \text{i.e., } Y = 0.106 \times x^{1.52} \) \((R^2 = 0.92)\). Gray: data from a 40 year old Norway spruce stand in a catchment of the Fichtelgebirge, Germany (Alsheimer et al., 1998).

Fig. 5. Average sap-flux densities for the sampled trees in 2010. For the mature stand only “internal” and “internal edge” trees were sampled (Table 2). Sap-flux densities in the young and mature Norway spruce stands were significantly different \((P < 0.001, \text{Welch two sample } t\text{-test})\) and the Grand fir stand was significantly different from both Norway spruce stands \((P = 0.05)\). The young Norway spruce stand showed a significant correlation between tree circumference and sap-flux density \((Y = 0.00015x - 0.00017, R^2 = 0.26, P = 0.05)\) while there was no such correlation in the mature and Grand fir stands \((P = 0.79\) and \(P = 0.85\) respectively).

between tree size and sap-flux density, with the largest sampled trees having about twice the flux density of the smallest sampled trees. For the mature Norway spruce and the Grand fir there was no dependency of sap-flux density on tree size.

To account for the sap-flux density dependency on tree size in the young Norway spruce stand, the sampled trees were compared with all trees in the stand (Fig. 6). The sampled trees were slightly larger than the natural distribution in the stand, and using the observed relations between (a) tree size and sap-flux density and (b) tree size and sapwood area, it was possible to correct the measured flux densities. On average, the measured flux densities were corrected by \(-6\%\).

In the mature Norway spruce stand heterogeneity and edge effect were explored in May 2011. On a typical cloudless day with dry canopy conditions, the peak sap-flux density for the internal edge trees was twice that of the internal trees, while the south edge trees had 2.5 times the peak flux density of the internal trees (Fig. 7). Statistically the internal trees are well separated from both edge tree classes during most of the day (standard deviations do not overlap), while the edge classes are less well separated. In terms of the daily sum of sap-flux density, Fig. 8 shows the difference between the classes for a 16-day period in May 2011. As also indicated by the half-hour values in Fig. 7, there is a statistically significant difference between the internal trees and the two edge classes for all days except those featuring very little transpiration. The two edge classes are not significantly different for most days, though the overlap between the error bars is generally small, and at no point do the error bars of one edge class overlap the mean values of the other edge class. This gives us some confidence, that there is a real difference between the internal edge and the south edge classes, and that the lack of significance is primarily a result of the limited number of probes installed in each class.

The internal edge and South edge trees make up a disproportionately large part of the stand transpiration (Table 3). While the
internal trees number 55% of the total stand, they are only responsible for 24.7% of the stand transpiration. The internal edge trees comprise 40% of the stand trees, but are responsible for 60.5% of the transpiration; while the south edge class, which only makes up 5% of the trees, is responsible for 14.8% of the stand transpiration. In 2010 the distribution of sampled trees in the mature Norway spruce stand was always 60% internal and 40% internal edge. This sensor distribution resulted in an underestimation of the stand transpiration by 16.3% on average according to the 2011 data. This percentage was used to correct the 2010 transpiration estimates for the mature stand.

The time delay between transpiration in the tree crown and sap-flux detectable in the stem at breast height varies considerably between the internal and the edge trees (Fig. 7). The onset of transpiration was delayed about 2 h compared with the EC-ET for the south edge trees while the internal trees showed a delay of 3 h. The internal edge trees had an intermediate delay. The timing of the peak sap-flux signals also differed. The peak flux in the internal edge trees occurred half an hour later than in the south edge trees, while the peak of the internal trees was 1.5 h delayed compared to the internal edge trees. There is no reason to believe that the actual timing of transpiration from the different trees is dissimilar, hence the difference in time lag at breast height must be related primarily to water storage capacity (sapwood volume) and transpiration rate of the average tree in each class. As such it will be difficult to establish a precise correlation between tree transpiration measurements and EC-ET estimates on short time scales, and care must be taken when comparing the two at timescales shorter than one day.

