The Significance of Soil Conditions for Sap Flow of Scots Pine in the Boreal Environment

Licentiate thesis

by

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Abstract

Conifers growing at high latitude are seasonally subjected to freezing temperatures both in the air and soil. The depth and duration of soil frost as well as the persistence of low soil temperature varies spatially, influenced to a large degree by the snow cover distribution. Silvicultural practice affects the snow cover distribution and thus the dynamics of soil warming during spring. The importance of soil temperature for growth and vitality has been seen on seedlings and saplings in the laboratory. But we know very little about the effect of cold soils on larger trees in the field and the potential loss of forest production after a stand is established. The objective of this thesis was to examine the effects of soil conditions on sap flow during spring. Water dynamics were examined in the field on Scots pine trees (*Pinus Sylvestris* L.) exposed to different soil temperature regimes. One attempt to quantify the sensitivity of tree water use to soil and atmospheric conditions in the boreal forest environment was made by manipulating the soil thermal regimes on tree-scale soil plots. Soil temperature, soil moisture content, snow and frost depth as well as above ground climatic parameters were measured, together with sap flow, needle water potential, stem increment and shoot elongation. In this study, low soil temperatures restricted tree water uptake most after the growing season had started. Before the start of the growing season, low soil temperatures had little apparent effect. Liquid water existed in the soil as soil frost successively thawed and snowmelt infiltrated. Water, however, was not available to the tree until the soil temperature in the upper rooting zone had reached a threshold temperature above 0°C, even if the evaporative demand was large due to above ground climatic conditions. The study has confirmed the importance of low soil temperatures for tree water uptake when soil warming is delayed beyond the start of the growing season, as defined by air temperatures. Another approach to elucidating the effect of soil conditions on tree water uptake was to compare the above and below ground climate at a forest edge with that of the forest interior. Differences in tree water uptake and stem increment were found that could be associated with the difference in soil thermal regimes associated with the forest edge. The estimated water use was larger at the edge zone than in the stand interior. The results of both field studies suggest that the effect of soil temperatures on tree water uptake during spring, in conjunction with above ground conditions, is a factor to consider in forest management in areas susceptible to soil frost and low soil temperatures.

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Introduction

In 1648 Joan-Baptista Van Helmont made an experiment by taking a vessel in which he placed two hundred pounds of oven-dried soil, and watered it with rainwater. In the vessel he planted the stem of a willow tree weighing five pounds. Five years later it had developed into a tree weighing one hundred and sixty-nine pounds and three ounces. Nothing but rain had been added. Finally he dried the vessel again and found the same two hundred pounds of soil diminished by only two ounces. From this he concluded that 164 pounds of willow tree had been created from only water (Brock, 1992). Van Helmont certainly stressed the importance of water being accessible for plant growth. But today we know that the system is rather more complex, involving dissolved nutrients, CO_2 and energy from the sun. We also know that these components, together with human activity, interact along the film of water that constitutes the soil-plant-atmosphere continuum. In cold climates water relations are complicated by the existence of water as ice. Resistance also increases along water flow paths due to conditions influenced by low soil and air temperature.

Conifers growing at high altitudes are seasonally subjected to low air and soil temperatures. Up to 30% of the annual photosynthesis can be lost in the boreal forest during a cold spring (Linder and Flower-Ellis, 1992). This loss of productivity is of the same order of magnitude as that during a summer of drought (Cienciala *et al.*, 1998). During winter photosynthetic capacity is severely reduced by the combined effect of both low air and soil temperatures (e.g. Troeng and Linder, 1982). In spring and early summer the recovery of photosynthetic capacity is strongly dependent on temperature. Many studies have shown a strong correlation between air temperature and rate of recovery (e.g. Lundmark *et al.*, 1998). However, no recovery of photosynthetic capacity was seen in Scots pine before the soil had thawed (Linder and Troeng, 1980; Troeng and Linder, 1982). Below ground, soil frost and low temperatures may delay the onset of water uptake by desiccation and reduction of root system efficiency. It is important to see how the below ground conditions may contribute to spring productivity loss, especially since this is related to silviculture.

Ångström (1936) has demonstrated the great influence which silvicultural practices have on the extent and duration of soil frost. Silviculture influence spring soil temperature dynamics through effects on heat flow related to the canopy, organic layer and snow cover, all of which are affected by forest management decisions. Although the canopy may be seen as a buffering layer due to its thermal properties, the canopy also effects spatial variability in snow depth. Snow and frost depths are often inversely related (Stadler *et al.*, 1996).

Simulations of forest growth based on soil warming experiments show that spring water stress has a large effect on the productivity of the forest (Bergh *et al.*, 1998; Gärdenäs and Jansson, 1995). In the boreal forest the timing of the growing season start can even be of significance for the global carbon balance (Rodhe *et al.*, 1995). Soil frost and cold soil temperatures are important factors in water stress that may contribute to these production losses. This is due in part to the importance of the early growing season, but also to the possibility of enduring damage to tree needles and roots. If needles are subjected to high solar radiation at times when water uptake is limited, the photosynthetic apparatus of needles may be permanently damaged (Lundmark, 1996). Desiccation of frozen roots may also attenuate tree water uptake during the entire growing season (Sutinen *et al.*, 1996; Robitaille *et al.*, 1994). Earlier studies have focused on how a lowering of soil temperature inhibits water uptake and gas exchange on seedlings or immature trees, often in laboratory experiments (e.g. Grossnickle, 1988; Day *et al.*, 1991; Pavel and Fereres, 1998; Wang and Zwiazek, 1999). Schwartz *et al.* (1997) found that net photosynthesis in red spruce saplings was more sensitive to changes in soil temperature than air temperature, with the strongest correlation between soil temperature and sap flow at temperatures below 10°C. One of the few field studies found that sap flow was strongly reduced as long as soil temperature was close to 0°C (Bergh and Linder, 1999). In that study, however, it was not possible to decide whether this was an effect of soil temperature, water availability or both. Our studies investigated the effect of soil conditions on sap flow in mature Scots pine trees along a gradient from the forest edge, and on plots where soil temperature was manipulated during spring.

Aims

The overall aim of this work was to examine the water relations of Scots pine trees (*Pinus Sylvestris* L.) exposed to different soil temperature regimes in the field. Further on, we intend to quantify the sensitivity of Scots pine water use to soil conditions as well as atmospheric conditions in the boreal forest environment as influenced by silvicultural practices. Quantifying that effect on forest growth may help provide a better basis for a more "frost-conscious" forest management. We began by finding out more about the water dynamics of mature trees in cold environments under field conditions. To achieve this, field studies were made by manipulating the soil thermal regimes on tree-scale soil plots, as well as by examining the effects of the thermal regimes caused by a forest edge. Measurements were made on:

- soil temperature and moisture content
- snow and frost depth
- air temperature and humidity
- sap flow in branches and stems
- needle water potential
- shoot elongation and stem increment

Soil-plant-atmosphere continuum

The soil-plant-atmosphere continuum is the film of water through the plant linking the rhizosphere to the atmosphere that allows water movement from the soil to the atmosphere. The water pathway through a tree is influenced by a number of physical conditions governing the potential gradient between the soil and roots across a semi-permeable membrane, the hydrostatic gradient in the tracheids and the water vapour pressure between the shoots and atmosphere (figure 1). These conditions are influenced by the structure of a stand, since the stand influences the microclimate and the local soil climate. The pressure gradients of the soil-plant-atmosphere continuum induce water movement to provide the transpiration favourable for nutrient and phytohormone transport, as well as for uptake of the CO_2 required for photosynthesis. The rate of transpiration is mainly dependent on the supply of water and energy to the shoots.

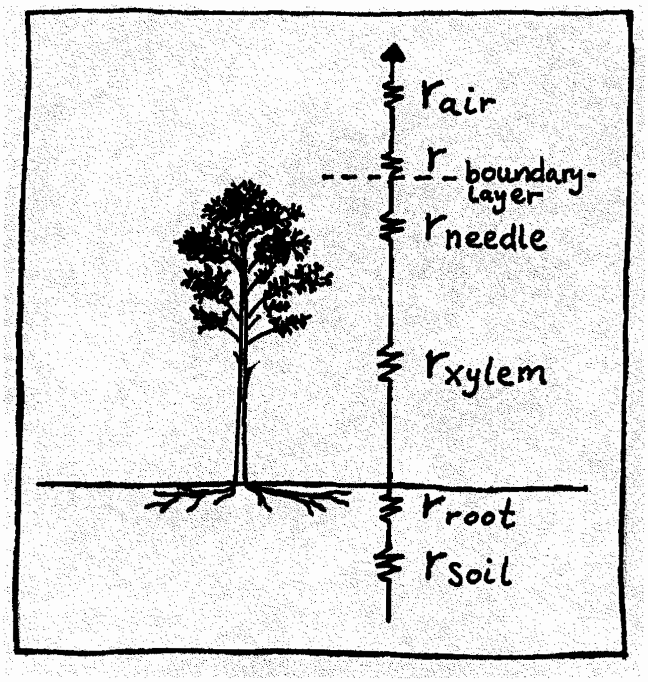

Figure 1 The electrical analogue of the water flow from the soil moisture store to the atmospheric sink via the soil-plant-atmosphere continuum.

As water moves through the soil-plant-atmosphere continuum there are several factors in the climate, soil and tree that can restrict that transport. Limitations of transpiration are often caused by soil drought, and the tree's phytochemical systems for controlling stomatal conductance (Havranek and Tranquillini, 1995). Liquid water may be absent either due to evaporation or freezing. If the soil is cold, the water uptake may also be limited by a lower production of new fine roots that are more conductive to water (e.g. Kramer and Boyer, 1995), a higher viscosity of water, as well as a lower root conductance and membrane permeability (Kaufmann, 1975). Low soil temperatures also affect the soil processes associated with nutrient fluxes.

Climate

The soil-plant-atmosphere continuum is part of a dynamic system where above ground climatic conditions are reflected in the soil climate. Climate variables regulate the daily and yearly supply of energy, carbon and water to the soil and plant. Gradients of air temperature and humidity induce heat and water flows between the soil and air. These parameters, together with solar radiation, vary strongly within time and space due to differences in the soil surface and vegetation. The gradients in water vapour pressure between a plant and air are the "engine" for transpiration that not only helps CO_2 assimilation but also cools the leaf or needle and prevents overheating.

Soil

The annual mean soil surface temperature and its amplitudes are both important characteristics for the soil temperature, and thus also for freezing of a soil. Other important features are the thermal properties of the soil and the damping effects on heat flow caused by vegetation canopy, organic layer and even more so by snow cover (figures 2 and 3). These are all factors that may be influenced by the structure of a stand. At the ground surface, i.e. soil or snow surface, the energy balance can be simplified as the relationship between net radiation, R_n and the incoming and outgoing heat flows between the atmosphere and ground surface:

$$R_n = LE + H + G \qquad (1)$$

Where LE is the latent heat flow, H the sensible heat flow and G is the soil heat flow. Latent heat is the heat associated with the state of water, i.e. liquid, gas or ice, and is transported by convection of soil water. Sensible heat is transported by conduction, expressed in Fourier's Law as a relation of the temperature gradient and thermal conductivity of the soil. Temperatures of the soil depend on these fluxes.

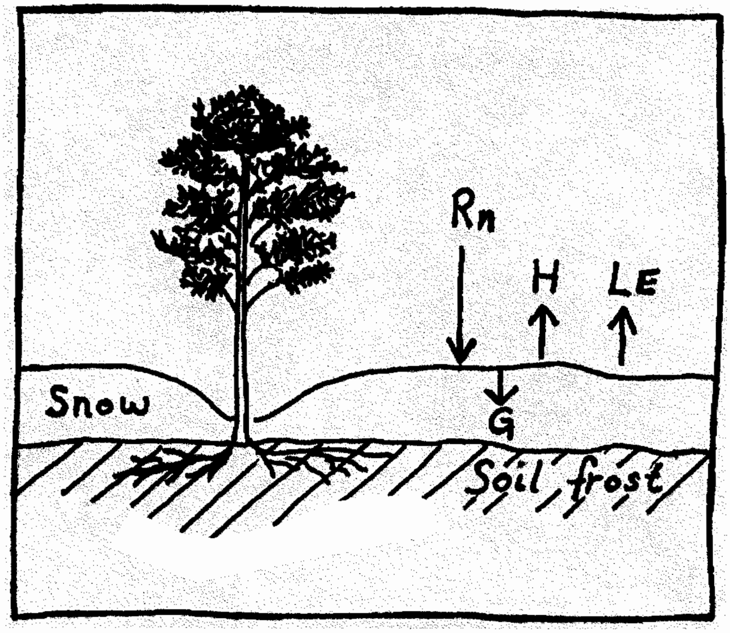

Figure 2 The energy balance during winter.

A soil freezes over a range of temperatures, where liquid water can be present in a continuous film adsorbed to mineral and organic surfaces even at temperatures well below the freezing point. The distribution of water and air in frozen soil is normally liquid water in the very fine pores, ice in the intermediary pores and air in the largest (Stähli *et al.*, 1996). The different proportions of these phases of water, in combination with soil type, complicates water movement on and through the frozen soil during snowmelt (Nyberg *et al.*, 2001; Stähli *et al.*, 2001).

The ability of a soil to transport liquid water is described by its hydraulic conductivity. It is dependent on the soil matrix and is largely controlled by the coupling between the heat and water regime.

It is important to understand the energy status of a soil when dealing with its water relations. Total potential of soil water is the sum of forces associated with gravitation, the attraction of water to soil particle surfaces and osmotic effects. Depending on particle size, distribution and water content, the soil will have different negative forces giving rise to different matrix potentials. As a soil successively dries, the water potential decreases and the retaining forces in the soil water become stronger, creating a water potential gradient in the soil profile. Water flow is then induced from higher to lower potential according to Darcy's Law:

$$q = kA\,(d\Psi/dZ) \qquad (2)$$

Where q is the flow (m^3s^{-1}), k is the hydraulic conductivity (ms^{-1}), A is a cross-sectional area of the flow path (m^2) and ($d\Psi/dZ$) is the potential gradient.

The phenomena of drying and wetting in an unfrozen soil are similar to those for freezing and thawing in a frozen soil. As a soil dries, water is removed and replaced by air, leaving the remaining water at a lower matrix potential. The same happens when a soil freezes, except that liquid water changes phase into ice. Therefore the capillary and osmotic forces that prevent a soil from draining also prevent it from freezing.

Tree

Soil water enters the root cells across a semi-permeable cell membrane driven by the water potential gradient between the soil and root. The soil temperature is important in determining the water uptake of roots. In conjunction with lowering the water viscosity, low soil temperature also reduces the root membrane permeability (e.g. Kramer, 1940). As the soil temperature decreases, the resistance in the plasma membrane increases due to less fluid membrane lipids. Cold soil temperature also inhibits growth of new unsuberized roots that are more conductive to water than older roots. Soil drying not only reduces the root water uptake by making water less available, but also by reducing the contact between the roots and soil due to shrinkage. Roots generally have access to available water within 6 mm of the root (Lambers *et al.*, 1998).

The water in the xylem of a stem is under a negative hydrostatic pressure. This pressure can be measured with a Scholander pressure chamber (Scholander, 1965; Waring and Cleary, 1967). Interactions of water molecules with the capillaries in the cell walls of transport vessels cause these suction tensions. The water is sucked up in the xylem to the top of the trees to replace the water transpired by the shoots. Capillary forces hold the water column in the xylem in place and cohesion among the water molecules, from hydrogen bonding, allows the water to rise. The xylem water flow, Q_w (mms^{-1}), described as the transport of fluids in ideal capillaries, can be expressed by the Hagen-Poiseuille equation:

$$Q_w = (\pi R^4 \Delta\Psi_p)/8 \eta L \qquad (3)$$

where $\Delta\Psi_p$ is the difference in hydrostatic pressure (MPa), R is the radius of the single capillary (mm) with the length L (mm) through which the transport takes place, and η is the viscosity constant ($mm^{-2}MPas$).

The steepest pressure gradient of the soil-plant-atmosphere continuum occurs at the transpiring surfaces of the shoots. This makes stomata the major point of regulation for water transport through trees. Stomata also respond to light to be open for CO_2 assimilation. Under clear sky conditions this causes a conflict in which the stomata have to compromise so as to maximise photosynthesis and at the same time minimise transpiration. However, it is not only irradiance, CO_2 concentration and air humidity that determine the stomatal conductance. Chemical and hydraulic signals triggered by insufficient water supply are also involved, although the details are still being investigated. Low water potential has been seen to cause a greater release of Abscisic acid (ABA) which will be concentrated in the shoots and lead to stomatal closure (e.g. Havranek and Tranquillini, 1995; Lambers *et al.*, 1998). Hydraulic signals may also be involved in initiating stomatal closure when exposed to low soil temperatures (Day *et al.*, 1991). De Lucia *et al.* (1991) found stomatal closure to be the dominant factor limiting net photosynthesis at low soil temperature for *Pinus sylvestris* seedlings. However, non-stomatal inhibition of photosynthesis was also found to be important in Loblolly pine at soil temperatures below 7°C (Day *et al.*, 1991).

Boreal forest

The boreal zone has a cold, temperate and humid climate covering a large part of the Northern Hemisphere; mainly in Russia, Fenno-Scandia and Canada. The daily average air temperature determines the length of the growing season. Commonly the start of the season is set to a threshold of +5°C for at least three days.

