



Effects of Thinning, Weather and Soil Moisture on Tree and Stand Transpiration in a Swedish Forest

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Abstract

The thesis investigates how thinning affects transpiration in a heterogeneous, but typical, mixed pine and spruce forest. Measurements were made during three years in a forest 30 km north of Uppsala, Sweden. The measured stand was divided into two plots, of which one was thinned by 25% of the basal area after the first year. The sapflow technique, by which transpiration was estimated, was evaluated. Sapflow was measured on five trees by the Cermak method and the Granier method. The methods diverged considerably. After comparison with eddy-correlation data, it was concluded that Granier measurements needed correction. The first year after thinning was very dry; transpiration of individual trees was modelled by means of weather and soil-moisture data. The response to soil moisture varied greatly; the number of days below the onset threshold for reduced transpiration varied between 21 and 111. The relationship between individual transpiration and growth, and three measures (diameter, needle mass and competition index), potentially useful as scaling-up factors, was also tested. Of the three, none was superior to the others. Thinning increased variation, and trees around the strip-roads from a thinning about ten years earlier were still affected. After thinning, transpiration on the thinned plot started at only 60% of that on the reference plot. The ensuing drought affected the thinned plot far less than the reference plot, and during the driest period, transpiration on the thinned plot was far higher than that on the reference plot. In the second year after thinning, the thinned plot transpired 20% more than the reference plot. Since neither an increase in LAI nor a reaction by the ground vegetation was detected, an increase in photosynthetic activity as a result of higher needle nitrogen concentration was a likely explanation. This hypothesis was supported by the results of a simulation.

Key words: *Picea abies*, *Pinus sylvestris*, forest management, MAESTRA, tissue heat balance.

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Abstract

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Appendix

This thesis is based on the following papers, which are referred to by their roman numerals:

- I. Lundblad, M., Lagergren, F. & Lindroth, A., 2001. Evaluation of heat balance and heat dissipation methods for sapflow measurements in pine and spruce. *Annals of Forest Science* 58, 625-638.
- II. Lagergren, F. & Lindroth, A., 200X. Transpiration of Pine and Spruce in a Swedish forest: response of individual trees to weather and soil moisture. *Agricultural and Forest Meteorology*. (Accepted).
- III. Lagergren, F. & Lindroth, A., 200X. Variation in sapflow and stem growth in relation to tree size, competition and thinning in a mixed forest of pine and spruce in Sweden. *Forest Ecology and Management* (Submitted).
- IV. Lagergren, F., Lankreijer, H., Kucera, J., Cienciala, E., Mölder, M. & Lindroth, A., 200X. Effects of thinning on transpiration in a mixed pine and spruce forest in central Sweden. *Agricultural and Forest Meteorology* (Submitted).
- V. Lankreijer, H., Lagergren, F. & Lindroth, A., 200X. Increased transpiration after thinning in a mixed coniferous forest: analysis with a model application (Manuscript).

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Fredrik Lagergren had the main responsibility for all fieldwork, except in Paper I, where the fieldwork was shared between Lagergren and Lundblad. Data were jointly analysed in the case of co-authored papers, while the senior author had the main responsibility for compiling such papers.

Introduction

Interest in the water relations of forests and other ecosystems has increased rapidly in recent decades, because of heightened concern about the consequences of global change. The study of different aspects of water use, the effects of water deficiency and of combined effects caused by increased temperature and CO₂ concentration, are important if we wish to understand how the Earth's vegetation may be affected in the future. The expected effect of global change is not only that the temperature may be a few degrees higher (Greco *et al.*, 1994), but that there may also be a change in precipitation, both in space and in time (Houghton *et al.*, 1996), and that extreme weather conditions may occur more frequently (Karl *et al.*, 1995; Fulton, 1999). The increase in CO₂ concentration itself affects plant water use. Although CO₂ is not normally considered to be a limiting nutrient for plant growth, there is a trade-off, regulated by the stomata, between a larger loss of water and better access to CO₂, or a smaller water loss and poorer access to CO₂. This has been shown in several experiments in which elevated CO₂ has increased water-use efficiency and the growth of plants (*e.g.* Beerling, 1997; Szente *et al.*, 1998).

International framework

Research related to the Earth's climate is at present largely organised within an international framework. In 1986, the International Geosphere Biosphere Programme (IGBP) was instituted, with the mission to 'deliver scientific knowledge to help human societies develop in harmony with Earth's environment'. IGBP is a scientific research programme built around a family of core projects. One such core project is Biospheric Aspects of the Hydrological Cycle (BAHC), which deals with the physical processes of the hydrosphere and its interaction with terrestrial ecosystems. Within this organisation, several large-scale land-surface experiments, mainly concerning water- and energy-exchange, were conducted in the early and mid-1990s. Two of them, BOREAS (Sellers *et al.*, 1995) and NOPEX (Halldin *et al.*, 1999), focussed on the boreal zone; the latter was conducted in the present study area. Increasing interest in the carbon balance of forests, in particular, promoted the development of flux networks, pioneered by EUROFLUX (Valentini *et al.*, 2000), which focussed on the long-term study of exchanges of both CO₂ and water vapour along a climatic gradient in Europe. Today, several flux networks are in operation, all of which are collated in a global network, FLUXNET (Gu *et al.*, 2001). Information about these networks is most easily available from the Internet, where the homepage of IGBP is a good starting point (<http://www.igbp.kva.se>: Accessed 9-Oct-2001).

The existence of a human impact on the functioning of terrestrial ecosystems with respect to the climatic system is evident, and has been considered in general terms in the international research projects described above. This question has, however, become more topical since the international agreements concerning the

reduction of greenhouse gas emissions, recently reached in Bonn, Germany (<http://www.unfccc.de/>: Accessed 9-Oct-2001). By this agreement, the signatory states, the 'Annex 1 countries', must account for the effect of management on the carbon balance of their forests. The strong link between the exchanges of water and CO₂ makes it equally important to understand how different management practices affect these exchanges.

Forests and forest management

On a global scale, the managed part of the total forest area is not very high; no more than *ca.* 27% of all forest can be considered to be actively managed (Sharma, 1992). However, in Europe most of the forest area is managed; in Sweden *ca.* 95%. Management consists of many different activities, of which thinning is one. At present, thinning is on the increase, because of technical developments which make it more profitable, and because of the existence of increasing areas of forest plantations (Kerruish & Shepherd, 1982; McNeel & Dodd, 1996). In a global perspective, this trend is expected to continue in the future.

Thinning has several aims, the most important of which are:

- to increase tree dimensions at future harvests,
- to direct growth to stems of good quality,
- to harvest trees which would die in any case,
- to change the species mix in a mixed stand,
- to obtain a net cash income before the final harvest,
- to improve tree health, and make trees less vulnerable to damage or pests.

Thinning is generally performed 3–4 times per rotation in southern, and 1–2 times in northern Sweden. Normally, *ca.* 20–40% of the basal area is removed at a thinning. About 1% of the Swedish forests are thinned annually, and about one-third of the total harvested volume is derived from thinnings. Advanced technology, relatively easy terrain and the fact that a pre-commercial thinning has already been carried out, make these rather light thinnings profitable.

The effect of thinning on stem growth has been widely studied in Sweden during the past century. The largest survey, 'Stora produktionsundersökningen' ('the big yield study'), was conducted between 1941 and 1965, on 2075 plots distributed throughout the country (Näslund, 1971). This study resulted in yield models for spruce (Eriksson, 1976), pine (Persson, 1992) and mixed stands (Agestam, 1985). The effect of thinning on single trees has been investigated by Jonsson (1995). Stand growth always decreases somewhat after a thinning. Spruce is, however, less sensitive to thinning than pine, and for thinning intensities of up to 40%, maintains its increment almost at the pre-thinning level. In all of these studies, growth is related to site, stand and tree variables by means of empirical relationships, with a time resolution of five years. Their low resolution in time, and the lack of relationships with physical driving variables,

make these studies less useful for making predictions in a future changing environment.

