

The effect of a north-facing forest edge on tree water use in a boreal Scots pine stand

Emil Cienciala, Per-Erik Mellander, Jiří Kučera, Magda Opluštilová, Mikael Ottosson-Löfvenius, and Kevin Bishop

Abstract: Tree water use and growth increment were studied in a north-facing forest edge of a 70-year-old monospecific Scots pine (*Pinus sylvestris* L.) stand growing on poor sandy soils in the northern boreal zone of Sweden. The forest edge in this study bordered a 20-year-old clearcut. There were differences in water use and growth increment during the growing season between trees growing at the forest edge and trees growing in the forest interior. These differences were likely related to soil conditions, such as access to soil moisture, soil temperature, and soil frost conditions, whereas an effect of aboveground microclimate was not found. The estimated tree water use and growth increment over one growing season tended to be greater for trees at the edge zone relative to those from the interior. The variability of the measured tree water fluxes was high, especially for the edge-zone trees. There were also structural differences between the two groups of trees, most notably in the radial profile of conductive xylem, in tree height, and in green crown length, but these differences were on the limits of statistical significance. The estimated seasonal transpiration was low, about 70 mm when estimated exclusively for trees in the forest interior and 107 mm when estimated exclusively for trees at the forest edge. This illustrates the likely magnitude of water use enhancement resulting from the conditions specific to the forest edge.

Résumé : La consommation d'eau et la croissance ont été étudiées dans la bordure nord d'un peuplement pur de pin sylvestre (*Pinus sylvestris* L.) âgé de 70 ans croissant sur un sol pauvre et sablonneux au nord de la zone boréale en Suède. La bordure de forêt qui a été étudiée longe une coupe à blanc âgée de vingt ans. Il y avait des différences de consommation d'eau et de croissance pendant la saison de végétation entre les arbres situés dans la bordure et ceux à l'intérieur du peuplement. Ces différences sont probablement liées aux conditions du sol, telles que l'accès à l'humidité du sol, la température du sol et les conditions de gel dans le sol, alors qu'aucun effet du microclimat épigé n'a pas été observé. La consommation d'eau par les arbres et leur croissance estimées pendant une saison de végétation tendent à être plus élevées chez les arbres en bordure que chez ceux à l'intérieur. La variabilité de la consommation d'eau des arbres est élevée, spécialement pour les arbres en bordure. Il y avait aussi des différences structurelles entre les deux groupes d'arbres, notamment dans le profil radial du xylème fonctionnel, dans la hauteur des arbres et dans la longueur de la cime vivante, mais ces différences étaient à peine statistiquement significatives. La transpiration saisonnière était faible, aux alentours de 70 mm lorsque estimée exclusivement chez les arbres à l'intérieur du peuplement et de 107 mm lorsque estimée exclusivement chez les arbres en bordure. Ces résultats illustrent l'ampleur potentielle de l'augmentation de la consommation d'eau due aux conditions particulières qui existent en bordure de la forêt.

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Introduction

At the zone of interface between a forest and an open field, specific microclimatic conditions develop that are dif-

ferent from those of the forest interior (Young and Mitchell 1994; Chen et al. 1995; Cadenasso et al. 1997). Depending on orientation, the forest edge may receive more or less radiation as compared with the forest interior. At the forest edge, enhanced turbulence can make advection much more effective. Wind penetration eases rapidly towards the forest interior, but may extend up to several hundreds of metres (Chen et al. 1995). At a forest edge, there are also specific soil temperature and moisture gradients that may extend deep into the forest interior. Stand structure and especially the forest edge itself have a large influence on the snow-cover distribution, which is important for the timing of soil warming. Many studies have illustrated the inhibiting effects that low soil temperature may have on water use and gas exchange (e.g., Grossnickle 1988; Day et al. 1991; Bergh et al. 1999; Wang and Zwiazek 1999). Trees situated at the forest edge have carbon allocations and growth patterns that differ from those of interior trees (Ranney et al. 1981). The edge-zone trees usually develop longer green crowns containing more foliage relative to the interior trees. This increases both

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E. Cienciala. Department of Soil Sciences, Swedish University of Agricultural Sciences, Box 7014, 750 07 Uppsala, Sweden.

P.-E. Mellander¹ and K. Bishop. Department of Environmental Assessment, Swedish University of Agricultural Sciences, Box 7050, 750 07 Uppsala, Sweden.

J. Kučera and M. Opluštilová. Environmental Measuring Systems, Turistická 5, 621 00 Brno, Czech Republic.

M. Ottosson-Löfvenius. Department of Forest Ecology, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.

¹Corresponding author

(e-mail: Per-Erik.Mellander@vfp.slu.se).

transpiration and interception evaporation fluxes relative to the interior forest.

Edge zones and associated landscape fragmentation may have important implications for water and carbon cycles, especially when scaling up stand-level fluxes using models parameterized from interior conditions. Extrapolating these fluxes to larger areas without considering the specific contribution of edge zones and other fragmented landscape elements, e.g., frequent small forest patches, may underestimate the actual fluxes. Obviously, this will depend on the degree of vegetation fragmentation in the landscape. Within a specific stand, one of the key characteristics of the forest edge zone is stand structure and density. In an intensively managed landscape, typical for most European countries, stands have sharp boundaries with agricultural land and pastures. In recent decades, more attention has been paid to biodiversity and aesthetic values of a landscape; hence forest boundaries have become more variable and more frequent, with a larger variety of tree species and extended transition zones to production forest.

For the boreal zone of northern Sweden, forests are usually more sparse and slow growing relative to those at more southern latitudes. Water is generally not considered as a factor limiting growth compared with nutrient deficiency and low temperature. Indeed, ongoing fertilization and heating experiments indicate that the forests in the northern boreal zone have a large production potential (Bergh et al. 1999). However, trees growing on sandy soils, which are common in some areas of northern Sweden, may not be able to fully utilize precipitation, because of the rapid drainage through the sandy soil layers. In such situations, trees growing at the forest edge boundary may benefit from less competition for water stored in the soil of the neighbouring open area and from more effective rainfall relative to the forest interior (Matlack 1993; Weathers et al. 1995). The size of a clearing affects both snow accumulation and snow ablation and may thus affect the timing of water yield (Swanson and Golding 1982). Another aspect that is specific to boreal forest ecosystems is soil frost. Frost duration, length of melting period, and low soil temperature are crucial variables in determining the production of boreal forests. It is thus essential to assess the gradients of soil temperature and moisture conditions from the forest edge towards the stand interior, together with their importance for tree function and growth.

In this paper we examine water use and growth conditions of a relatively sparse boreal forest growing on sandy soil that is typical for some areas of northern Sweden in two contrasting situations: the edge zone and the forest interior. Our aim was to determine the differences between a north-facing edge zone and the forest interior with respect to both above- and below-ground factors.

