

Spring Water Stress in Scots Pine:

Interaction of snow and soil temperature

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Abstract

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Water use and net carbon assimilation during spring was examined on Scots pine trees exposed to different soil warming dynamics in the field. Sap flow, needle water potential and net carbon assimilation were measured on trees that were exposed to a wide range of soil temperature regimes caused by manipulating the snow cover on tree-scale soil plots. This made it possible to quantify the sensitivity of water uptake and recovery of gas exchange by Scots pine in the critical transition from winter dormancy to the growing season, which can be influenced by silvicultural practices. A part of the study was to find a tool for estimating the coupled effect of belowground and aboveground climate on transpiration, as well as to adapt this tool to the harsh climate of the boreal forest. Combining the results of field experiments on tree susceptibility to water stress with a physically based SVAT-model as well as a model for estimating the recovery of photosynthesis helped to predict spatial and inter-annual variability of snow depths, soil warming, water uptake and net primary productivity during spring within different Scots pine stands across the landscape. This could provide a better basis for a more frost-conscious forest management. The studies have confirmed the importance of low soil temperatures in combination with aboveground climate for root water uptake and net carbon assimilation during spring, when soil warming occurs after the start of the growing season. The studies have also confirmed that earlier, controlled laboratory studies on the inhibiting effects of low soil temperature on water relations and gas exchange for seedlings or saplings also hold true on mature trees in the field. The experimental data served well as the basis for model analyses of the interaction between belowground and aboveground conditions on water use and net photosynthesis. The results of the field studies and model analyses suggest that the effect of soil temperature on tree water uptake and net photosynthesis during spring, in conjunction with aboveground conditions, are factors that need to be considered in forest management in areas susceptible to soil frost and low soil temperatures.

Keywords: Low temperature, soil warming, transpiration, root water uptake, carbon dioxide assimilation, soil frost, silvicultural practice, *Pinus Sylvestris*.

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“If it seems soulless to attribute the glories of arboreal form to natural design alone this underestimates an appropriate sense of wonder at the extraordinary and creative inventiveness which life has repeatedly shown.”

(Richard Fortey (1999) when describing the evolution of trees in “Life: a natural history of the first four billion years of life on earth.”)

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Appendix

Papers I – VI

This thesis is based on the following papers, which will be referred to in the text by their respective Roman numerals.

- I. Mellander, P-E., Bishop, K. & Lundmark, T. The influence of soil temperature on transpiration: a plot scale manipulation in a young Scots pine stand. *Forest Ecology and Management* (Accepted).
- II. Strand, M., Lundmark, T., Söderbergh, I. & Mellander, P-E. 2002. Impact of seasonal air and soil temperatures on photosynthesis in Scots pine trees. *Tree Physiology*, 22: 839-847.
- III. Mellander, P-E., Stähli, M., Gustafsson, D. & Bishop, K. Modelling the effect of low soil temperatures on water uptake by Scots pine. (Manuscript).
- IV. Mellander, P-E., Bergh, J. Lundmark, T. & Bishop, K. Recovery of photosynthetic capacity in Scots pine: a model analysis of forest plots with experimentally manipulated winter/spring soil temperature regimes. (Manuscript).
- V. Cienciala, E., Mellander, P-E., Kučera, J., Opluštilová, M., Ottosson-Löfvenius, M. & Bishop, K. 2002. The effect of a north-facing forest edge on tree water use in a boreal Scots pine stand. *Canadian Journal of Forest Research*, 32: 693-702.
- VI. Mellander, P-E., Bishop, K. & Lundmark, T. Modelling a decade of soil temperature in the Scots pine stands of a boreal landscape (Manuscript).

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Introduction

Long cold winters, short growing seasons and long rotation periods to harvest are characteristic of boreal forest ecosystems. Another feature is the mosaic of microclimate conditions throughout the landscape in different stands. In northern Sweden the ground is normally covered with snow for half of the year. The insulating effect of the snow cover reduces soil heat loss, which influences the soil temperature regime and the depth of soil frost. Many laboratory experiments have stressed the inhibiting effects of cold soils on water and gas exchange for seedlings or saplings (*e.g.* Grossnickle, 1988; Day *et al.*, 1991; Wang and Zwiazek, 1999). For newly planted seedlings in the field the importance of soil temperature for seedling establishment and early root growth has been demonstrated (Örlander, 1984). Field studies have also suggested that sap flow is reduced in larger trees by low soil temperature (*e.g.* Bergh and Linder, 1999; Zweifel, 1999). The timing of soil warming in spring, in combination with the above-ground climate, helps to determine when the trees can utilize the liquid water in the soil after snow melt and frost thaw (Paper I and III) for net carbon assimilation (Paper II). 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).

The depth of soil frost generally varies inversely with snow depth (Kubin and Poikolainen, 1982; Stadler *et al.*, 1996), and the snow cover distribution is influenced by the choice of silvicultural method (Ronge, 1928; Ångström, 1936; Pierce *et al.*, 1958). The size of a clearing affects both snow accumulation and snow ablation and may thus affect the timing of water yield (Swanson and Golding, 1982). More recently several observations of the impact of forest management on the soil temperature in northern forests have been made. Canopy removal during harvest influenced both soil temperature and moisture regimes (literature review by Ballard, 2000). A wide variety of soil temperatures during the same spring were observed at different boreal forest stands within a 10 km radius in a study by Kluge (2001). Löfvenius *et al.* (2003) reported a relation of snow and soil frost depths to the stem density in shelterwoods. A possible climate change can also influence the timing of soil warming. In the boreal forest, however, climate change to warmer conditions as is usually predicted does not necessarily lead to warmer soil temperatures at springtime. Hardy *et al.* (2001) suggested that a climate shift towards less snowfall, or shorter duration of snow on the ground, would induce increases in soil freezing in northern hardwood forests. Given the variability of microclimate within a landscape, it is desirable to know how the stand structure and landscape variability will affect the snow cover distribution at a stand level, how that will affect the soil frost depths and how that can lead to different timings of soil warming during spring and early summer. This, in turn, may affect the availability of water in spring and thus the productivity of the forest (Figure 1). Incorporating such knowledge into available bio-geophysical models can provide us with guidelines for a more “frost-

conscious” forest management, and possibly help us to better understand the feedback effects that a boreal forest has on the climate.

There is a need to understand how trees respond to different combinations of belowground and aboveground conditions and how different silvicultural measures may affect abiotic factors such as soil temperature. This thesis seeks to use field manipulations to provide basic data on the response of Scots pine to different soil temperature and soil water conditions during spring, as well as to explore these data and their potential implications with the help of models.

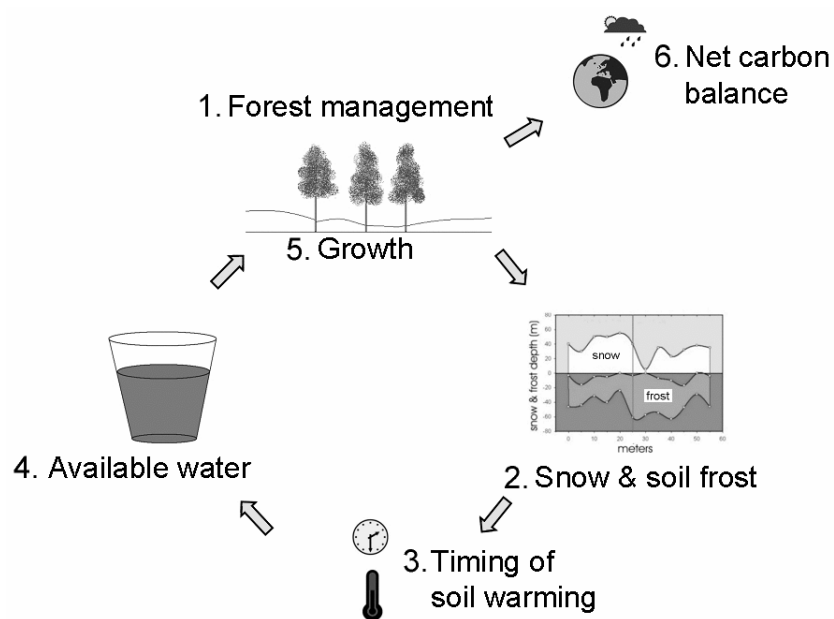


Figure 1 Illustration of how the stand structure and landscape variability interacts with snow cover distribution and soil frost depths, timings of soil warming during spring and early summer, the availability of water in spring, productivity of the forest as well as possible feedback effects on the climate.

Background

Despite the long history of investigations into tree – soil water relationships, the field remains an area of intense and productive research. Before turning to the experiments and models employed in this study, a brief summary of the field is provided.

Plants and water

In 1648 Joan-Baptista Van Helmont made an experiment by taking a vessel in which he placed 200 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 169 pounds and three ounces. Nothing but rain had been added. Finally he dried the vessel again and found the same 200 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 highlighted the importance of water being available for plant growth. But today we know that the system is rather more complex, involving dissolved nutrients, CO₂ 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.

Water constitutes as much as 80 to 95% of the non-woody biomass in trees. Even though the water molecule is one of the most common on earth, the most restricting factor for plant production, on a global scale, is water availability. Since large quantities of water are needed relative to the availability at particular places and times in the soil, water plays an important role in the physiological processes of plants.