Fifty-five per cent of the area of Sweden is forest. Since the country covers 13° of latitude, the general character of the forests varies widely, but it can also vary on a local scale, *e.g.* from a pine heath to deciduous fen forest. The only native forest-forming conifers, Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) are dominant throughout Sweden. After the latest glaciation, pine migrated into Scandinavia from the south, while spruce came from the north. The natural distribution of spruce has not yet reached the extreme south-west of Sweden. Pine, which is a pioneer species, is normally found in drier habitats with limited nutrients, and is dependent on disturbances such as wildfire or storms for its natural regeneration. Spruce is a secondary species, which prefers wetter habitats that are not often disturbed. Spruce can exist both in the main canopy layer and in the undergrowth, and can survive as a small shrub under a dense canopy, with the potential to grow to a large tree if released. In moderately fertile stands, pine and spruce often coexist, and spruce usually invades and takes over pine sites if no disturbance occurs. Pine and spruce also differ morphologically; pine has a generally deeper root system, often with a taproot, which anchors the tree and gives access to deeper soil horizons. In southern and central Sweden, spruce retains its needles for 5–10 years, pine for only 2–5 years; pine therefore exhibits greater variation in needle biomass during the year.

Mixed stands have the potential to produce a higher yield than pure stands, by sharing a common resource in space or time (Auclair, 1983). Root distribution at different depths is an example of the former, different growth curves over the season or over a rotation an example of the latter. Birch (*Betula pendula* Ehrh. and *B. pubescens* Ehrh.) is the third most common tree species in Sweden. Natural, pure stands of birch are common in mountain regions and may also develop elsewhere after a major disturbance, but birch mainly coexists with pine and spruce in mixed stands. Birch has rapid growth in its youth, but growth declines at an early stage; birch in admixture with spruce is therefore a combination with the potential for increased growth, and this has also been verified (Fries, 1974; Andersson, 1984; Tham, 1994). If economic factors are considered, mixed stands can increase the overall yield, when species such as pine, oak or beech, which have a high timber value at the final harvest but a low pulpwood value, are grown in mixture, *e.g.* with spruce or birch. A mixed stand also implies that less damage will be caused by pathogens and natural disasters, since such events often affect single species. Mixed stands of pine and spruce do not, however, show an increased yield compared to pure stands (Agestam, 1985). A review of several different combinations of tree species and their interaction may be found in Oliver & Larson (1996).

Background

An understanding of the factors which regulate the opening and closing of stomata is crucial for understanding the exchange of both water and CO₂. The conductance of the stomata can be described by empirical relationships with radiation, vapour pressure deficit, temperature and soil moisture (Stewart, 1988) (Figure 1). Even though efforts have been made to describe these relationships in general terms (Granier *et al.*, 2000), wide variation in the parameters estimated for the same functions under similar conditions has been reported (Cienciala *et al.*, 1994; Morén, 1999). Such empirical relationships are often used in ‘big-leaf models’ to describe the conductance of the entire canopy (*e.g.* Jansson & Karlberg, 2001). More physiologically-based approaches also exist, in which conductance is a function of intercepted radiation and photosynthetic capacity (Farquhar *et al.*, 1980). Such models require a good estimate of light absorption in the canopy, and for conifers which have a clumped leaf distribution in particular, to make such estimates is not a trivial task.

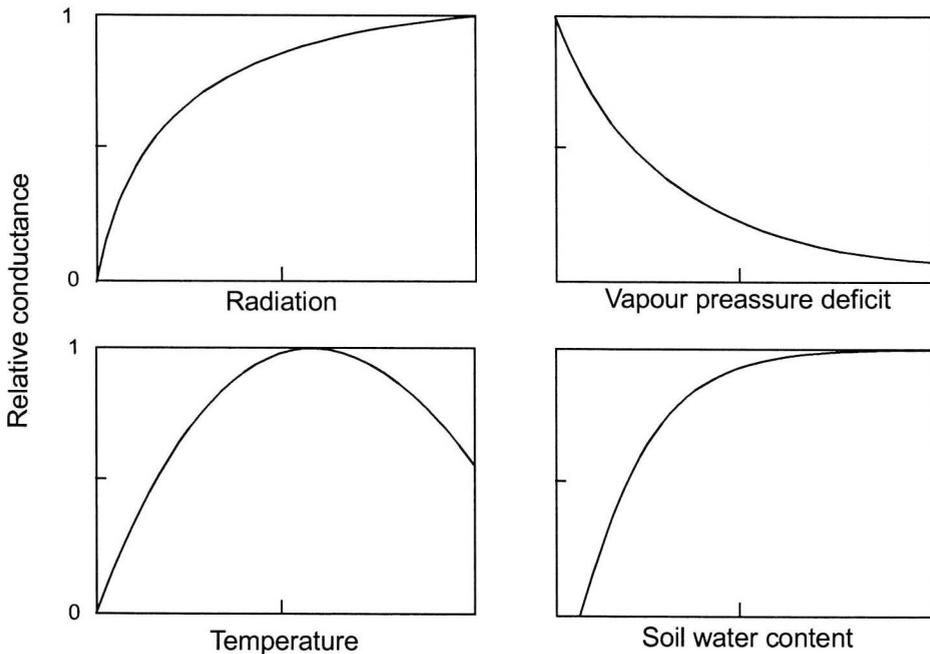


Figure 1. The principle of the dependence of relative stomatal conductance on weather and soil moisture.

The response of stomatal conductance to reduced soil-water availability is an important component many water-balance models (Vertessy *et al.*, 1993), in growth models (*e.g.* McMurtrie & Landsberg, 1992), in local ‘SVAT schemes’ (Jansson & Karlberg, 2001), in weather-forecasting models (Bringfelt *et al.*, 1999), as well as in general circulation models, GCMs (Viterbo & Beljaars, 1995). The dependency of transpiration on soil moisture is normally modelled in

two ways; either there is a direct dependency between conductance and soil moisture, which reduces transpiration, or potential transpiration is first estimated, and is then reduced as a function of soil moisture. In forests in which there is a strong, almost linear relationship between canopy conductance and transpiration, the difference between these two approaches is minor. The function that describes the relationship between soil moisture and conductance or transpiration can either be a continuous function (Granier *et al.*, 2000), or a discontinuous, threshold-type function (Irvine *et al.*, 1998). The existence of a specific threshold can be explained by hormonal signals from the roots to the stomata, which commence at a certain soil-moisture content. It has been shown that abscisic acid (ABA) affects stomata in such a way that conductance decreases when ABA increases; and it has also been shown that ABA can be produced by the roots (Zhang & Davies, 1989; Liu *et al.*, 2001). The response to reduced water availability can differ greatly between different species and soils.

Carbon gain and water loss in vascular plants are strongly linked through their common passage through the stomata. The ratio between these, *i.e.* the amount of CO₂ taken up by photosynthesis per unit of water transpired, is most commonly denoted 'water-use efficiency' (WUE). WUE appears to be relatively conservative within a species, its variation largely being explained by the vapour pressure deficit (Aphalo & Jarvis, 1991; Morén *et al.*, 2001). This provides an interesting opportunity for modelling carbon exchange from measurements of water use by the trees (Morén *et al.*, 2001; Widén *et al.*, 2001).

Measurement technique

Water and carbon fluxes from forests or other ecosystems can now be efficiently measured by the eddy correlation technique (Grelle & Lindroth, 1996). This technique, however, requires a large, uniform and relatively flat area. This requirement restricts its use if a specific stand in a patchy forest, or different treatments in small plots, are to be studied. Gas-exchange measurements at branch or tree level are another option, but to scale up to stand level from branches is difficult, and the use of whole-tree chambers is restricted to relatively small trees. A useful way of estimating water use by a tree is to measure the flow in the most concentrated passage, the stem xylem. This can be done by various thermal sapflow techniques. The oldest method, the heat pulse velocity (HPV) technique, originates from early work by Huber (Huber, 1932), but it has gone through many modifications since then (see Swanson, 1994). The HPV method measures the velocity of the flow, rather than the mass-flow rate. More recently, thermal heat-balance methods have been developed, which utilise either constant or variable heating. From the difference in temperature between the heated wood and a reference point, the flow can be calculated as the volume of water that corresponds to the energy input and the rise in temperature. The heating can be external (Sakuratani, 1981), internal within a stem segment (Cermak *et al.*, 1973; Cermak *et al.*, 1976), or internal along a heated probe (Granier, 1985; Granier, 1987). In the last method, the heated cross-sectional area is not defined, and

calculation of the flow depends on an empirical calibration. The advantage of the sapflow technique is that it is relatively cheap, it is fairly easy to scale up measurements to stand level, compared to branch measurements, and it is possible to study individual trees or small plots. Transpiration from the trees is also separated from forest-floor transpiration and from the evaporation of intercepted water. This is an advantage if the trees alone are of interest, but a disadvantage if the entire water balance is to be studied, in which case additional measurements are needed. If a high time-resolution is desired, the time-lag between sapflow and transpiration must be considered. The time-lag is caused by the presence of capacitances that exist in the flow pathway from the soil to the atmosphere. If measured sapflow in the trunk is to be used to calculate conductance, a time correction is usually needed, from some 15 minutes (Cienciala *et al.*, 1998) to more than an hour (Köstner *et al.*, 1998b).