3.3. Transpiration and meteorological conditions

The seasonal totals (1 April–30 September) of transpiration and EC-ET are listed in Table 4. The young Norway spruce stand and the Grand fir stand transpired at about the same rate with a total of 221 mm and 219 mm respectively. The mature Norway spruce stand transpired about 30% less at 154 mm for the season. Compared with the EC-measurements the forest transpiration made up 46% of the total ET. If only dry days are considered, the forest transpiration comprised 65% of the total ET, while the distribution of transpiration among the stands remained unchanged.

The forest transpiration was calculated using the average distribution of young Norway spruce, mature Norway spruce and Grand fir within the EC footprint – 47.4%, 47.0% and 5.6%, respectively. The validity of using the average distribution was tested by relating the difference between EC-ET and transpiration + modeled moss ET to wind direction (Table 5). While there was a lot of variability in the daily values, no significant differences were found between the wind sectors indicating that the spatial variance in stand composition within the footprint does not need to be treated explicitly.

The average daily course of forest transpiration, EC-ET and selected meteorological parameters are shown in Fig. 9. The figure is composed only of days without precipitation. The average daily transpiration rates ranged from about 1 mm d$^{-1}$ in April to 2 mm d$^{-1}$ in June and back to 1 mm d$^{-1}$ in September. On average transpiration made up about 65% of the observed ET. Transpiration and ET generally followed the global radiation, peaking around noon. This is out of sync with temperature and VPD, which peaked later in the afternoon between 15:00 and 16:00 h. 2010 was a relatively wet year, with precipitation spaced evenly throughout the summer season and no periods with drought. Only on the warmest and driest days did we observe a high-VPD induced depression of transpiration, where the peak of the transpiration rate occurred before noon (data not shown).

3.4. Moss ET

The spatial variability of moss ET is small in Gludsted Plantation. One example of moss ET measurements is presented in Fig. 10. On two days in early September 2010 moss ET was estimated by weighing five trays once every hour. In general the trays agreed well with each other (CV ~10% at midday) and no clear trend between ET rates under the closed mature stand and open young stand can be identified. The only exception is tray D on DOY 248 which experienced direct sunlight for about one and a half an hour in the early afternoon. This is in agreement with the observations of Bond-Lamberty et al. (2011). Working in Canadian Black spruce forests they found no relation between moss ET rates and stand age and moss species, respectively, for well drained sites.

Modeled moss ET amounted to 77 mm for the months of April–September, about 18% of the total EC-ET. If only dry days are considered, moss ET amounted to 45 mm. The modeled ET values follow the diurnal course in temperature and VPD, with small changes in VPD having a large impact on the ET rate (Fig. 11). The model is less sensitive to changes in resistance as long as the
Table 4
Seasonal sum (April–September) of transpiration and evapotranspiration in 2010. The “forest” transpiration is calculated based on an average EC-footprint distribution of 47.4%/47.0%/5.6% for the young Norway spruce, mature Norway spruce and Grand fir stands respectively. Dry days are defined as days with zero precipitation.

<table>
<thead>
<tr>
<th></th>
<th>Young Norway spruce (mm)</th>
<th>Mature Norway spruce (mm)</th>
<th>Grand fir (mm)</th>
<th>Forest (footprint) (mm)</th>
<th>EC-ET (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All days</td>
<td>221</td>
<td>154</td>
<td>219</td>
<td>189</td>
<td>412</td>
</tr>
<tr>
<td>Dry days</td>
<td>167</td>
<td>122</td>
<td>157</td>
<td>145</td>
<td>221</td>
</tr>
</tbody>
</table>

Table 5
Comparison of the difference between EC-ET and transpiration + modeled moss ET versus wind direction. Means and standard deviations are based on daily sums for dry days (no precipitation).