Material and methods

Site description

The experiment was conducted at the Heden site within the Vindeln Experimental Forests (64°14'N, 19°46'E) in the boreal zone of northern Sweden, 60 km NW of Umeå. The Heden study site is located 175 m above sea level on a level pine heath on glaciofluvial deposits. The forest of the Heden area is mostly composed of monospecific Scots pine (*Pinus*

sylvestris L.) stands. The soil is a podzolised sandy silt classified by Giesler et al. (2000) as a Haplic Arenosol (FAO 1988). The open heath has only a thin organic layer of about 1–2 cm. In the forest stand this layer is somewhat thicker. The soil is annually subjected to soil frost. The groundwater level at the site is estimated to be several metres below the surface.

Typically, the area has winters with continuous snow cover from the end of October until the end of April, and the growing season lasts from the middle of May until the end of September. The mean annual precipitation is close to 600 mm, of which one-third falls as snow. The mean average temperature is about 1.0°C (1980–1999). The flat plain of the Heden area is slightly colder in wintertime than its surroundings, and the site is frequently subjected to summer frosts (Odin and Degermark 1990).

Meteorology and soil conditions

Meteorological data were obtained from a climate station located in the centre of the open heath. The climate station is part of a reference monitoring program of the Vindeln Experimental Forests, which includes measurements of standard meteorological variables such as air temperature, humidity, precipitation, and short-wave radiation (Anonymous 1981–1999). In addition, soil temperature and soil moisture content were measured in the clearing in a vertical profile from 0.2 to 2 m below the mineral soil surface using thermistors and soil water content reflectometers (CS615, Campbell Scientific, U.S.A.) connected to a Campbell CR-10 data logger via a relay scanner. Relative humidity and air temperature were also measured in the stand with ventilated Rotronic air probe YA100 (Rotronic AG, Bassersdorf, Switzerland) sensors at two additional locations. One was located at the very edge of the stand, the other was located 40 m from the edge boundary. Both sensors were situated about 9 m above the ground, in the upper part of the tree canopy.

The potential evapotranspiration (PET, mm/day) was estimated from the equation by Turc (1961):

$$[1] \quad \text{PET} = \left(\frac{R_g + 50}{41\,868} \right) \times 0.013 \times \frac{T_a}{T_a + 15}$$

where R_g (W/m²) is the daily mean global radiation, and T_a (°C) is the daily mean air temperature. The equation is adjusted to SI units and does not include relative humidity, as PET is defined for conditions when the daily mean of relative air humidity is within 50–100%. This equation was found to be a practical estimate when comparing evaporative conditions between years in the same location (Cienciala et al. 1999), and it is also comparable to other, more commonly used estimates of forest evaporation (Federer et al. 1996).

The depth of snow and soil frost was measured manually, twice a week, with frost tubes (Gandahl 1957; Rickard and Brown 1972). Measurements were made from 12 frost tubes, one every 5 m along a line from the open area into the forest interior. The measuring range was 100 cm above ground (snow) and 100 cm below ground (soil frost). There was also a frost tube at the climate reference station in the centre of the open area.

Stand properties and treatments

The study site was established as a 50 × 80 m rectangle in the 70-year-old, monospecific Scots pine stand. One 50-m side of this rectangle extended along the 20-year-old forest edge. From there the rectangle extended 80 m into the forest interior. Tree height was about 10 to 11 m for the stand, with a mean diameter at breast height (DBH) of slightly over 12 cm. The distribution of tree DBH was narrow, typical for planted even-aged stands. Stand basal area was slightly over 20 m²·ha⁻¹. Live crowns had a length of about 5 m and formed a relatively sparse canopy. The stand formed a distinct forest edge oriented to the north (20°); where it faced a 0.9-ha open area. This open deforested heath area was sparsely covered by ground vegetation including lichen (70%), heather (20%), and grass (10%). In the forest stand the lichen and heather cover fell to 50% in favour of lingonberries (*Vaccinium vitis idaea* L.).

Most of the biophysical measurements used in this study were designed to identify possible differences between two stand situations, i.e., the north-facing forest edge zone and the forest interior. The edge zone was defined as extending 13 m into the forest from the edge itself. Thus defined, the length of the edge zone corresponds to the mean tree height (10.7 m) plus one standard deviation (2.2 m). This definition was chosen because there are a number of environmental gradients that are strongly influenced by tree height. These gradients continue into the stand but are likely to be steepest near the edge. The interior zone was defined as an equally deep (13 m) swath located 32 to 45 m from the forest edge. The mean distance from the interior zone to the forest edge (39 m) was chosen to be three times the mean tree height and its standard deviation.

Stand biometry and increment

Basal area increment was monitored with dendrometer tapes made of thin metal. They were placed at breast height on 17 trees as well as on the trees used for sap-flow measurements (see Sap-flow measurements section). Readings were taken at 2- to 4-week intervals. Other stand biometry variables were measured on one occasion from 30 June to 1 July. These measurements included DBH (1.3 m), tree height, and height of crown base from which a green crown length could be derived.

Xylem water content

Core samples of xylem were taken on 2 and 3 July. The weather conditions during the measurements were mild and windy, with an air temperature of about 15°C. Six trees (three for each treatment, i.e., edge zone and interior) were sampled, with two samples taken on each tree stem from opposing directions. Cores were taken using an increment borer (4 mm inner diameter). The sampled cores were immediately covered with plastic foil, stored in a shaded place, and put in a freezer as quickly as possible. In the laboratory, the section of bark and phloem was removed, and the cores were cut into segments of about five successive growth rings from the outer end to the inner part of the core. The segments were weighed with an accuracy 0.1 mg for estimation of fresh biomass and then dried in an oven at 80°C. The segment's length was measured immediately after weighing with an accuracy 0.1 mm. The dried segments were weighed

and the values of relative water content (w , %) in the individual segments were calculated as

$$[2] \quad w = \frac{FM - DM}{FM} \times 100$$

where FM (mg) and DM (mg) represent fresh and dry biomass of a segment, respectively. The depth of individual segments was set to one-half of the segment's length plus the total length of the preceding segments. The radial profile of water content for each core was established from the values of the water content in different segments. The relative water content in 1-mm steps was calculated by a linear interpolation between real values.