Earlier work on thinning and water relations

There are numerous studies on the effects of thinning, and for Europe, a comprehensive review of early work was made by Braathe (1957). However, where the effects of thinning on water relations are concerned, the studies are less frequent, and for the species studied here, Scots pine and Norway spruce, few results have been published. Morikawa *et al.* (1986) measured transpiration in a *Chamaecyparis obtusa* Endl. stand before and after a 24% thinning. They found that transpiration increased for single trees, while stand transpiration decreased. Donner & Running (1986) studied the effect of thinning on pre-dawn leaf water potential in three different forests of Lodgepole pine (*Pinus contorta* Engelm.). Thinning intensities between 37 and 78% were compared with control plots. They found that the water potential in late summer was significantly higher, *i.e.* less negative, (0.17–0.35 MPa) in thinned stands. The effect of thinning on transpiration, obtained from the depletion of soil water, was studied by Aussenac & Granier (1988) for five years after a 50% thinning of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). They observed reduced water stress during dry years. Transpiration from the thinned stand increased from 83 to 103% of that of the reference stand during the five-year period. Breda *et al.* (1995) measured transpiration and growth response after a 35% thinning in a Sessile oak forest (*Quercus petraea* (Matt.) Liebl.). The ratio of actual to potential transpiration increased from 38% during the first year, to 48% during the second year after thinning, without any increase in leaf-area index. The effect of thinning and drought on transpiration and growth of Eucalyptus (*E. globulus* Labill.) for three intensities of thinning, was studied by McJannet & Vertessy (2001). They found that mortality was lowest in the most heavily thinned stands after drought, and that transpiration was higher on a heavily thinned than on a lightly thinned plot.

Aims

The overall aim of this study was to increase our understanding of how a common silvicultural practice, such as thinning, affects water relations in

deciduous forests; and to assess the interaction between abiotic and biotic factors in this context. The main emphasis was placed on the study of transpiration, and how it was affected at both tree level and stand level, on a diurnal to seasonal time scale, and less emphasis on the study of tree growth in relation to thinning.

The specific aims were: (i) to assess the methods used (a) to measure water uptake by trees, and (b) to scale up from tree to stand level; (ii) to quantify the dependency of tree conductance on weather parameters and soil moisture; (iii) to quantify the effects of thinning on tree and stand transpiration and growth; and (iv), to assess the sensitivity of transpiration to both abiotic and biotic factors. The study was performed in a typical mixed coniferous forest in central Sweden.

Material and methods

Site and stand

The studied stand was *ca.* 50 years old, naturally regenerated and situated in central Sweden *ca.* 30 km north of Uppsala (60°5'N, 17°29'E, 45 m a.s.l.). The age of the trees was rather uneven. Cores from twelve medium-sized trees gave a mean age at breast height of 43 years; the lowest and highest ages found were 33 and 54 years, respectively. The stand was a mixture of Scots pine (*Pinus sylvestris* L., *ca.* 60% of the basal area (BA)), Norway spruce (*Picea abies* (L.) Karst., *ca.* 35%) and Common birch (*Betula pubescens* Ehrh., *ca.* 5%). There were also a few specimens of Silver birch (*B. pendula* Ehrh.), and in the wetter parts, some Black alder (*Alnus glutinosa* (L.) Gaertn.). The trees were growing on a deep, boulder-rich, sandy glacial till. Feather mosses dominated the bottom layer vegetation and on the wetter parts there were *Sphagnum* mosses. The field layer was dominated by *Vaccinium* dwarf shrubs and grasses (see Table 1 in Paper IV for details). The area is rather flat, but small differences in elevation caused large variations in the groundwater table, and the soil moisture was therefore highly variable.

Table 1. *Stand characteristics of the reference and the thinning plot before and after thinning. Basal area (BA) and stem density (SD) are expressed per hectare, diameter (D) and height (H) are arithmetic means*

	BA	Pine	Spruce	Decid.	SD	D (cm)	H (m)	LAI
Reference	28.9	64%	33%	2.8%	872	19.9	16.9	5.0
Thinned before	29.1	57%	40%	3.4%	939	19.2	16.7	4.6
Thinned after	22.0	56%	40%	3.6%	703	18.9	16.5	3.5

In 1997, the position and diameter of all trees more than 5 cm in diameter at breast height were measured on a 120 × 120 m thinning plot and a 120 × 60 m reference plot, respectively. In November 1998, *ca.* 25% of the BA on the thinning plot was removed. The trees were harvested by chainsaw, and a

forwarder extracted the logs. The strip-road system used at the previous thinning, in the winter of 1990/91, was again used; this road system was also located and mapped. A buffer zone *ca.* 10 m wide, bordering the thinning plot, was also thinned. Trees were selected with three goals in mind; to remove trees of low quality, damage or a poor growth potential; to maintain the size and species mixture unchanged; and to distribute the removals evenly over the area. The stand properties before and after thinning are summarised in Table 1. Even if the properties of the plots are rather similar, variation on a smaller scale was large; for subplots of 15×15 m, the BA-weighted mean diameter varied from 17 to 26 cm, and the proportion of pine from 0 to 100% (Figure 2).

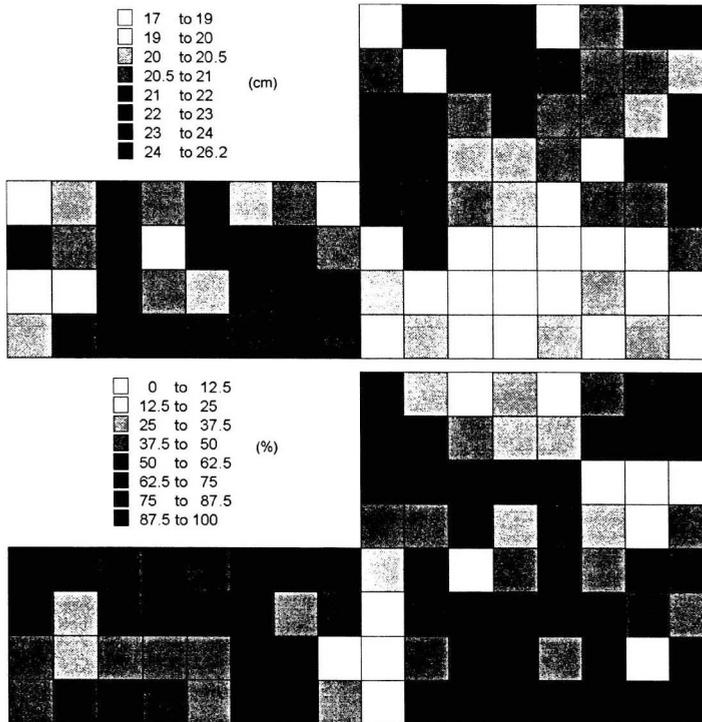


Figure 2. Variation in BA-weighted mean diameter (cm, above) and percentage of the BA that is pine (below), for subplots 15×15 m. The left 4×8 squares are the reference plot, and the right 8×8 squares are the thinning plot.

Sapflow

Sapflow was measured by the tissue heat balance technique (Cermak *et al.*, 1973; Cermak *et al.*, 1976; Cermak *et al.*, 1982), using commercially available flow-meter systems (P4.1 and P690.3, Ecological Measuring Systems Inc., Brno, Czech Republic). A segment of the stem was constantly heated with a power of 1 W, supplied through five parallelly inserted electrodes. The temperature difference between the heated segment and the remainder of the stem was measured with a battery of four pairs of thermocouples, of which two are used to

compensate for the natural temperature gradient (Cermak & Kucera, 1981) (see Figure 1 in Paper I). The mass flow of water through the heated segment can be calculated from the energy balance of the segment, since the net loss of energy per unit time corresponds to the energy gained by the water during the same time interval. The gross energy loss also includes a convective heat-loss term; this term can be calculated during zero-flow conditions.