<table>
<thead>
<tr>
<th>Wind sector</th>
<th>NE</th>
<th>E</th>
<th>SE</th>
<th>S</th>
<th>SW</th>
<th>W</th>
<th>NW</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean (mm)</td>
<td>0.27</td>
<td>0.42</td>
<td>0.27</td>
<td>0.26</td>
<td>0.26</td>
<td>0.50</td>
<td>0.39</td>
<td>0.43</td>
</tr>
<tr>
<td>SD</td>
<td>0.30</td>
<td>0.21</td>
<td>0.30</td>
<td>0.14</td>
<td>0.32</td>
<td>0.31</td>
<td>0.27</td>
<td>0.23</td>
</tr>
</tbody>
</table>

Fig. 9. Average daily course of forest transpiration, EC-ET, global Radiation, temperature and VPD. Only dry days (no precipitation) included. The timing of the transpiration signal has been modified to coincide with the evapotranspiration signal (see Fig. 7 for example of transpiration signal delay).

resistance is below 1000 s m⁻¹. During the seven days the daily sum of moss ET varied between 0.30 mm (6/19) and 0.87 mm (6/21).

4. Discussion

4.1. Age versus spacing effects on stand transpiration?

In the present study the 40 years old mature stand transpired about 30% less than the 20 years old stand. The difference in sap-flux densities was even larger, with the young stand having on average 2.5 times the flux density of the mature stand. Age-related decline in transpiration has been widely observed (e.g., Alsheimer et al., 1998; Köstner et al., 2002) and is mainly linked to decreased leaf area index in older stands, and increased hydraulic constraints as water has to be transported further in older taller trees (Ryan et al., 1997; Delzon and Loustau, 2005). However, in the present study both stands are relatively young in the sense that decreasing in LAI due to tree mortality and wind damage is not yet detectable in the mature stand. If only the “internal edge” and “south edge” trees of the mature stand are considered, the “south edge” trees had about the same sap-flux densities as the young stand average, and the “internal edge” trees had only about 20% less. Our results seem to confirm the part of Hypothesis 1, which related differences in transpiration to variations in canopy structure, but rejects the second part where age is a controlling factor. Thus, a typical age effect is
unlikely to be the main reason for the observed differences in sap-flux density. Instead we will now discuss the potential impact of (1) stand structure in terms of needle mass and crown architecture, and (2) spatial variations in microclimate in terms of irradiance, VPD and wind speed.

Needle mass per tree (NM) was not measured in this study. However, BHD can serve as a proxy because BHD and NM are linearly related in spruce stands, independent of stand age or thinning regime (Kantola and Mäkelä, 2004). Thus, if sap-flux density in the 40 years old stand is related to tree position (Table 3) but not BHD (Fig. 5), NM cannot be the reason for the different sap-flux densities observed. Among the structural differences within the mature stand and between the mature and young stands, crown length, being the distance from the lowest living branch to the canopy top, was the most prominent. Lowest living branches were found at 2 m in the young stand, at 8–10 m in the inner part of the old stand, at 5 m at the inner edges and at less than 1 m at the south edge of the old stand, on the side facing the aisle. The corresponding crown lengths are ca. 13 m, 10 m, 5–7 m and 19 m (south side only), respectively. Crown length is not necessarily related to NM, yet it is known that spruce trees with smaller distance to their neighbours will have shorter crowns and denser foliage with a maximum closer to the tree top compared to more widely spaced trees (Kantola and Mäkelä, 2004). As a consequence of the denser crown, a higher percentage of the needles will be in the shade and thus NM will be less important for the control of sap-flux density, since shaded needles have a lower stomatal conductance than sunlit needles and contribute less to transpiration. We conclude that the spatial variability of canopy structure induced a large variation in the proportion of needles being exposed to light and that this variation was mainly responsible for the reported edge effects in the closed stand.

This interpretation of the edge effect in the closed 40 years old stand is in agreement with the study of Lagergren and Lindroth (2004), who observed that, in a closed 50 year old stand, not needle mass but the distance to the neighbours, was best correlated with sap-flux density in shade-tolerant spruce. In contrast, shade-intolerant conifers such as pine only maintain needles in the sunlit canopy layer and thus sap-flux correlates best with NM. The difference in light environment is also a logical explanation for the difference in sap-flux density between equally sized trees in the old and young stands (Fig. 5). The crowns of the young trees were widest at approximately one-third of the tree height, which left most of the living canopy with spaces between the individual trees and thus a higher percentage of the foliage exposed to light when compared to the closed, mature canopy.