At the cellular level, water is needed to transport metabolites through the cell. And at the whole plant level, water helps to transport nutrients from the bulk soil into the roots, as well as transport of carbohydrates, nutrients and phytohormones from the roots to the shoots. Water is also essential for building up a positive pressure against the cell walls (turgor), which is the basic structural support mechanism in plants. If the plant loses its turgor, it can no longer carry out vital processes such as cell expansion and photosynthesis.

Only one percent of the absorbed water is stored in the biomass, the rest is lost by transpiration. This is due to the process of photosynthesis. When the stomata are open for CO₂ to enter the leaf, they also provide a pathway for water loss. This has an important effect on the leaf, as water evaporating from the mesophyll cell surface cools the leaf and protects it from damagingly high temperatures due to high solar irradiance.

In cold climates, water relations are further complicated by the existence of water as ice. There are also resistances that increase along water flow paths due to conditions influenced by low soil and air temperature.

Soil-plant-atmosphere continuum (SPAC)

An important contribution to the study of plant-water relations was conceptualising water as a film through the plant that connects the rhizosphere to the atmosphere, with an array of closely linked processes governing water movement from the soil, into the roots, through the plant, and out in the air along a soil-plant-atmosphere continuum (SPAC). This idea was introduced by Philip in

1966, and has helped us to achieve an integrated view of water relations when studying the water balance of plants.

In the pathway of water through a tree there are a number of physical, biological and chemical conditions influencing the potential gradient between the soil and roots across a semi-permeable membrane, the hydrostatic gradient in the tracheids and the water vapour pressure gradient between the shoots and atmosphere. There are a number of resistances in this pathway that often have been illustrated as an electrical analogue (Figure 2). For trees, these conditions are influenced by the structure of a stand, since the microclimate and the local soil climate are affected by the stand (*e.g.* Chen *et al.*, 1993; Ottosson-Löfvenius *et al.*, 2000). The pressure gradients along 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 potential evapotranspiration and the supply of water and energy to the shoots.

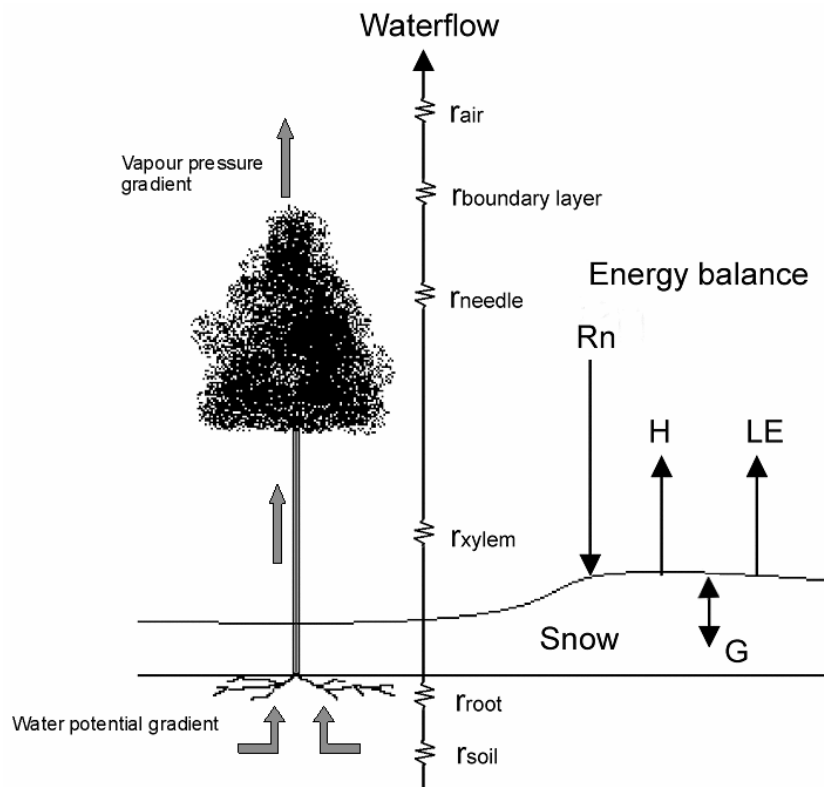


Figure 2 Illustration of the driving gradients along the water pathway through a tree, the electrical analogue of the water flow from the soil moisture store to the atmospheric sink via the soil-plant-atmosphere continuum and the energy balance.

The status of water in soils, plants or the atmosphere is commonly described in the terms of water potential, *i.e.* the chemical potential of water in a specific part of the system compared with the chemical potential of pure water at the same temperature, elevation and atmospheric pressure. The total water potential, in any part of the system, is the sum of the gravitational potential, the pressure potential and the osmotic potential.

Soil

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

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

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

A soil freezes over a range of temperatures, with water freezing first in the larger pores (Stähli, 1996). Liquid water can be present in a continuous film on mineral and organic surfaces even at temperatures well below the freezing point. The different proportions of water's three phases, *i.e.* solid, liquid and gaseous, in combination with soil type, complicates water movement on and through 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, which depends on the soil matrix and its water content. The coupling between the heat and water regime largely controls the movement of water during periods of freeze and thaw. It is important to understand the energy status of a soil when dealing with its water relations. The total potential of soil water is the sum of gravimetric potential, pressure potential and osmotic potential. The forces associated with the attraction of soil particle surfaces to water are a component of the pressure potential, commonly referred to as the matrix potential. 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 total water potential decreases and the retaining forces in the soil water become relatively stronger, changing the water potential gradient in the soil profile. Water flows from higher to lower potential according to Darcy's Law:

$$q = -kA (d\Psi/dZ) \quad (2)$$

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 water is removed and replaced by air, soil is getting drained and drier, 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 force that hinders soil drainage also hinders it from freezing.

Plant

The most important plant factors affecting the water pathways in the SPAC are: leaf area, leaf exposure, canopy structure, stomatal aperture, and effectiveness of the roots as absorbing surfaces (Kozlowski & Pallardy, 1996).

Absorption of water

Water moves relatively easily from the soil toward the unsuberized root tips of a transpiring plant following a water potential gradient. The plant absorbs ions (both passively and actively), which gives rise to a higher concentration of solutes in the root cells. Water can then enter the root cell across a semi-permeable cell membrane driven by the osmotic potential gradient created between the soil water and the root cell solution. The water will choose either a symplastic or an apoplastic pathway. If there is no exodermis the water will take an apoplastic pathway through the cell walls (apoplast) and other spaces outside of living cells. The symplastic pathway goes through the space comprising all the cells of a plant's tissues (symplast) connected by membrane-lined channels through the cell wall (plasmodesmata) and surrounded by a plasma membrane. Eventually the water must enter the symplast at the innermost cortical layer of suberized cells (endodermis). At the endodermis or exodermis, water has to enter the cells, passing the plasma membranes, before it arrives in the xylem vessels. There are also water channel proteins, or so-called aquaporins, which are present in the membranes and allow water passage in a single file (Chrispeels and Agre, 1994).

For developing an efficient root system, the roots must be free from stresses caused by the soil physical environment, such as mechanical impacts, low-water, low-oxygen and low-temperature conditions. As early as the 18th century Hales (1727) observed that cold soil reduces water absorption (in Kramer and Boyer, 1995). In high latitude stands low soil temperatures are known to reduce plant growth in several ways, including by 1) reducing the growth rate of new fine roots (*e.g.* Barney, 1951) that are more conductive to water, 2) influencing stomatal behaviour by abscisic acid (ABA) (*e.g.* Havranek and Tranquillini, 1995; Lambers *et al.*, 1998) that has originated in the roots (Zhang *et al.*, 1987), and 3) reducing the permeability of the cytoplasmic membranes due to lower production of

lubricating lipids (e.g. Kramer, 1940). In the latter mechanism, the aquaporins become somewhat immobilized and the resistance of the plasma membrane to water increases. Also the viscosity of water increases with lower soil temperatures.

Lyr and Garbe (1995) demonstrated that root temperature significantly influenced the growth rates of all organs of *Pinus sylvestris* L. Running and Reid (1980) calculated root resistance of lodgepole pine to be 67% of the total plant resistance at a soil temperature of 7 °C and 93% at 0 °C. Also the root growth of aspen (*Populus* L) was found to be completely inhibited at a soil temperature of 5 °C and inhibited by 97% at 10 °C (Wan *et al.*, 1999). This suggests a significant change with temperature in the membrane permeability and thus the pathway of water into the root system, as well as less exposed absorption area on the roots since low soil temperature reduces root growth. Even a mild soil freezing has been observed to cause significant shifts in fine root dynamics (Tierney *et al.*, 2001). Low temperatures can also decrease the respiration and thus lower the production of ATP, which is needed for the active transport of water into the roots to build up a root pressure. However, many plants, including conifers such as pine, do not develop root pressure (Raven, 1998).

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. In such situations, mucilage can help the root to keep contact with the soil and ease the water uptake. Roots generally have access to available water within 6 mm of the root (Lambers *et al.*, 1998).

Mycorrhizal fungi, which influence the diameter size and dendritic pattern of the root tips, commonly infect the fine roots of forest trees. Root hydraulic conductance was found to be higher in mycorrhizal plant species compared to non-mycorrhizal plants in a study by Landhäusser *et al.* (2002). There was however no soil temperature effect found on the root hydraulic conductance in either species at soil temperatures of 4 and 8 °C.