Three selections of sapflow trees were used. The first selection was installed in the summer of 1997, and was used until July 1998. Data from the 1997 season were almost entirely lost, as a result of damage to the instruments by thunderstorms, and were not used in the present study. The second selection of trees was measured from July 1998, and throughout the 1999 growing season, while the third selection was used in 2000. The trees were selected along transects on which there was an even diameter and species distribution. Two flow-meters were used on the thinning plot and one on the reference plot; in the year 2000, a fourth system was used, which was shared between the plots. The position of the trees, together with the strip-road system, is shown in Figure 3.

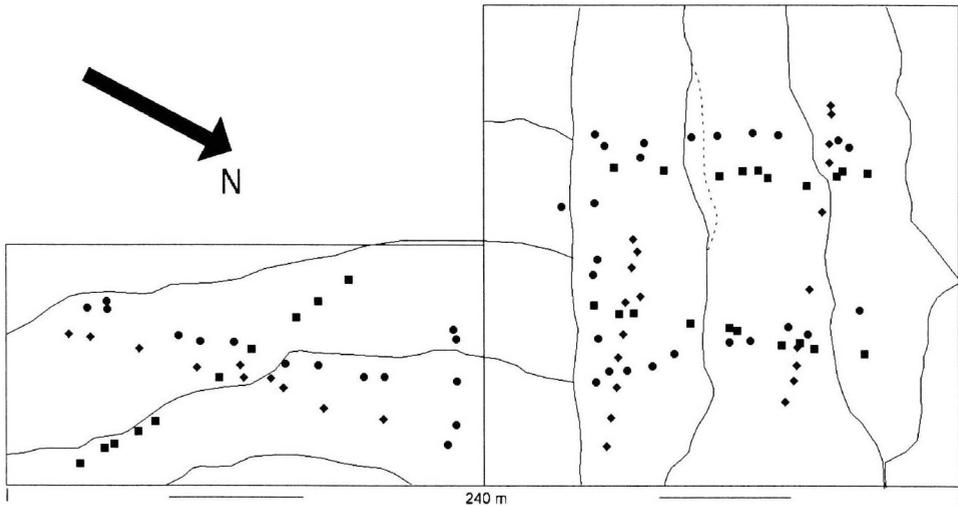


Figure 3. The position of the sapflow trees and the strip road system. The dotted part was moved to the position left in the thinning of 1998. The diamonds represent trees from the first sample of trees measured in 1997–98, squares represent the trees measured in 1998–99, and circles trees measured in 2000.

Each flow-meter was used for the simultaneous measurement of sapflow on ten trees. Meters were installed on both the east and the west side of all ten trees. Since there are twelve sapflow channels on each instrument, only one pine and one spruce had both sides continuously connected. For the remaining trees, the side connected to the instrument was shifted once or twice each season. The correlation of daily total sapflow with that of the continuously-measured tree of

the same species, was used to correct for differences between opposite sides (Figure 4, see also Paper I).

Stand transpiration was calculated according to the recommendations of Cienciala *et al.* (1999), whereby the ratio of foliage mass according to Marklund (1988) between the sapflow trees and the entire stand was used. Values were scaled up separately for pine and spruce. Deciduous trees were measured only in 2000; it was assumed that their relative contribution to the total was the same in all years (Paper IV).

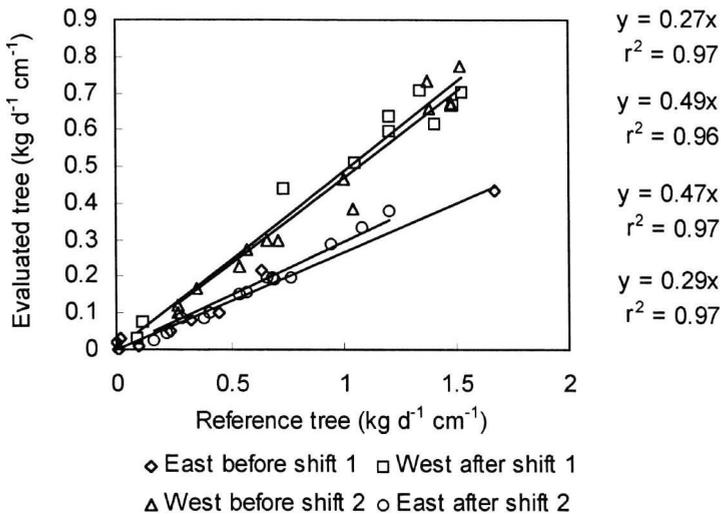


Figure 4. An example of the relationships with a reference tree, used to obtain a mean value that represents both sides of the tree. The unit is water flow (kg) per day and circumference (cm), (the base unit from the software delivered with the sapflow systems).

In 1998 and 1999, a ‘Granier heat decapitation sapflow system’ (Granier, 1985; Granier, 1987) was installed in five of the sapflow trees on the reference plot (Paper I). This method uses two needles: one contains a heating wire and a thermocouple, the other contains a reference thermocouple, to heat the sapwood along the heated probe and to measure the temperature difference. Sapflow is normally calculated from the measured temperature difference, according to an empirical relationship established under laboratory conditions (Granier, 1985; Granier, 1987). The two systems were compared and evaluated. The effect of radial gradients in sapflow and natural temperature gradients in the stem was also analysed.

Other measurements

The growth of 40 pines and 40 spruces on the thinning plot, and 20 pines and 20 spruces on the reference plot, was measured by dendrometer bands. The bands were installed in July 1997 and were read about every fourteenth day during the growing seasons.

Climatic data were taken from the Norunda central tower (Lundin *et al.*, 1999) *ca.* 500 m from the site, and, for missing values, from a scaffold tower 50 m from the site. The data from the central tower were preferred, because the instruments in the scaffold tower were slightly below the height of the tallest trees and could, therefore, be affected at low solar elevations. Soil-water content was measured by the TDR-technique (Topp *et al.*, 1980) in 16 positions on the thinned plot and eight positions on the reference plot, at both the 0–20 and the 0–50 cm level (Paper IV). Readings were taken manually about every tenth day during the growing seasons. ThetaProbes (ML1, Delta-T Devices, Inc., Cambridge, UK), connected to a data-logger, were also used to measure the soil-water content. The day-to-day variation obtained from the ThetaProbes was combined with data from the mean of the TDR-measurements, to obtain daily values for soil-water content from the 0–20 and the 0–50 cm level. The groundwater table was measured by one tube in each stand; because of the boulder-rich soil, tubes could not be installed deep enough to give readings during the driest periods. The tubes were read manually about every fourteenth day.

Projected leaf-area index (LAI) was measured three times each season with the LAI-2000 plant canopy analyser (Li-Cor Inc., Lincoln, NE, USA). Since no seasonal trends were found, LAI was represented by a mean value for each year (Table 1). The needle area of every individual tree was calculated from relationships with diameter, established by a detailed biomass sampling in an adjacent stand (Morén *et al.*, 2000). The projected leaf areas per tree were corrected to sum to the level of the LAI-2000 measurement; these data were used in Paper V.

Calculations

On a sample of 115 pines and 85 spruces, including the dendrometer trees, and on all sapflow trees, the height and the length of the green crown were measured. The needle mass according to Marklund (1988) was calculated from diameter at breast height, height and live-crown length. Relationships between diameter and needle mass could then be established and applied to all trees in the stand. It was then possible to establish relationships between the leaf area of all trees in the stand, and needle mass. These relationships were used to estimate the projected leaf area of the sapflow trees, whereby the height and length of the living crown were taken into account. The needle mass was used when sapflow was scaled up to tree level (Paper I, IV), and its relation to sapflow and growth was evaluated (Paper III). The leaf areas of the sapflow trees were also used to normalise sapflow (Paper II).

The relationship of stem growth and sapflow to diameter, needle mass and a distance-dependent competition index, were also analysed (Paper III). A competition index is a relative measure of the sum of certain biometric relationships, and the distance between a single tree (e) and its competitor (i).