In Northern Sweden, forests are usually more sparse and slower growing relative to those in more southerly latitudes. Water is, however, considered to be abundant in summer, and thus not a factor limiting carbon assimilation. More restricting for growth are low air and soil temperatures, and nutrient deficiency. Soil frost commonly occurs in the boreal forest ecosystem during winter and sometimes persists into the spring. Frost depth and duration will affect the soil temperatures and availability of water during spring.

Forest management affects several parameters of importance for both climate in the stand and in the soil, and thus indirectly affects the water transport in the soil-plant-atmosphere continuum. The stand structure strongly influences the soil temperature dynamics during spring by its effects on the heat flow (figures 2 and 3). The soil warming dynamics vary at one site from one year to another, but also spatially across the landscape during the same year due to differences in snow cover distribution (Kluge *et al.*, in prep).

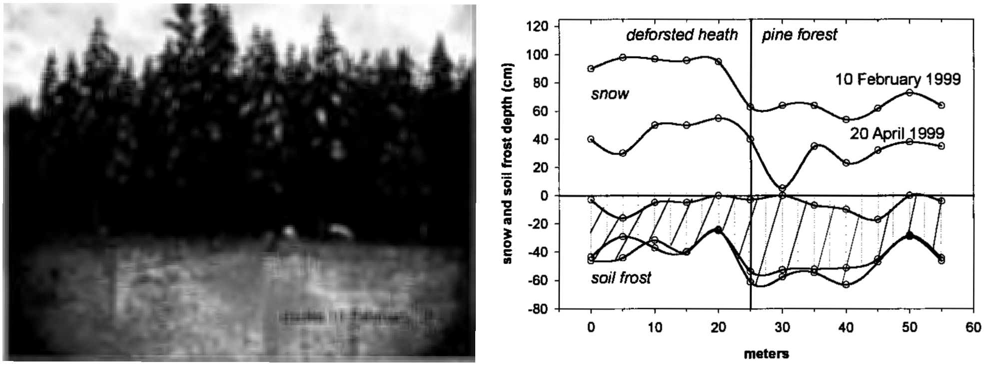

Figure 3 Distribution of snow and soil frost depth (February 10 and April 20, 1999) along a transect stretching from an open deforested heath into a 70 year old Scots pine forest at Heden. This is the forest edge treated in paper II during 1998.

Sap flow measurements

There are several methods for measuring sap flow, including gravimetric and volumetric measurements, as well as measurements of water vapor and sap flow velocity. The method used in this study is the heat balance method (Cermak *et al.* 1973; Kucera *et al.* 1977) using the commercially available sap flow meters from EMS (Environmental Measuring Systems, Brno, Czech Republic). The method is based on the analysis of how much heat, applied to a well-defined space in the conductive xylem, is carried away by the water flow. This is an absolute method giving values of the sap flow rate in mass per time units. The sap flow rate (Q_w) is assessed from:

$$Q_w = P/(\Delta T c_w) - k/c_w \qquad (4)$$

where P (W) is the heat input, ΔT (K) is the temperature difference between the heated and non-heated parts of the xylem, c_w is the specific heat of water (4186.8 J kg^{-1} K^{-1}) and k is the coefficient representing the heat loss from the measuring point. The system can be used on both branches and tree trunks. The device consists of a heater, thermocouples and a device for controlling and monitoring the measurements.

In the experiments presented in this work, the field measurement technique has been refined to measure sap flow more accurately during spring when there are large fluctuations in temperature from well below freezing during the night to warm temperatures during day time. Sap flow measurements typically show a disturbed signal during periods of freezing temperatures. When the temperature rises and eventually permits flux to occur, the measured signal becomes “undisturbed”, showing the actual values. It is relatively easy to distinguish these periods of water flux during daytime for measurements from the branch gauges. The measurements at the stem are however more robust and slightly less sensitive to the very fine fluctuations that can be observed on branches. This is because the stem measurements involve larger quantities, i.e.; more heat is usually applied and processed by the system to calculate the actual water flux. Consequently the amplitude of very small fluxes are more difficult to determine, in comparison to the measurement system for branch gauges, which have a better resolution to detect the early onset of transpiration during the first weeks of spring. On the other hand, the flux measurements on the stem give reliable data across the whole season and provide an independent check for branch measurements during the measurement period.

Experimental sites

The experiments to study the water relations of Scots pine trees were conducted at Västomån (paper I) and at Heden (paper II). The sites lie near or within Vindeln Experimental Forests (64° 14' N, 19° 46' E) in the boreal zone of northern Sweden (figure 4), and are located approximately 180 m above sea level on flat plains of glacifluvial deposits. The soils are ferric, podzolized sandy silts and have only thin layers of humus (1- 2 cm). Both the eluvial and the illuvial horizons are approximately 10 cm thick. The soil profiles are dominated by the sand and silt fractions, and have only low clay contents. In this region soils are annually subjected to soil frost, normally lasting from November until June (Odin, 1992).

The Heden site has a mono-specific, naturally regenerated 70-year-old Scots pine (*Pinus Sylvestris* L) stand. At Västomån the stand is mixed but dominated by naturally regenerated 20-year-old Scots pine.

Standard climatological data were obtained from the Heden climatic reference station (Degermark, 1981-1997). The climate is characterised by a long-lasting winter with a continuous snow cover from the end of October until the beginning of May, followed by a growing season lasting from the beginning of May until the end of September. The mean annual precipitation is 600 mm, of which one-third falls as snow. The mean 20 year average temperature is 0 °C. The flat plain of the Heden area is slightly colder than its surroundings, and the site is frequently exposed to summer night frosts.

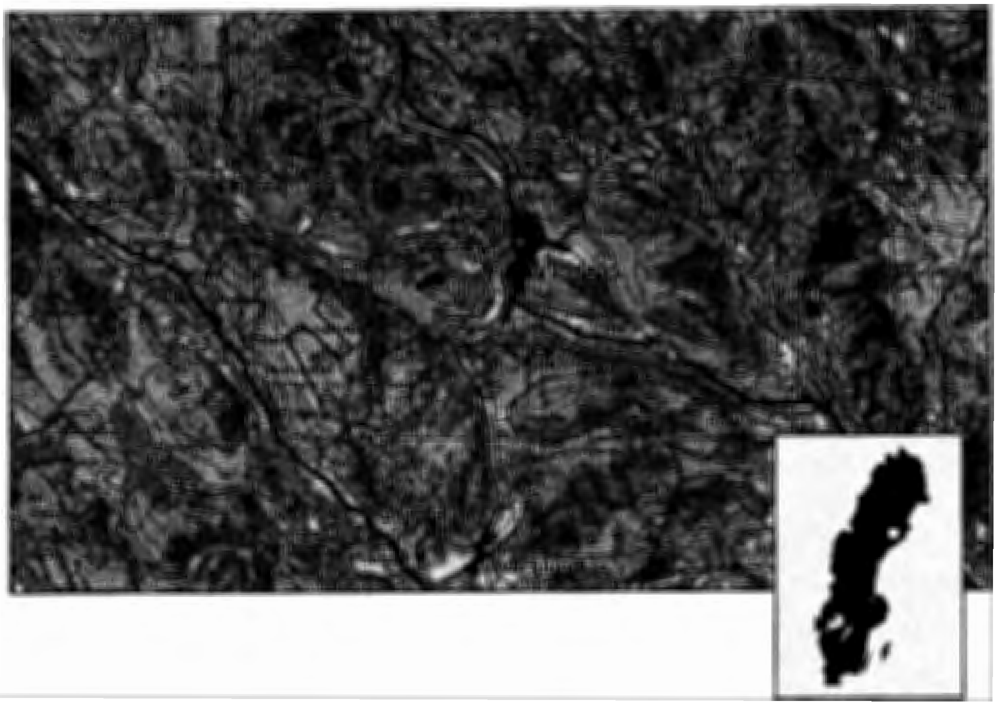

Figure 4 Location of Vindeln Experimental Forests. The Västomån site is marked with V, Heden with H and the Svartberget field station with S.

Paper I:

In this paper we examined the water relations of 20-year-old Scots pine trees exposed to different soil temperature regimes in the field by soil manipulations. An attempt to quantify the sensitivity of spring tree water uptake to soil temperature and/or the presence of plant available water was made. This involved distinguishing the effect of the atmospheric and rhizospheric conditions for sap flow. The soil temperature was manipulated on different plots and the response of sap flow, needle water potential and shoot elongation was measured. The study was conducted during 1999 at the Västomån site.

The duration of soil frost and cold soils affect tree water uptake both by inhibiting tree water uptake and by inhibiting the development of water conductive fine roots. Cold soil temperatures give rise to a higher viscosity of water. Together with a lower root conductance at low temperatures in the rhizosphere and possibly a release of phytochemical and hydraulic signals increasing the stomata resistance, this may limit transpiration and thus also carbon assimilation. Soil frost and associated cold soils at spring may be linked to silvicultural practices. This study was an attempt to see if a "frost-conscious" forestry is necessary throughout the life of the stand, rather than just during the stand-establishment phase.

Paper II:

In this paper we examined the water relations of 70-year-old Scots pine trees exposed to different soil and air temperature regimes in the field by the effect of a northerly orientated forest edge. An attempt to distinguish the climate and soil influences caused by the forest edge effect was made. The study was conducted during 1998 at the Heden site.

The forest edge creates a specific microclimate. Depending on orientation, it may receive more or less radiation in comparison to the forest interior. At the edge the turbulence is enhanced which can make the ventilation much more effective. The forest edge also creates specific soil temperature and moisture gradients. These are all factors affecting, water use and thus also the carbon allocation.

The edge zones in the landscape and the associated fractionation of vegetation may have important implications for water and carbon cycles, especially when scaling up the stand level fluxes using models parameterised from the interior conditions. Extrapolating these fluxes into large areas without considering the specific contribution of edge zones and other fractionated landscape elements such as frequent forest patches may underestimate the actual fluxes from the landscape.

Results and discussion

The methods for manipulating the soil conditions by snow removal and ground insulation, in paper I, effectively created large differences in the depth and duration of soil frost (figures 5 and 6). This allowed us to study the tree water dynamics in the field during a wide range of soil temperatures in combination with different climatic parameters. The soil temperature at 10 cm was used when analysing soil temperature effects on tree water uptake, as this was the level of highest density of living fine roots (<2 mm) and the highest saturated hydraulic conductivity. A Principal Component Analysis of the soil temperatures at different depths also confirmed that this was an appropriate level to study. Our results indicate that the thawing of soil frost together with infiltrating water from the snowmelt was not sufficient for tree water uptake during spring on the study plots, even when above ground climate generated a large evaporative demand. For substantial water uptake to occur, the soil temperature needed to rise above zero in the upper soil layer where most of the fine root bio-mass and a layer of higher water conductivity are located (figure 6).

Figure 5 Above: photo of the "cold soil plot" April 20, 1999. The snow was removed during the cold period to create deep soil frost, until March 24 when the snow was replaced. The "added" snow was covered with sawdust to help preserve the snow and soil frost as spring progressed. **Below:** photo of the "warm soil plot" April 28, 1999. The presence of soil frost was minimised by insulating the ground with Styrofoam pellets in large, porous bags from November 10 to April 20.

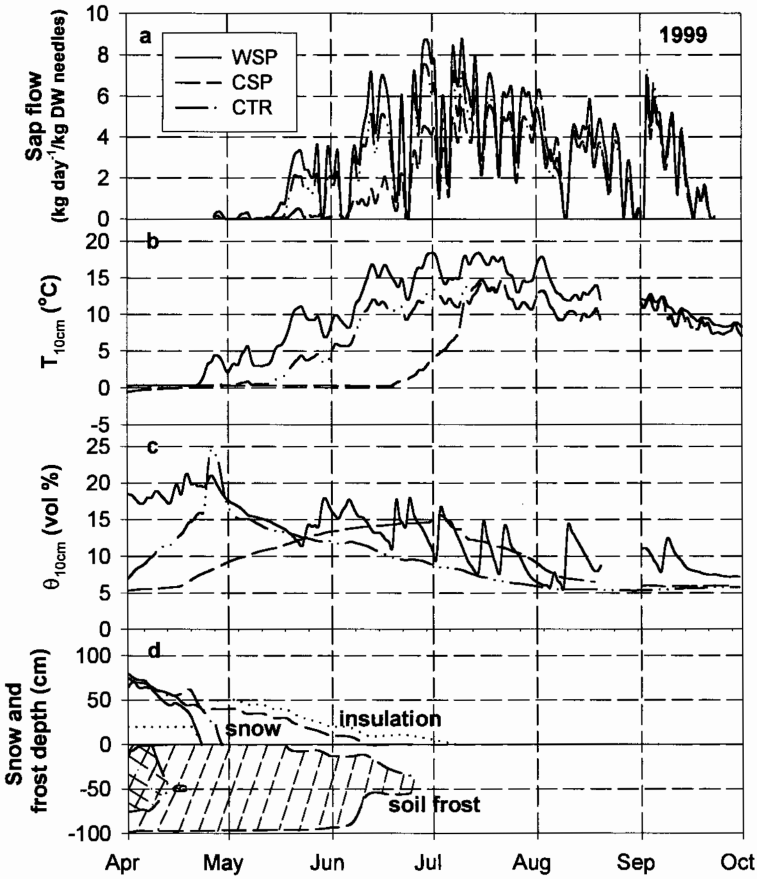

Figure 6 The response of sap flow for the plots with different soil temperature on the WSP (Warm Soil Plot), CSP (Cold Soil Plot) and CTR (Control Plot) at Västomån during the growing season 1999. **a)** Daily sum of branch sap flow averaged from four branch gauges per plot, **b)** daily average of soil temperature at 10 cm averaged from three soil profiles, **c)** daily average of soil moisture content at 10 cm and **d)** snow and soil frost depths as indicated by frost tube measurements.

The measured branch sap flow in paper I was normalised to the dry weight (DW) of needles and presented in kg per kg DW needles. Since needle bio mass was sampled at the end of the growing season, 1999, the values of sap flow during development of the current year needles (i.e. the first half of the growing season) was somewhat underestimated. Since the shoots developed at the same relative rate on each plot, the relation of sap flow rates between the plots was the same.

When the growing season had started, low soil temperatures restricted tree water uptake. On the cold soil plot the soil warming was delayed by one month and low soil temperatures persisted well into the growing season, which started in May 15 (figure 6). The delay of soil warming severely restricted the sap flow on the cold soil plot in comparison to the control, during May and June (figure 7). The cause of water uptake differences between the warm soil plot, which warmed before the start of the growing season, and the control were less clear (figure 7). Since a somewhat greater uptake in the warm soil plot persisted into the autumn there could be an intrinsic difference between the plots. Apparently it is not related to soil temperature differences, unless root growth was enhanced in the warm soil treatment and allowed it to transpire more water throughout the growing season. An interesting feature in this study is the variation in sap flow during the day, and the tendency for a midday depression on days with high potential evapotranspiration (PET). This tendency was found throughout the season. It will be interesting to ascertain the causes and significance of this phenomenon. At the end of the growing season the measured branches on the warm soil plot had transpired a total of 490 kg per kg DW needles, the branches on the control plot 402 kg per kg DW needles, and the branches on the cold soil treatment 312 kg per kg DW needles.

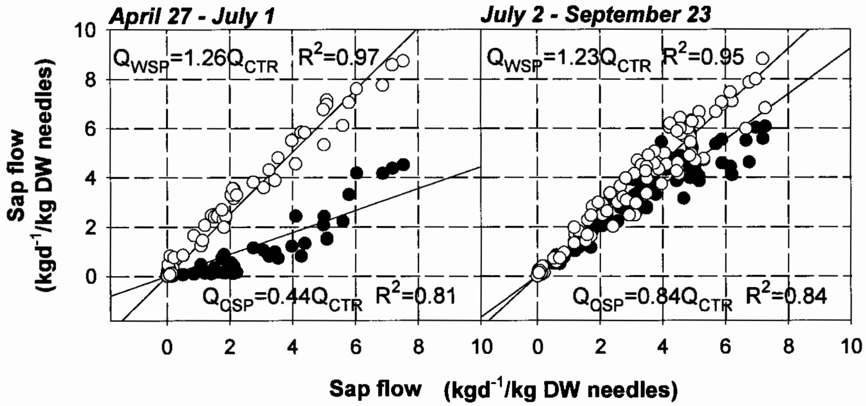

Figure 7 Daily total sap flow on the WSP (warm soil plot, open circles) and on the CSP (cold soil plot, filled circles) plotted against the sap flow on the CTR (control plot). The time series is separated into a period when below-ground conditions differed between the plots (left) and a period when soil conditions were similar (right).

The studies extended throughout the whole growing season. However, the period May 1 – July 1, 1999 was chosen in paper I to find any correlation of sap flow to soil temperature and PET, since this was likely a period when the sap flow was somehow restricted by soil factors in conjunction with above ground conditions. Soil temperatures at 10 cm correlated well with the rate of sap flow (when weather conditions were favourable for transpiration). In conjunction to this, a higher soil temperature allowed a higher sap flow for the same value of PET on each plot (figure 7 in paper I). While soil temperature had an effect on water uptake in relation to PET, the effect of a specific soil temperature was not the same at different times. Since the plots achieved a particular temperature approximately one month after each other, this indicates that soil temperature during spring influence water uptake in combination with other factors such as length of the day, a period of warm air temperature, or the tree's recovery from winter damage. The soil temperature effect was most evident on the cold soil plot, due to its low soil temperatures during the first month of the growing season.