Sap-flow measurements

Sap flow was measured using a heat balance method (Cermak et al. 1973; Kucera et al. 1977) with commercially available sap-flow meters from EMS (Environmental Measuring Systems, Brno, Czech Republic). One unit (P4.1) was designed to operate on tree stems, using internal heating and internal sensing of temperature gradient. The other unit (PT4.1) combined the stem measurements with branch gauges that utilize external heating and subsurface temperature sensing, using needles inserted through a thin bark layer. The branch gauge arrangement was similar to that previously used in a short-rotation stand of willow (Lindroth et al. 1995; Cienciala and Lindroth 1995). Stem sap flow was measured using 18 measuring channels applied on 10 trees, of which six were in the edge zone and four in the forest interior (Table 1). Stem sap-flow measurements were usually taken on two opposite sides of a tree to account for flux variability along the stem circumference. Additionally, branch sap-flow gauges were applied on six branches distributed in the middle of the green crowns of two trees that were located between the edge zone and the forest interior. All sample trees were dominant or codominant.

The water fluxes at tree level were also extrapolated to stand level on the basis of stem circumference. This simplified scaling approach assumed a linear relationship between tree circumference and tree water use. Tree growth at the studied site was small (mean DBH was 12.1 cm at the age of 70), which indicates that the band of effectively conductive tissue will also be thin. Hence tree circumference was assumed to be a better scaling parameter than basal area. To establish a continuous transpiration record for the whole growing season, some missing stemflow values from July and August ($n = 20$ days) were extrapolated on a daily basis using the branch sap-flow data that ran continuously.

Results

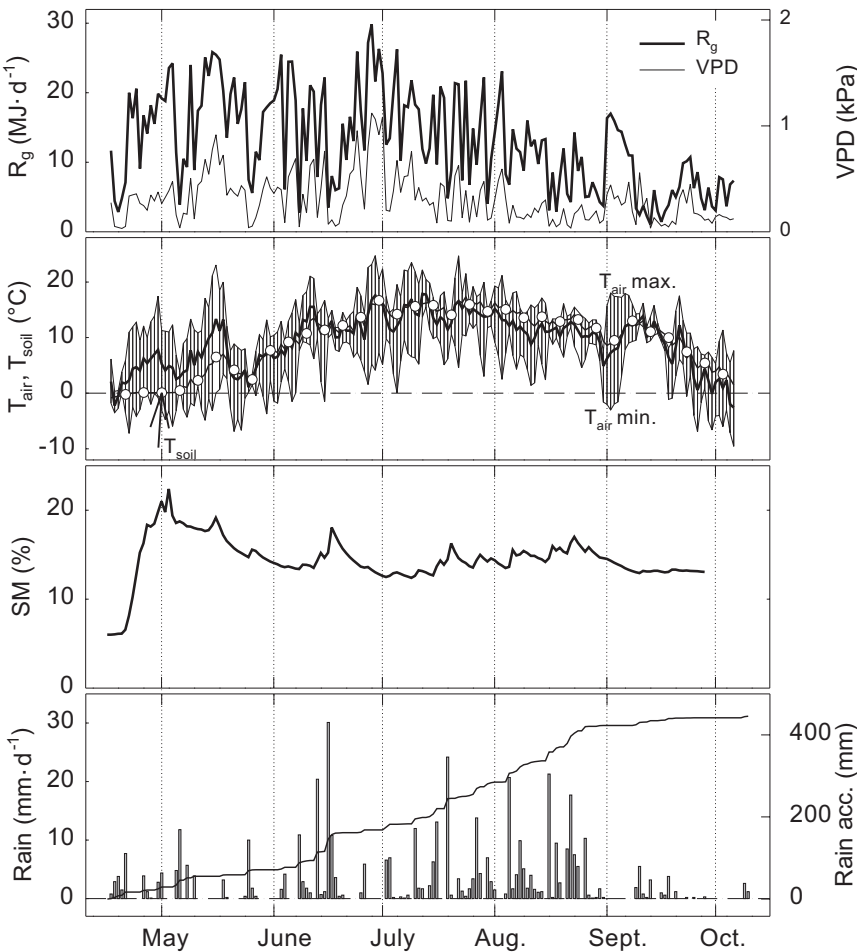
Meteorology and soil conditions

In 1998, the growing season started on 26 April, which was about 2 weeks earlier than normal, and lasted until 24 September (using a temperature threshold of 5°C). The winter snow cover was established about 2 weeks later than normal, but in January the snow depth was greater than normal. The date of snow-free ground was close to normal. The depth of soil frost at the reference station was less than normal, although the maximum depth was close to 70 cm. The

Table 1. Trees selected for the measurement of sap flow and basic tree biometry.

Treatment	Tree No.	DBH over bark (cm)	DBH without bark (cm)	Total height (m)	Crown height (m)
Edge	191	17.5	15.9	11.7	6.4
	193	17.5	14.6	12.8	7.0
	201	19.1	15.6	9.8	6.4
	202	16.9	13.4	10.0	7.2
	203	15.9	13.1	13.3	8.0
	204	16.2	13.7	13.6	9.6
	Mean±SD	17.2±1.0	14.4±1.1	11.9±1.5	7.4±1.1
Interior	205	19.1	15.9	13.0	5.3
	206	17.2	15.3	13.8	6.5
	207	17.2	14.6	13.9	5.6
	208	19.1	14.6	13.7	7.5
	Mean±SD	18.2±1.0	15.1±0.5	13.6±0.4	6.2±0.9

Fig. 1. Climatic conditions at the site: solar radiation (R_g), daily mean vapour pressure (VPD), daily mean, minimum, and maximum air temperature (T_{air}), soil temperature (T_{soil}), soil moisture content at 20 cm (SM), and daily and accumulated precipitation (rain).

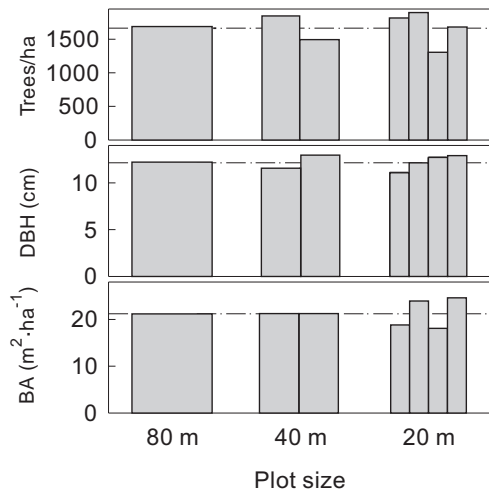


climatic conditions for the measurement period are shown in Fig. 1.

The comparative measurements of temperature and humidity gradients into the forest interior performed by ventilated sensors from July to September did not reveal any

significant differences between the forest edge and stand interior (40 m apart). Air temperature and relative humidity differed, on average, by about 0.2°C and 1.5%, respectively, between the the forest edge and the forest interior (data not shown). These differences are also within the specified accu-

Fig. 2. Stand biometry as measured on the segments extending 80 ($n = 1$), 40 ($n = 2$), and 20 m ($n = 4$) into the stand interior: tree density (top panel), mean diameter at breast height (DBH, middle panel), and stand basal area (BA, bottom panel).



racy of the used instruments (Rotronic AG, Bassersdorf, Switzerland).