Here, the relative difference in diameter (D_i/D_e), and a function of distance ($f(l)$) were used. A function that gave different weight to trees from different azimuthal directions ($f(v)$) was also tested, but did not improve the performance of the index.

$$CI_e = \sum_{i=1}^n f(l) \times \left(\frac{D_i}{D_e} \right) \times f(v)$$

Many different indices exist; the above competition index can be referred to the category ‘distance-weighted size ratio indices’ (Tomé & Burkhart, 1989), first introduced by Hegyi (1974). In the analysis of the relationships between competition index and growth and sapflow, respectively, the reciprocal of the competition index was used ($1/CI$).

The total BA-growth was calculated by relationships established with the competition index for each year. For trees within five metres of the centre of a strip-road, a relationship with diameter was used instead.

The functions shown in Figure 1 were used to model conductance for single trees in the reference stand in 1999. Conductance was calculated from the daily totals of sapflow per unit needle area per tree, and vapour pressure deficit (VPD) according to Monteith & Unsworth (1990). Functions were fitted stepwise, first for VPD, then for radiation, temperature and soil moisture, in that order. Functions were fitted for periods when conditions for the parameters not included in the function were considered to be non-limiting (paper II).

To analyse thinning effects in a theoretical framework, an array model (Wang & Jarvis, 1990) was used (Paper V). The model originates from early work by Norman & Jarvis (1975). In the work by Wang & Jarvis (1990), it was named MAESTRO, but it has recently been revised, and renamed MAESTRA, by Belinda Medlyn (see: <http://www.ed.ac.uk/~bmedlyn/maestra/>: Accessed 9-Oct-2001). In this model, the position and characteristics of single trees are used to simulate photosynthesis and transpiration, on the basis of light absorption in the canopy. The tree characteristics that must be included are: vertical needle density distributions, projected leaf area, crown radius, living crown length, height and diameter, respectively. Since the model is restricted to a maximum of 250 trees, a smaller area of 50 × 49 m on the thinned plot, and a 65 × 45 m area on the reference plot, were used.

Results and discussion

Climate and soil moisture

The growing seasons of 1998–2000 contrasted in weather condition (Table 2). The summer of 1998 was cool and wet; May to August received 145% of the normal precipitation, and especially June and August were colder than normal. The growing season of 1999 was dry and warm; July was warmer than normal, by 1.9 °C, and September by 3.2 °C. In July, only one-third of the normal precipitation fell; the totals in June, August and September were kept up by some heavy rainstorms, but in the intervals between them, there were long, dry periods. In 2000, June and July were wet and cool; July had only six days without rain. The spring and late summer were, however warm and dry; in Uppsala, September was the driest since records began in 1723 (Hans Bergström, personal communication 2001).

Table 2. *Monthly mean temperature (T) and precipitation for the three years and the mean for Uppsala, 1960–1990 (Ref)*

	April	May	June	July	Aug.	Sept.	Oct.
T Ref	4.0	10.2	15.0	16.4	15.2	10.8	6.4
T 1998	3.3	9.3	12.0	14.8	13.0	11.4	4.8
T 1999	5.7	8.6	15.7	18.3	14.9	14.0	6.3
T 2000	5.6	11.3	13.4	14.9	14.5	10.1	9.1
Prec Ref	29.1	32.7	44.8	75.2	64.8	59.2	50.6
Prec 1998	31.8	41.2	101.7	98.7	74.0	58.0	60.2
Prec 1999	54.6	22.6	45.9	24.7	60.9	55.4	32.5
Prec 2000	12	32	71.6	119.1	36.9	18.8	103.6

The soil-water content varied widely within the stands, especially in spring, when the water table was close to or at the soil surface (Figure 5). In 1998, the level was kept fairly constant throughout the season by frequent rains. The winter and spring of 1999 were wet, and the growing-season began with the water table at the surface at many points. During the dry periods, the soil-water content reached very low values at the beginning of August and in September. In 2000, the dry period after a rainy July reduced the soil-water content to minimum values at the end of September.

The groundwater table never fell below 75 cm in 1998 (Figure 6). In 1999, the level was too deep to be measured on the reference plot from 2 July, when it was below 110 cm; on the thinned plot, it was too deep for measurement from 30 August (>150 cm). The difference between the plots appears to be larger in 2000 than it was before thinning, but was at the same level as in November 1997 (data not shown).

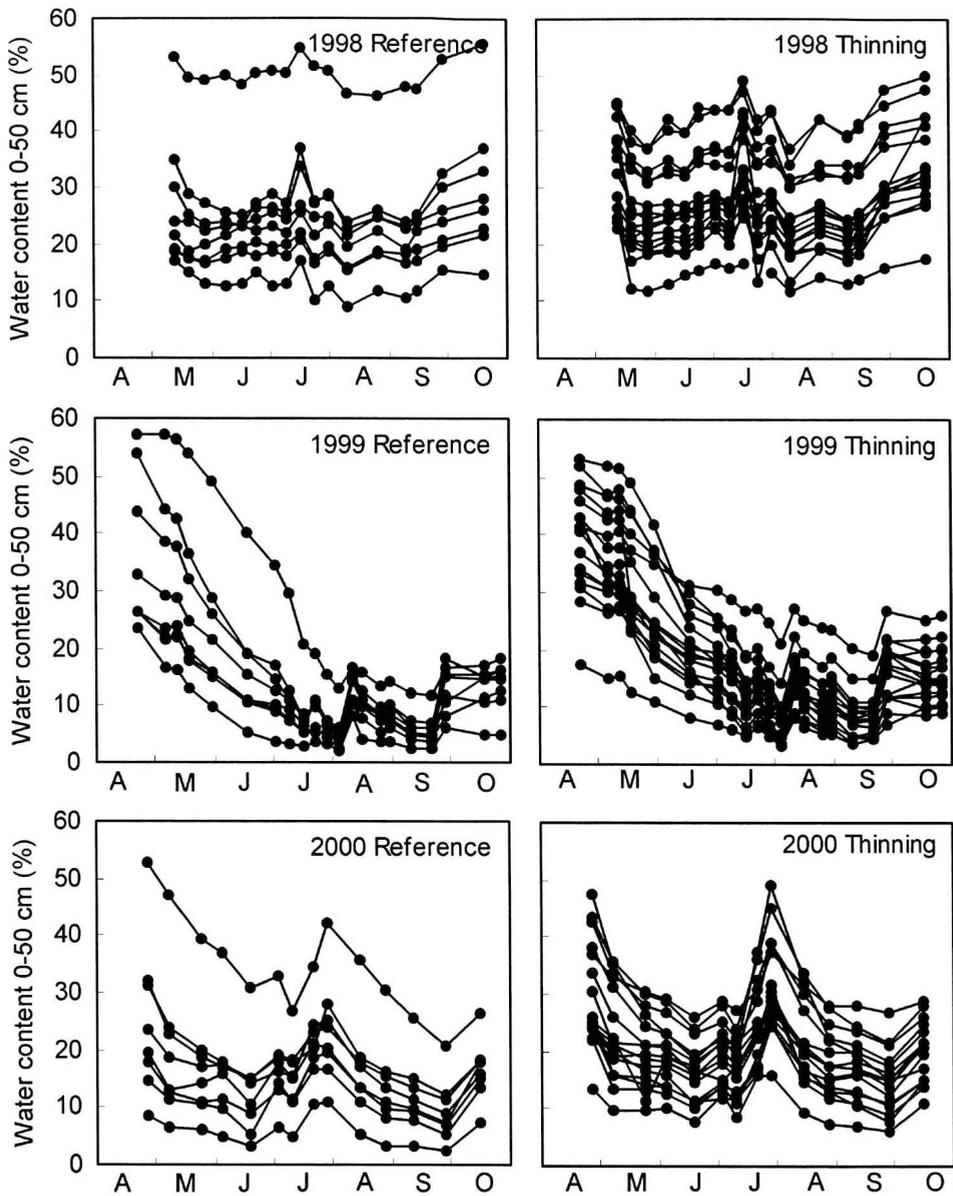


Figure 5. Variation in soil-water content at 0–50 cm depth in 8 positions on the reference and 16 positions on the thinned plot during 1998–2000.