When the evaporative demand was not satisfied due to the low soil temperatures, the trees were water stressed. The needle water potentials were lower on the cold soil plot than the other plots during the measuring period April 16 – June 22 (figure 8). When soil potentials are low, stomatal and biochemical effects are likely to be involved in determining the rate of transpiration (see theory part). A comparison of the needle water potential with sap flow gave a clear linear relation with different slopes for the different soil treatments (figure 8b). Since the water transport in a tree is driven by the difference in needle water potential and soil water potential, the slope in figure 8b indicated the conductance for the entire system. The conductance was largest in the warm soil plot and lowest in the cold soil plot.

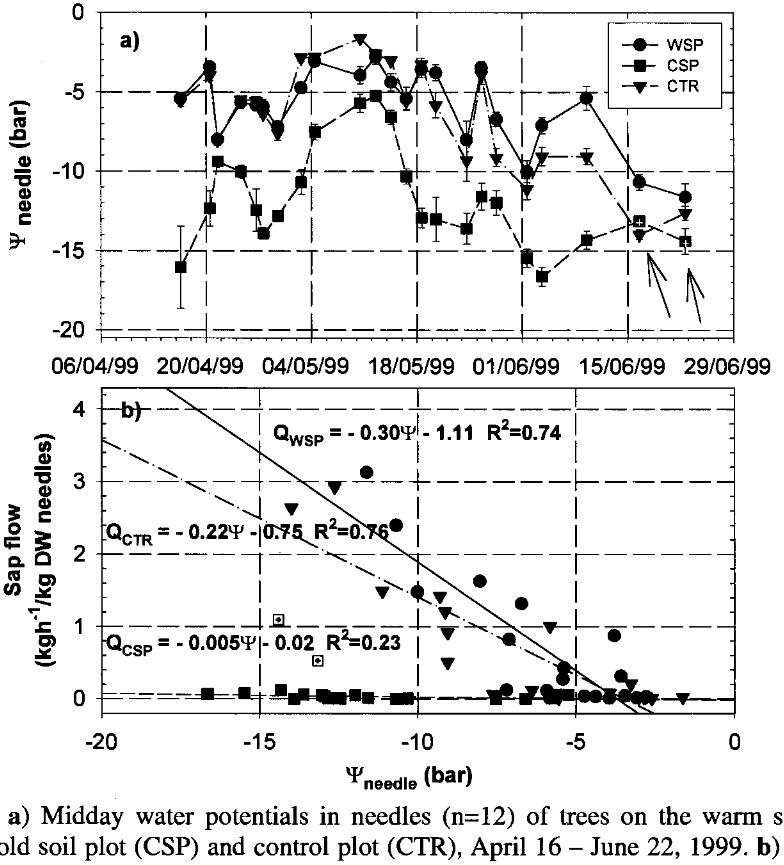

Figure 8 **a)** Midday water potentials in needles (n=12) of trees on the warm soil plot (WSP), cold soil plot (CSP) and control plot (CTR), April 16 – June 22, 1999. **b)** Hourly values of branch sap flow as a function of needle water potential. At the two last measurements on the CSP (marked with arrows) the soil warming had started and the transpiration demand was high. These two deviating points are not taken into account for the function in b).

As the water and carbon fluxes of a tree share the stomata as a common pathway, the reduced water flow in the trees, in conjunction with the low soil temperatures, also reduced net photosynthesis. This was observed in a study by Strand *et al.* (in prep.) who examined the light saturated rate of net photosynthesis and stomatal conductance on the same study plots as in paper I (figure 9). Compared to the control plot, the long duration of low soil temperature on the cold soil plot severely restricted the recovery of net photosynthesis, and especially stomatal conductance. The warm soil treatment had little effect on gas exchange compared to the control, although the average soil temperature was 3.8°C higher than on the control plot during the first half of the growing season. This was another indication that the rate of net photosynthesis and stomatal conductance were not limited by low soil temperature alone.

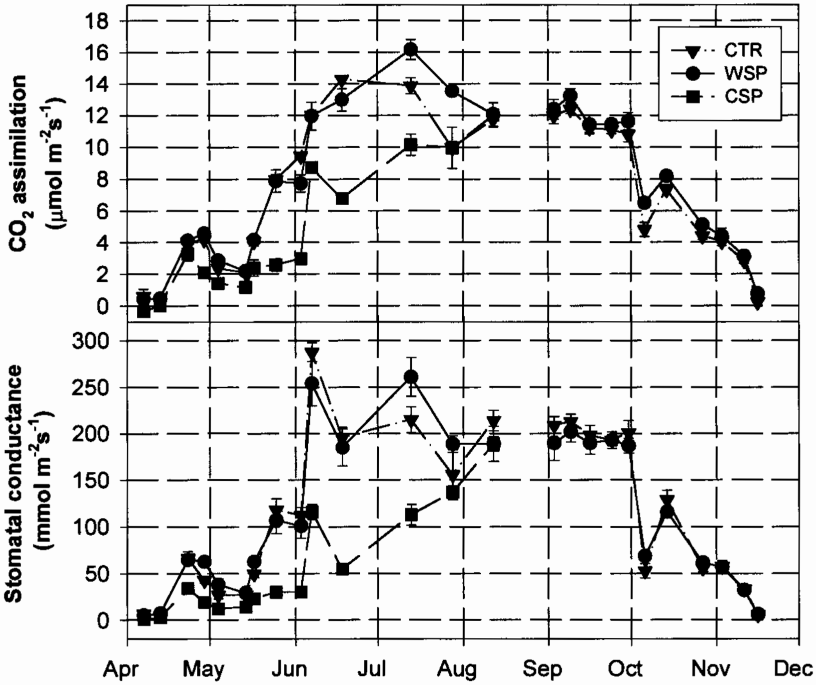

Figure 9 a) CO$_2$ assimilation and **b)** stomatal conductance in needles from three branches per tree (n=9) on the warm soil plot (WSP), cold soil plot (CSP) and control plot (CTR). The cold soil plot was excluded from September to November (Strand *et al.*, in prep.).

In comparison to earlier published literature, the study in paper I demonstrated that many results with seedlings and saplings hold true in our field study with regards to the restricting effects of cold soils on water uptake and carbon exchange. In particular this fits with the finding by Bergh and Linder, (1999) that cold soil temperatures had less effect early in the spring (which is when the CTR was colder than WSP), than later in the spring (when only the CSP was markedly colder).

The differences in soil warming created by the experimental plot manipulations in paper I span the range of soil warming dynamics that can be expected at a single site due to inter-annual variations in climate. However, this range of warming dynamics was also found within a 10 km radius of Vindeln Experimental Forests during the same year (Kluge *et al.*, in prep). Thus the links between silvicultural practice and timing of soil warming seems to be important to have in mind for forest productivity, not only when establishing a stand, but throughout the productive lifetime of the stand.

The variation in soil conditions found across the landscape could also be seen when comparing the forest edge with the forest interior in paper II. The study showed that the forest edge had a considerable effect on frost depth. In comparison with the interior forest, the soil frost depth at the forest edge was deeper during winter, but thawed earlier and left an ice lens at a greater depth below the rooting zone during spring. In the forest interior, the remaining lens of frost was more superficial and coincided with the zone of the largest root density (Plamboeck et al, 1999). The importance of cold soils as a limitation to water uptake and transpiration was apparent during the beginning of the growing season at Heden 1998.

There were differences in water use and annual ring increment during the growing period between trees growing at the forest edge and trees growing in the forest interior (paper II). The variability, however, was higher at the edge zone. Earlier published literature have stressed the edge effect on microclimate (Carmago and Kapos, 1995; Chen *et al.*, 1993; Chen *et al.*, 1995; Matlack, 1993). The difference in water use and increment in this study, however, could not be explained by above ground climatic conditions, since these effects were very small due to the stand structure and orientation to the north. Air temperature and relative humidity only differed on average by about 0.2°C and 1.5%, respectively, between the location at the forest edge and 40 metres inside the stand. These observations also indirectly excluded wind as a variable that could affect transpiration at the edge zone relative to its interior. Thus soil conditions caused by the stand edge seemed to be of importance for water use.

The tree and stand biometry of the edge zone trees and the stand interior trees did not reveal any strong differences of importance for the transpiration fluxes. The only significant difference that could be found was in tree heights, which tended to increase towards the stand interior. This is likely explained by the competition for light among the trees in the interior stand.

The estimated tree water use and increment was larger at the edge zone. At the interior, the estimated transpiration was 70 mm and at the edge zone 107 mm during the 1998 growing season (figure 10). This indicates that the frequency and structure of forest edges may have importance for calculating fluxes from a landscape.

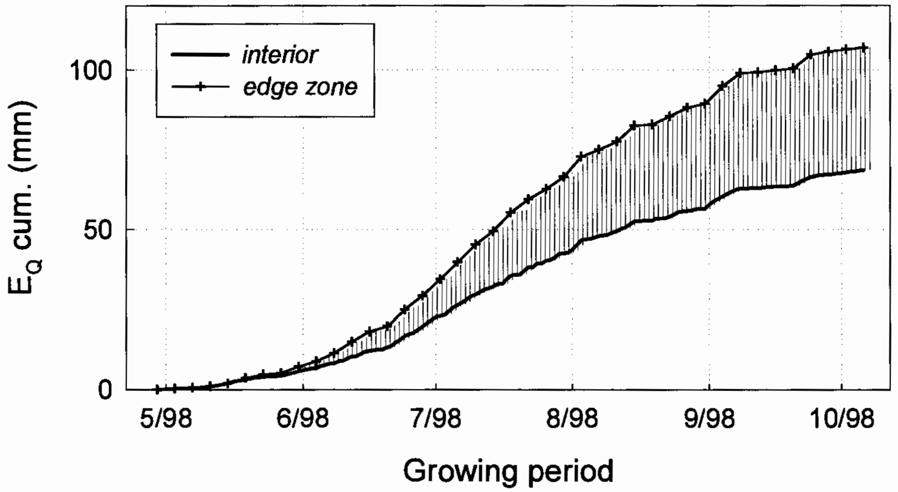

Figure 10 Cumulative values of estimated canopy transpiration (E_Q) calculated from edge zone and interior trees, respectively. Some missing values in summer were filled from the regression to mean daily branch sap flow. Shaded area shows a likely range of E_Q that depends on the weight given to particular situations, i.e., edge zone and forest stand interior.

Conclusions

In this Licentiate thesis the water relations of Scots pine trees exposed to different soil temperature regimes in the field was examined. The field scale experiments have confirmed the importance of low soil temperatures for tree water uptake during spring when soil warming is delayed beyond the start of the growing season as defined by air temperatures. Before the start of the growing season however, low soil temperatures had little effect. The release of liquid water, as soil frost melted and snowmelt infiltrated, was not in itself enough to satisfy the demand for water during spring when the above ground conditions were suitable for photosynthesis by *P. sylvestris*. The water was not available to the tree until the soil temperature in the upper rooting zone had reached a threshold temperature above 0°C, even if the transpiration demand was large due to above ground climatic conditions.

The start of soil warming varies in time and space due to snow cover distribution. These variations were found within a small area due to a forest edge. The observations of the edge effect have confirmed that there were differences in water use and stem increment of trees at the edge zone relative to the interior ones. These differences were most related to soil conditions, including water availability, soil temperature and frost formation in the root zone.

Since silvicultural decisions effect soil temperature, the effect of soil temperatures on tree water uptake during spring in conjunction with above ground conditions seems to be a factor worth investigating further with regards to forest management in areas susceptible to soil frost and low soil temperatures.

Ongoing and future work

A comparison between the different aged stands at Heden and Västomån will be made with regard to water conductance and water use sensitivity to soil physical conditions. The time series of soil temperature and moisture content, micro climate and sap flow will also be used to calibrate the SOIL/COUP-model (Jansson, 1996) to investigate the current formulations in the model with regard to reduction in water uptake during spring. Further investigations will be made on the influence of spatial arrangement of snow cover around trees on frost depth and root water uptake, as well as simulating different scenarios to extend the range of our knowledge beyond our range of measurements to include the effects of different silvicultural treatments. A 20-year time series of climatological data from Heden and two other sites (Degermark, 1981-1997) is available to support this work. These measurements are a part of the climate reference measurement program at Vindeln Experimental Forests.

Data from this project will also be used for further parameterization and validation of a boreal version of the BIOMASS-model (Bergh *et al.*, 1998). The final step is, with the help of BIOMASS simulations, to quantify the effect of spring soil temperature, as mediated by silvicultural practices, on photosynthesis and forest growth.

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The Influence of Soil Temperature on Spring Water Stress: a Plot Scale Manipulation in a Young Scots Pine Stand

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Abstract

Classic studies have stressed the importance of forest management for soil frost and the dynamics of soil warming during spring. But we know very little about the potential loss of forest production due to cold soils. Liquid soil water may not be available to trees due to cold soil conditions, thus reducing transpiration and photosynthesis. We believe that these effects need to be quantified in order to keep silvicultural practices from inadvertently reducing forest growth through effects on soil temperature. In order to test this hypothesis it is important to know more about water uptake in the field by trees in cold environments.

The amount and persistence of soil frost was manipulated on two plots in a young stand of *Pinus Sylvestris* L. to create one plot with relatively warm soil conditions and another with prolonged cold soil conditions. A third plot served as a control. Soil profile temperature and liquid water content, as well as snow and frost depths, were measured together with tree physiological parameters such as sap flow, needle water potential and shoot elongation.

The cold soil treatment severely restricted sap flow. The absence of frost (and hence the presence of liquid water) was not sufficient to enable water uptake. It was rather elevation of soil temperature above zero in the upper soil layers that was required for substantial water uptake, in combination with other site factors. When soil temperature at 10 cm depth was below ca 8°C, that temperature correlated with the rate of sap flow on each plot when weather conditions were favourable for transpiration. The effect of a certain soil temperature, though, is not the same at different times due to its interaction with other factors such as day-length. The importance of cold soil increases with the persistence of low temperatures after the start of the growing season. The delays in soil warming induced by our study are within the spatial, and interannual variation of soil warming in this region. Thus we conclude that forest management influences on soil temperature can effect the transpiration deficit during spring, with potential implications for forest productivity.

Key words

Soil frost; soil temperature; water stress; sap flow; transpiration; water potential; roots; Scots pine; Pinus sylvestris.

Introduction

Conifers growing at high latitude are subject to seasonal freezing temperatures in both in the air and the soil. The depth and duration of soil frost as well as the persistence of low soil temperature varies spatially, influenced to a large degree by the snow cover distribution. There are strong links between silvicultural practice and spatial variability of snow cover and soil frost (Ångström, 1936; Pierce *et al.*, 1958). The combined effects of stress factors such as low air and soil temperatures (e.g. Troeng and Linder, 1982) and excessive light (Hällgren *et. al*, 1991) severely reduce net photosynthetic capacity during winter (Strand and Lundmark, 1987; Troeng and Linder, 1982). The recovery of net photosynthetic capacity in spring and early summer is strongly temperature dependent and many studies have shown a strong correlation between air temperature and rate of recovery (e.g. Lundmark *et al.*, 1988, 1998). However, no recovery of net photosynthetic capacity was seen in Scots pine before the soil had thawed (Linder and Troeng, 1980; Troeng and Linder, 1982). Soil temperature is an important factor for tree water dynamics and consequently for the growth and vitality of trees.

Tree water dynamics are influenced by a number of physical conditions governing the water potential gradient between the absorbing roots and soil, the hydrostatic pressure gradient in the stem and the vapour pressure gradient between the transpiring surfaces of the shoots and the atmosphere, thus involving both the rhizosphere and atmosphere. Many factors are involved in explaining the dynamics of water flow in trees. Above ground the PET is important for transpiration by creating a water potential gradient between the shoots and atmosphere. Below ground, the soil temperature is important in determining water flow resistance by changing the water viscosity and reducing root permeability (Kaufmann, 1975), as well as by inhibiting root growth (Kramer and Boyer, 1995). Thus both PET and soil temperatures are involved in determining the conductance of the plant water system, although there are uncertainties in the exact mechanisms. This principal resistance is usually between the stomata and atmosphere, with the effect of soil conditions mediated by the trees own feedback mechanisms for controlling stomatal conductance. Limitations of transpiration are often caused soil drought, where liquid water is absent either due to evaporation or freezing. At low soil temperatures the water uptake may also be limited by a lower production of new fine roots that are more conductive to water (e.g. Kramer and Boyer, 1995), a higher viscosity of water as well as lower root conductance and membrane permeability. Low soil temperatures also affect the soil processes associated with nutrient fluxes.

Many studies have focused on the inhibiting effects which cold soils may have on water relations and gas exchange for seedlings or saplings, often in laboratory experiments (e.g. Grossnickle, 1988; Day *et al.,* 1991; Pavel and Fereres, 1998; Wang and Zwiazek, 1999). Schwartz *et al.* (1997) found that net photosynthesis in red spruce saplings was more sensitive to changes in soil temperature than air temperature, with the strongest correlation between soil temperature and sap flow at temperatures below 10°C. These studies clearly illustrate how lowering soil temperature increases the water flow resistance through the soil-plant-atmosphere continuum, mainly by a lowering of the root permeability and increased stomatal resistance. Due to differences in experimental design, the thresholds at which soil temperature has been reported to have a pronounced effect on photosynthesis and transpiration varies by more than 10°C. This variation in temperature thresholds, and the fact that there are few field studies on the water dynamics of conifers in cold climates makes it difficult to assess how silvicultural decisions that contribute to colder soils during spring may reduce forest productivity. One important field study, however, has suggested that sap flow was strongly reduced as long as soil temperature was close to 0°C (Bergh and Linder, 1999). In that study, however, it was not possible to decide whether this was an effect of soil temperature, water availability or both. Another field study, Cienciala *et al.* (2001), found soil conditions to be more decisive for the transpiration than the microclimatic variations when comparing the interior of a stand with the forest edge.