Tree and stand biometry

The mean stand DBH was 12.1 cm. A tree density of 1660 trees/ha was estimated on the 50 × 80 m study area. The stand's tree density tended to decrease from the edge towards the interior, while the DBH tended to increase towards the interior. This resulted in a basal area that was relatively homogeneous with respect to distance from the forest edge (Fig. 2). Using areal segments that were only 20 m deep revealed some variation in the basal area. The standard deviation of the mean for the four successive stand segments from the forest edge to the stand interior was about 15%.

The length of the green crown tended to be greater for the edge trees (6.0 m) compared with the interior trees (5.3 m). The sample group of edge-zone (0–13 m from the edge) trees had a similar mean DBH (12.8 cm; $n = 33$) compared with the interior-zone (32–45 m from the edge) trees (13.0 cm; $n = 17$). On the contrary, the total tree height was significantly smaller for the edge-zone trees compared with the interior ones, with mean values of 10.2 and 12.1 m, respectively ($P = 0.014$; Fig. 3).

Within a growing season, there was a systematic tendency of greater stem circumference increment for the edge-zone trees as compared with the interior trees (Fig. 4). However, since tree-level variability was large for both groups of trees, the observed difference in stem growth increment was non-significant or just approached the limits of statistical significance (t test, e.g., $P = 0.05$). The stems typically shrank during May, when soil temperature remained low.

Radial profile of stem moisture content

The radial profile of xylem water content for the edge trees was deeper into the stems than that of the interior trees (Fig. 5). The shape of the water content profile was, however, similar in both groups of trees. Xylem water content at depths of 2, 17, and 22 mm differed between the edge-zone trees and interior trees (t test, $P = 0.05$). An analogous pat-

Fig. 3. Tree height versus diameter at breast height (DBH). Values are shown for the total data set (total) and for the edge-zone trees and interior trees. A two-parameter logarithmic function ($r^2 = 0.64$; solid line) was fitted to all data ($n = 89$).

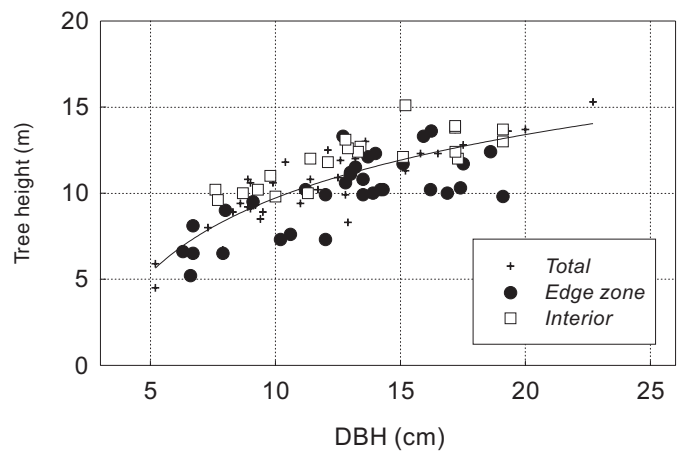


Fig. 4. Mean stem increment at breast height (\pm SD) for edge-zone and interior trees, for May–October 1998.

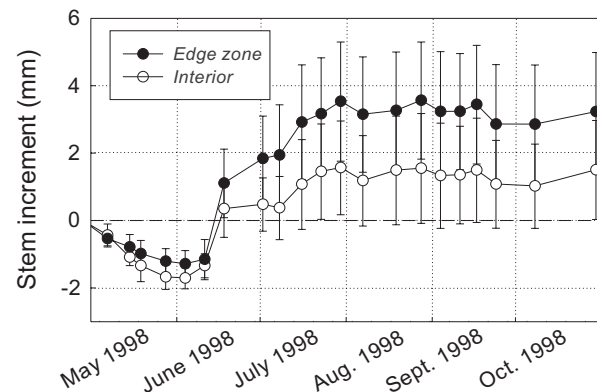


Fig. 5. Mean radial profile of xylem water content (RWC) in stems of the edge and interior trees (mean values). The 0-mm depth locates the boundary of xylem sapwood and phloem (or vascular cambium); the depth increases towards the stem centre.

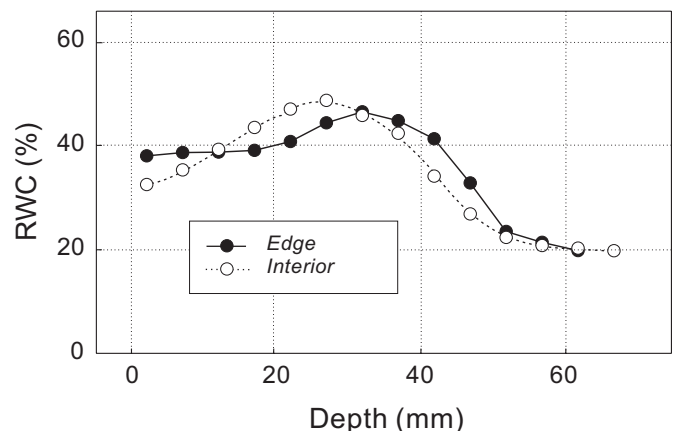


Fig. 6. Specific sap flow per unit of stem circumference. Values are daily means for sample trees of the edge zone and interior forest.

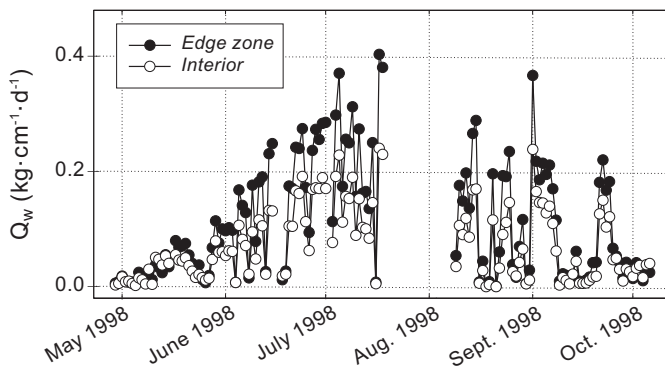
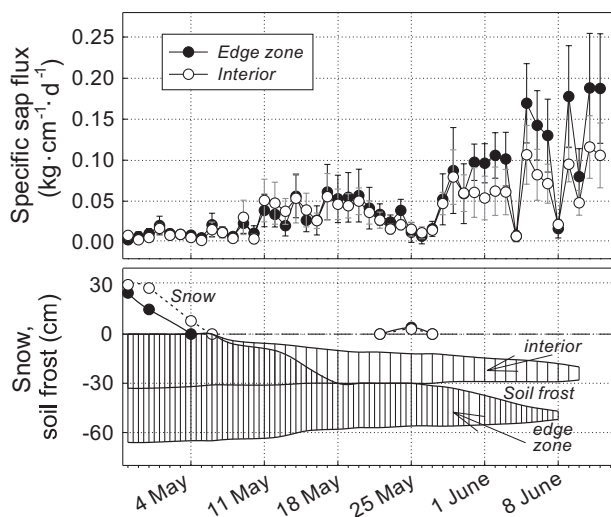


Fig. 7. Transpiration per unit of stem circumference (specific sap flux) of edge-zone and interior trees with standard deviation of the mean shown (top panel) and snow layer and depth of frozen soil for edge and interior zones (bottom panel).