Whether microclimatic factors other than irradiance had a role in explaining the differences in sap-flux density cannot be answered with certainty. However, when looking at other studies that have investigated the variability of meteorological factors within and above spruce canopies (Constantin et al., 1998; Radler et al., 2010; Staudt et al., 2011), it seems unlikely that differences in air temperature or vapour pressure deficit between open and closed stands or between “inner” and “edge” trees may have caused the observed differences in transpiration between those tree classes. Whilst the irradiance in the lower canopy differed by a full order of magnitude between the forest interior and a south-facing edge in a mature spruce forest according to Radler et al. (2010), the corresponding difference in air temperature was only 0.3 °C. Also, humidity gradients within and above spruce canopies are usually very small and, in combination with temperature gradients of less than 1 °C, result in VPD differences of only 0.1 kPa between exposed and inner canopy layers (Constantin et al., 1998; Staudt et al., 2011). The absence of larger micrometeorological gradients indicates a close coupling between spruce canopies and the atmosphere and thus a limited influence of spatial variations in wind speed on transpiration.

Total stand transpiration may vary considerably in response to canopy structure in terms of row configuration. Table 6 gives an estimate of what would happen to the transpiration rate of the mature stand if the row configuration were to be changed. Assuming fixed average sap-flux density and sapwood area for the three classes, the theoretical stand transpiration rate is calculated for a fully closed canopy (max internal) and a more open canopy (max internal edge). A fully closed canopy would result in a decrease in transpiration rate of about 17% compared with the current row layout, while a more open canopy would result in an increase of about 15%. In essence the presence of aisles and access roads seems to add to the forest transpiration. This confirms Hypothesis 2.

**Fig. 11.** Modeled moss ET and the relevant meteorological driving variables for a seven-day period in June 2010. See Section 2.4 for model details.
structure plays an important role in determining the total stand transpiration, and for models to accurately evaluate and predict evapotranspiration from Norway spruce plantations, information on canopy structure has to be included. However, predictions about possible consequences of different thinning regimes on total stand transpiration should be treated with caution, because the timing of thinning activities can make a large difference to tree growth and water use. Shade-tolerant and shallow-rooted Norway spruce trees will need many years to acclimate to new artificial canopy edges, and at the beginning they may experience thinning activities as stress rather than as competitive advantage (Lagergren and Lindroth, 2004). The actual enhancement of transpiration following thinning might therefore be less than predicted from the observations at Gludsted Plantation where the investigated trees had been exposed to the edges for many years. Nonetheless we believe the variability to be large enough to have implications for the control of transpiration in heterogeneous stands and potentially for catchment hydrology, too.

### 4.2. Tree size and sap-flux density

In the young stand we found a significant relation between tree size (breast height circumference) and sap-flux density while there was no such relation in the mature stand. In the literature observations support no relation (e.g., Alsheimer et al., 1998; Köstner et al., 1998a, 2002; Gartner et al., 2009) but all of these studies have looked at stands aged 30 years or older. This implies that the observed relation between tree size and sap-flux density in the young stand might be a transient phenomenon. In the open, immature canopy of the young stand the tree size distribution is asymmetrical compared with the mature stand (Fig. 6) and the largest trees are spaced more evenly throughout the stand whereas the larger trees in the mature stand occur in clusters along the internal and external edges. This has two effects: (1) the larger trees in the young stand have disproportionately more access to light than the smaller trees and (2) the larger trees are more exposed to turbulence than the smaller sheltered trees. Both these effects will work towards creating the observed tree size dependence on sap-flux density. As the stand matures the smallest trees will either die off naturally or be removed by thinning, to leave a more homogeneous stand. As a result there is less difference in height between the smaller and the larger trees in the stand, and as the tree density decreases the individual trees will have more space to develop their canopy. Both will serve to minimize the sources of sap-flux variability, and might explain why no relation between tree size and sap-flux density is observed once a stand matures.