Sap flow

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 drawn 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. This process described by the cohesion theory which has developed to explain how 100 m tall trees are able to hold a water column when cavitation would occur if pressure gradients were all that was involved. 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:

$$Q_w = -[\pi R^4/8 \eta] [\Delta\Psi_p /L] \quad (3)$$

where $\Delta\Psi_p$ is the difference in water 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^2MPa).

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 of the water transport in trees. Stomata also respond to light to be open for CO_2 assimilation. At clear sky conditions in combination with a shortage of water this causes a conflict in which the stomata have to compromise so as to maximise photosynthesis and at the same time minimise transpiration.

Photosynthesis

Photosynthesis is the reduction of atmospheric CO_2 to carbohydrates by the use of light energy, with a release of oxygen from water. The energy absorption and CO_2 fixation takes place in the chloroplasts. The photochemical reactions involve pigment protein complexes (mainly including chlorophyll molecules). These protein complexes are known as reaction centres. There are two such reaction centres that commonly are described as photosystems I and II.

It is well known that as the temperature in both the air and the soil decreases, so does the rate of CO_2 uptake. Relatively little, however, is known about the interplay between aboveground and belowground temperature influences on net primary production (NPP). Hurst (1987) showed that lowering the transpiration in the root zone reduced the wood production of mature beech trees. The boreal conifers alternate summer growth with long periods of winter dormancy. Even if conditions for photosynthesis are favourable in spring, the rates will be low because of damage to the photosynthetic apparatus due to low winter temperatures and high photon flux densities while needles are still frozen (Öquist *et al.*, 1987). The photosynthetic inhibition is strongly dependant on how low the soil temperature is and to what extent the tree is adapted to the environment. The development of winter hardiness is essential for resisting extreme sub-freezing temperatures and must be maintained throughout the winter until the prolonged spring recovery period arrives (Havranek and Tranquillini, 1995).

The water stress caused by chilling roots reduces stomatal conductance and can cause reduction in photosynthesis. De Lucia (1986) reported that both photosynthetic and leaf conductance declined sharply in Engelmann spruce at soil temperatures below 8°C . Strand *et al.* (Paper II) found the same critical temperature for *Pinus sylvestris*. The climate stress on photosynthesis is regulated both by stomatal conductance and the photosynthetic capacity of the mesophyll. However, the resistance caused by the stomata normally dominates the effect of the mesophyll capacity (De Lucia, 1991). The non-stomatal inhibition of photosynthesis was only found important in loblolly pine at soil temperatures below 7°C (Day *et al.*, 1991).

A large part of the carbohydrates assimilated from photosynthesis are spent by respiration. Under non-stressed conditions, photosynthesis substantially exceeds respiration. This creates a surplus of photosynthesis products, which are available

at times when photosynthesis cannot occur and provides carbohydrates for building up an efficient root system. If a tree is stressed and the photosynthesis is inhibited but respiration continues, the photosynthetic reserves will be depleted. In an experiment where autotrophic respiration (root respiration) was separated from heterotrophic respiration (respiration from microorganisms and animals), root respiration was not found to be more sensitive to soil temperature, however there were links of seasonal root respiration to sap flow (Bhupinderpal-Singh *et al.*, 2003).

Atmosphere

The soil-plant-atmosphere continuum is a part of a dynamic system where aboveground climatic conditions are reflected in the soil climate. The climate variables regulate the daily and yearly supply of energy, carbon and water to the soil and plant. The most important environmental factors affecting transpiration are light intensity, vapour concentration gradient between leaf and air, temperature, wind, and soil water supply. The gradients induce heat and water flows between the soil and air. These parameters, together with solar radiation, vary strongly with time and in space due to differences in the soil surface and vegetation. The gradient in water vapour pressure between a plant and air is the “engine” for transpiration.

Trees intercept solar radiation and precipitation. Thus trees have a large impact on the soil temperature and soil moisture regimes that will vary at one site from one year to another, and also spatially across the landscape during the same year due to differences in snow cover distribution. The structure of a stand also has an important impact on the microclimate as it influences the position of the active surface with regard to the exchanges of heat, mass and momentum. Most of the exchange takes place at the leaves, making the vertical foliage distribution of the stand very important. The resistances influencing this exchange lie within the mesophyll, the stomata, the boundary layer and the air.

Objectives

The aim of this study was to examine the water use and net carbon assimilation of Scots pine trees (*Pinus Sylvestris* L.) exposed to different soil temperature regimes, in combination with the accumulated effects of aboveground climate in the field. This would then be used to quantify the sensitivity of water uptake and recovery of gas exchange by Scots pine to soil and atmospheric conditions in the boreal forest environment, as influenced by silvicultural practices. Another intention was to evaluate possible risks for enduring damage to roots and needles. An additional aspect of the study was to find a tool for estimating the coupled effect of belowground and aboveground climate on transpiration, as well as to adapt this tool to the harsh climate of the boreal forest. By combining the results of the field experiments on tree susceptibility to water stress with a physically-based

soil-vegetation-atmosphere-transfer-model (SVAT) as well as a model for estimating the recovery of photosynthesis, the response of water uptake and gas exchange to silvicultural choices and some aspects of climate change may be predicted. The modelling approach was intended to be used for quantifying spatial and inter-annual variability of snow depths and soil warming during spring within different Scots pine stands across the landscape in order to help provide a better basis for “frost-conscious” forest management.

Materials and methods

Site description

The experiments were conducted in Scots pine stands at Västomån (Paper I, II and IV), Heden (Paper III and V) and observations were used from an additional eight stands (Paper VI). All stands lie near or within Vindeln Experimental Forests (64° 14' N, 19° 46' E) in the boreal zone of northern Sweden (Figure 3). Västomån and Heden are located approximately 180 m above sea level on flat plains of glacial deposits. The soils are ferric and podzolised and have only thin layers of humus (1- 5 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. The ground vegetation is sparse and consists mainly of lichens.

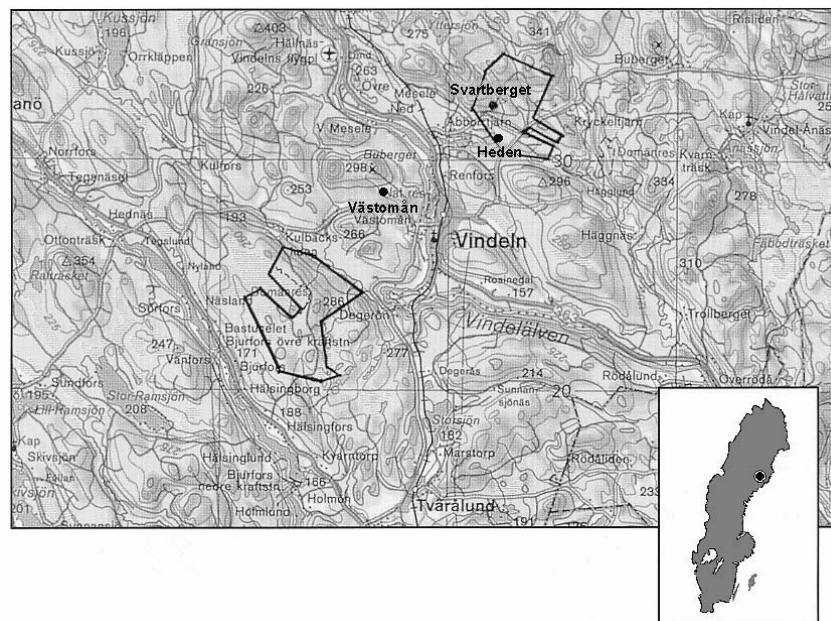


Figure 3 Map of the Vindeln Experimental Forests (2531 ha, 64° 14' N, 19° 46' E, 150 - 290 m.a.s.l.) in the boreal zone of northern Sweden.

The Heden site has a mono-specific, naturally regenerated 70-year-old Scots pine stand. At Västomån the stand is open, mixed and dominated by 20-year-old, naturally regenerated Scots pine.

The climate of the area is characterized by cold winters, and the yearly average air temperature is 1.3 °C (20-year average). The mean annual precipitation is close to 600 mm, of which one-third normally falls as snow (20-year average). The soils are annually frozen, normally lasting from November until June (Odin, 1992). The mean annual period with snow cover is 171 days (20-year average). The growing season is short and normally lasts from the middle of May until the end of September (Odin, 1992). The flat plain of the Heden area is slightly colder than its surroundings, and the site is frequently exposed to summer night frosts.

Experimental design

In the papers I – IV studies were made on manipulated forest plots. Three 30 m² plots were established in the stands at both Västomån and Heden. Each plot had three study trees (Scots pine). The plots were situated ca. 10 m from each other. On two plots per site, the snow cover was manipulated during the winter 1998/1999 in a manner similar to that of Robitaille *et al.* (1994) and Hardy *et al.* (2001). One treatment was made to delay soil warming by maximizing the depth and persistence of soil frost (Cold plot). This was achieved by removing the snow during the coldest period (November – March). At the end of March, this snow was returned 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. The sawdust was removed in the beginning of July, when the snow had melted (Figure 4). Another treatment was made to hasten the soil warming by minimizing the amount and persistence of soil frost (Warm plot). This was achieved by insulating the ground with Styrofoam pellets in large, porous bags late in September. At the end of the snowmelt, in late April 1999, the ground insulation was removed. A third plot was not manipulated and served as a control. During the second year of measurements no manipulations of the snow cover were made.