The objective of this study was to quantify the sensitivity of water uptake by Scots pine trees to soil temperature and/or the presence of plant available water. In order to do this we have studied the soil temperature, water availability in the soil, sap flow, needle water potential, shoot elongation and potential evapotranspiration of Scots pine trees exposed to different soil temperature regimes in the field.

Materials and methods

Site description

The experiment was conducted at Västomån, near to Vindeln Experimental Forests (64° 14' N, 19° 46' E) in the boreal zone of northern Sweden. The stand is located 185 m above sea level on a flat plain of glacifluvial deposits. It is a mixed stand dominated by 20 year old, naturally regenerated Scots Pine (*Pinus Sylvestris* L). The ground vegetation is sparse and consists mainly of lichens.

The soil is a ferric, podzolised sandy silt and has only a thin humus layer of 1- 2 cm. The soil profile is dominated by the sand and silt fractions, with a low clay content. Both the eluvial and the illuvial horizons are approximately 10 cm thick. In this region soils are annually subjected to soil frost, normally lasting from November until as late as June on some sites (Odin, 1992).

The climate is characterised by a long winter with a continuous snow cover from the end of October until the beginning of May, followed by a growing season (i.e. daily average air temperature >= +5°C for at least three days) lasting from the beginning of May until the end of September. The mean annual precipitation is 600 mm, of which one-third falls as snow. The 20 year average temperature is 0 °C.

Experimental design and treatments

Three 30 m^2 plots, each with three study trees (*Pinus sylvestris* L), were used in this experiment. The pines are oriented in an east-west line and are all southerly exposed. The amount and extent of soil frost was manipulated during the winter 1998/1999 in a manner similar to that of Robitaille *et al.*, 1994. On one soil plot the soil frost was maximised (referred to in this study as the Cold Soil Plot, CSP) by removing the snow during the coldest period. Near the end of winter, this snow was replaced to insulate the frost and at the same time re-establish the hydrological inputs to the plot. The "added" snow was covered by a 10 cm layer of sawdust to help preserve the snow as spring progressed. At the other plot (referred to as the Warm Soil Plot, WSP), soil frost was minimised by insulating the ground with Styrofoam pellets in large, porous bags during the autumn. At the end of snowmelt in late April 1999, the ground insulation was removed. The third plot served as a control (CTR) where the conditions were kept as natural as possible. To make sure that the trees on the CSP were subjected to the manipulated soil conditions and reduce the effect of the warmer, surrounding soil, the plot was root isolated. This was done by cutting the roots around the plot to a depth of 40 cm. All plots were equipped with a tower to facilitate the tree physiological measurements.

Climate

Standard climatological data including air temperature, humidity, precipitation and global radiation were obtained from the Heden climate reference station (Degermark, 1981-1997). The climatological site is situated at an open heath in a pine stand within Vindeln Experimental Forests (10 km from the experimental site). Parallel measurements during 2000 confirmed the similarity of potential evapotranspiration (PET) at the two sites.

The depth of snow and soil frost at the experimental site was measured manually with frost tubes (Gandahl, 1957; Rickard and Brown, 1972). The measuring range was 100 cm above ground and 100 cm below ground. These measurements were made once a week until snowmelt began, when the frequency was increased to twice a week. One frost tube per plot was placed 1.5 meters from the nearest tree.

Each plot contained three soil temperature profiles and one soil moisture content profile with sensors at 0, 10, 20, 40, 60 and 90 centimetres depth from the top of the mineral soil. Soil temperature (T_s) was measured with thermistors and soil moisture content (θ) with Campbell CS 615 soil moisture reflectometers. The measurement profiles were placed at different distances from the nearest tree. The measurements were automatically read every 10 minutes, and a two hour average was stored in Campbell CR10 data loggers. Soil temperatures are presented as averages of the three soil profiles integrated over the plot, as these measurements revealed no significant effects caused by the different distances from the nearest tree.

Soil physics and Root Mass Distribution

Two profiles of soil were sampled adjacent to the plots, to determine texture and saturated hydrological conductivity (k_s). Samples were taken vertically every 5 cm to a depth of 45 cm and then at depths of 60 and 90 cm. For determination of k_s, samples were taken with 5 cm high cylinders (core diameter 7.20 cm) for analysis in the laboratory with a constant-head permeameter.

For distribution of fine-root mass, twenty soil cores (volumetric samples, core diameter 22.8 mm) were taken every four meters along a transect in the stand during October 1999. The core was divided vertically into four 10 cm layers of mineral soil. The samples were stored frozen until analysis in the laboratory, where the roots were washed free from soil, classified, dried (80°C for 48h) and weighed (Makkonen and Helmisaari, 1998; Vanninen and Mäkelä, 1999). The roots were classified into living or dead and into diameters larger or smaller than 2 mm. The root mass was expressed in dry weight per cm^3 soil.

Sap flow, shoot elongation and needle potential measurements

Sap flow was measured in southerly exposed branches with commercially available sap flow meters from EMS (Environmental Measuring Systems, Brno, Czech Republic). This system is based on the heat balance method (Cermak *et al.*, 1973; Kucera *et al.*, 1977). The branch gauges utilise external heating and sub-surface temperature sensing using needles inserted through a thin bark layer. These gauges are soft and flexible and the system causes practically no damage to plant tissues. Four gauges per plot were used (one per tree plus one extra) and connected to a PT4.1 logger unit from EMS. The measured branch sap flow was normalised to the dry weight (DW) of needles and presented here in kg h^{-1} per kg DW needles as averages of measurements from four branches per plot (three on the control plot). The needle DW averaged approximately 0.07 kg per branch. This needle biomass was sampled at the end of growing season, 1999. To measure water uptake over the full growing season is a challenge, since dry weight changes. The development of needle bio-mass was therefore estimated from tree physiological measurements and used for normalisation of the measured branch sap flow, in order to see how this might have affected the interpretation of sap flow (data not shown). The results illustrated that sap flow is somewhat underestimated during the period of needle development (i.e. the first half of the growing season), as the values were normalised to the dry weight of needles in October. The relations between the plots were, however, the same.

During the period June 9 to July 10 1999, the shoot elongation was measured with a measuring tape on six occasions. On each plot four to five shoots per tree were measured on branches with different azimuths (n=12 to 14 per plot).

During the period April 16 to June 22 1999, the needle pressure potentials (Ψ_n) were measured. One year old needles were collected on 23 occasions between 1200 and 1500 h. Samples were immediately put in glass vials lined with moistened filterpaper and covered with aluminium foil. The vials were stored in a cooling box during transportation (< 30 minutes) to the laboratory where Ψ_n was immediately measured with a Schollander pressure chamber (Waring and Cleary, 1967). On two trees per plot, three pairs of needles were sampled from each of two southerly exposed branches for analysis (n=12 per plot).

Results

Climate

The annual average air temperature for 1999 was warmer than normal, +1.7°C compared to 0°C. The winter 1998/99 was however cold with a minimum daily average air temperature of -34.1°C in January (with an instantaneous minimum of -41.3°C). Not until April did the daily average air temperature exceed 0°C. Thereafter the air temperature fluctuated with several frost nights, until mid May when the temperature stayed above 0°C. There was a warm period between June and August (figure 1e) with a maximum daily average temperature of +20.2°C (instantaneous maximum +26.6°C). Early autumn was also warmer than a normal year. The growing season lasted for 143 days between May 15 and October 4 (using an air temperature threshold of +5°C).

The methods for manipulating the soil conditions on the plots effectively created large differences in the depth and duration of soil frost and soil temperature (figure 1). These differences were within the natural range of soil warming for the area within a 10 km radius of the study site(Kluge *et al.* in prep.). In the WSP, the measured soil frost lasted from early February until the beginning of April 1999. Soil frost reached a maximum depth of 9 cm. The soil in the CSP was frozen (i.e. $T_s < 0°C$) from early November 1998 until late June 1999, and frost reached a maximum depth of >=100 cm in late February. On the CTR, soil frost persisted from mid November 1998 until mid April 1999, and had a maximum depth of 78 cm. These frost conditions were reflected in the soil temperature and soil moisture content of the plots. The timing of soil warming was delayed by approximately one month between each plot. The measured daily average soil temperature at 10 cm reached 5°C on May 6 for the WSP, June 2 for the CTR and July 4 for the CSP.

The annual precipitation during 1999 was slightly less than normal, 539 mm compared to 600 mm (figure 1f). In April there were several large rain events. May, however, was dry, which allowed the PET to increase, and thus created a large water demand in the trees. Rain events occurred frequently during the whole summer. Plant available water (i.e. a moisture content above the permanent wilting point of ca. 6% in these soils), was observed in all the plots after the snowmelt. This occurred in the beginning of April for the WSP and CTR, but at the end of April for the CSP. During the first half of the growing season the liquid water content in the upper soil layer was very similar to that at 20 and 40 cm on all the plots. As spring and summer passed, the liquid water content slowly decreased until October (figure 1c and 3d).

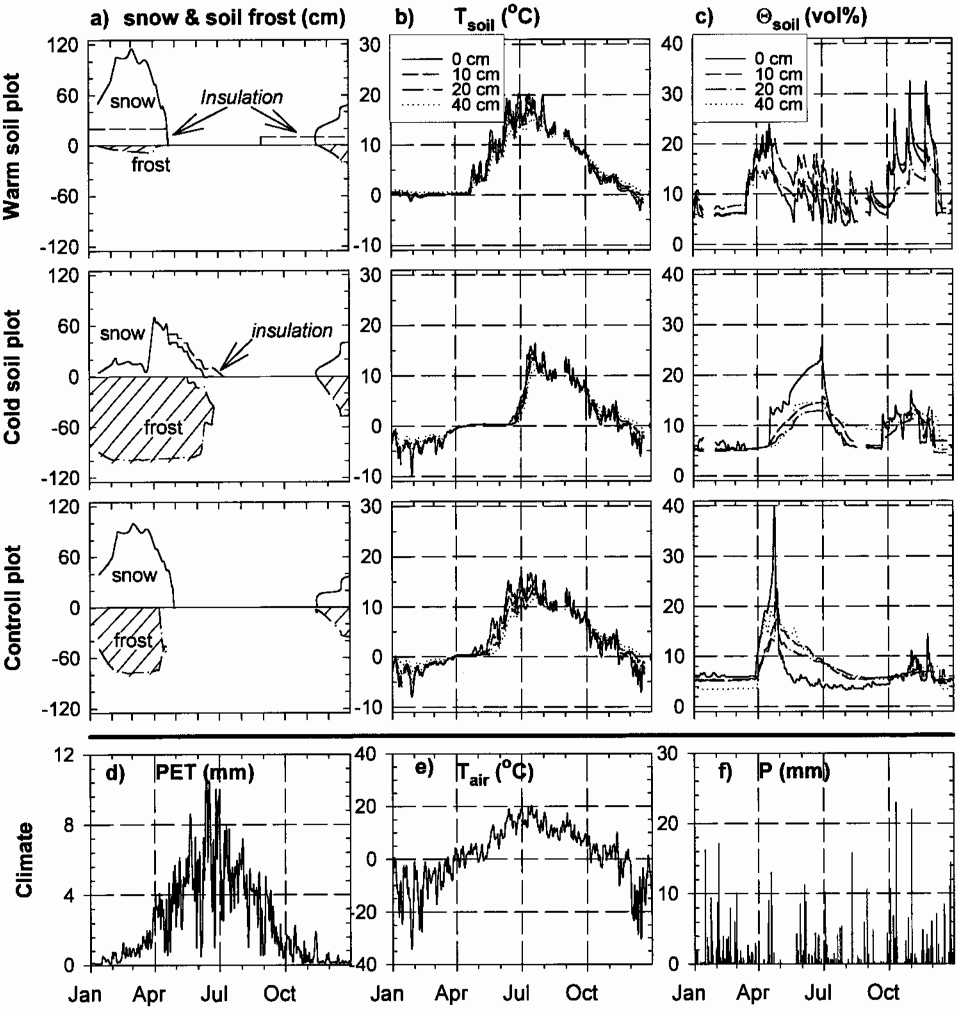

Figure 1 Time series of snow cover manipulation on three plots at Västomån 1999, and its effect on: **a)** soil frost as indicated by frost tube measurements, **b)** soil temperature at 10, 20 and 40 cm, averaged from three soil profiles per plot and **c)** soil moisture content at 10, 20 and 40 cm. The lowest row shows daily averages of **d)** potential evapotranspiration (PET) according to Pennman, **e)** air temperature at 170 cm and **f)** precipitation from the climate reference station at Heden.

Soil profile

The total root mass decreased with depth in the soil profile (figure 2a). The amount of living fine roots (<2 mm) was consistently higher than that of dead fine roots. The ratio of living and dead roots, however, decreased with soil depth. The topsoil level (0 – 10 cm) had the highest root bio-mass density (4.2 mg/cm^3). The average saturated hydraulic conductivity (figure 2b) through the profile (0 – 90 cm) was 0.7 cm min^{-1}. The topsoil layer at 0 – 5 cm was most conductive to water; k_{sat} = 1.14 cm min^{-1}.

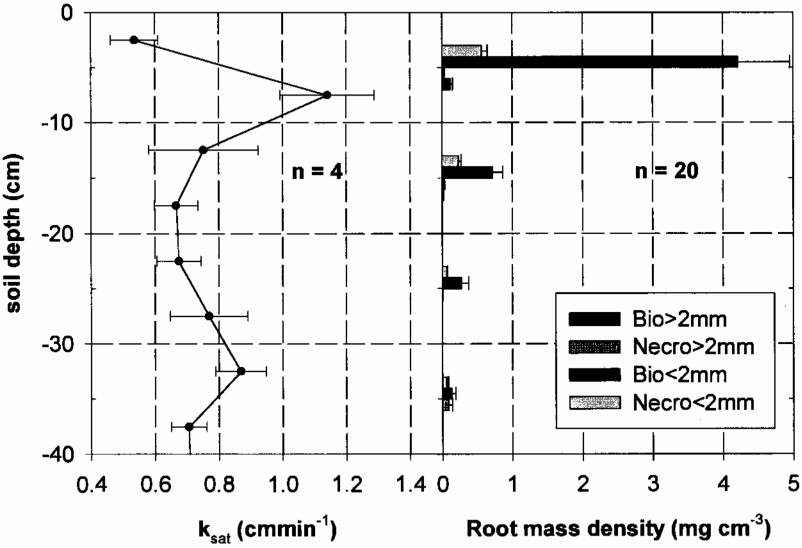

Figure 2 Left: soil profile of saturated hydraulic conductivity (k_{sat}) from 0 – 40 cm. **Right:** soil profile of root mass density (bio = living roots and necro = dead roots) from 0 – 40 cm, measured in laboratory. The horizontal bars illustrate the standard error of the measurements.

Sap flow

The onset and amount of water flow in the tree branches was related to the soil temperature when liquid soil water was available (figures 3, 4, 5 and 6). There were some minor water fluxes in all trees on several days at the end of April and beginning of May. The first major increase of sap flow on the WSP coincided well with the start of the growing season in May 15. Then, with slightly lower rates and some days delay, the sap flow increased on the CTR. After several more days delay, and at much lower rates, sapflow increased on the CSP. On June 5 the flow in all trees was interrupted by a period of rain and low air temperatures. After this period the flow increased rapidly on the WSP, until it became five times higher than that on the CSP. On the CSP the sap flow slowly increased until July 15 when it reached similar rates as on the WSP and CTR. The flow on all plots declined and stopped entirely in the beginning of August, due to rain. In mid-August and at the beginning of September, there were two warm periods which kept soil temperatures above +10°C. Water flow at these times reached the same levels as during the middle of the growing season. At the end of the growing season the measured branches on the WSP had transpired a total of 490 kg per kg DW needles, the CTR branches had transpired 402 kg per kg DW needles and on the CSP 312 kg per kg DW needles.

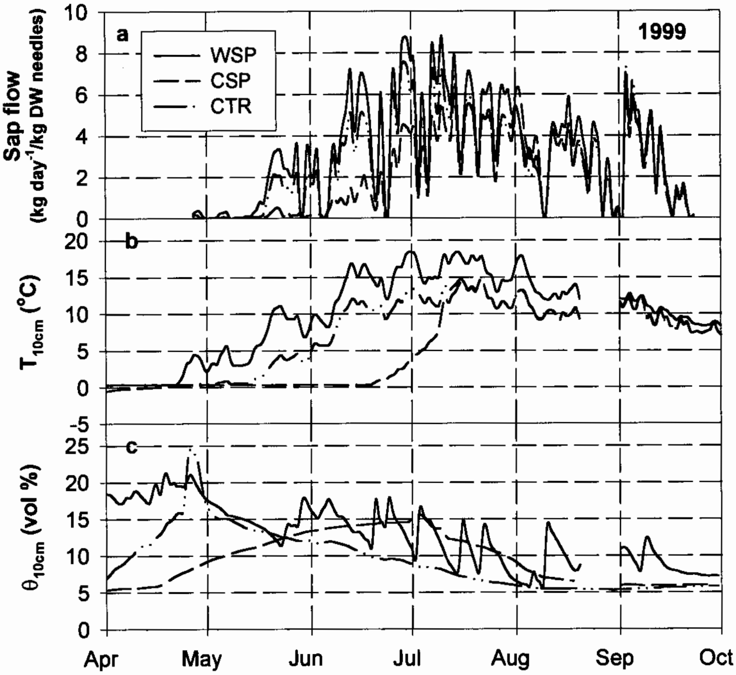

Figure 3 The response of sap flow for the plots with different soil temperature on the WSP (Warm Soil Plot), CSP (Cold Soil Plot) and CTR (Control Plot) at Västomån 1999. **a**) Daily sum of branch sap flow averaged from four branch gauges per plot, **b**) daily average of soil temperature at 10 cm averaged from three soil profiles and **c**) daily average of soil moisture content at 10 cm.