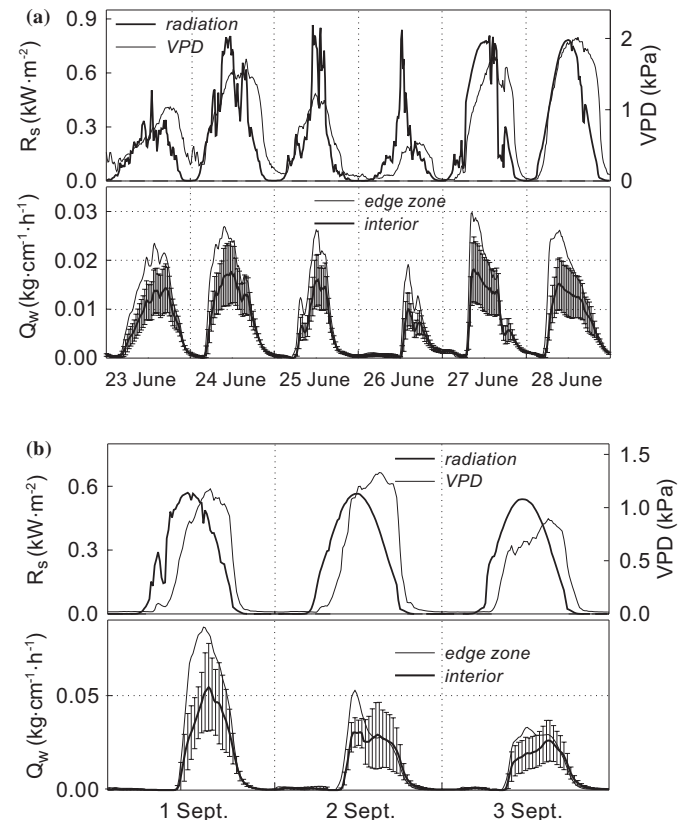


tern was observed for stem moisture profiles in the two groups of trees when testing a new measurement method based on electrical conductivity (data not shown).

Tree water use

The daily mean xylem sap flow (Q_w) reached its maximum of about $0.4 \text{ kg}\cdot\text{cm}^{-1}$ in July. It was greater for the edge-zone trees than for the interior trees for most of the season (Fig. 6). When compared by monthly periods, the daily mean specific sap flow was significantly higher for the edge trees only in July (t test, $P = 0.043$). For the other periods, the differences in specific sap flow between edge and interior trees were statistically non-significant because of large variability among trees within the sample groups. Water uptake was detected earlier in the interior trees (27 April) and their mean Q_w was also temporarily higher or of a similar magnitude at the onset of the growing season compared with the edge-zone trees (Fig. 7). The mean daily Q_w became greater for the edge-zone trees in June, about 1 month

Fig. 8. Diurnal course of mean specific sap flow (Q_w) of edge-zone and interior trees, with standard deviation shown for the interior trees. Short-wave radiation (R_s) and vapour pressure deficit (VPD) are also shown. Data are shown for (a) early summer period, 23–28 June 1998, and (b) late summer period, 1–3 September 1998.



after the onset of detectable transpiration. This situation persisted until the end of the growing season (Fig. 6).

On a diurnal scale, the Q_w pattern was similar for edge and interior trees. As seen during the early summer period, the pattern of Q_w for both edge and interior trees showed a similar correspondence to evaporative drivers when evaporative demand was rather low (Fig. 7, 23–26 June). However, the water uptake curve under high evaporative conditions peaked quite abruptly in the morning and then gradually decreased (Fig. 8a, 27–28 June). This was in contrast to vapour pressure deficit and radiation, both of which peaked later in the afternoon and decreased in a different manner than Q_w . These observations indicate water deficit conditions or conditions of low conductance for water transport along the conductive pathway. Quantitatively, water flux was higher for edge-zone trees than for the interior trees, though variation among trees remained high. Another indication of water and (or) conductive limitations is evident in the late summer period of 1–3 September (Fig. 8b). This period followed a rainy spell from 16–31 August that brought 90 mm of rain to the site (Fig. 1). Q_w was highest on 1 September for both interior and edge trees, but decreased rapidly the following day for the interior trees and remained considerably lower than that of edge-zone trees, despite higher or similar evaporative conditions. The mean tree fluxes for the two groups had distinctively different diurnal dynamics, and the edge-

Table 2. (A) Measured fluxes of sap flow and (B) climatic variables for the early and late summer periods.

(A) Sap-flow fluxes.				
Treatment and tree No.	23–28 June		1–6 September	
	Q_w (kg·cm ⁻¹ ·d ⁻¹)	Q_{wt} (kg·d ⁻¹)	Q_w (kg·cm ⁻¹ ·d ⁻¹)	Q_{wt} (kg·d ⁻¹)
Edge				
191	0.194	9.72	0.196	9.78
193	0.218	10.9	0.238	11.9
201	0.225	11.7	0.278	14.4
202	0.304	14.0	0.383	17.6
203	0.129	5.69	0.124	5.47
204	0.219	10.1	0.171	7.87
Mean±SD	0.215±0.056	10.3±2.7	0.232±0.091	11.2±4.4
Interior				
205	0.086	4.55	0.089	4.70
206	0.162	7.79	0.203	9.75
207	0.148	7.23	0.149	7.29
208	0.184	9.74	0.201	10.7
Mean±SD	0.145±0.042	7.33±2.1	0.160±0.054	8.10±2.7
(B) Climatic variables.				
Air temperature (°C)	12.9		8.6	
Relative humidity (%)	63.7		80.7	
Short-wave radiation (W·m ⁻²)	241		175	
VPD (kPa)	0.70		0.33	

Note: Sap flow is shown both as a specific value (Q_w), expressed per centimetre tree circumference, and a tree-based (Q_{wt}) value. Climatic variables are mean daily values for each period.