In Paper V a northerly orientated forest edge at the Heden site was used for analysing how the exposure to different soil and air temperature regimes in the field affected the water use of mature Scots pine. And in Paper VI the variability in soil temperature caused by different stand structure in the landscape was analysed at eight different Scots pine stands within Vindeln Experimental forests.

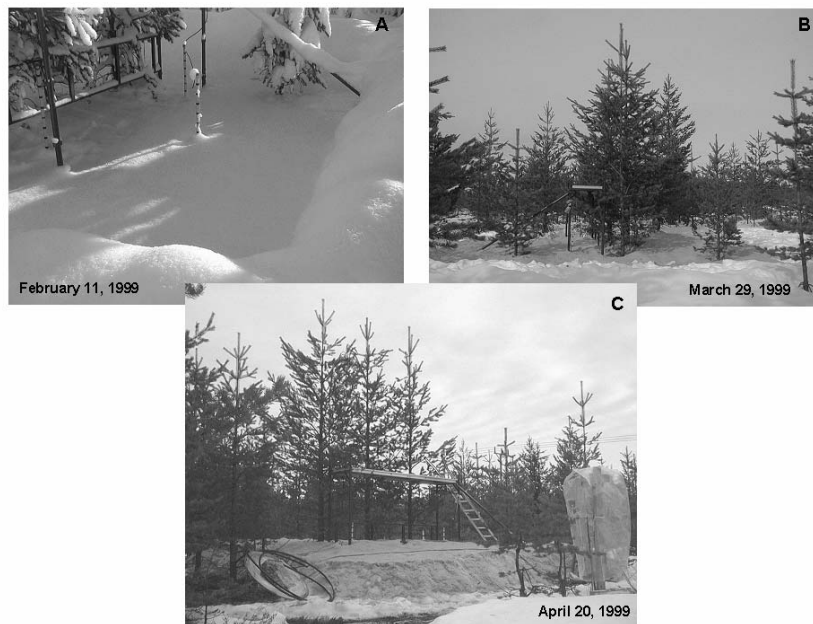


Figure 4 Photos of the snow manipulations made on one of the plots to create a delay of soil warming in the Västomån stand in 1999. A) The snow was removed during the coldest period (November – March). B) At the end of March, snow was returned to insulate the frost and to re-establish the hydrological inputs. The snow was covered by a 10 cm layer of sawdust. C) The sawdust helped to preserve the snow as spring progressed.

Measurements

Climate

Standard climate data were obtained from a climate station located in the centre of a 0.9 ha clear-cut, at the Heden site (180 m.a.s.l.). The station is part of the reference-monitoring program of the Vindeln Experimental Forests, which includes measurements of standard meteorological variables such as air and soil temperature, humidity, precipitation, global radiation, and wind speed (Anonymous, 1981-1998). In Paper VI another reference climate station was used. This is situated in a 1.4 ha open clear-cut (220 m.a.s.l.) near to the field station of Svartberget.

Each plot, in Paper I – IV, contained three soil-temperature profiles located at different distances and compass directions from the trees with sensors at depths of 0, 10, 20, 40, 60 and 90 cm measured from the top of the mineral soil. One soil moisture content profile was located at each plot near to one of the temperature profiles. Soil temperature was measured with thermistors, and soil moisture content with Campbell soil moisture reflectometers, based on the TDR-technique (model CS 615, Campbell Scientific, Logan, UT, USA). The temperature measurement profiles were placed at different distances from the nearest tree. The

sensors were automatically measured every 10 minutes, and a two-hour average was stored in data loggers (model CR10, Campbell Scientific, Logan, UT, USA).

Snow and soil frost depths were manually measured at the experimental sites with frost tubes (Gandahl, 1957; Rickard and Brown, 1972). The measuring range was 100 cm aboveground and 100 cm belowground. These measurements were made once a week until snowmelt began, when the frequency was increased to twice a week. In the plot studies (Paper I – IV) one frost tube per plot was placed 1.5 meters from the nearest tree. In Paper V twelve frost tubes were placed in a 55 m transect (every five meters) leading from a 0.9 ha open clear-cut into the forest.

Sap flow, needle water potential and shoot elongation

Sap flow was measured using the heat balance method (Cermak *et al.*, 1973; Kučera *et al.*, 1977) with commercially available sap flow meters from EMS (Environmental Measuring Systems, Brno, Czech Republic). A logger unit (PT4.1) was designed to combine measurements on tree stems and in branches. The stem measurements used internal heating and internal sensing of temperature gradients. The branch gauges utilized external heating and sub-surface temperature sensing using needles inserted through the thin bark layer. On the Heden site, measurements from the trunks were made and the branch sap flow gauges were used as extra controls. On the Västomån site only measurements with branch sap flow gauges were made.

Tree-trunk sap flow was measured using two measuring channels for each tree. These measurements were taken on opposite sides of each tree in order to account for flux variability along the stem circumference. Branch sap flow gauges were placed on southerly exposed branches in the middle of the green crowns of the trees. On Heden the water fluxes at tree level were 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. On Västomån the measured branch sap flow was normalized to the dry weight (DW) of needles.

During spring and early summer, 1999 the water pressure potentials were measured on one-year-old needles on southerly exposed branches. These were collected between 1200 and 1500 h. Samples were immediately placed in glass vials lined with moistened filter paper and covered with aluminium foil. The vials were stored in a cooling box during transportation (< 30 min.) to the laboratory where measurements were made with a Schollander pressure chamber (Waring and Cleary, 1967).

At Västomån, in the beginning of the growing season in 1999, the shoot elongation was measured with a measuring tape. On each plot four to five shoots per tree were measured on branches with different azimuths.

Gas exchange measurements

Determinations of CO₂ and water vapour exchange were made at Västomån (Paper II and IV) with a portable computerized open-path system IRGA (LI-6400, Li-Cor, Lincoln, NE). Measurements were made from April to November 1999

between 1000 and 1600 h on clear and partly cloudy days. Gas exchange was measured on detached needles of 1-year-old sun-exposed shoots from the upper third of the crown. Each measurement was completed within about 5 minutes. Ten needles were placed across the short dimension of a 2 x 3 cm leaf cuvette. Saturating light ($1500 \mu\text{mol m}^{-2} \text{s}^{-1}$) was provided by a LED light source (Li-Cor 6400-02B) mounted on the leaf chamber and CO_2 concentration was controlled by the Li-Cor LI6400 CO_2 injection system. Measurements were taken at near ambient air temperatures and relative humidities. The same branches on each tree were sampled on each occasion throughout the study occasion.

After the measurements of gas-exchange, the needles were kept cool and moist for up till 24 h until the projected needle area was determined, based on the mean of five measurements made with a leaf-area meter (Li-Cor LI3000). Light-saturated rate of CO_2 assimilation at a CO_2 concentration of $360 \mu\text{mol mol}^{-1}$ (A_{360}) or $2000 \mu\text{mol mol}^{-1}$ (A_{2000}) were then calculated on a projected leaf-area basis.



Figure 5 Photo collage of some of the measurements made at the Heden and Västomån site in 1999 and 2000.

Soil physical properties and root mass distribution

Two profiles of soil were sampled adjacent to the plots, to determine texture and saturated hydraulic conductivity (k_{sat}). 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_{sat} , samples were taken with 5 cm high cylinders (core diameter 7.20 cm) for analysis in the laboratory with a constant-head permeameter.

On Västomån the vertical distribution of fine-root mass was estimated. This was achieved by taking twenty soil cores (volumetric samples, core diameter 22.8 mm) every four meters along a transect in the stand during October 1999. The cores were 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).

COUP model

The COUP model (used in Papers III and VI) was originally developed by Jansson and Halldin (1979) in order to quantify and increase the understanding concerning basic hydrological and biological processes in the soil-plant-atmosphere system.

The model treats the soil profile as a series of horizontal layers having specific hydraulic properties, the snow pack as a homogeneous layer and the vegetation as a single big leaf. The driving variables of the model are standard meteorological data, such as: air temperature and humidity, global radiation, precipitation and wind speed. The central part of the model is represented by two coupled differential equations for water and heat flow. These equations are solved numerically, and the basic assumptions behind them are: (1) the law of conservation of mass and energy and (2) flows occur as a result of gradients in water potential (Darcy's Law) or temperature (Fourier's law). The model also includes processes such as: water uptake and transpiration by vegetation, rain and snow interception, soil evaporation, evaporation of intercepted water, surface runoff, soil freezing and thawing.

The calculations of water and heat flows are based on soil properties such as: the water retention curve, functions for unsaturated and saturated hydraulic conductivity, the heat capacity including the latent heat at thawing/melting and functions for the thermal conductivity. The most important plant properties are: development of vertical root distributions, the surface resistance for water flow between plant and atmosphere during periods with a non limiting water storage in the soil, how the plants regulate water uptake from the soil and transpiration when stress occurs, how the plant cover influences both aerodynamic conditions in the atmosphere and the radiation balance at the soil surface.

The transpiration is defined in the model as a potential rate when there are no water deficits or low soil temperatures to influence the water loss. In this case the potential transpiration is derived from the combined Penman-Monteith equation (Monteith, 1965). The actual transpiration is calculated in two steps: (1) reduction from the potential to actual water uptake that accounts for drought, over-saturation, and temperature effects, which is calculated for each soil layer where roots are available, (2) an additional uptake of water by roots in layers where no water stress is calculated to compensate for other layers that are exposed to water stress.