Assessment of sapflow measurements

The natural temperature differences along tree stems, found in this stand (Paper I), varied between -0.8 and $+0.8$ K over a distance of 10 cm during the course of the day. This is high, compared to differences found in other studies, where a typical maximum difference is *ca.* 0.5 K (Cermak & Kucera, 1981; Goulden & Field, 1994). Since the sapflow rate is proportional to the reciprocal of the

temperature difference, and since the temperature difference is small when the flow rate is high, a relatively small error in determining the temperature difference can cause a large error in the estimated flow rate. At the maximum flow rate, a typical temperature difference is *ca.* 0.7–2 K; with a natural temperature difference of 0.1 K, the error in the flow rate will be *ca.* 5–15%. Even if the heating applied is five times higher in the Cermak system than in the Granier system, the heated volume is much larger, and the rise in temperature is lower. Compensation for the natural temperature gradient is therefore important when the Cermak system is used. If no compensation sensors are used, the gradient should occasionally be measured by turning the heating off for a few days. The fact that the correlation between the two systems was so much improved when both systems were compensated for the natural gradients, indicates that compensation worked well in both systems (Paper I).

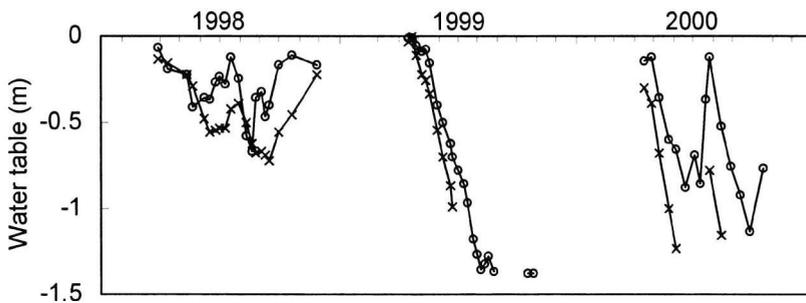


Figure 6. The groundwater table on the thinned (circles) and reference (crosses) plots.

The variation in sapflow density along the radius of a tree stem illustrates the difficulty of scaling up to tree level; the flow at 0–4 cm depth was in the range 28–107% of that at 0–2 cm depth, when measured with Granier system (Paper I). When the Granier method is used, the measured sapflow density is usually treated as samples of the entire sapwood in the stand, not that of single trees, and the tree level is not used (*e.g.* Granier & Loustau, 1994; Oren *et al.*, 1998) in the process of scaling up. At first sight, the concept of taking samples of the sapflow density of the stand, and scaling it up to stand level by means of the total sapwood area, might be regarded as a robust method. The sapwood area of the stand can probably be estimated quite well, but it is more difficult to obtain representative samples of sapflow density. The variation between trees may be large (Köstner *et al.*, 1996; Oren *et al.*, 1998), as may also variation along the radius of a tree (Cermak *et al.*, 1992; Cermak & Nadezhdina, 1998), and around the circumference of a tree (Paper I, Cermak & Kucera, 1990; Cermak *et al.*, 1992); and dry conditions can impose even larger variations along the radius (Cermak & Nadezhdina, 1998) and around the circumference (Cermak & Kucera, 1990).

When the tissue heat-balance method is used, the entire sapwood depth is usually covered, and a larger part of the circumference is measured, as compared to the Granier system. There is, however, still uncertainty in the estimate of the

share of the sapflow measured, and about how representative sapflow density is in the area measured. Sapflow from the Cermak systems was scaled up to tree level by multiplying sapflow density, expressed per unit circumference, by the circumference of the tree. This is a rather crude method, since the electrodes are inserted in parallel, and the method therefore underestimates the sapwood area measured. But since sapflow is higher in the outer xylem, the method is probably still satisfactory. Errors can also arise if the segments between the five electrodes have different resistances, which will cause uneven heating. If the two outer segments, in which temperature is not sensed, differ from the two middle ones in this respect, an error is created. The manufacturer of the sapflow system used in the present study therefore now recommends that only three electrodes be used. The measured variation between different sides of a stem then decreases, but a new problem arises, in that the effective width of the measured segment then varies with sapflow velocity (Jiri Kucera, personal communication, 2001).

The Cermak and Granier systems differed greatly in measured quantities, especially at high flow rates (Paper I). Since the Cermak method, in this study and in previous studies, has shown good agreement with independent methods in the same area (Grelle *et al.*, 1997), it was considered to be the more reliable. The two methods have generally shown good agreement in previous studies (Granier *et al.*, 1996; Köstner *et al.*, 1998a) but underestimates by the Granier system have earlier been reported (Hogg *et al.*, 1997; Offenthaler *et al.*, 1998). From these observations, it was therefor judged to be most appropriate to estimate new coefficients for the Granier system, and to keep the Cermak system unchanged.

In the present study, the relation between the needle mass of the sapflow trees and the total for the stand, was used to scale up sapflow to unit ground area. This method has earlier been used in the studied forest (Cienciala *et al.*, 1998; Cienciala *et al.*, 1999). Simpler approaches, using only diameter, were also tested; they gave results within 10%. Needle mass was used, since it generally showed a better relationship with sapflow than did diameter (Paper III). It is also more appropriate, from a physiological point of view, to use that part of a tree that is fully active in the process, *i.e.* the needles, than to use a less 'active' part, such as diameter, in scaling up (Cermak & Kucera, 1990). The competition index also appeared to be a potentially useful scaling factor; if trees close to the strip-road system (< 5m to the centre) were excluded, the index explained the variation in sapflow in 1998 best of all parameters tested. It also has the advantage that it immediately assumes a new value after thinning, but on the other hand, it requires that the position of all trees in the stand is known.

Individual tree transpiration

There was wide variation in the parameter values in the conductance models for the individual trees in the reference stand in 1999 (Table 3; Paper II). The hypothetical conductance at zero vapour pressure deficit (VPD), g_{imax} , was ca 5–10 times higher for pines than for spruces, because of a steeper dependence on

VPD for pine. This was also the weather-related parameter, which varied most within species. The dependency on radiation was very consistent among the pines; for spruce, one tree acted more like a pine. A temperature dependency, such as that shown here, without an optimum or a maximum level, does not accord with the known physiological behaviour of plants. Normally, no dependency, or a function with an optimum at *ca.* 15–20 °C, is used (Stewart, 1988). The functions applied here, however, did not primarily attempt to describe the physiological responses, but aimed rather to produce an adequate, empirically-based model of conductance, which could be used for normalising the weather-dependent variables, in order to discover and establish good relationships with soil moisture. Without normalisation of the weather-dependent variables, the variations in conductance are so large that they overshadow any dependency on soil moisture.

Table 3. *The parameters for modelling tree conductance, from Paper II*

	P1	P2	P3	P4	P5	S1	S2	S3	S4	S5	Pine	Spruce
g_{max} (mm s ⁻¹)	11.05	10.43	14.31	5.91	7.12	1.55	1.31	2.35	2.60	1.76	10.44	1.48
$a \cdot 1000$	2.15	2.12	2.44	1.46	2.04	1.29	1.08	0.92	0.99	1.55	2.12	0.92
b	0.563	0.555	0.573	0.582	0.576	0.458	0.497	0.457	0.471	0.615	0.578	0.470
c	2.51	2.49	2.60	2.50	2.57	1.84	2.21	1.87	1.93	2.79	2.59	1.91
$f(T_{\text{day}})$	1	1	1	2	1	2	3	3	3	3	1	3
k	0.160	0.170	0.123	-	0.222	-	-	-	-	-	0.171	-
l	0.114	0.113	0.130	-	0.095	-	-	-	-	-	0.110	-
m	-	-	-	0.063	-	0.066	-	-	-	-	-	-
x_{0-20}	0.219	0.065	0.256	0.328	0.207	0.205	0.368	0.267	0.200	0.329	0.207	0.239
x_{0-50}	0.205	0.042	0.260	0.371	0.196	0.188	0.392	0.303	0.176	0.384	0.195	0.214

The wide variation in soil-water content could probably explain some of the large differences in the response of conductance to soil moisture (Figure 5). For most of the time, there was typically at least a fourfold difference in soil-water content between the highest and lowest measured value on a given plot. The variation at single measurement points was, of course, larger than that in the mean conditions to which a tree is exposed, but there is no doubt that trees encountered different moisture conditions. The variation in response to the soil-water content was much larger within species, than between pine and spruce, even if there was a tendency for the spruces to be more sensitive.

As in many other studies, trees on the thinned plot were less affected by drought than were trees on the reference plot. The behaviour of the most extreme pine and spruce in each treatment is shown in Figure 7, for twelve days in July–August 1999 without rain, and with a very high atmospheric demand during the second half of the period. On the thinned plot, the trees that coped best with drought maintained their transpiration at almost the same rate during the entire period.