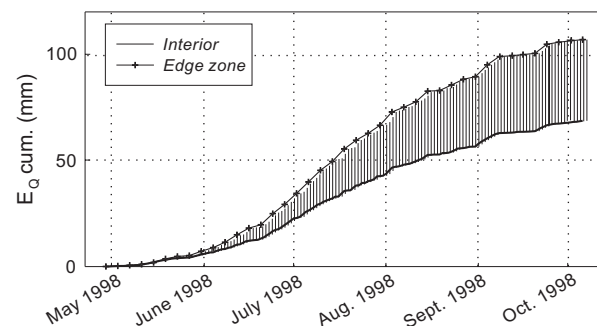
zone trees reached higher values than the interior trees (Fig. 8b).

Maximum sap flow for the largest trees at the edge of the stand was close 25 kg·d⁻¹. The typical values of summer daily tree sap flow were about 15 kg·d⁻¹. A comparison of sap fluxes expressed both per unit of stem circumference and per tree was performed for two 6-day periods (Table 2), representing early summer (23–28 June) and late summer (1–6 September) periods. Sap flow reached higher values in the late summer period despite the generally lower evaporative demand and radiation compared with the climatic conditions in early summer. The variability of measured Q_w fluxes was high for the trees of the edge zone, whereas it was somewhat smaller for the interior trees (Table 2).

The total stand transpiration (E_Q) for the growing season, calculated with the assumption that tree flux is linearly related to tree circumference, reached 107 mm when based exclusively on the measurements of edge-zone trees and 69 mm if based only on stand-interior trees (Fig. 9). Thus, depending on the weight given to particular situations, a range of transpiration values can be obtained, with the maximum extent defined by the values as above, when transpiration in the interior forest was about 64% of that in the edge zone.

The qualitative relationship of E_Q to evaporative demand was assessed in relation to potential evapotranspiration. Throughout the whole growing season, this relation was weak for both the edge zone ($r^2 = 0.51$) and the interior forest ($r^2 = 0.52$). This relationship was weak at the beginning of the growing season but improved later in summer. When cal-

Fig. 9. Cumulative values of canopy transpiration (E_Q) calculated for edge-zone and interior trees. Some missing values in the summer period were extrapolated from the regression to mean daily branch sap flow. Shaded area shows a likely range of E_Q values that depends on the weight given to particular situations, i.e., edge zone and forest stand interior.



culated for each month, the coefficient of determination (r^2) of the linear regression between E_Q and evapotranspiration was 0.22 and 0.33 in May, 0.74 and 0.75 in August, and 0.67 and 0.64 in September, for the edge trees and interior trees, respectively.

Discussion

This study revealed some notable differences in water use and growth increment between trees in the edge zone and those in the forest interior. Though the variability in the

measured variables was generally high and the differences were on the limits of statistical significance, the results for water uptake, increment growth, and radial moisture profiles gave a consistent pattern. This discussion considers the extent to which these differences can be explained by differences in microclimate, stand structure, and (or) soil conditions.

Microclimate

The published literature on microclimate reports significant edge effects on light, temperature, litter moisture, vapour pressure deficit, humidity, shrub cover, and wind (Camargo and Kapos 1995; Chen et al. 1993, 1995; Matlack 1993; Weathers et al. 1995). However, in this study site, those effects are not likely to be large because of the edge orientation and stand structure. Many of those cited studies found that a forest edge with a northern exposure has the smallest gradients of microclimatic variables. In particular, a northern exposure minimizes any enhancement of radiation effect.

The above observation also indirectly excludes wind as a variable that could affect transpiration at the edge zone relative to the forest interior. Wind has been mostly reported to exponentially decrease within 60 m into the stand interior (Raynor 1971; Fritschen 1985), obviously depending on the density of the forest edge. We may consider that increased ventilation at the forest edge increased aerodynamic conductance, promoting transpiration there. However, the northern coniferous forests have a large aerodynamic roughness and represent a well coupled system where transpiration is mainly controlled by stomatal conductance and vapour pressure deficit (McNaughton and Jarvis 1983; Jarvis and McNaughton 1986). This means that the increased ventilation at the forest edge was not large enough to cause a difference in vapour pressure deficit between the two locations that might help explain the enhanced water flux in the forest edge zone.

The combined effects of low air and soil temperatures are a common limitation on water use and growth in the boreal forest. The limitation is related to low soil temperatures extending beyond the start of the growing season (P.-E. Mellander, personal observation) and to soil water retention capacity. The duration of frost and low soil temperatures affects tree water uptake directly and indirectly. Directly by inhibiting tree water uptake, and indirectly by inhibiting the development of fine roots that are more conductive. Our study showed a considerable effect of frost depth at the forest edge zone (Fig. 7). Differences were also apparent in the vertical location of the frozen profile. In the forest interior zone, the lens of frost coincided with the zone of greatest root density at 0–10 cm depth (Plamboek et al. 1999). The amount and persistence of soil frost affects the timing of soil heating, and winter conditions are reflected in the soil temperature well into the growing season. In conjunction with frequently occurring night frost events, this is of great importance for the water uptake of trees, affecting overall growth and production. Water stress has negative consequences for the foliage, especially during the spring when air temperature increases and evaporative demand is not met during periods of high insolation (Berg and Chapin 1994).

In this study, the importance of cold soils as a limitation to water uptake and transpiration was apparent during the beginning of the growing season at the end of April and in May. At that time, soil temperature either indicated frost or remained low, whereas air temperature was frequently over 12°C during daylight but below 0°C during the night (Fig. 1). The limitation by low soil temperature with extended soil frost and likely delayed development of the rhizosphere was also confirmed by the correlation of stem-flow with Turc's (1961) potential evaporation (not shown). This relation was generally weak during spring, whereas it improved towards the end of the growing season, when root uptake limitations by low temperatures diminished and permitted a stronger response to evaporative drivers.

Low soil temperatures may be the reason for the enhanced water uptake and growth observed at the edge zone relative to the interior. However, a more detailed analysis of soil effects on water uptake requires a more detailed measurement program, which should notably include soil temperature profiles at different locations, and preferably also monitoring of root growth by the rhizotron technique (e.g., Taylor et al. 1970; Majdi 1996).

Stand structure and tree growth

The tree and stand biometry did not reveal any strong difference between the edge-zone trees and those in the stand interior. The edge zone should generally support longer green crowns, as supported by the difference of 0.6 m found here. This difference represents about 10–11% of the mean crown length, which is too little to be of major importance for transpiration fluxes. The difference in DBH between the two groups was also non-significant. This was expected, because the forest boundary was orientated towards the north, where the overall effect of edge conditions is likely to be smallest (Chen et al. 1995). The only significantly different biometric variable between the edge and interior zones was tree height, which tended to increase towards the stand interior. If this growth pattern was a typical one, it would also be reflected in differences in the mean stem diameters between the two groups. As this was not the case, we conclude that these differences were amplified only in the recent phase of stand development, when stand canopy became denser and the overall competition among trees increased. This hypothesis could be tested by a detailed microscopic analysis of increment cores, which will be a subject of the next study at the site.