A detailed model description can be found in Johnsson and Jansson (1991), Jansson and Karlberg (2001), and in the Appendix of Paper III.

BIOMASS model

The BIOMASS model describes processes of radiation absorption, canopy photosynthesis, phenology, allocation of photosynthate among plant organs, litterfall, and stand water balance. BIOMASS consists of a series of equations; some processes being described by a single equation, others by several. The equations are in principle based on established theories of plant-physiological processes and soil-water dynamics. For a detailed description of the BIOMASS model, see McMurtrie *et al.* (1990). A boreal version of BIOMASS is described in Bergh *et al.* (1998), in which effects of frozen soils, post-winter recovery of photosynthetic capacity, frost-induced decline of photosynthetic capacity and phenology pattern have been included.

The date of soil thawing is required as an input to BIOMASS, and can be obtained directly from soil and sap-flow measurements or by modelling soil-thawing processes. The recovery of light-saturated photosynthesis and quantum yield is strongly dependent on air temperature (Pelkonen, 1980; Linder and Lohammar, 1981; Bergh, 1997), and the recovery is related to an accumulated degree-day sum in BIOMASS. Frost-nights and cold days with sub-zero temperatures can slow and even reduce photosynthetic recovery. The autumn decline of photosynthetic capacity is hastened by severe frost-nights (Bamberg *et al.*, 1966; Strand, 1995). Photosynthesis declines progressively after each successive frost until it is reduced below a "dormancy level", which is set at approximately 20% of potential capacity. The decline is irreversible until recovery occurs the following spring. The control of budburst in Norway spruce and Scots pine has been incorporated into BIOMASS as a sub-model. As recommended by Heide (1993), the onset of budburst is determined by a thermal sum, which accumulates when daily mean air temperature exceeds 0 °C. The date of soil thawing promotes the photosynthetic recovery, mainly determined by the aboveground temperature. Before the date of soil thawing, recovery and photosynthesis is reduced.

Results and discussion

The snow cover manipulations made in 1999 effectively created large differences in the depth and duration of soil frost and thereby the timing of soil warming (Figure 6). This made it possible to study the *in-situ* tree water dynamics and net carbon assimilation of mature Scots pine trees over a wide range of soil temperatures in combination with the same aboveground climate. The soil temperature at 10 cm was used when analysing soil temperature effects on root water uptake, as this was the level of the highest density of living fine roots (<2 mm) and the highest saturated hydraulic conductivity (Paper I).

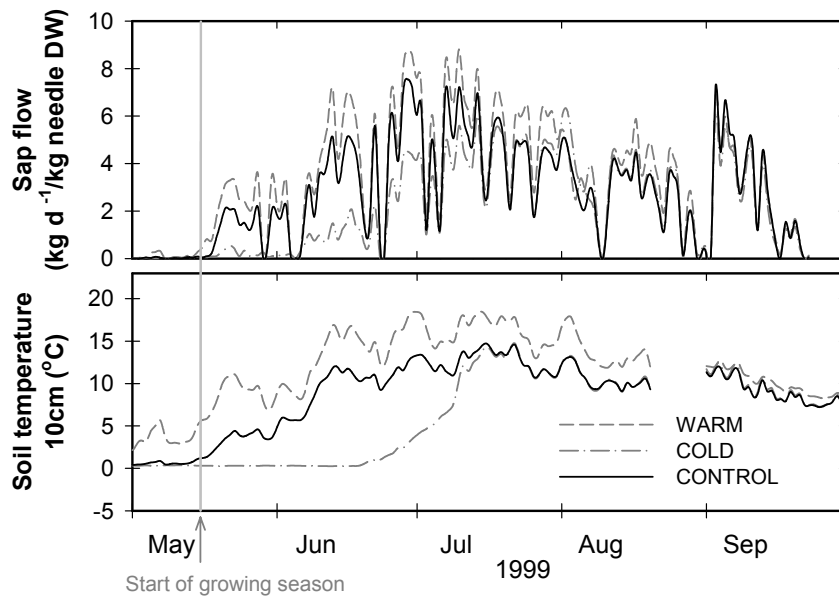


Figure 6 The response of sap flow for 20-year-old, naturally generated Scots pine trees on plots with different timing of soil warming created by snow cover manipulations at the Västomån site in 1999 (WARM = plot with early soil warming and COLD = plot with late soil warming). Above: daily sum of branch sap flow averaged from four branch gauges per plot and normalised to the dry weight (DW) of needles. Below: daily average of soil temperature at 10 cm, averaged from three soil profiles per plot. The growing season started on May 15.

Temperature effects

The release of liquid water, as frost thawed and snowmelt infiltrated, was not sufficient to satisfy the demand for water during spring when the aboveground climate was suitable for photosynthesis (Paper I). Thus the transition of water from frozen to liquid could not be seen as a “switch” that turned on the water uptake. The difference in the timing of soil warming between the plots was well reflected in the measurements of sap flow (Figure 6). The water was not available for the tree until the soil temperature in the upper rooting zone had reached a certain temperature above 0 °C, even when the transpiration demand was large. The trees with favourable soil temperature, *i.e.* with an early start of soil warming, did not take up water until the start of the growing season. However, these trees were more efficient in their water uptake, which could be an effect of the more favourable growing conditions for the water-conductive fine roots. As the start of soil warming was delayed into the growing season the water uptake was severely reduced. In the cold plots, the onset of sap flow was delayed almost a month into the growing season. Classical stress factors for limitations of root water uptake, such as drought, lack of oxygen or high salinity were not involved as the liquid soil water content has a low ionic strength and was constantly above the wilting point during the growing season, while the residual, air-filled porosity was never

less than 4%. The restricted water uptake was rather attributed to the soil temperature (e.g. Grossnickle, 1988; Day *et al.*, 1991; Wang and Zwiazek, 1999). Soil temperatures below +8 °C restricted the transpiration (Paper I and III). It was likely that the aboveground climate was more important for the start of transpiration, and the belowground climate had greater influence on the membrane pathway of the root water uptake system as well as reducing the area of new, water-conductive fine roots. Measurements of transpiration and midday needle water potential indicated that low soil temperatures during the growing season induced an increased resistance in the root membranes and in the stomata and thus caused water stress (Paper I).

The stomatal conductance was measured together with net carbon assimilation and intercellular CO₂ concentration (*C_i*) on the Västomån site (Figure 7, Paper II). In terms of CO₂ assimilation, only the cold plot differed from the control by being constantly reduced until the end of July. Stomatal closure partly explained the depression of CO₂ assimilation in the needles from the trees with low root soil temperatures, since *C_i* was lower in needles from the cold plot than in the control during most of the time in the first half of the growing season. However, on a few occasions during late spring similar values of *C_i* in needles of the cold plot and the control indicated that non stomatal factors were also responsible for the depression of CO₂ assimilation.

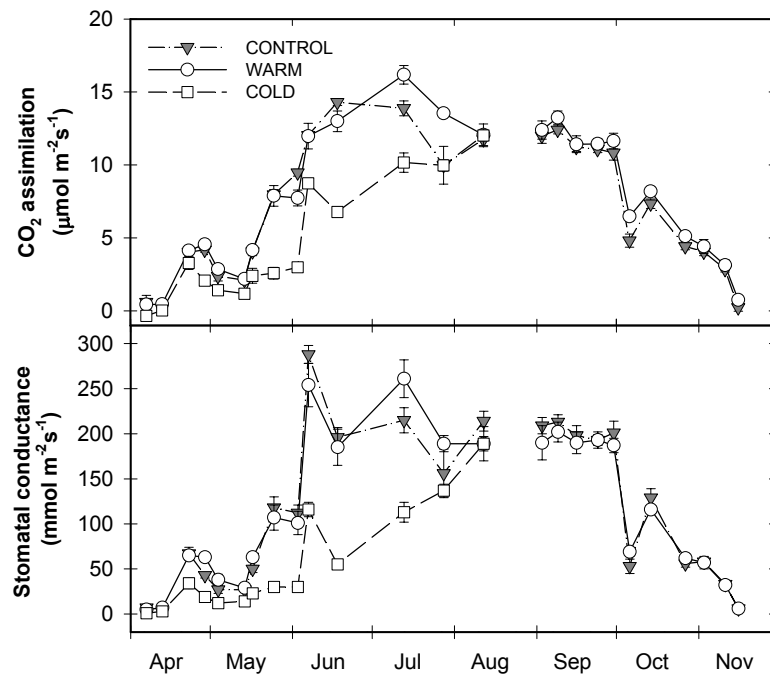


Figure 7 Above: seasonal course in light-saturated rate of CO₂ assimilation, below: stomatal conductance to water vapour. Measurements were made in needles from three branches per tree (n=9) on 20-year-old, naturally regenerated, Scots pine trees on plots with different timings of soil warming at the Västomån site in 1999. The cold soil plot was excluded from September to November.