### 4.3. Closing the evaporation balance

The sum of transpiration and modeled moss ET made up 86% of the observed EC-ET for dry days in the measurement period April–September 2010 (Table 4 and Section 3.4). In broad terms this confirms Hypothesis 3 and is in line with a general trend observed in the literature – the sum of individually estimated ET components in forests seems to underestimate the EC-ET by up to 20% (Bernhofer et al., 1996; Wilson et al., 2001; Oishi et al., 2008; Staudt et al., 2011). The main sources of errors that might explain this discrepancy include (1) processing of the raw sap-flux signal and scaling of sap-flux to tree and stand level, (2) estimation of understory ET, (3) estimation of other ET components and (4) estimation of EC footprint and scaling of sap-flux to the footprint area.

In processing the raw sap-flux density signal great care was taken to account for nocturnal flux and periods of drift in sapwood water content as recommended by Lu et al. (2004). Oishi et al. (2008) found that not taking nocturnal fluxes into account underestimated growing season transpiration by 22% on average for an oak-hickory forest in North Carolina, USA. In the present study the effect is much smaller (<10%), which can in part be explained by nocturnal fluxes being relatively rare and small in magnitude (a true zero flux state is reached at dawn on most days) and in part by the fact that 2010 was a wet year with no periods of significant soil moisture stress and relatively low variability in sapwood water content.

In scaling flux density measurements from tree to stand level uncertainty may be introduced by inadequate description of the tree-to-tree variability. Coefficient of variation (CV) of the sap-flux density signal was 35% for the young Norway spruce stand, 38% for the mature Norway spruce stand and 20% for the Grand fir. These numbers are somewhat high compared with other studies of Norway spruce. According to Köstner et al. (1998a) CV can be expected to be about 25–30% for a sample size of 9–11 trees, and Staudt et al. (2011) reports a CV of 12% from a 54 years old stand in the Fichtelgebirge, southern Germany. The high coefficient of variation can be ascribed in part to the limited number of sensors available (5 trees, 10 sensors per stand at any time) and in part to the unusually large variability within the stands caused by the flux density dependence on tree size in the young stand and the edge effect in the old stand. It is possible to quantify the variability due to the edge effect using the data from 2011. At this time the sensors were installed in distinct tree classes in the mature stand and as a result the coefficient of variation was only 17%, 18% and 20% for the “internal”, “internal edge” and “south edge” trees respectively. Thus a large part of the observed variation in 2010 in the mature stand is due to the fact that the probes were installed in a mix of “internal” and “internal edge” trees. This suggests that the tree-to-tree variation is described reasonably well despite the high CV, and it gives us confidence that the sap-flux measurements can be used to estimate stand level transpiration.

Another potential source of uncertainty when scaling sap-flux measurements is radial gradients in sap-flux density. Although Köstner et al. (1998a, 2002) did not find any radial gradients in sap-flux density in Norway spruce stands in southern Germany, studies from other Norway spruce stands did (Čermák et al., 1992; Phillips et al., 2001; Ewers et al., 2001). Čermák et al. (1992) observed a Gaussian distribution of sap-flux density along a radial profile with peak flux densities at 3 cm depth. Sap-flux in spruce trees like this could be measured accurately with 3 cm long TDP probes, because they would capture a representative average of the true flux
density. However, Phillips et al. (2001) and Ewers et al. (2001) observed a different pattern with the inner part of the xylem having a lower sap-flux density than the outer part which, according to Phillips et al. (1996), may be explained by a transition from mature sapwood in the outer part of the xylem to juvenile sapwood formed in the first 10 or so years of the tree’s life in the inner part. Phillips et al. (2001) found that for a stand of Norway spruce in northern Sweden, sap-flux density in the inner part (2–4 cm depth) of the xylem was on average only 26% of the sap-flux density in the outer part (0–2 cm depth); however, this gradient disappeared when the trees were fertilized and grew faster.