The enhanced transpiration observed in the edge-zone trees (Fig. 6) is supported by the analysis of radial profiles of stem moisture content (Fig. 5), which shows a wider band of conductive xylem in the stems of edge-zone trees of similar diameter. The conductive xylem area is strongly related to amount of tree foliage (Shinozaki et al. 1964; Dvorak et al. 1996) and hence also to transpiration (Cermak 1989).

Tree water use

The daily pattern of water uptake indicated water limitation during the growth period (Figs. 8a and 8b), despite relatively frequent precipitation (Fig. 1). This limitation could arise because of the properties of readily drainable soils with a small water retention capacity, resulting in a small amount of water available to plants. Water uptake may also be re-

stricted by the harsh above- and below-ground climatic conditions in the area. The observed difference in the amount of soil frost between the edge and interior zone has a large effect on the timing of soil warming. Low soil temperatures inhibit water uptake and gas exchange (e.g., Grossnickle 1988; Day et al. 1991). Another factor contributing to a decoupling of water uptake from the diurnal patterns of evaporative drivers could be a high resistance to flow along the conductive pathway in plants, caused by a lowering of the root permeability and increased stomatal resistance related to low soil temperatures. However, since the trees were able to transport a considerable quantity of water immediately after an intense precipitation event (Sept. 1, Fig. 8b), this vascular conductivity limitation was likely of minor importance. In the case of the rain period in September (Fig. 8b), the shape of the water uptake curve differed between the edge-zone and interior trees with the interior stand transpiring less. During this time of the year these differences were not likely explained by different soil temperatures, but more likely reflect a better access to soil moisture at the edge zone with more water available to plants (Kapos 1989). In conjunction with other factors such as a possibly lower density of new fine roots and higher competition for water, this may limit the transpiration in the interior forest and thus help explain the observed enhancement of water use by the edge-zone trees. Unfortunately, detailed measurements of soil tension were only available from the open area outside the stand during the period reported here. The measurements of water content in the open area do not indicate severely dry conditions except for the period when the soil was still frozen (Fig. 1).

The estimated seasonal quantity of transpiration was lower than the reported 243 mm (Grelle et al. 1997) and 113 and 193 mm reported for a dry year (Cienciala et al. 1997) for denser and more productive southern boreal mixed spruce–pine forest stands in central Sweden. It is also lower than the average 200 mm estimated for a range of Swedish pine stands on sandy soil in a simulation exercise by Gärdenäs and Jansson (1995), but it was about the same as the 69 to 169 mm estimated for a range of jack pine (*Pinus banksiana* Lamb.) stands in the BOREAS northern study area (Kimball et al. 1997). It should be noted that our estimate of stand transpiration was based on the assumption that tree transpiration is linearly proportional to tree circumference. Trees, however, commonly contribute to stand transpiration in a more complex, nonlinear manner, with a larger weight attributed to dominant trees within a stand (e.g., Cermak 1989; Cermak and Kucera 1990). Also, the choice of the most suitable scaling parameter is more complex and depends on actual species and stand properties. A rigorous scaling approach hence requires tree measurements to be performed across the whole range of tree diameters in the stand, which was not done in this study. A larger sample size of measured trees that would permit a more rigorous estimation of stand transpiration would, however, most likely reveal similarly low seasonal transpiration. This is because transpiration was primarily constrained by a short growing season and further limited by the unfavourable soil moisture and nutrient conditions, which limited growth at the site. On the other hand, the simplified extrapolation of measured sap flow from tree to stand level does not affect the observed

relative differences between the fluxes estimated from edge-zone trees and from the stand-interior trees.

The fact that the estimated difference in annual stand fluxes depends on whether one uses the edge-zone or the interior data (Fig. 9) indicates that the structure of forest vegetation cover in a region may be important for calculating fluxes for larger areas. The importance of edge-zone enhancements will increase with the patchiness and heterogeneity of the forest cover in the landscape. However, the assessment of the above effects would require a much more extensive measurement program that would cover the variety of edge conditions in a region and permit quantification of the area exhibiting edge-zone effects on microclimate. This might enhance edge-zone transpiration fluxes more than seen in this study where soil conditions appear to have a major role in causing the edge effect.

Conclusions

There was a tendency of higher water use and higher stem increment for trees at the north-facing edge zone relative to interior trees. The differences were likely related to soil conditions, including water availability, soil temperature, and frost formation in the root zone. Trees at the north-facing edge zone benefitted from better access to soil moisture relative to the interior trees. Additionally, trees at the edge zone gradually develop a more conductive stem structure than found in the interior trees. The edge-zone trees tended to have larger sapwood area, longer green crowns, and smaller height. The latter is likely related to the competition for light. While these findings indicate the potential importance of considering edge effects in landscape-scale estimates of gas and water exchange, a more extensive measurement program is needed to quantify the observed patterns and also to explore the edge effects with different edge expositions and higher stand densities.

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References

- Anonymous. 1981–1999. Climate and water chemistry of water at Svartberget. Reference measurements (1981 to 1999). *Edited by* C. Degermark. Vindeln Experimental Forests, Swedish University of Agricultural Sciences, Umeå.
- Berg, E.E., and Chapin, F.S., III. 1994. Needle loss as a mechanism of winter drought avoidance in boreal conifers. *Can. J. For. Res.* **24**: 1144–1148.
- Bergh, J., Linder, S., Lundmark, T., and Elfving, B. 1999. The effect of water and nutrient availability on the productivity of Norway spruce in northern and southern Sweden. *For. Ecol. Manage.* **119**: 51–62.
- Cadenasso, M.L., Traynor, M.M., and Pickett, S.T.A. 1997. Functional location of forest edges: gradients of multiple physical factors. *Can. J. For. Res.* **27**: 774–782.
- Camargo, J.L.C., and Kapos, V. 1995. Complex edge effects on soil-moisture and microclimate in central Amazonian forest. *J. Trop. Ecol.* **11**: 205–221.