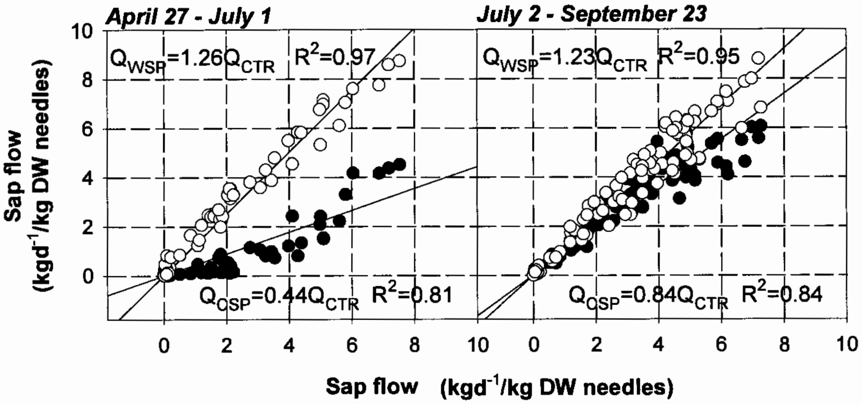

Figure 4 Daily total sap flow on the WSP (warm soil plot, open circles) and on the CSP (cold soil plot, filled circles) plotted against the sap flow on the CTR (control plot). The time series is separated into a period when below-ground conditions differed between the plots (left) and a period when soil conditions were similar (right).

A comparison of sap flow on the WSP and the CSP against that on the CTR illustrated possible influences of the soil treatments on sap flow (figure 4). During the period April 27 – July 1 when soil temperatures differed between the CTR and CSP, the sap flow on the CSP was restricted to 44 % of that on the CTR. Later on, during July 2 – September 23, when soil temperatures were similar, this ratio of water flow on the CSP compared to CTR increased to 84%. The WSP had 26% higher sap flow rates than the CTR during the period April 27 – July 1. This difference between sapflow on WSP and CTR, however, persisted largely unchanged into the autumn when soil temperature and photosynthesis rates (Strand et al, in prep.) were similar.

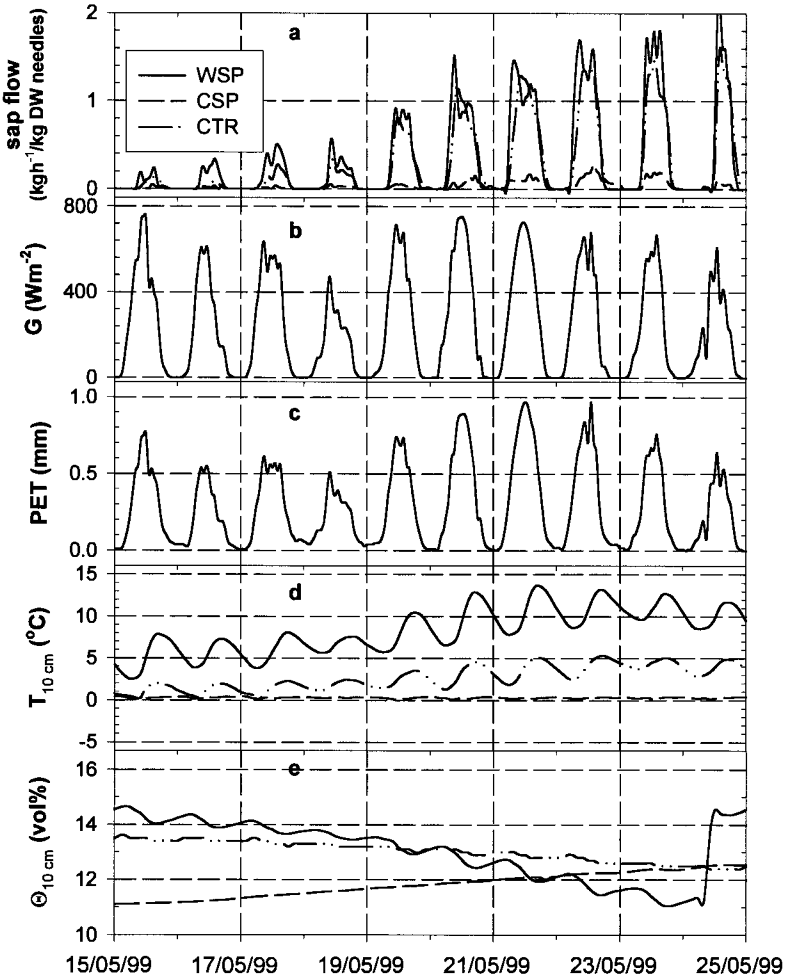

Figure 5 Diurnal patterns of **a)** branch sap flow, **b)** global radiation, **c)** potential evapotranspiration according to Pennman, **d)** soil temperature at 10 cm and **e)** soil moisture content at 10 cm, at the first ten days of the growing season, May 15 – 25 1999. The sap flow and aboveground climate parameters are hourly averages, while soil parameters are two hour averages.

At the beginning of the growing season, the TDR-measurements (time domain reflectometry) revealed more than 10 volumetric percent liquid water on all plots (well above the wilting point). From May 15 to 25, the evaporative demand for water increased. Soil temperature also increased several degrees on the WSP and CTR. On the CSP however, the soil temperatures remained between 0 and +1°C. These conditions were reflected in the hourly water flow rates in the trees (figure 5). On the CSP there were only very low fluxes of sap flow during this period, but on the WSP and CTR the rate of sap flow increased daily. On the WSP the rate was only slightly higher than on the CTR. Each morning, however, the CTR took slightly longer to reach its daily maximum rate than what the WSP did, but the decline after midday was synchronised in both plots. This made the daily total sap flow higher in the WSP than in the CTR even if they reached almost the same magnitudes. This was especially clear during the clear sky conditions on May 20, 21 and 22. On days with a high PET, there was a distinctive midday depression in the WSP and CTR during the entire growing season.

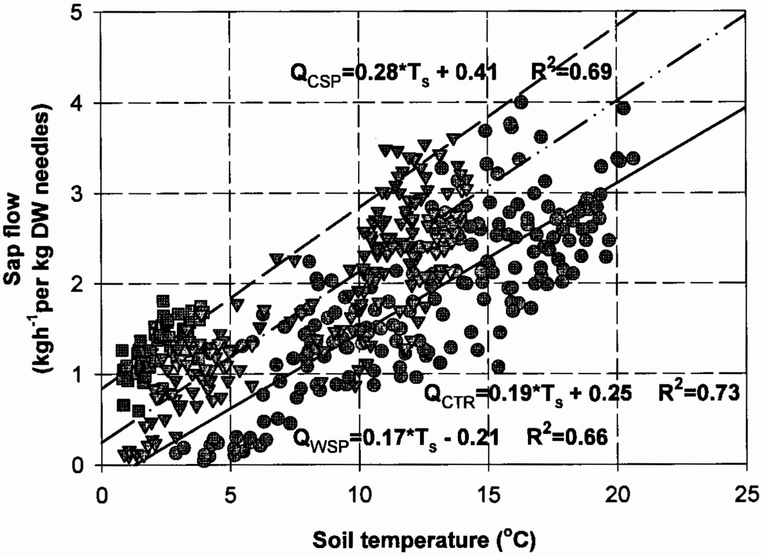

Figure 6 Relationship between hourly averages of branch sapflow and soil temperature at 10 cm, for measurements when the global radiation was equal to or greater than 500 W/m^2. The warm soil plot (circle), control (triangle) and cold soil plot (square). The measurements were compared during the period May 1 – July 1 1999, when the transpiration on all plots had not reached its potential.

By the beginning of July, the soil temperature was above +5°C in all plots. Transpiration was near its potential, and varied in relation to atmospheric conditions. For this reason the time period May 1 – July 1 was used to look for soil temperature influences on the relation between sap flow and PET. The soil temperature at 10 cm showed a clear relationship on each plot to hourly averages of sap flow when aboveground conditions were conducive to gas exchange (figure 6). This relationship was weaker with soil temperature at lower depths (data not shown), although the availability of liquid water did not differ much within the different soil layers. There was a positive correlation of sap flow to soil temperature on all plots, but within different ranges of sap flow for the different plots. The CSP had the highest sap flow for a certain soil temperature, whereas the WSP had the lowest. When comparing hourly averages of PET with sap flow, the correlation was good but varied between the plots and within different ranges of soil temperature (figure 7). The higher the soil temperature range, the higher the sap flow at a certain PET. On the CSP there was a correlation of very low rates of sap flow to PET before the start of soil warming, when soil temperature was just above 0°C. After the start of soil warming, but below +3°C, the sap flow could reach a higher rate for a certain PET on the CSP than on the CTR (on the WSP the soil temperature had already exceeded +3°C at the start of this period). Within the soil temperature interval of 3 – 8°C the response of sap flow to PET was similar on the CSP and CTR but in the WSP the rates of sap flow were very low, similar to those of the pre soil warming on the CSP. (N.B. The WSP exceeded these soil temperature at the start of the period being compared, i.e. before the growing season had begun, whereas the other plots entered this soil temperature range weeks later, after the WSP had soil temperature > 8° C). At soil temperatures exceeding 8°C, the correlation was similar on the WSP and the CTR. On the CSP the soil temperature never exceeded 8°C during this period.

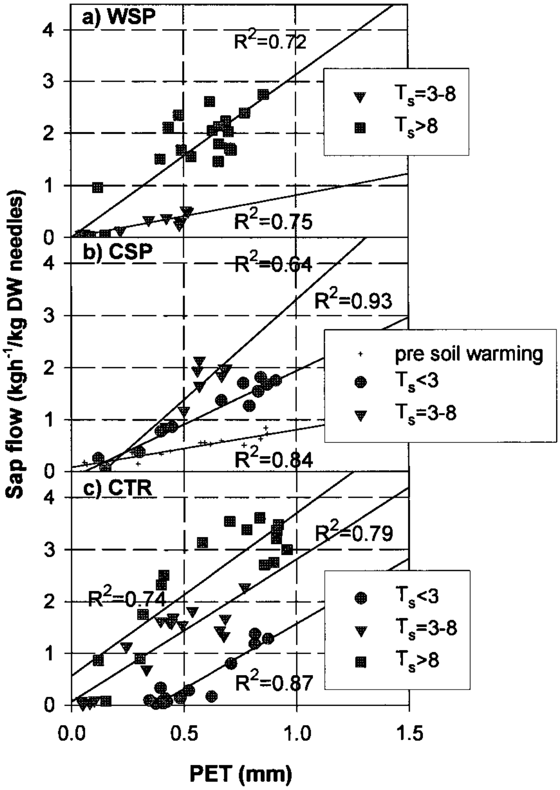

Figure 7 Hourly values of branch sap flow as a function of potential evapotranspiration (PET) according to Pennman, during the period May 1 – July 1, 1999, when the transpiration on all plots had not reached its potential. Data are selected by the maximum sap flow rate during a day, and plotted for different soil temperature ranges (<3°C, 3 – 8°C and >8°C) at 10 cm depth for **a)** warm soil plot, **b)** cold soil plot and **c)** control plot.

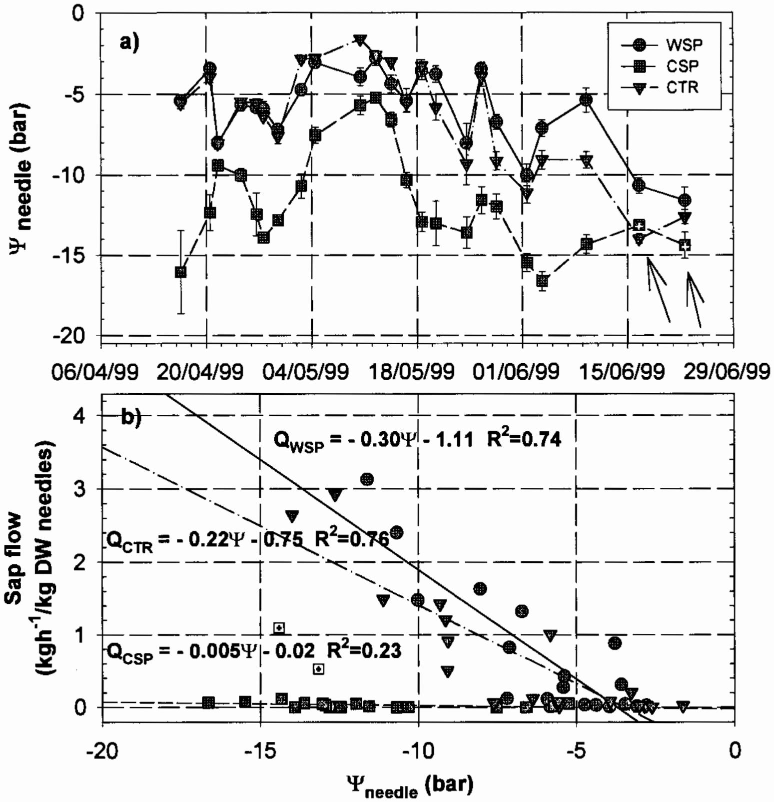

Figure 8 a) Water potentials in needles of trees on the manipulated plots (n=12), April 16 – June 22, 1999. **b)** Hourly values of branch sap flow as a function of needle water potential. The two deviating points on the CSP from June 16 and 22 are marked with arrows and are not taken into account for the regression function.

When the transpiration demand was not satisfied due to inclement soil conditions, the trees were water stressed. This was observed in the water potentials of needles on the CSP (figure 8 a). During the measurement period (April 16 – June 22) the soil temperature interval on the WSP was 0.3 – 14.9°C, on the CTR it was 0.4 – 11.0°C, and on the CSP 0.0 – 1.0°C. The needle water potentials on the CSP were constantly lower than on the other two plots, with the exception of the last two measurements in June 16 and 22 when a difference between the plots was no longer evident. The needle water potentials in the WSP and CTR did not differ much. There was a clear relationship between needle water potentials and sap flow (figure 8 b). This relationship differed between the plots. Since the difference in needle water potential and soil water potential drives water transport through the tree, the slope of the relationship (figure 8 b) gives an indication of the conductance for the entire system between the needle and the soil. The conductance was greatest in the WSP and lowest in the CSP. In the CSP the sap flow was very low during the period of potential measurements, regardless of the water potential in the needle. The only exceptions were the last two occasions in June 16 and 22 (the two deviating points marked in figure 8), when the soil temperature was just staring to rise above 1°C and the PET was high. (These two measurements are not taken into account for the function in figure 8 b).

The shoot elongation followed the same growth pattern on all plots (figure 9) but the lengths varied greatly between the plots. At the end of the growing season the shoots on the WSP averaged 13.3 cm, those on the CSP averaged 7.7 cm and on the CTR 10.1 cm.

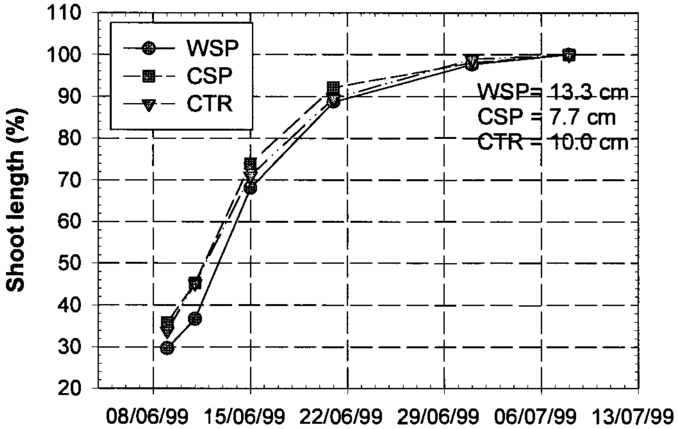

Figure 9 Time series of shoot elongation as percentage of the lengths at the end of the growing season in 1999 from six measurement occasions (n=14 per plot) during June 9 - July 10, 1999.

Discussion

Soil manipulations allowed us to study the *in-situ* tree water dynamics during different combinations of soil and climate conditions covering a wide range of the physical parameters that can potentially influence tree water uptake and the amount of transpiration.

The first question to be addressed was whether the absence of free water resulting from soil frost was a major limitation on water uptake by trees during spring. There is no clear definition of soil frost as the frozen soil may contain different proportions of liquid water and ice even below 0°C, especially at spring when snowmelt water infiltrates into the soil. The TDR measurements, however, revealed available water in the CSP from April 20, well before the start of the growing season. But it took more than a week after the start of growing season before any measurable amount of water uptake occurred (figure 3). Even rain infiltrating through the snow into the soil did not lead to significant water uptake on the next day when PET rose. Before the start of the growing season (May 15) there were some fluxes revealed in the measurements, but these fluxes coincided with rain events and it is possible that sap flow resulted from direct uptake through the bark rather than root water uptake (Katz, 1989; Zweifel, 1999) or from stored water in the bole. We interpret these results as an indication that the absence of soil frost (and hence the presence of liquid water) was not sufficient for tree water uptake during spring on the study plots, even when aboveground climate generated a large PET. For substantial water uptake to occur once the growing season had commenced above ground, the soil temperature needed to rise above zero in the upper soil layer where most of the fine root biomass and a layer of higher water conductivity was.