The potential impact of such a radial gradient on the measurements from Gludsted Plantation was explored by recalculating the individual tree and stand transpiration with the modification that for all trees with a sapwood depth greater than 3 cm (the length of the probes), the sapwood was divided into two sections; Section 1 (0–3 cm) and Section 2 (3 cm – sapwood depth). For Section 1 the sap-flux density was calculated from the probe signal as usual, whereas for Section 2 it was assumed to be only 26% of the sap-flux density in Section 1. When compared with the data from the individual stands (Fig. 5), the average sap-flux density is reduced by 9% in young Norway spruce, by 13% in mature Norway spruce and by 24% in Grand fir. In essence, a radial gradient such as the one observed by Phillips et al. (2001) would increase the difference between the young and the mature Norway spruce stands. The magnitude of the reduction in sap-flux density is dependent on tree size, and the presence of a radial gradient would weaken the relation between tree size and sap-flux density observed in the young stand. Using the gradient from Phillips et al. (2001) the relationship would no longer be significant at the 85% level ($P = 0.15$), though a clear trend towards higher sap-flux densities in the larger trees would remain.

For the mature Norway spruce stand, a correction for potential radial gradients would reduce the sap-flux density by 9% in the internal trees, by 14% in the internal edge trees and by 20% in the south edge trees. The relative contribution to stand transpiration would change only slightly to 25.9%, 60.3% and 13.8% for the internal, internal edge and south edge trees respectively. Despite the greater reduction of sap-flux density in the edge classes compared with the internal trees, the statistically significant difference between internal trees and edge trees would remain.

In terms of total forest transpiration, the total for dry days would be reduced to 151 mm for the young Norway spruce, 106 mm for the mature Norway spruce and 119 mm for the Grand fir. The total forest (footprint) transpiration would be reduced by 12% to 128 mm. The original transpiration estimates only make up 86% of the eddy-covariance evapotranspiration when forest floor evaporation is subtracted. This suggests that radial gradients in sap-flux density, which would make the transpiration estimate even lower, are only of minor importance in Gludsted Plantation. It is quite possible that in terms of wood structure the investigated stand has more similarities with Norway spruce stands in Germany (Küstner et al., 1998a, 2002) and southern Sweden (Čermák et al., 1992) than with slow growing stands in northern Scandinavia (Ewers et al., 2001; Phillips et al., 2001) where 33 year old trees were only 5 m high, compared to 15–20 m at Gludsted Plantation.

The relative importance of understory ET is influenced by forest structure and composition (Baldocchi and Vogel, 1996). In an open boreal pine stand Baldocchi and Vogel (1996) found that understory ET contributed 50% of the stand ET. In denser temperate stands understory ET ranges from about 10–20% depending on LAI (Bernhofer et al., 1996; Wilson et al., 2000; Staudt et al., 2011). The modeled sum of “moss ET” in Gludsted Plantation made up 18% of the total ET for the period April–September 2010, and 17% if all of 2010 is considered. This fits within the higher range observed for temperate forests and suggests that the forest had a relatively open canopy in terms of below canopy evaporative demand. This is obviously the case for the young Norway spruce stand where the open canopy structure allows both light and some degree of turbulence to reach the forest floor. Comparing the moss ET trys between the young and mature canopy however, no significant differences in ET rate are observed. It may be that the presence of the aisles in the mature stand and the distinctive structure of small 0.25 ha interspaced young and mature stands resulted in a higher evaporative demand under the mature stand compared to a larger homogeneous stand. Conversely, there is evidence suggesting that the ET rate of an understory comprised primarily of mosses may simply be less sensitive to the density of the overstory compared with an understory containing higher plants. In a chronosequence of boreal Black spruce stands in Canada, the absolute moss ET rate was constant across four stands that had LAI values ranging from 2 to 6 (Bond-Lamberty et al., 2002, 2011).