- Cermak, J. 1989. Solar equivalent leaf area: an efficient biometrical parameter of individual leaves, trees and stands. *Tree Physiol.* **5**: 269–289.
- Cermak, J., and Kucera, J. 1990. Scaling up transpiration data between trees, stands and watersheds. *Silva Carelica*, **15**: 101–120.
- Cermak, J., Deml, M., and Penka, M. 1973. A new method of sap flow rate determination in trees. *Biol. Plant.* **15**: 171–178.
- Chen, J.Q., Franklin, J.F., and Spies, T.A. 1993. Contrasting microclimates among clear-cut, edge, and interior of old-growth Douglas-fir forest. *Agric. For. Meteorol.* **63**: 219–237.
- Chen, J.Q., Franklin, J.F., and Spies, T.A. 1995. Growing-season microclimatic gradients from clear-cut edges into old-growth Douglas-fir forests. *Ecol. Appl.* **5**: 74–86.
- Cienciala, E., and Lindroth, A. 1995. Gas-exchange and sap flow measurements of *Salix viminalis* trees in short-rotation forest. 1. Transpiration and sap flow. *Trees*, **9**: 289–294.
- Cienciala, E., Kucera, J., Lindroth, A., Cermak, J., Grelle, A., and Halldin, S. 1997. Canopy transpiration from a boreal forest in Sweden during a dry year. *Agric. For. Meteorol.* **86**: 157–167.
- Cienciala, E., Kucera, J., and Lindroth, A. 1999. Long-term measurements of stand water uptake in Swedish boreal forest. *Agric. For. Meteorol.* **98–99**: 547–554.
- Day, T.A., Heckathorn, S.A., and DeLucia, E.H. 1991. Limitations on photosynthesis in *Pinus taeda* L. (loblolly pine) at low soil temperatures. *Plant Physiol.* **96**: 1246–1254.
- Dvorak, V., Oplustilova, M., and Janous, D. 1996. Relation between leaf biomass and annual ring sapwood of Norway spruce according to needle age-class. *Can. J. For. Res.* **26**: 1822–1827.
- Federer, C.A., Vorosmarty, C., and Fekete, B. 1996. Inter-comparison of methods for calculating potential evaporation in regional and global water balance models. *Water Resour. Res.* **32**: 2315–2321.
- Food and Agriculture Organization (FAO). 1988. FAO/UNESCO soil map of the world. Revised legend. Food and Agriculture Organization, Rome. *World Resour. Rep.* 60.
- Fritschen, L.J. 1985. Characterization of boundary conditions affecting forest environmental phenomena. In *The Forest–Atmosphere Interaction: Proceedings of the Forest Environmental Measurements Conference*, 23–28 Oct. 1983, Oak Ridge, Tenn. Edited by B.A. Hutchison and B.B. Hicks. D. Reidel, Dordrecht, the Netherlands. pp. 3–23.
- Gandahl, R. 1957. Bestämning av tjalgrans i mark med enkel typ av matare. [In Swedish.] *Grundforbättring*, **10**(1): 7–19.
- Gärdenäs, A.I., and Jansson, P.E. 1995. Simulated water balance of Scots pine stands in Sweden for different climate change scenarios. *J. Hydrol.* **166**: 107–125.
- Giesler, R., Ilvesniemi, H., Nyberg, L., van Hees, P., Starr, M., Bishop, K., Kareinen, T., and Lundstrom, U.S. 2000. Distribution and mobilization of Al, Fe and Si in three podzolic soil profiles in relation to the humus layer. *Geoderma*, **94**: 249–263.
- Grelle, A., Lundberg, A., Lindroth, A., Moren, A.S., and Cienciala, E. 1997. Evaporation components of a boreal forest: variations during the growing season. *J. Hydrol.* **197**: 70–87.
- Grossnickle, S.C. 1988. Planting stress in newly planted jack pine and white spruce. Factors influencing water uptake. *Tree Physiol.* **4**: 71–83.
- Jarvis, P.G., and McNaughton, K.G. 1986. Stomatal control of transpiration: scaling up from leaf to region. *Adv. Ecol. Res.* **15**. pp. 1–49.
- Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* **5**: 173–185.
- Kimball, J.S., White, M.A., and Running, S.W. 1997. BIOME-BGC simulations of stand hydrologic processes for BOREAS. *J. Geophys. Res.* **102**: 2943–2951.
- Kucera, J., Cermak, J., and Penka, M. 1977. Improved thermal method of continual recording the transpiration flow rate dynamics. *Biol. Plant.* **19**: 413–420.
- Lindroth, A., Cermak, J., Kucera, J., Cienciala, E., and Eckersten, H. 1995. Sap flow by the heat-balance method applied to small-size *Salix* trees in a short-rotation forest. *Biomass Bioenergy*, **8**: 7–15.
- Majdi, H. 1996. Root sampling methods—applications and limitations of the minirhizotron technique. *Plant Soil*, **185**: 255–258.
- Matlack, G.R. 1993. Microenvironment variation within and among forest edge sites in the eastern United-States. *Biol. Conserv.* **66**: 185–194.
- McNaughton, K.G., and Jarvis, P.G. 1983. Predicting effects of vegetation changes on transpiration and evaporation. In *Water deficits and plant growth*. Vol. V. Edited by T.T. Kozlowski. Academic Press, New York. pp. 1–48.
- Odin, H., and Degermark, C. 1990. The spring in the forest terrain at Svartberget, Northern Sweden. *Geogr. Ann.* **72A**(2): 167–178.
- Plamboeck, A.H., Grip, H., and Nygren, U. 1999. A hydrological tracer study of water uptake depth in a Scots pine forest under two different water regimes. *Oecologia*, **119**: 452–460.
- Ranney, J.W., Bruner, M.C., and Levenson, J.B. 1981. The importance of edge in the structure and dynamics of forest islands. *Ecol. Stud. Anal. Synt.* **41**: 67–95.
- Raynor, G.S. 1971. Wind and temperature structure in a coniferous forest and a contiguous field. *For. Sci.* **17**: 351–363.
- Rickard, W., and Brown, J. 1972. The performance of a frost tube for determination of soil freezing and thawing depths. *Soil Sci.* **113**: 149–154.
- Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T. 1964. A quantitative analysis of plan form: the pipe model theory. I. Basic analysis. *Jpn. J. Ecol.* **14**: 97–105.
- Swanson, R.H., and Golding, D.L. 1982. Snowpack management on Marmot watershed to increase late season streamflow. In *Proceedings, 50th Annual Meeting, Western Snow Conference*, 19–23 April 1982, Reno, Nev. IAHS Press, Wallingford, U.K. pp. 19–23.
- Taylor, H.M., Huck, M.G., Klepper, B., and Lund, Z.F. 1970. Measurement of soil-grown roots in a rhizotron. *Agron. J.* **62**: 807–809.
- Turc, L. 1961. Évaluation des besoins en eau d'irrigation, évapotranspiration potentielle. *Ann. Agron.* **12**: 13–49.
- Wang, Y., and Zwiazek, J.J. 1999. Spring changes in water relations, gas exchange, and carbohydrates of white spruce (*Picea glauca*) seedlings. *Can. J. For. Res.* **29**: 332–338.
- Weathers, K.C., Lovett, G.M., and Likens, G.E. 1995. Cloud deposition to a spruce forest edge. *Atmos. Environ.* **29**: 665–672.
- Young, A., and Mitchell, N. 1994. Microclimate and vegetation edge effects in a fragmented podocarp–broadleaf forest in New Zealand. *Biol. Conserv.* **67**: 63–72.