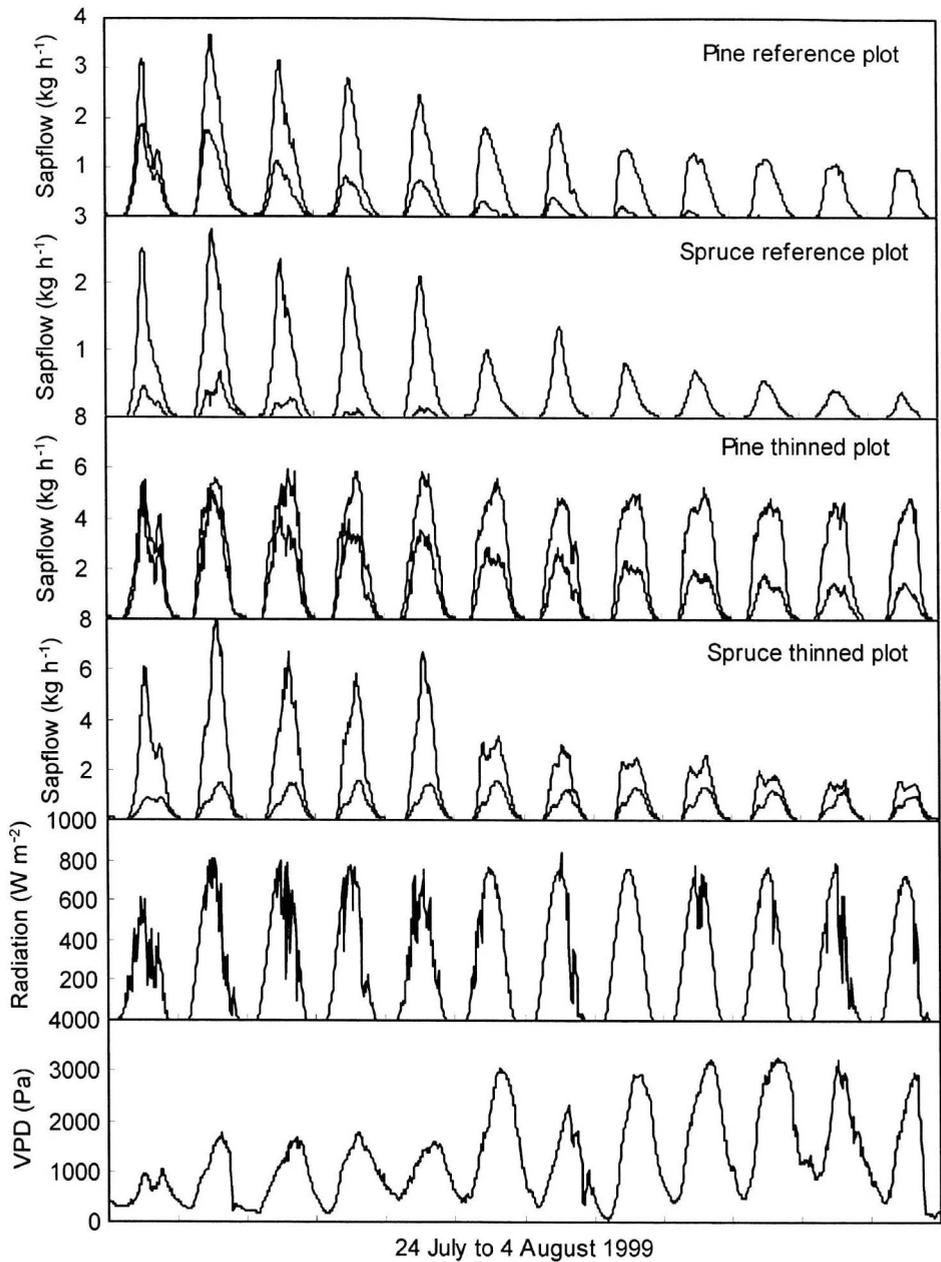


Figure 7. The most extreme trees, with respect to decreased sapflow, of pine and spruce for the thinned and reference plot, respectively, during 12 dry days.

On the reference plot, transpiration was reduced by at least 65% during the same period, and the most sensitive trees had no measurable sapflow (one pine and two spruces, of ten trees). From 28 to 29 July, there was a change in the weather. The maximum air temperature rose from *ca.* 21 °C to *ca.* 28 °C, and vapour pressure deficit reached *ca.* 3000 Pa. This affected spruce much more

than pine, which probably is an effect of different rooting depth; at that time, the topsoil was almost completely depleted of water.

In the spring immediately after thinning, the transpiration per tree (normalised by needle mass) was larger for trees on the reference plot. It appeared that the trees on the thinning plot were stressed in some way, especially the pines (Figure 8 in Paper IV). However, they recovered rapidly; from 19 May 1999 onwards, the transpiration per unit needle mass was always larger for spruces on the thinned plot, as compared to the reference (Paper IV). The corresponding date for pine was 9 June 1999.

According to the simulations by MAESTRA, transpiration per tree should increase by 8.8% for pines and 8.1% for spruce, as a result of increased light interception (Paper V). The most efficient way of simulating the *ca.* 50% higher transpiration per tree observed in 2000, was to increase the nitrogen content of the needles (Table 4 in Paper V). From the dead roots and the thinning slash there is normally a flush of nutrients; the 'assart effect', which is taken up by the ground vegetation or by the trees. Since no large increase was observed in the ground vegetation or in the leaf-area index after thinning, it is likely that the nutrient content of the needles had increased.

To find a parameter which is strongly correlated to sapflow is, of course, important when scaling up the data to stand level. In an homogeneous forest, diameter is often sufficient to describe the variation. The stand in the present study was, however, rather heterogeneous, and for a stand 400 m away it has previously been shown to be difficult to find strong relationships with diameter (Cermak *et al.*, 1995; Cienciala *et al.*, 1997). It is unlikely that sapflow should be linearly related to diameter over a broad range of dimensions, since diameter is non-linearly related to the water-conducting area of the stem. Therefore, basal area or sapwood area is often used instead (Cienciala *et al.*, 1994), although the latter is not easily estimated. In the present study, needle mass generally explained the variation in sapflow best, if all trees were included, but it was not much better than diameter. Trees close to the strip-road system deviated in many respects from the common trends, and regressions were therefore calculated without those trees. This resulted in a better explanation for all measures, but improvement was greatest for the competition index, which was then the best predictor in 1998. Trees close to the strip-roads had generally lower transpiration than could be expected from the relationship between sapflow and competition index for the other trees. This pattern was not as clear for diameter or needle mass (see Figure 2 in Paper III).

The sampling strategy for sapflow measurements, whereby trees were selected along transects laid out without reference to the strip roads, proved to be unfortunate, particularly for the second selection of sample trees on the reference plot. It transpired that six out of ten trees were within five metres of the centre of a strip road (Figure 3). As regards the transpiration of pine, this caused no

problems, but it could have caused stand transpiration to be underestimated, owing to reduced transpiration by spruce in the second half of 1998 and in 1999 (Figure 8).

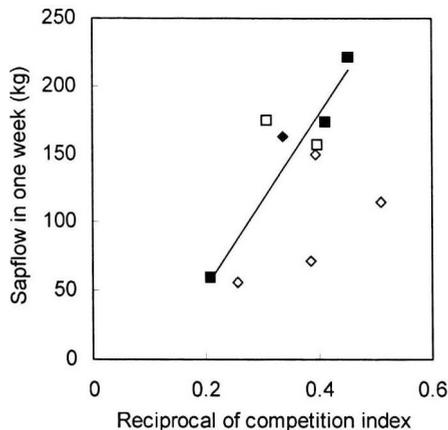


Figure 8. The reciprocal of the competition index, plotted against total sapflow for one week in June 1999, for trees on the reference plot. Squares represent pine, and diamonds spruce. Open symbols represent trees closer than 5 m to the centre of a strip-road.

Variation between trees was significantly greater on the thinned than on the reference plot after thinning (Figure 9). Such a reaction has been shown earlier for oak (Breda *et al.*, 1995). The reason for this may be that trees remaining after thinning are exposed to a combination of stimulation and stresses; which of the two dominates may differ from tree to tree.