Low soil temperatures restricted tree water uptake when the growing season had started. Before the start of the growing season however, low soil temperatures had little effect. On the CSP the soil warming was delayed by one month after the start of the growing season in May 15 (figure 3). This severely restricted the sap flow on this plot (figures 3 and 4). The cause of water uptake differences between the WSP, which warmed before the start of the growing season, and the CTR were less clear (figure 4). Since a somewhat larger uptake in the WSP relative to the CTR persisted into the autumn, it is hard to attribute any differences between the WSP and CTR during May to soil conditions, unless root growth was enhanced in the WSP which allowed it to transpire more water throughout the growing season. There were, however, small variations of daily patterns of sapflow between the WSP and CTR in May (figure 5). This corresponds with the work of Zweifel (1999) who found that for a soil temperature lower than 3°C at spring there was a reduction of daily uptake but not in daily maximum transpiration rate in mature *P. abies*. Soil temperature in that study did not affect the water uptake rate but rather controlled the duration of the uptake period. It seemed from our cold soil treatment however, that if soil temperatures are persistently low during the early growing season, both the period and rate of transpiration were restricted by soil temperature.

During clear sky conditions (global radiation > 500 Wm^{-2}) there was a relationship between soil temperature and water uptake on all plots (figure 6). But for a certain soil temperature, though, the CSP allowed more sap flow than the CTR did, and the CTR more than the WSP. During spring and early summer the relationship between PET and sap flow also varied with soil temperature, with a higher soil temperature allowing a higher sap flow for a certain PET (figure 7). This further suggests that soil temperature is of importance for the quantity of sap flow.

But a given temperature on one plot did not correspond to the water uptake seen on the other plots at that same soil temperature. Although low soil temperatures restricted the water uptake, the effect of a certain soil temperature was not the same at different times of the year, which could also be seen in the variation of sap flow during periods of cold soil temperatures (figures 3 and 5). Because the soil warming on each plot is delayed by one month, the effects of factors on the trees recovery from winter damage (day length, a period of warm air temperature) contribute to this difference in sap flow at a given soil temperature. This indicates that factors other than soil temperature are also involved in describing sap flow/water.

Another factor potentially contributing to the soil temperature effect is the possibility of a difference in development of new unsuberized roots. A delay of soil warming inhibits the root growth (Kramer and Boyer, 1995). In such a case it is likely that antecedent soil temperatures are of importance. Delay of root growth influences water uptake during a large part of the growing season, but cold soils can have an even more long-lasting effect on productivity if the roots are damaged (Sutinen *et al.*, 1996; Robitaille *et al.*, 1994).

Due to the importance of aboveground conditions, soil temperature was not found to have an effect on water uptake before the start of the growing season. But the longer cold temperatures persisted into the growing season, the more it limited water uptake. The effect of this restriction was also seen in the reduced net photosynthesis on the CSP in May/June by Strand *et al.* (in prep.) At soil temperatures between 3 and 8°C the role of the aboveground climatic conditions increased and allowed more sap flow.

After July 1 the soil temperatures reached well above 8°C (up to 20°C in the WSP) and sap flow did not correlate well with either soil temperature or PET in any of the plots (data not shown). At high soil temperatures it is likely that the transpiration can reach its potential level. During autumn 1999 (with no severe night frost) data from Strand *et al.* (in prep.) revealed that at soil temperatures above 8°C, soil temperature did not affect net photosynthesis or stomatal conductance at saturating light. Soil temperature is often said to be important below a certain threshold, but there are large variations in published values for the threshold. Our data do not allow us to accurately determine a threshold, but suggests that it lies between 0 and 8°C.

Figure 8b illustrates that low soil temperatures induces water stress in the trees and gives rise to a lower conductance in the system. The soil temperature is clearly important in determining the water flow resistance through the soil-plant-atmosphere continuum. In conjunction with lowering the water viscosity, it also reduces the membrane permeability of roots (e.g. Kramer, 1940). As the soil temperature decreases, the resistance in the plasma membrane increases due to less fluid membrane lipids. An insufficient water supply will lower needle water potential, which we also observed on the CSP (figure 8). This may increase the release of Abscisic acid (ABA) which accumulates in the shoots and leads to stomatal closure (Lambers *et al.*, 1998). Not only chemical signals, but also hydraulic signals may be involved in initiating stomatal closure when exposed to low soil temperatures (Day *et al.*, 1991). De Lucia *et al.* (1991) found stomatal closure to be the dominant factor limiting net photosynthesis at low soil temperature for *Pinus sylvestris* seedlings. However, non stomatal inhibition of photosynthesis was also found to be important in Loblolly pine at soil temperatures below 7°C (Day *et al.*, 1991).

Lyr and Garbe (1995) found that root activity is more important than air temperature for shoot extension. Our soil manipulations however, did not reveal any effects of low soil temperature on the timing and growth pattern of the shoots, but it did affect the shoot lengths (figure 9). On July 10, 1999 the shoots on the WSP averaged 13.3 cm, while on the CTR they were 10 cm and on the CSP 7.7 cm. This suggests that aboveground climatic conditions affect the timing and pattern of shoot extension but, as seen when compared to the previous year (data not shown), low soil temperature seem to restrict the capacity.

In comparison with earlier work, this study demonstrated that many of the results on seedlings and saplings also hold true on larger trees in the field. There was an increase of the water flow resistance in the soil-plant-atmosphere continuum with lower soil temperature, and the importance for water uptake was greatest when cold soil temperatures persisted into the growing season (defined by aboveground conditions). This was seen on the CSP where low soil temperatures reduced water uptake, created water stress, and presumably reduced growth.

A decrease of root permeability and stomatal conductance is the likely explanation of our observed decrease in transpiration rate and low needle water potential at soil temperatures below 8°C (figures 3, 4, 5 and 7) and thus also the large differences in shoot lengths between the WSP and CSP (figure 9).

While the cold soil treatment delayed warming by one month relative to the control, and two months relative to WSP, it is important to note that a two month span in the date of soil warming is found between years on forest soils in the area (Kluge *et al.*, in prep.).

Conclusion

This field scale experiment has confirmed the importance of low soil temperatures for tree water uptake during spring when soil warming occurs after the start of the growing season as defined by above ground climate. The release of liquid water, as soil frost melted and snowmelt infiltrated, was not sufficient to satisfy the demand for water during spring when the above ground conditions were suitable for photosynthesis by *P. sylvestris*. The water was not available to the tree until the soil temperature in the upper rooting zone had reached a threshold temperature above 0°C, even if the transpiration demand was large due to above ground climatic conditions. Between a soil temperature of >0 and ca. 8 C, soil temperature was a factor in the restriction of sap flow. While soil temperature had an effect on water uptake in relation to PET, the effect of a specific soil temperature was not the same at different times. Since the plots achieved a particular temperature approximately one month after each other, this indicates that soil temperature during spring influences water uptake in combination with other factors such as length of the day, and the tree's recovery from winter dormancy. The soil temperature effect was most evident on the CSP where soil warming occurred a month after the start of the growing season.

Soil temperatures below 8°C are common in spring and early summer in the northern boreal zone, and changing the dynamics of soil warming below this threshold will likely influence tree growth. The differences in soil warming created by our study span the range of soil warming dynamics that can be expected at a single site due to interannual variations in climate. This range of warming dynamics was also found within Vindeln Experimental Forests during the same year. Thus our results support the hypothesis that forest management has an influence on soil temperature, especially the timing and rate of soil warming during spring. This will affect the transpiration deficit during spring and presumably forest productivity. Important influences on spring soil temperature dynamics, which can be affected by forest management decisions, are the crown canopy, organic layer and snow cover. Each of these are insulating layers that effect heat fluxes. The canopy, however, also affects spatial variability in snow depth.

Thus we consider it important to quantitatively assess soil temperature effects and the effect which silviculture has on soil temperature to see if they should be given more consideration in forest management in areas susceptible to soil frost and low soil temperatures.

Acknowledgements

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Forest Edge Effect on Tree Water Use in a Boreal Scots Pine Stand on Sandy Soil

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Abstract

The effect of the forest edge on tree water use and increment was studied in a 40-60 year old mono-specific stand of Scots pine (Pinus sylvestris) trees growing on poor sandy soils in the northern boreal zone of Sweden. The forest edge in this study was oriented towards the north where the stand bordered on a clear-cut established about 50 years ago. There were differences in water use and increment during the growing period between trees growing at the forest edge and trees growing in the forest interior. These differences were mostly related to soil conditions, including access to soil moisture, low soil temperature and soil frost conditions, whereas an effect of above ground microclimate was not found. The estimated tree water use and increment over one growing season was larger 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, tree height and green crown length, but these differences were also on the limits of statistical significance. The estimated seasonal transpiration was low, about 70 mm when estimated exclusively from forest interior and 107 mm when estimated exclusively from trees at the edge. This illustrates the likely magnitude of water use enhancement due to the conditions specific to the forest edge.

Key words

edge effects, sap flow, transpiration, sapwood, increment, microclimate

Introduction

At the edge zone interface of a forest with open field, specific microclimatic conditions develop that are different from those in the interior forest (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 to the interior forest. At the forest edge, enhanced turbulence can make ventilation much more effective. Wind penetration eases rapidly towards the forest interior, but it may extend up to several hundreds meters (Chen et al. 1995). The forest edge also creates specific soil temperature and moisture gradients that may extend deep into the interior forest. These factors affect tree water use and carbon allocation. Trees situated at the forest edge have carbon allocation 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 transpiration and interception evaporation fluxes relative to interior forest.

The edge zones in the landscape and the associated fractionation of vegetation 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 fractionated landscape elements, e.g., frequent small forest patches, may underestimate the actual fluxes. Obviously, this will depend on the degree of vegetation fractionation in the landscape. Within a specific stand, one of the key characteristics of the forest edge zone will be stand structure and density. In an intensively managed landscape, typical for most European countries, stands create sharp boundaries with agricultural land and pastures. In recent decades more attention has been paid to biodiversity and esthetic 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 in more southern latitudes. Among the factors affecting growth, water is generally considered to be abundant, and thus not a limiting production, especially compared to nutrient deficiency and low temperature. Indeed, the current fertilization and heating experiments indicate that the forests in the northern boreal zone have a large production potential (Bergh et al. 1999). However, trees grown on sandy soils, which are common in some areas of Northern Sweden, may not be able to utilize precipitation, because water is effectively drained through the sandy soil layers. In such situations, trees grown at the forest edge boundary may benefit from less competition for water stored in the soil of the neighboring open area and from more effective rainfall relative to the forest interior (Matlack 1993; Weathers et al. 1995). Another aspect that is specific to boreal forest ecosystems is formation of soil frost. Frost duration, melting period and generally low soil temperatures are crucial parameters that determine production of boreal forests. It is thus essential to assess the gradient of soil temperature and moisture conditions from the forest edge towards the stand interior, together with its importance for tree function and growth.

In this paper we examined water use and growth conditions of a relatively sparse boreal forest grown on sandy soil that is typical for some areas of Northern Sweden. In this initial experiment, we focussed on two contrasting situations, namely the edge zone and the interior forest. We aimed at detecting the likely differences that are established at the edge zone relative to the forest interior with respect to factors both above and below ground.

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 glacifluvial deposits. The forest of the Heden area is mostly composed of mono-specific Scots pine (Pinus Sylvestris L.) stands. The soil is a podzolized sandy silt classified by Giesler et al. 2000, as a Haplic Arenosol (FAO 1988) and has only a thin organic layer of about 1- 2 cm at the open heath. In the forest stand this layer is somewhat thicker. The soil is inclined to freezing and is annually subjected to soil frost. The ground water level at the site is estimated to be several meters.

Typically, the area has winters with continuous snow cover from the end of October until the end of April, and growing seasons lasting from the middle of May until the end of September. The mean annual precipitation is close to 600 mm, 35 % of which falls as snow. The mean average temperature is about +1,0°

C. The flat plain of the Heden area is slightly colder than its surroundings and the site is frequently subject to summer frosts.

Meteorology and soil conditions

Data were used from a climate station located at the open heath. The climate station is part of a reference monitoring program of the Vindeln Experimental Forests that includes standard meteorological variables such as air temperature, humidity, precipitation and short wave radiation, but also soil temperature and soil moisture profiles to a depth of 2 meter below ground (Anonymous 1981-97). In the studied year, the growing period started on April 26, which was about two weeks earlier than normal and lasted until September 24 (using a temperature threshold of +5°C). The preceding winter snow cover was established about two 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 actual climatic conditions for the measurement period are shown in Fig. 1. Relative humidity and air temperature were also measured by ventilated Rotronic Hygromer HP100 (Rotronic AG, Bassersdorf, Switzerland) sensors at two additional locations at the upper part of the canopy: 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.

Stand properties and treatments

The study site was established as a 50x80 m rectangle in a 50-60 year old, monospecific Scots pine (Pinus Sylvestris L.) stand. One 50-m side of this rectangle stretched along the forest edge. From there the rectangle extended 80 m deep into the forest interior. Tree height was about 10 to 11 m for the stand, with a mean diameter at breast height (DBH) slightly over 12 cm. The distribution of tree DBH was narrow, typical for planted even-aged stands. Stand basal area was slightly over 20 m^2ha^{-1}. Tree green crowns stretched to about 5 m and formed a relatively sparse canopy. The stand formed a distinct forest edge boundary oriented to the North (20°), where it faced an open area. This open deforested heath area was sparsely covered by ground vegetation represented by lichen (70%), heather (20%) and grass (10%). In the forest stand the lichen and heather cover declined to 50% in favor of lingon berries.

Most of the biophysical measurements used in this study were designed to identify differences between two stand situations, namely the forest edge zone and the forest interior. The edge zone trees were located in the forest edge zone extending from the forest edge 13 m back into the forest. The 13 m depth of the edge zone corresponds to the average tree height plus one standard deviation (10.7 and 2.2 m, respectively). The interior zone was defined as an equally deep (13 m) swath 32 to 45 m from the forest edge. The average distance of the interior zone from the forest edge (39 m) was chosen to be three times the mean tree height and its standard deviation.

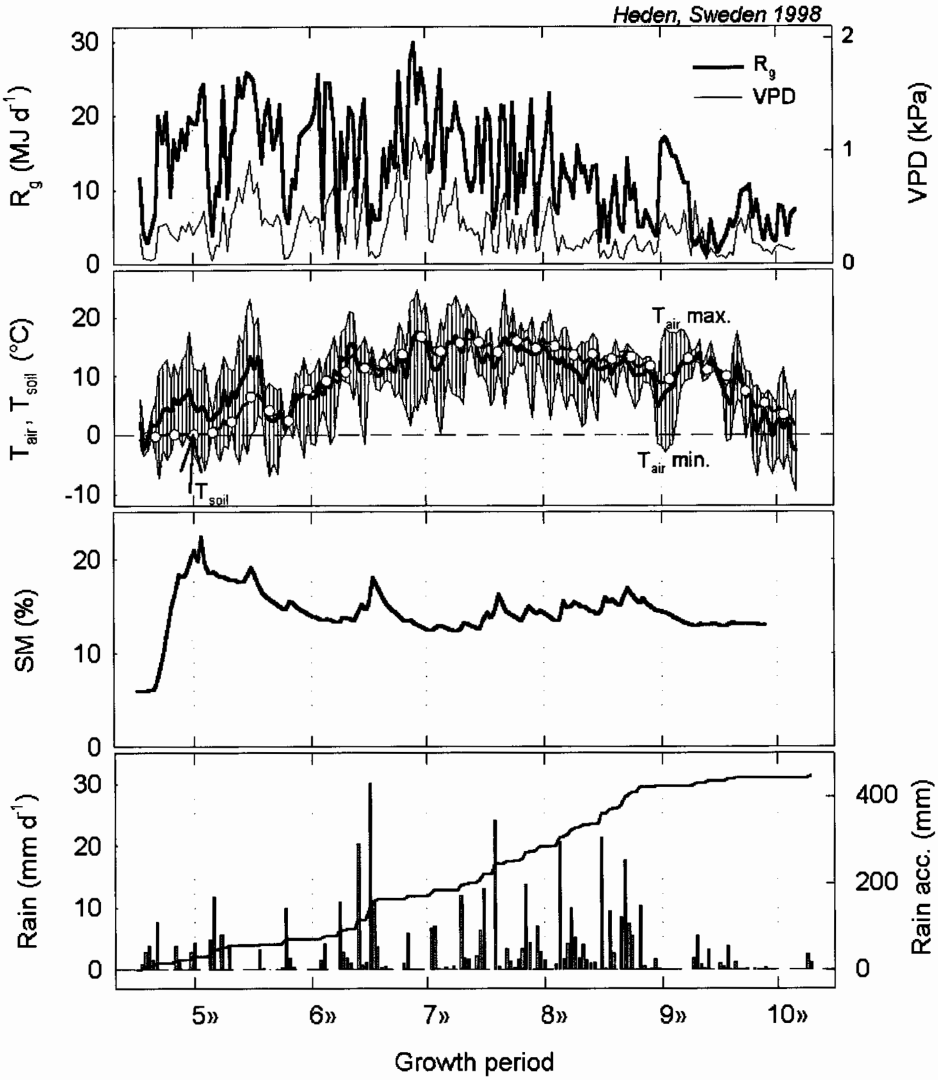


Fig. 1: Climatic conditions at the site: solar radiation (R_g), daily mean vapor pressure deficit (VPD), daily mean, minimum and maximum air temperature (T_{air}) and soil temperature (T_{soil}), soil moisture content at 20 cm (SM), daily and accumulated precipitation (Rain).