Since water vapour and CO₂ share the stomata as a common pathway, the stomatal aperture plays an important role in both water and CO₂ flux. There are, however, some additional resistances associated with the inward CO₂ flux leading to a partial stomatal closure and thus higher resistance to water movements than to CO₂ movements (Gaastra, 1959; Slatyer and Bierhuizen, 1964). In such cases the transpiration will be more reduced than the photosynthesis. This can explain why the CO₂ assimilation could start much earlier than the sap flow did, as observed in the measurements. Further on, the differences between the plots were clearer when looking at the measurements of sap flow in comparison to the CO₂ assimilation where there was little difference between the warm plot and the control plot. An alternative explanation to this can, however, be seen when looking at the diurnal pattern of sap flow (Paper I) where there is little difference between the control and warm plot during the hours when the gas exchange was measured, even though the total sap flow during the day was different. The positive relationship between measured CO₂ assimilation and sap flow followed the same pattern in all of the plots, regardless of the timing of the soil warming (Paper IV).

The different timings of soil warming did not reveal any effects of soil temperature on the timing and growth pattern of the shoots. There were however large differences in the shoot lengths between the different treatments. An early soil warming increased the shoot length by 33%, and the delay of soil warming decreased the shoot length by 23% (Paper I).

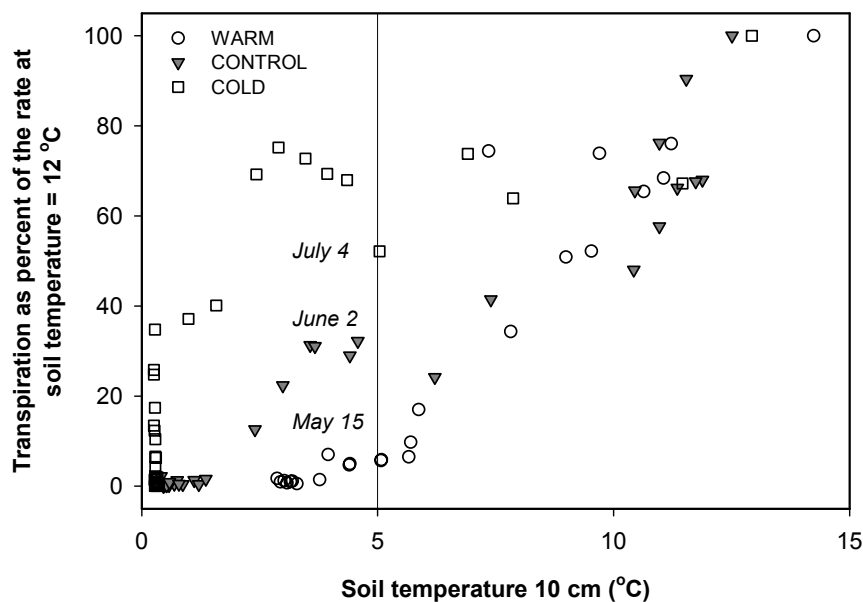


Figure 8 Transpiration presented as percent of the rate at a soil temperature of 12 °C, plotted against the soil temperature at 10 cm, on the plots with different timing of soil warming at the Västomån site in 1999.

Coupling of belowground climate and accumulated aboveground climate conditions

Soil temperature does not alone determine the onset of transpiration and net carbon assimilation in isolation from other factors (*e.g.* Bergh and Linder, 1999). It is rather the combined effect of soil temperature and the accumulated aboveground conditions such as air temperature, day length and time after winter dormancy. As seen in Figure 8, a certain soil temperature did not have the same effect on the transpiration, but depended on when that soil temperature occurred. In the warm soil treatment, the soil reached +5 °C on May 15 and transpired only 6% of its maximum rate at a soil temperature of +12 °C, whereas in the cold soil treatment the soil reached +5 °C on July 4 and transpired as much as 52% of its maximum rate at a soil temperature of +12 °C. There is clearly a time-dependency between the soil temperature and the transpiration, which was investigated in Paper III.

Modelling the temperature effects

For ecosystem modelling of the Boreal forest it is important to include a detailed process description relating snow cover to soil frost as well as the timing of soil warming, and how this affects tree water uptake. With the study on the Heden site in Paper III, we demonstrated the potential for a considerable overestimation of transpiration if the reduction of the trees' capacity to transpire due to low soil temperatures is not taken into account. It was of great importance to consider the soil temperature in combination with the accumulated effect of aboveground conditions. The simulation suggests that there is no unique threshold temperature for determining the start of water uptake but rather a flexible threshold temperature, changing with time. This threshold soil temperature was modelled as a linear function of the sum of positive daily air temperature starting from the beginning of the growing season (Figure 9). This accounts for the development of the aboveground plant conditions. The threshold soil temperatures for each of the three plots were each calculated from the intercepts of the soil temperature and plotted against the ratios of actual and potential transpiration. Although Figure 9 agreed well with the temperature range for limitation of water uptake and photosynthesis reported in the literature (*e.g.* Langlet, 1935; Kramer, 1942; Kramer, 1969; Running and Reid, 1980 and Day *et al.*, 1991), it could also be that it illustrated a more site-specific relation to the air temperature degree sum due to specific tree physiology combined with the soil heat and water conducting characteristics. It would be interesting to see if this relation of the soil threshold temperature and the air temperature sum also holds true for other sites.

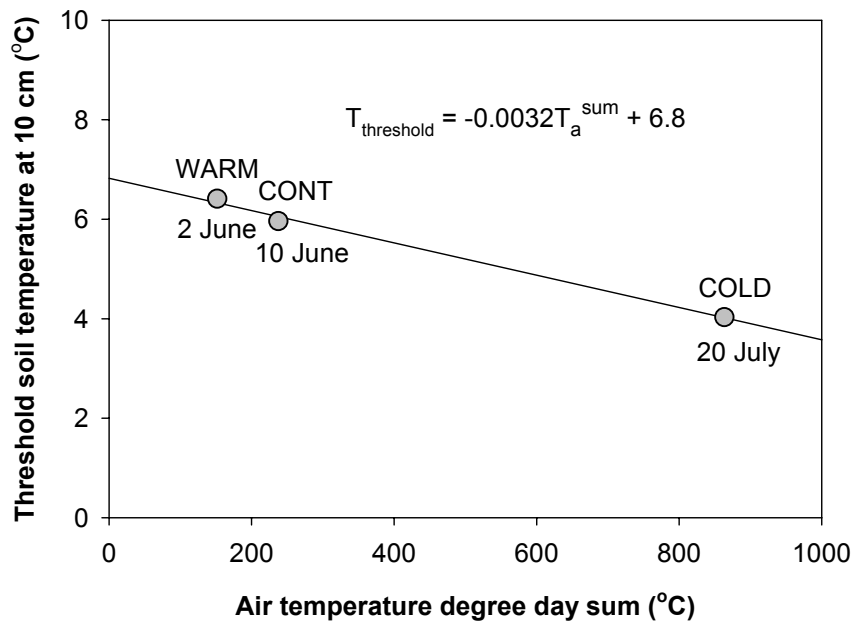


Figure 9 A simple model of the combined effect of soil temperature and the accumulated effect of aboveground conditions (air temperature degree day sum) on the threshold soil temperature, for determining the onset of transpiration in the COUP model. Threshold soil temperatures were calculated from measurements made on the plots with different timing of soil warming at Heden in 1999.

When using a water uptake reduction function with a threshold soil temperature that was determined by degree-day sums (dynamic function), the simulation of transpiration was improved in 1999 for the control plot and for the cold plot (Figure 10). For the warm plot however, there was a large underestimation, possibly due to the model simulation not including the positive effect that the absence of soil frost and an early start of soil warming may have on root growth. As the COUP model was run for the years 1999 and 2000 without including root growth, the effects of the snow cover manipulation on root growth in 1999 were hypothesized to cause the underestimation on the warm plot, and the overestimation on the cold plot of total transpiration during 2000 when no snow cover manipulation was made.

The COUP model was successfully used for reproducing the snow depth and timing of soil warming after snowmelt and frost thaw (Paper III and VI). The model was tested under a wide range of frost conditions and proved to be suitable for estimating water uptake in Boreal forest stands. We therefore believe that this is a useful tool for optimising forest management in forests exposed to harsh winter conditions.

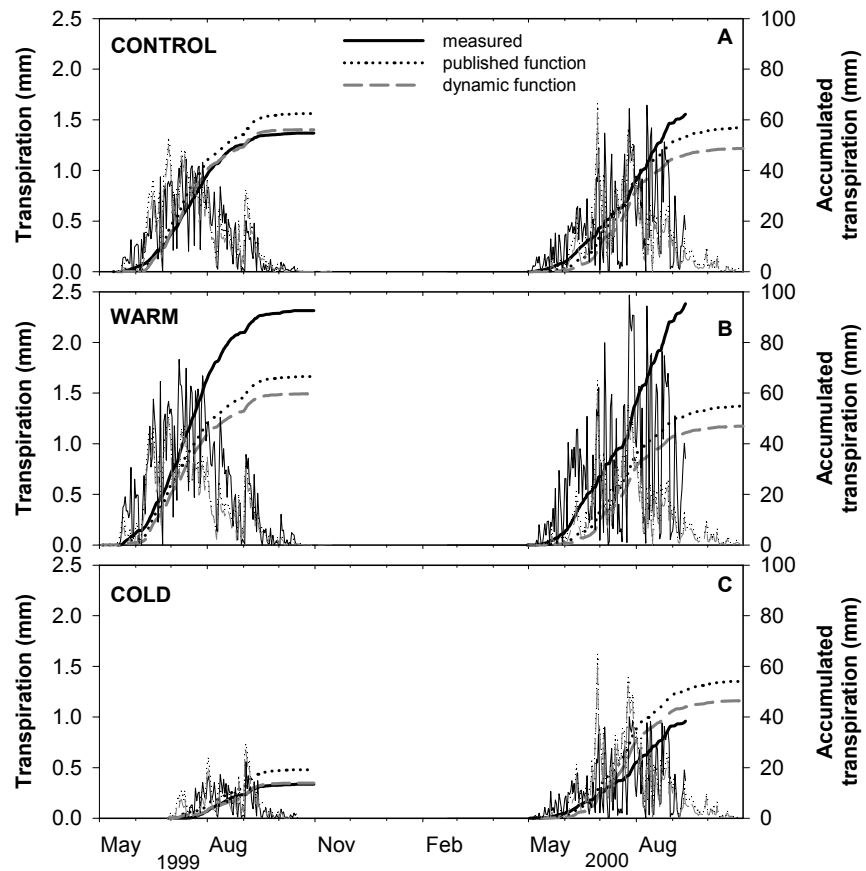


Figure 10 Measured (solid line) and modelled transpiration, for the three plots at Heden, using the previously published version of the root water uptake reduction function (dotted line) and the new dynamic root water uptake reduction function (dashed line). The manipulation of the snow cover, to create different timings of soil warming, was only made in 1999.