The present study looks at dry days only, as good estimates of interception evaporation are not yet available from Gludsted Plantation. Intercepted water may still be present at the beginning of a dry day if the canopy has not experienced at least 8 h of daylight since the last precipitation event (Herbst et al., 2008). Fig. 12 plots the difference between EC-ET and transpiration + moss ET versus number of daylight hours since last rain. Indicated by the dashed oval are days with unusually high differences between ET estimated by tree transpiration + moss ET, and ET estimated by EC. This group of days all had less than 8 h of dry daylight the previous day, further suggesting the presence of interception evaporation. If these days are not considered, tree transpiration + moss ET makes up 88% of the observed EC-ET. Indicated by the solid oval in Fig. 12 is another group of days with unusually high EC-ET. For this group up to two days with no precipitation had passed. Staudt et al. (2011) discussed whether a similar discrepancy between EC and tree transpiration estimates could be ascribed to interception evaporation up to four days after the last precipitation event. They concluded that a change in wind direction (EC-footprint) was a more likely cause, but did not rule out interception evaporation. For Gludsted Plantation we can find no link to wind direction. If interception evaporation does still contribute to the total ET after two days, the most likely source in our opinion is the understory and not the Norway spruce canopy. The moss ET model in its current form can only reduce the resistance to evaporation to that of a moss water content corresponding to field capacity. Thus it is unable to properly simulate interception evaporation from the understory, which may help explain the discrepancy between tree transpiration, moss ET and EC-ET. In the same way, interception evaporation from the forest floor may also be partly responsible for the large scatter observed in Fig. 12.
Dew formation may also contribute to the scatter in Fig. 12. While the EC method is in principle capable of detecting both the formation and evaporation of dew, the EC sensors may not function when covered in dew (Wilson et al., 2001). As this issue is likely to arise at the beginning of dewfall and disappear quickly as the dew starts evaporating, it can lead to an overestimation of ET by the EC instruments. Dew can under favorable conditions reach a magnitude of 0.3–0.5 mm per night (Richards, 2004) which is within the range of the scatter seen in Fig. 12. At present however we do not have sufficient data to establish a satisfactory relationship between dewfall and the discrepancy between transpiration, moss ET and EC-ET. A forthcoming study will look specifically at dew dynamics in the forest, utilizing leaf wetness sensors.

The precision of the EC footprint may be improved by the use of a dynamic footprint model. It is doubtful how much this will decrease the discrepancy between EC estimates however. The variation in stand types within the typical footprint range is relatively small, and no significant statistical relationship between the discrepancy and wind direction could be found. Using a reasonable estimate of the average distribution of the stand types does matter though: if the entire footprint is assumed to consist only of mature Norway spruce stands, tree transpiration and moss ET would only make up 72% of the April–September dry day EC-ET estimate. If the entire footprint was covered with young Norway spruce, the tree transpiration and moss ET would make up 101% of the EC estimate.

4.4. Canopy structure and transpiration in relation to climate change

Under present climatic conditions soil moisture availability is already considered as a constraining parameter in Danish forestry, especially for the sandy soils of western Denmark (Beier et al., 1995). Climate scenarios for the coming century predict drier and warmer summers in this region (Christensen and Christensen, 2007). Such a trend would imply a decrease in water availability and thus an increase in water stress especially in edge and internal edge trees in stands like the one in the present study. Consideration should therefore be given to the structure of forest stands and the ability to withstand increased soil moisture deficits.

5. Conclusion

The forest in this study creates a rare chance to examine the effect of canopy structure on the variability and rate of tree transpiration. The tree level sap-flux variability in the young open–canopy stand could be ascribed to a relationship between tree size and sap-flux density, while sap-flux variability in the mature closed–canopy stand could be ascribed to edge effects near access roads and aisles. Transpiration in the open canopy was about 30% higher than transpiration in the closed canopy. This difference was caused by low average sap-flux densities for the closed canopy trees that were not affected by edge effects, and can be viewed as a functional difference in transpirational capacity between open and closed canopies of Norway spruce. The presence of edge effects in the closed canopy allowed the affected mature trees to reach similar transpiration rates as those in the open canopy. Our data suggests that it may be possible to minimize stand transpiration of the mature stand by optimizing management practices to limit the impact of edge effects.

By incorporating the observed variance in tree transpiration it was possible to make transpiration and a modeled estimate of forest floor ET sum to 86% of the eddy covariance estimate of ET on dry days. This agreement is similar to that reported in studies from more homogeneous forests, and suggests that the measured tree and stand level variation is also valid at the larger scale of the EC footprint. This result also holds implications for the modeling community. Unless the variance in transpiration due to canopy structure and edge effects is incorporated, the model may fail to predict the tree transpiration correctly for forests with a heterogeneous structure like Gludsted Plantation.

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