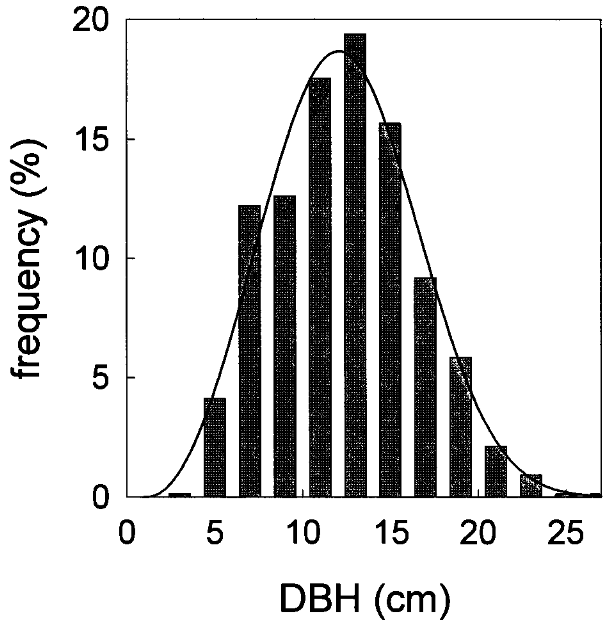


Fig. 2: Stand structure: a symmetric distribution of diameters at the breast height (DBH)

Stand biometry and increment

Basal area increment was continuously measured with dendrometer bands made of a thin metal sheet. They were placed at breast height on 17 trees and on those trees used for sap-flow measurements. Readings were taken at 2-4 week intervals. Other stand biometry was measured during one occasion 30 June and 1 July. These measurements included tree DBH, tree height, and a crown base from which a green crown length could be derived.

Xylem water content and electrical conductivity

The core sampling used in this study was performed on 2-3 July together with the measurements of electrical conductivity. The weather conditions during the measurement were mild, windy, with air temperature of about 15°C. Six trees (three for each treatment, i.e., edge zone and interior) were used for sapwood core and conductivity analyses, with two samples taken on each tree stem from opposing directions.

Sapwood core analyses

A radial profile of water content was estimated from xylem cores taken by increment borer (4 mm inner diameter). The sampled cores were immediately covered by plastic foil, stored in a shaded place and put into 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 set 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

$$w = (FW-DW)/FW*100 \quad (1)$$

where FW (mg) and DW (mg) represent fresh and dry biomass of a segment, respectively. The depth of individual segments was set to one half of the segment length and 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.

Electrical conductivity

A new method for estimation of the radial profile of water content in the stem xylem was applied. The method is based on the assumption that electrical conductivity is directly proportional to xylem water content provided both temperature and ion concentration are constant.

A stabilized AC voltage is applied between a small spot electrode inserted in the xylem and the second, larger one, is put into the soil close to the measured tree. Then, the electrical conductivity is proportional to the current passing between the two electrodes. If the dimensions of the grounding electrode (diameter and length) are at least one order larger than those of the electrode inserted in the xylem, then the bulk electric conductivity relates to the xylem tissue surrounding the electrode according to the equation

$$G = 2*\pi*g*d \quad (2)$$

where G (Siemens, S) is measured electrical conductance of the xylem surrounding the probe, g (S m^{-1}) is specific electrical xylem conductivity and d is the probe diameter. For simplification, a ball-shaped probe is supposed here. This way about 90 % of the conductance estimated with the probe of 2.5 mm in diameter is related to the circumambient xylem in a 10-mm radius. Therefore, the measurement is nearly independent of the tree size and of other circumstances with the exception of those that influence the electrolytic properties of xylem tissue (temperature and ion concentration).

The field application of the method was as follows: the hole of 1.8 mm diameter was drilled in a radial direction into a tree stem. Using a screw-shaped probe of 2.5 mm in diameter and 5 mm long with a metric thread and a lead of 0.45 mm, the probe was carefully screwed into the hole and the value of electrical conductivity at certain different insertion depths was read. The battery operated measuring equipment supplied the probe with a sinus shaped alternating voltage of 50 V. Conductivity values in µS were shown on an LCD display.

Twelve sample trees (six for each treatment, edge zone and interior trees, respectively) were used for electrical conductivity measurements. Each tree was measured in two to four directions. The readings of electrical conductivity were performed in 5 mm steps. The first one or two readings were usually rejected from subsequent analyses. This was because these represented the phloem and vascular cambium tissues, which are easily distinguishable by a conductivity two to three times higher conductivity than that of sapwood.

Sap flow measurements

Sap flow was measured using a heat balance method (Cermak et al. 1973; Kucera et al. 1977) using the 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 sub-surface 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). Tree-trunk sap flow was measured using 18 measuring channels applied on 10 trees that were distributed in two groups, namely edge zone trees and interior trees. This distinction was given by the position of a sample tree relative to the forest/open field boundary (Table 1). Trunk sap flow measurements were usually applied at two opposite sides of a tree in order 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 not classified with respect to the position in the stand (edge zone or interior). All sample trees were dominant or co-dominant in the studied stand.

Table 1: Selected trees for the measurements of sap flow and basic tree biometry

Treatment	Tree Number	DBH/o.b. [cm]	DBH/w.b. [cm]	Height [m]	Crown [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
	average	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
	average	18.2±1.0	15. 1±0.5	13.6±0.4	6.2±0.9

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. To establish a continuous transpiration record for the whole growing period, some missing values in July and August (n= 20 days) were extrapolated on a daily basis using the branch sap flow data that ran continuously.

Results

Tree and stand biometry

The mean stand DBH was 12.1 cm, with and a tree density was1660 trees ha^{-1} as estimated on the 50 m wide study area and extending 80 m from the forest boundary towards the stand interior. 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 moderately homogeneous with respect to distance from the forest edge. The variability of these stand parameters increased when comparing smaller areal units. When the site was divided into two 40-m deep plots, the differences in stand tree density between the edge and interior plots were compensated by the differences in the mean DBH and the resulting basal area was almost identical (Fig. 3). Using areal segments that were only 20 m deep revealed some variation in the basal area. The standard deviation in the mean for the four successive stand segments from forest edge towards the stand interior was about 15%.

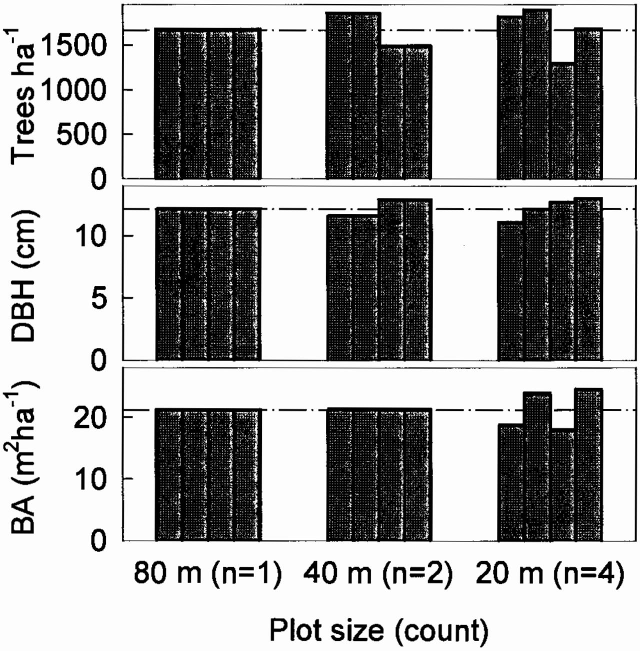


Fig. 3: Stand biometry as measured on the segments extending 80 m (n=1), 40 m (n=2) and 20 m (n=4) towards the stand interior: tree density (top, trees ha^{-1}), mean diameter at the breast height (DBH, middle) and stand basal area (bottom, BA, m^{2}ha^{-1}).

The sample group of edge zone (0-13 m) trees had an insignificantly smaller mean DBH (12.8 cm; n=33) compared to the interior zone (32-45 m) trees (13.0 cm; n=17). At the same time, the length of the green crown was larger for the edge trees (6.0 m) as compared to the interior trees (5.3 m). This difference, however, was still statistically insignificant (t-test P=0.154). On the contrary, the total tree height was significantly smaller for the edge zone trees compared with the interior ones, with mean values 10.2 and 12.1 m, respectively (P=0.014; Fig. 4).

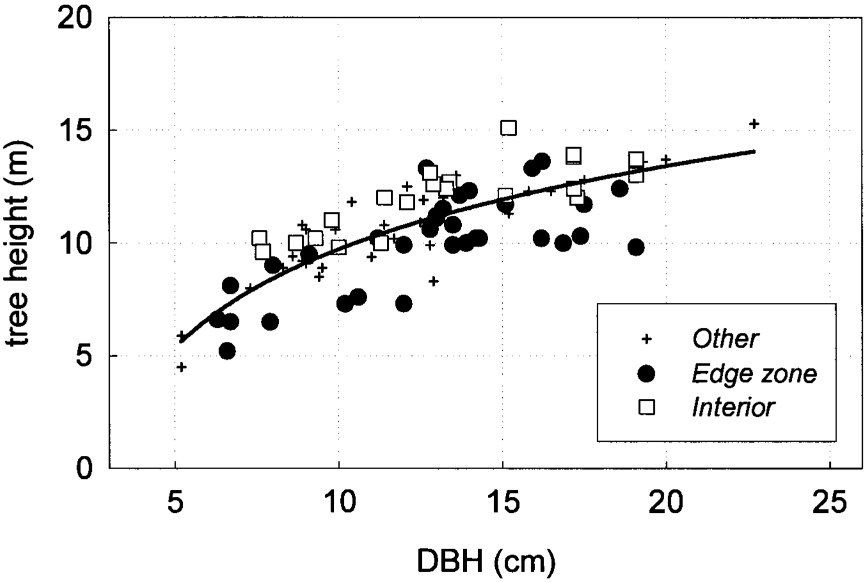


Fig. 4: Tree height against diameter at the breast height (DBH). The total data sets (cross symbol) and the marked groups of edge and interior trees. Two–parameter logarithmic function (r^2=0.64; solid line) was fitted to all data (n=89).

The increment measured during the growing season of 1998 was higher for the edge zone trees as compared to the interior trees (Fig. 5), although a large variation existed among the trees within each group, especially among trees at the edge zone. The stems typically shrank during the spring period of May, when soil temperature remained low.

Radial profile of stem moisture content and conductivity

The radial profile of relative water content for edge and interior trees is shown in Fig. 6. The water content profile for the edge trees was deeper and its shape was different as compared to that of the interior trees. These differences were statistically significant in some cases, e.g., at the radial stem depths of 2, 17 and 22 mm (t-test, P = 0.05). An analogous pattern was observed for the profiles of electrical conductivity for the two groups of trees. The xylem electrical conductivity reached a similar maximum, but the extent of high values was larger for the group of edge trees. The differences between edge and interior trees were statistically significant in the depth of 17-22 mm (t-test, P = 0.05).

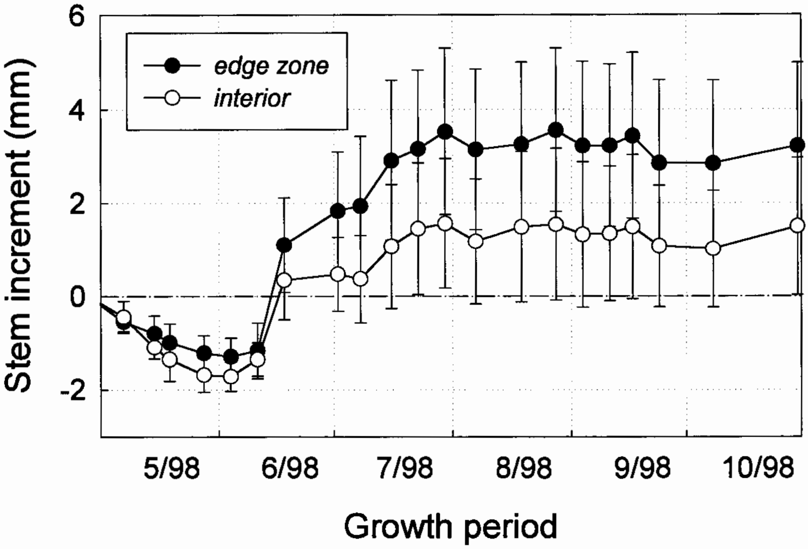


Fig. 5: Mean stem increment at the breast height and standard deviation for the trees growing at the edge zone and for interior trees.

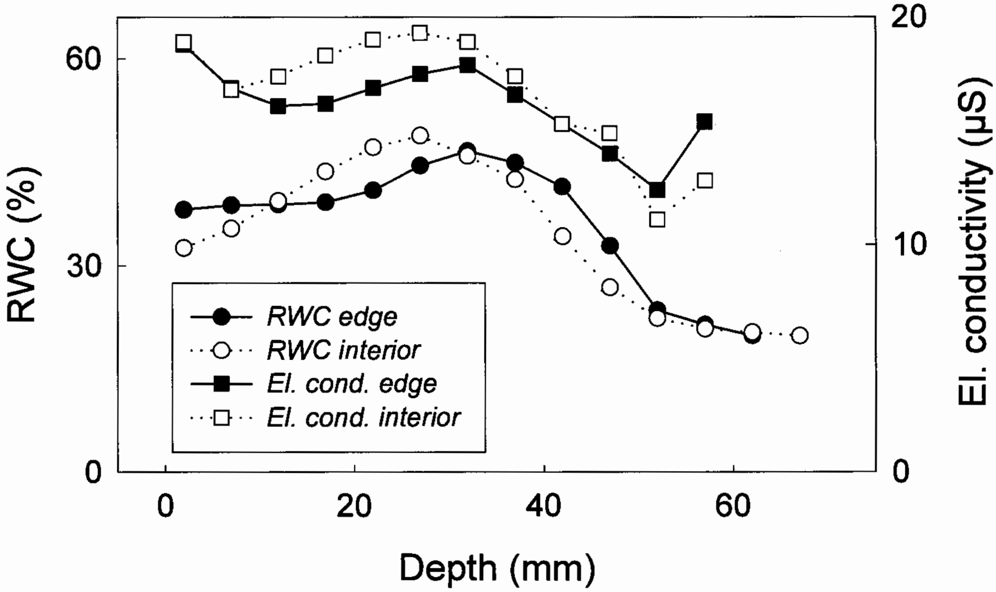


Fig. 6: Mean radial profile of xylem water content (RWC) and electrical conductivity in stems of the edge and interior trees (mean values). The depth 0 mm locates the boundary of xylem sapwood and phloem (or vascular cambium); the depth increases towards the stem center.

Tree water use

The daily mean specific sap flow (xylem sap flow per unit of stem circumference, Q_w) reached its maximum of about 0.4 kg cm^{-1} in July. It was larger for the edge zone trees than for the interior trees for most of the season (Fig. 7). However, water uptake was detected earliest 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 period in spring compared with the edge zone trees (Fig. 8). The mean daily Q_w became larger for the edge zone trees starting in June, about a month after the onset of detectable transpiration. This situation continued towards the end of the growing season (Fig. 7). The quantitative differences in Q_w were mostly insignificant, as the standard deviation of the mean remained relatively large. Tested on monthly periods, the differences in mean Q_w became significantly different (higher) for the group of edge trees only in July (t-test, $P = 0.043$).

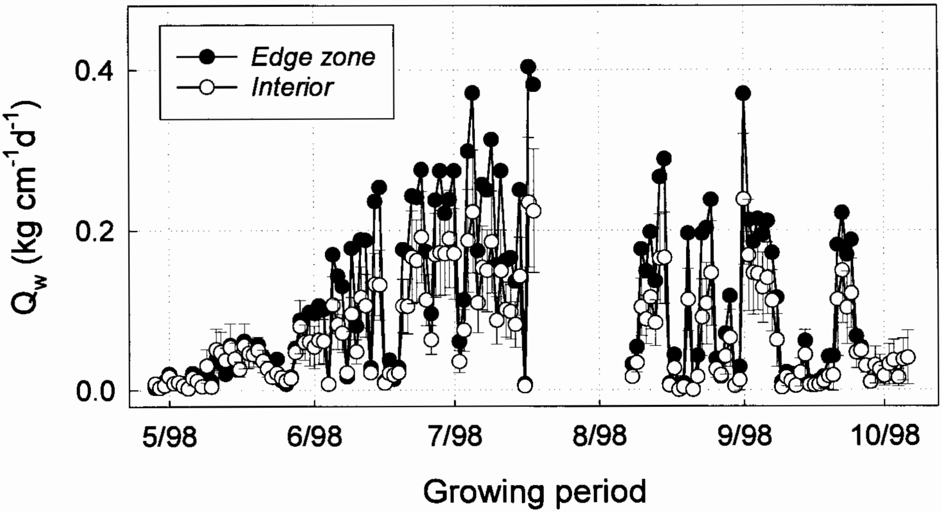


Fig. 7: Specific sap flow per unit of stem circumference – mean daily values for sample trees of the edge zone and interior trees. Standard deviation is noted for the group of interior trees.