The BIOMASS model was well suited to simulate the annual NPP at the Västomån site (Paper IV) since BIOMASS has been adapted to boreal coniferous forests (Bergh *et al.*, 1998). Applying BIOMASS to the results of the soil temperature experiment made it possible to assess the implications of changed soil temperature on NPP. The comprehensive experimental data and the hydrological predictions from the COUP model made it possible to test the performance of the “boreal features” in BIOMASS against a new set of data. The model performed well in capturing the development of photosynthetic recovery. The simulated values followed the same pattern as in the measurements, in all the plots and over a wide range of soil temperatures. BIOMASS took account of when the soil thawed, but there was no attenuation of the of root water uptake reduction as the soil warming progressed, as implemented in the COUP model (Paper III). Also no account of the time course of soil warming was taken in simulating the recovery of

photosynthesis. Despite the lack of accounting for more than the date of soil thawing, the differences created by the soil temperature manipulation were reflected in the measured and simulated photosynthetic recovery. It seemed possible to integrate the complexity of the soil climate effects into this threshold date for soil thaw, together with information about air temperature using a day degree sum to steer recovery of light-saturated photosynthesis, as long as water availability is not limiting the water uptake of the roots. A more realistic mechanism than that currently in BIOMASS may, however, be desirable as climate change shifts the typical patterns of interplay between air and soil temperature dynamics.

Recovery

The recovery of net photosynthetic capacity in spring and early summer is strongly temperature dependent, and many studies have shown a strong correlation between the air temperature and rate of recovery (e.g. Lundmark *et al.*, 1988, 1998). However, no recovery of net photosynthetic capacity has been seen in Scots pine before the soil had thawed (Linder and Troeng, 1980; Troeng and Linder, 1982). Bergh and Linder (1999) found that the time course of recovery of photosynthetic capacity in Norway spruce was mainly controlled by air temperature and by the frequency of severe night frost, rather than soil temperature, although observations of water availability indicated that soil temperature also had some effects on the rate of recovery. In Paper I and III the recovery was also observed to be a feature of when the soil starts to warm, since the availability of free water at temperatures around zero was not sufficient to allow for transpiration when there was considerable potential evapotranspiration. This is clearly illustrated in Figure 11, where the sap flow on the cold plot was reduced to 44% of that on the control during the period April 27 – July 1, even though liquid water was available in the soil. During July 2 – September 23 this had recovered to 84% of the control plot value. In that case it is likely that the roots' water uptake capacity was a major stress factor as indicated by the rate of sap flow and midday needle water potential. Also in Paper II and IV the relatively early photosynthetic recovery and the 7.5% increase of NPP on the warm plot, as well as the delay of photosynthetic recovery and the 13.7% reduction of NPP, on the cold plot, indicated that soil temperature needs to be accounted for as well as air temperature when analysing photosynthesis and NPP in the boreal environment.

Even though the trees on the cold plots recovered from the delayed soil warming in 1999, in terms of transpiration, there were still large differences in transpiration between the plots during 2000, when there were no longer any differences in the soil temperature that rose above 0 °C on nearly the same date (Figure 12). The measured yearly transpiration totals were reduced by 39% relative to the control on the cold plot in 2000, which could be the result of the long-lasting effect on productivity that can occur if the roots are damaged (Robitaille *et al.*, 1994; Sutinen *et al.*, 1996). Possibly there was also a long-lasting effect of the favourable soil conditions on the warm plot in 1999, which facilitated the development of a more efficient root system, thus increasing measured yearly transpiration totals in 2000 by 53% relative to the control. For a better

understanding of the recovery and the processes controlling the efficiency of water uptake by roots, it would have been valuable to measure the year before the manipulation of soil temperature (to ascertain any pre-manipulation differences between the plots) and to continue the measurements for several years thereafter.

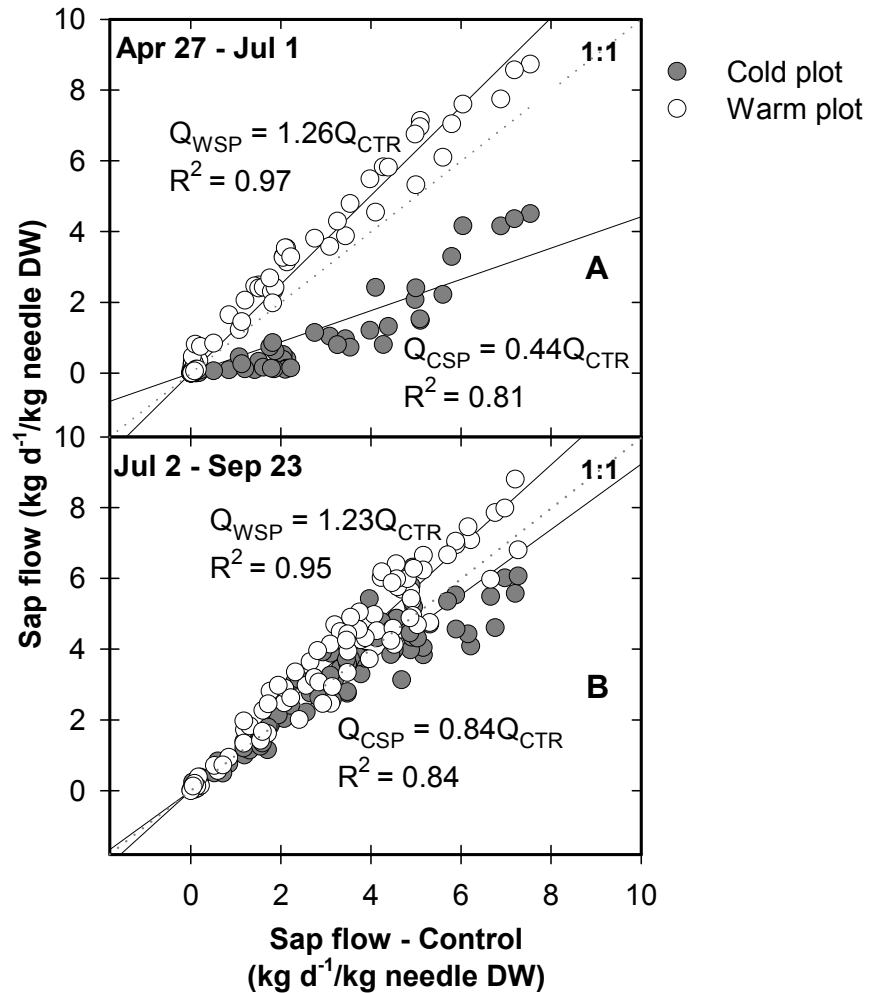


Figure 11 Total daily sap flow for the trees on the plot with an early soil warming (WARM) and the plot with a late soil warming (COLD) plotted against the sap flow for the trees on the control plot (CONT). The time series is divided into a period when A) the soil temperatures differed between the plots, April 27 – July 1, 1999 and B) a period when the soil temperatures were similar, July 2 – September 23, 1999 on the site at Västomån.

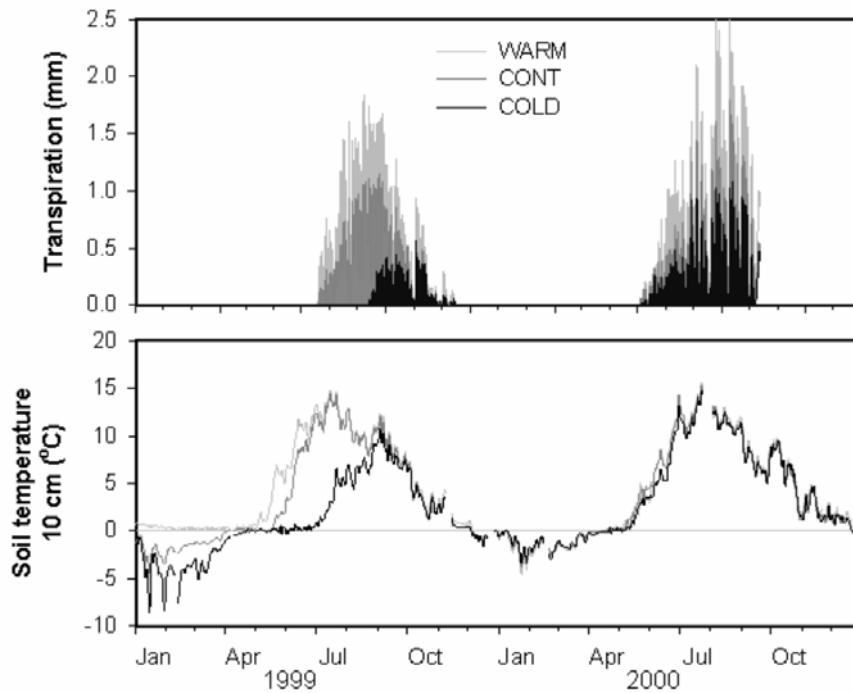


Figure 12 The response of sap flow for 70-year-old, naturally regenerated Scots pine trees on plots with different timing of soil warming created by snow cover manipulations at the Heden site in 1999, and without manipulations in 2000. Above: daily sum of transpiration extrapolated to stand level on the basis of stem circumference. Below: daily average of soil temperature at 10 cm, averaged from three soil profiles per plot.