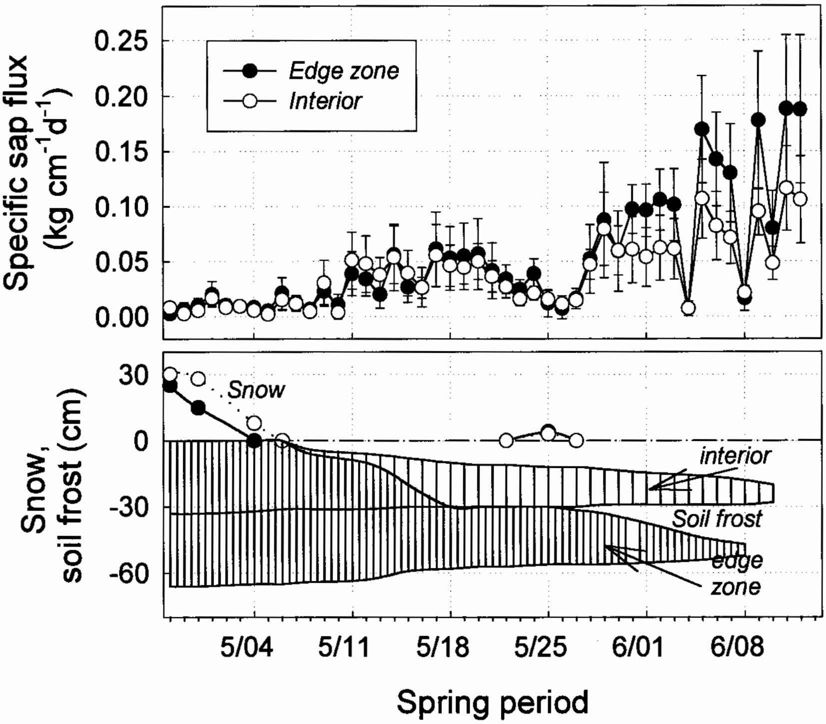
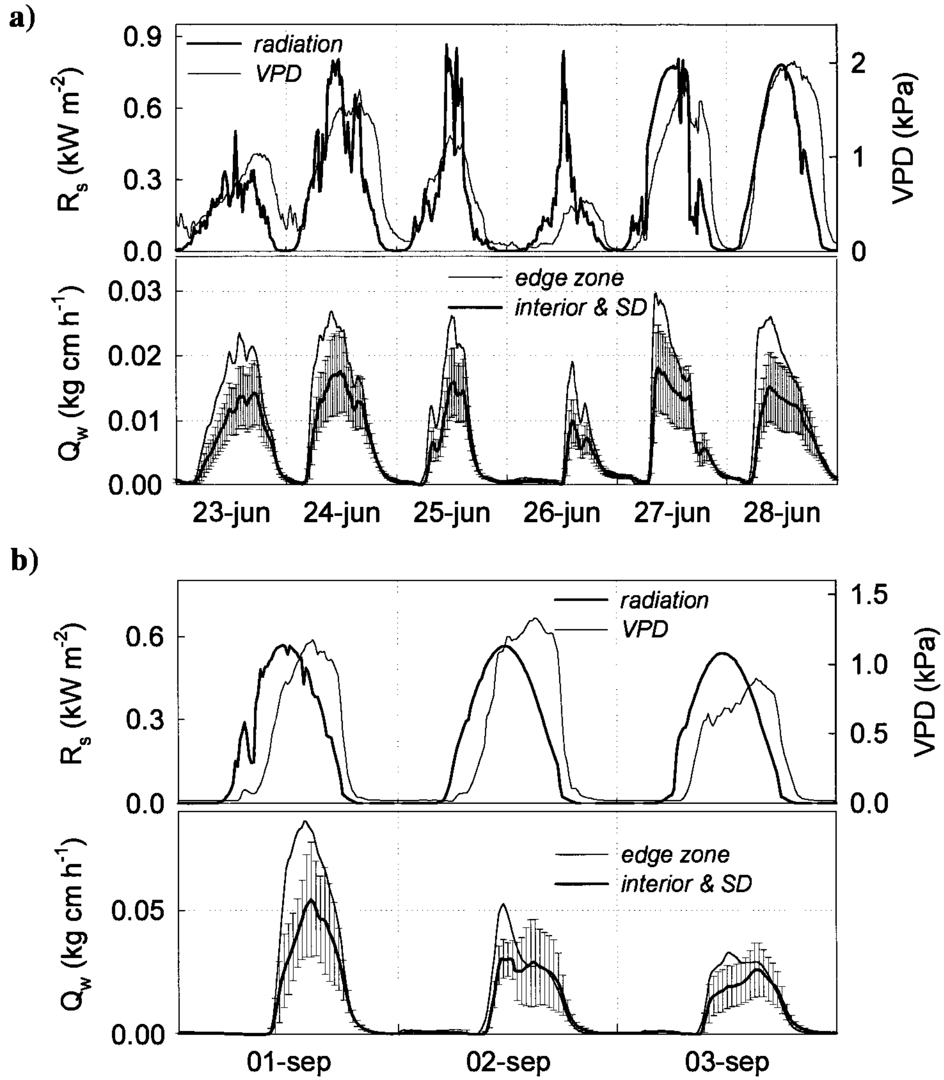


Fig. 8: Spring period: transpiration per unit of stem circumference (specific sap flux) of edge zone trees and interior trees, with standard deviation of the mean shown. Below: snow layer and depth of frozen soil for edge and interior zones, respectively.

On a diurnal scale, the Q_w pattern was similar for edge and interior trees. As shown during the early summer period, Q_w for both edge and interior trees had a good correspondence to evaporative drivers when evaporative demand was rather low (Fig 8a, days 23-26 June). However, the water uptake curve under high evaporative conditions peaked quite abruptly after it reached its maximum in the morning and then gradually decreased (Fig. 9a, 27-28 June). This was in contrast to the course of vapor pressure deficit and radiation in that both peaked later in the afternoon and decreased in a different manner than Q_w, which indicates water deficit conditions or conditions of low conductance for water transport along the conductive pathway. Quantitatively, water flux was higher for edge zone trees relative to 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. 9b). This period followed a rainy spell of August 16-31 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 it decreased rapidly the following day and remained considerably lower, despite higher or similar evaporative conditions. The mean tree fluxes for the two groups had distinctively different diurnal dynamics, and the edge zone trees reached higher values as compared to those in interior conditions (Fig. 9b).



Figs. 9a, 9b: Diurnal course of mean specific sap flow (Q_w in kg h^{-1} per cm of stem circumference) of trees at the edge zone and of the interior trees with standard deviation shown for the interior trees. Climatic drivers - short-wave radiation (R_s) and vapor pressure deficit (VPD) are also shown. Data are shown for **a)** early summer period 23-28 June and **b)** late summer period 1-3 September.

The specific sap fluxes, expressed on a tree basis, gave tree sap flow with a maximum of about 25 kg d^{-1} for the largest trees at the edge of the stand. The typical values of daily tree sap flow were about 15 kg d^{-1}. A detailed comparison of sap fluxes expressed both in the 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 generally the 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).

Table 2: Measured fluxes of sap flow and climatic variables for the early and late summer periods, respectively. Sap flow is shown either as a specific (Q_w) value, expressed per cm tree circumference, and a tree-based (Q_{wt}) value expressed per tree. Climatic variables are mean daily values for the two periods.

	June 23-28		**September 1-6**	
Sap flow	Q_w (kg/d/cm)	Q_{wt} (kg/d)	Q_w (kg/d/cm)	Q_{wt} (kg/d)
Edge #191	0.194	9.72	0.196	9.78
Edge #193	0.218	10.9	0.238	11.9
Edge #201	0.225	11.7	0.278	14.4
Edge #202	0.304	14.0	0.383	17.6
Edge #203	0.129	5.69	0.124	5.47
Edge #204	0.219	10.1	0.171	7.87
Int. #205	0.086	4.55	0.089	4.70
Int. #206	0.162	7.79	0.203	9.75
Int. #207	0.148	7.23	0.149	7.29
Int. #208	0.184	9.74	0.201	10.7
Mean edge ±SD	0.215±0.056	10.3±2.7	0.232±0.091	11.2+4.4
Mean int. ±SD	0.145±0.042	7.33±2.1	0.160±0.054	8.10±2.7
Meteorology				
Air temperature	12.9 °C		8.6 °C	
Relative humidity	63.7 %		80.7 %	
Short-wave radiation	241 W m^{-2}		175 W m^{-2}	
VPD	0.70 kPa		0.33 kPa	

The total of stand transpiration (E_Q) for the growing season, calculated with the assumption that the tree flux is linearly related to tree circumference, reached 107 and 69 mm based exclusively on the measurements of edge zone trees and stand interior trees, respectively (Fig. 10). 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 the interior forest transpired just about 64% compared with the edge zone.

The qualitative relationship of E_Q to evaporative demand was assessed on the relation to potential evaporation by Turc (1961). Across the whole growing period, this relation was weak for both edge zone ($r^2 = 0.51$) and interior forest ($r^2 = 52$). This relationship was weak at the beginning of the growing season but improved later in summer. Performed for the monthly periods, the coefficient of determination (r^2) of the linear regression between edge zone (interior) E_Q and Turc evaporation reached values of 0.22 (0.33) in May, but 0.74 (0.75) in August and 0.67 (0.64) in September.

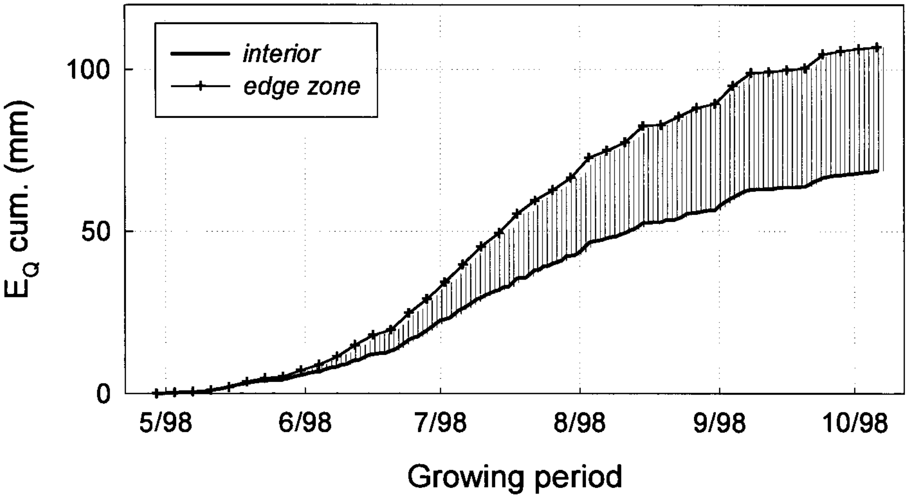


Fig. 10: Cumulative values of canopy transpiration (E_Q) calculated from edge zone and interior trees, respectively. Some missing values in summer period were filled from the regression to mean daily branch sap flow. Shaded area shows a likely range of E_Q that depends on the weight given to particular situations, i.e., edge zone and forest stand interior.

Discussion

The measurement campaign revealed some notable differences in water use and growth increment of the trees in the edge zone relative to 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 of water uptake, increment 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 in light, temperature, litter moisture, vapor pressure deficit, humidity, shrub cover and wind (Carmago and Kapos 1995, Chen et al. 1993, Chen et al. 1995; Matlack 1993; Weathers et al. 1995). However, on 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 exposition has the smallest gradients of microclimatic variables. In particular, the northern exposure minimized any enhancement of radiation effect.

We checked the differences in two other variables, namely air temperature and relative humidity, since the vapor pressure deficit is the primary driving force for transpiration. The comparative measurements of temperature and humidity gradients into the forest interior performed by ventilated sensors over July to September did not reveal any significant differences between the forest edge and stand interior (40 m distant). Air temperature and relative humidity differed on average by about 0.2°C and 1.5%, respectively between the location at the forest edge and 40 m inside the forest stand (data not shown). These differences are also within the specified accuracy of the applied instruments (Rotronic AG, Bassersdorf, Switzerland).

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 towards the stand interior (Raynor 1971, Fritschen 1985), obviously depending on the density of the forest wall. We may consider that increased ventilation at the forest edge increased aerodynamic conductance, herewith promoting transpiration there. However, the northern coniferous forests have large 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 vapor pressure deficit at the two locations that might help explain the enhanced water flux in the forest edge zone.

Stand structure and tree growth

The tree and stand biometry did not reveal any strong difference in the edge zone trees as compared to those in the stand interior. The edge zone should generally support longer green crowns, and an indication of this was the difference of 0.6 m found here. This difference represents about 10-11% of the average crown length, which is too little to be of major importance for transpiration fluxes. Similarly insignificant was the difference in DBH for the two groups. 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 significant difference in a biometric parameter between the edge and interior zones was tree height, which tended to increase towards the stand interior. This likely reflects an intensified competition for light among trees in the interior stand. On the basis of the above findings it is surprising to observe the enhanced stem increment over bark for the group of edge trees relative to the interior ones. If this growth pattern was a typical one, such a difference must have been pronounced also in the average 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 from the edge zone trees (Fig. 7), is, however, supported by analysis of radial profiles of stem moisture content and conductivity (Fig. 6). The two independent methods both show 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 1964; Dvorak et al. 1996) and hence also to transpiration (Cermak 1989). The pattern of moisture content and conductivity differed only in the reading that was adjoining cambium. At that place, some intruded remains of the phloem tissues with very high electrical conductivity could have affected conductivity measurements. Similarly, the increased electrical conductivity near the stem axis suggests a presence of pathogen tissues, or some metabolites affecting conductivity by their concentration. Nevertheless, the measurement of conductivity in the radial profile of stems proved to be a promising method that is considerably more efficient and less disturbing compared with the traditional moisture content estimations from drilled xylem cores.

Soil conditions

Apart from nutrition, low temperatures in soils are a common limitation on water use and growth in the boreal forest. This limitation is most often related to extended frost/cold soil conditions, and soil water retention capacity. Our study showed a considerable effect on frost depth at the forest edge zone (Fig. 8). 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 the largest root density (Plamboek et al. 1999).

The duration of frost and cold soils affect tree water uptake directly and indirectly. Directly by inhibiting tree water uptake, and indirectly by inhibiting fine root development. This affects 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 solar insolation (Berg and Chapin 1994). 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 negative during the night (Fig. 1). The limitation by low soil temperature with extended soil frost and likely delayed development of rhizosphere was also indicated by the correlation to Turc (1961) potential evaporation. This relation was generally weak during spring, whereas it improved a great deal towards the end of the growing season, when root uptake limitations by low temperatures diminished and permitted a stronger response to evaporative drivers.

These soil factors may be the likely reason for enhanced water uptake and growth observed at the edge zone relative to the interior. More detailed analysis of soil effects (Fig. 8) on water uptake requires a more detailed measurement program. This should notably include soil temperature profiles at different locations, and preferably also monitoring of root growth by rhizotron technique (e.g., Taylor et al. 1970; Majdi 1996). To analyze the influence of soil frost on tree water uptake, a new experiment was recently set up at two sites in the area (K. Bishop – personal communication 1999).

Tree water use

The daily pattern of water uptake indicated water limitation during the growth period (Fig. 9a,b), despite relatively frequent precipitation (Fig. 1). This limitation could arise because of soil properties with generally low unsaturated hydraulic conductivity and small water retention capacity, resulting in a small amount of water available to plants. Other factors contributing to a decoupling of water uptake from the diurnal patterns of evaporative drivers might also be high resistance to flow along the conductive pathway in plants. However, because plants were able to transport a considerably larger water quantity directly after an intensive precipitation event (Sept. 1, Fig. 9b), this vascular conductivity limitation was likely of minor importance. In the case of the September rain period (Fig. 9b), the shape of the water uptake curve differed between edge zone and interior trees. This may reflect better access to soil moisture at the edge zone with generally more water available to plants (Kapos 1989). 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). However, water content measurements in the forest interior were performed the following year. Then the water content averaged 3% units of volumetric water content less in the interior forest than the open area during September (data not shown). Such values would most likely limit transpiration in the interior forest and thus help explain the observed enhancement of water use by the edge zone trees.

The estimated seasonal quantity of transpiration is considerably lower relative to the values reported for a denser and more productive southern boreal mixed spruce/pine forest in central Sweden (Grelle et al. 1997; Cienciala et al. 1999). It is also lower as compared to the values estimated for a pine stand on sandy soil in a simulation exercise by Gärdenäs and Jansson (1995), but it was about the same as estimated for jack pine stand in the BOREAS northern study area by Biome-BGC (Kimball et al. 1997). It should be noted that the presented 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 determined by a short vegetation period, further enhanced by the unfavorable soil moisture and nutrient conditions limiting growth at the site. On the other hand, the simplified extrapolation of the measured sap flow from tree to stand level does not affect the observed relative differences between the fluxes estimated from edge zone trees or from the stand interior trees.

The simple exercise of expressing stand fluxes based either on the edge zone or the interior data (Fig. 10) indicates that the structure of forest vegetation cover in a region may have importance for calculating fluxes for larger areas. Clearly, the importance of edge zone enhancements will increase for a patchy and highly heterogeneous 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 that would permit quantification of the edge zone extent where edge zone effects on microclimate were present. This might enhance edge zone transpiration fluxes more than seen in this study where only the soil conditions appear to have caused the edge effect.

Conclusions

There were differences observed in water use and stem increment of trees at the edge zone relative to interior ones. The differences were mostly related to soil conditions, including water availability, soil temperature and frost formation in the root zone. Trees at the edge zone benefited from better access to soil moisture relative to the interior trees. Additionally, trees at the edge zone gradually develop a specific structure relative to the interior trees. They tend to have larger sapwood area, longer green crowns and smaller height, which is likely related to the competition for light. However, the overall effect of edge conditions at the site was found to be too small for further analysis of the gradients towards the stand interior and of the significance of edge zone at larger scales, unless a considerably more extensive measurement program is applied. Further investigations of edge effects should target more productive and denser forests in the southern boreal zone with contrasting expositions.

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