Variations in the landscape

The large differences in the timing of soil warming that were created by the snow cover manipulations may seem extreme. However, these differences were within the natural range of soil warming for the area within a 10 km radius of the study sites (Kluge, 2001).

The variation in soil conditions found across the landscape could also be seen when comparing a north-facing forest edge with the forest interior in Paper V. 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 low soil temperatures as a limitation to water uptake and transpiration was apparent during the beginning of the growing season at Heden in 1998. The estimated tree water use and increment was larger at the edge zone. In the interior, the estimated transpiration was 70 mm and at the edge zone 107 mm during the growing season in 1998 (Figure 13). This indicates

that the frequency and structure of forest edges may have importance for calculating gas and water exchange from a landscape.

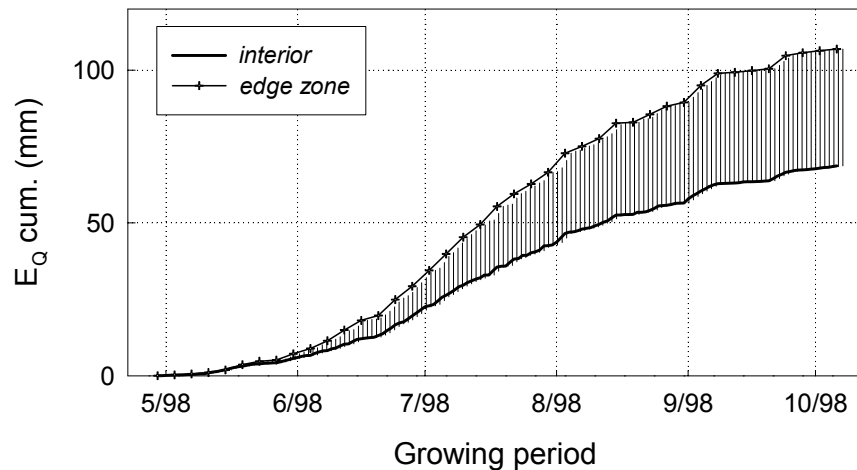


Figure 13 Cumulative values of estimated canopy transpiration (E_Q) calculated from edge zone and interior trees, respectively at the Heden site in 1998. Some missing values in summer were filled in from the regression to mean daily branch sap flow. Shaded area shows a likely range of E_Q that depends on the weight given to particular situations, *i.e.*, edge zone and forest stand interior.

In the boreal forest the stand structure and the climate are important features for the snow cover, the soil temperature and soil moisture regimes. This affects the spatial distribution of the water use and net primary production of these forests, as well as the sensitivity of the landscape to changes related to the climate and silviculture. In Paper VI the COUP model proved to be a functional tool for simulating the intra-landscape variations in snow depth and soil temperature. Application to eight different Scots pine stands for eleven years (1991 – 2001) revealed the variability that existed in the timing of soil warming between the stands and between the years (Figure 14), as well as the factors contributing to that variability. The model was also used to give an indication of how stand transpiration varies. The stands with the most favourable snow/soil temperature conditions for an efficient water uptake in relation to leaf area index (LAI), had certain characteristics in common, namely lower tree heights, high direct precipitation throughfall and low stem densities (paper VI). The model can help us in understanding both the effects of climate change and forest management on forest productivity in a landscape perspective, and, at a larger scale, possible feedback effects on climate change.

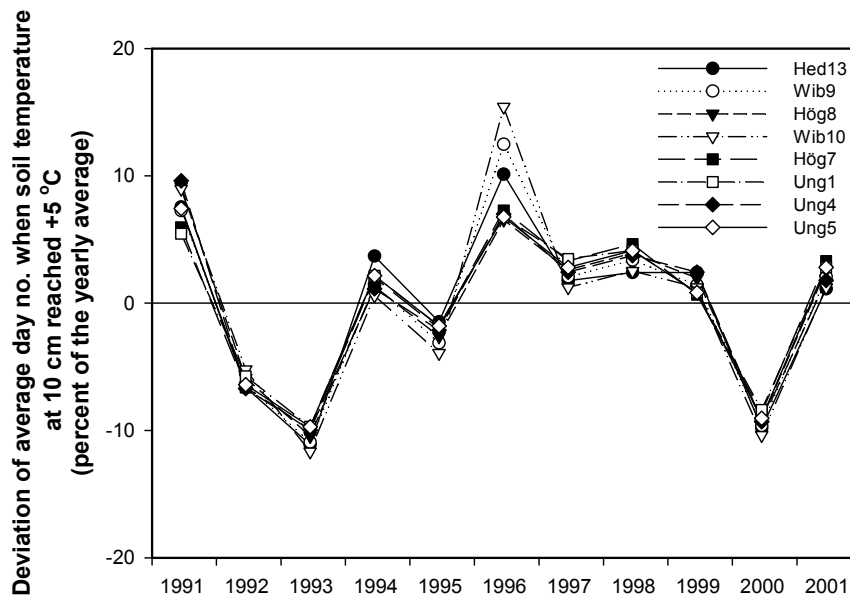


Figure 14 Deviation of the estimated day number for each year between 1991 and 2001 when the soil temperature at 10 cm reached +5 °C, relative to the average day number when this threshold was passed in the period from 1991 – 2001, expressed in percent, for eight different Scots pine stands within the Vindeln Experimental Forests.

Conclusions

These field scale experiments on mature Scots pine trees in the boreal zone of northern Sweden have demonstrated that the disappearance of soil frost was not in itself sufficient to enable tree water uptake, since some degree of soil warming was necessary even when aboveground conditions were favourable for transpiration. This confirmed and helped quantify the importance of low soil temperatures as a limitation on root water uptake and net carbon assimilation during spring when soil warming occurs after the start of the growing season as defined by aboveground climate. The experiments also indicate that earlier controlled laboratory studies (see Introduction) on the inhibiting effects of low soil temperature on water relations and gas exchange for seedlings or saplings hold true on mature trees in the field. The experimental data have also been the basis for model analyses that investigated the interaction of belowground and aboveground conditions on water use and net photosynthesis. This was scaled up to look at inter-annual and spatial variability within stands. This type of information could be of use in forest management that is more frost conscious throughout the entire life of a forest stand, as opposed to just at the establishment stage which is currently the period when most attention is given to temperature effects.

Some of the main findings were:

- The absence of frost (and hence the presence of liquid water) was not sufficient to enable water uptake. It was rather the elevation of soil temperature above zero in the upper soil layers that was required for substantial water uptake.
- A delay of soil warming into the growing season severely restricted the water uptake, the light saturated rate of net photosynthesis and the stomatal conductance.
- An early start of soil warming had little effect on the onset of water uptake, the light saturated rate of net photosynthesis and the stomatal conductance, which was rather controlled by the start of the growing season as defined by aboveground conditions. Earlier soil temperature increases did, however, appear to increase the roots capacity to absorb water through the growing season and into the subsequent year.
- The inhibiting effect of low soil temperature on water uptake was mainly attributed to reductions in the capacity of roots to absorb water.
- The inhibiting effect of low soil temperature on light saturated rate of net photosynthesis was attributed to both stomatal closure and effects on the biochemistry of photosynthesis. However, stomatal closure was dominant.
- When the soil temperature at 10 cm depth was below ca. 8 °C during spring, that temperature correlated with the rate of sap flow when weather conditions were favourable for transpiration. This was also the limit of soil temperature for when the light saturated rate of net photosynthesis and stomatal conductance was affected during autumn.
- The effect of a certain soil temperature on water uptake was not the same at different times due to interaction with the accumulated effect of aboveground conditions such as air temperature, day length and time after winter dormancy.
- The long lasting effect of the spring soil temperature on the roots' capacity to absorb water was observed during the second year of measurements after the snow cover/soil temperature manipulation had been conducted.
- The COUP model illustrated how transpiration was considerably overestimated if the reduction of trees' capacity to transpire, due to low soil temperatures, was not taken into account.
- The accumulated effect of the aboveground climate could be included in a new, dynamic water uptake reduction function for the COUP model that better estimates the transpiration for trees in the harsh climate experienced by boreal forest stands.
- The boreal version of the BIOMASS model was suitable for estimating the development of photosynthetic recovery in boreal forest stands.
- The COUP model proved to be a functional tool for simulating the intra-landscape variations in snow depth and soil temperature.

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