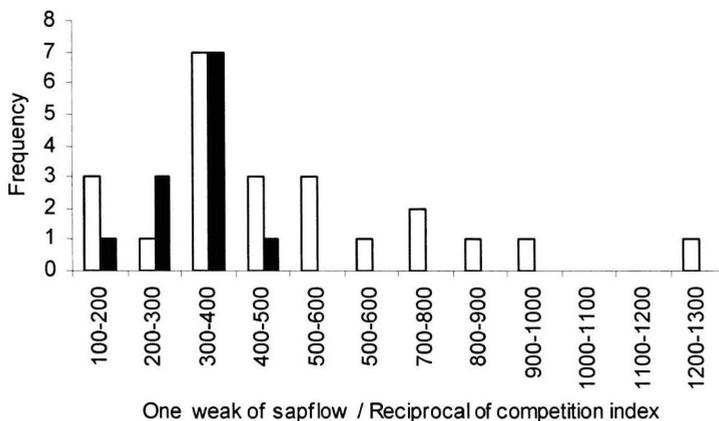


Figure 9. Histogram of the variation in sapflow for one week in July 2000, normalised with division by the reciprocal of competition index. Open bars, thinned plot; filled bars, reference plot.

Individual tree growth

Variation in basal area (BA) growth at tree level was best explained by the competition index, but the most simply acquired measure, diameter, also explained the variation well (see Table 3 in Paper III). For spruce especially, the exclusion of trees close to strip-roads increased the degree of explanation. Spruces close to roads generally grew less well than expected; pines grew somewhat better than expected, which was most clearly shown when competition index was used as the dependent variable (Figure 10). Pine has a deeper root system, and is less sensitive to rot than spruce, and it is possible that the pines could take advantage of decreased competition from disadvantaged spruces, and increase their growth in areas close to roads.

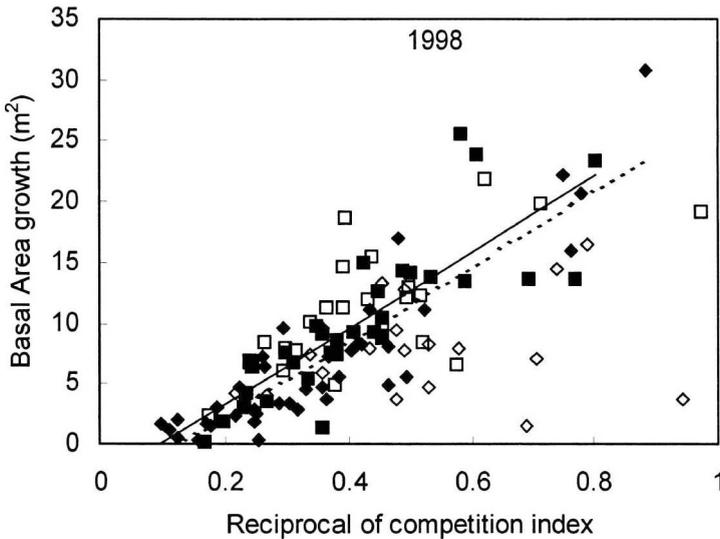


Figure 10. The reciprocal of the competition index, plotted against BA growth in 1998 for the trees on both plots. Squares represent pine, and diamonds spruce. Open symbols represent trees closer than 5 m to the centre of a strip-road. The lines are linear regressions for pine (solid line) and spruce (dashed line), excluding trees close to a road.

Stand transpiration

The level of the daily transpiration rates for the stand was relatively high. Maximum daily totals reached *ca.* 4.2 mm d⁻¹ in 1998 and 2000 (Figure 11 and Figure 3 in Paper IV). Compared to other studies in the same forest, this is about 1 mm d⁻¹ higher than in Cienciala *et al.* (1999), but within the range of the rates found for a further six stands in the same area (Lundblad & Lindroth, 2001). The stand is also rather young, and a negative correlation with age has previously been reported (Cienciala *et al.*, 1997; Lundblad & Lindroth, 2001). Transpiration was rather similar on the two plots in 1998, with $r^2=0.98$, and a slope of 1.04 (Figure 4, paper IV). However, after the shift of measured trees in July, there was

a small change in the contribution of pine and spruce, respectively, on the thinning plot, which emphasises that transpiration is difficult to measure.

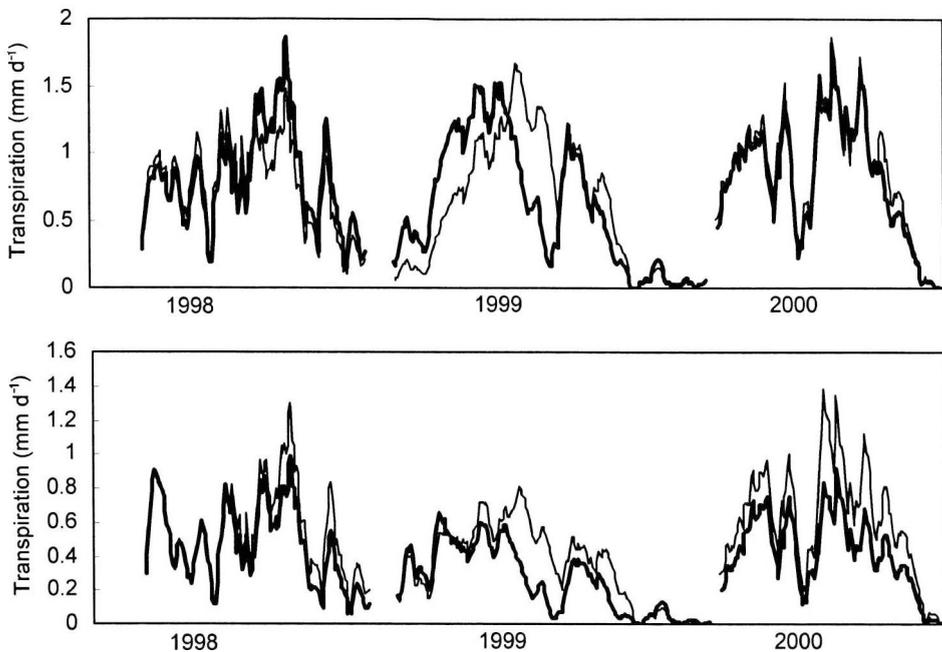


Figure 11. Seven-day running means of transpiration for pine (above) and spruce (below), for the reference (thick line) and the thinning (thin line) plots.

In 1999, after thinning, the transpiration of spruce started at about the same rate as that on the reference plot, but for pine, transpiration was less than 50% of the reference. The proportion of pine was higher on the reference plot (Table 1), which served to reinforce this, but can explain only a small part of it. The transpiration of pine successively recovered, and at the end of June, both plots transpired at the same rate (Figure 3, paper IV). During the drought that followed in July, transpiration of both pine and spruce was much less affected on the thinned plot than on the reference plot. In addition, during the dry period in the early weeks of September, the thinned plot transpired at a higher rate. The maximum transpiration in 1999 reached 3.1 mm on 7 July on the thinned plot, and 2.8 mm on 28 June on the reference plot, *i.e.* it was far lower than in 1998 and 2000. It was not unexpected that the thinned plot should perform better during drought, since more water is available per unit needle area (Jarvis, 1975; Whitehead *et al.*, 1984), which has also been shown in other studies (Donner & Running, 1986; Aussenac & Granier, 1988). It was, however, rather surprising that the difference in the reaction to drought between the two plots was so large, since the thinning was relatively weak; during the one-month dry period in July–August, the thinned plot transpired *ca.* 45 mm more than the reference plot, and for the season as a whole, the transpiration of the thinned plot was *ca.* 125% of the reference (paper IV).

Part of the difference in the response to drought can probably be explained by the difference in soil moisture. The difference between the two plots in mean soil-water content, at both the 0–20 and the 0–50 cm levels, was small, ca. 3–4% in the 0–50 cm layer (Figure 5 in paper IV), and to the advantage of the thinning plot. However, when the soil-water content approaches wilting point, a small difference in volumetric water content can make a large difference in soil-water potential, which is clearly shown by the pF-curves for the soils in a nearby stand (Stähli *et al.*, 1995). The rate of depletion of soil water at 0–50 cm could not explain the difference between the transpiration rates of the plots at the beginning of July; the depletion rates were almost identical from 1 July to 15 July, but the transpiration rates had already begun to diverge strongly on 8 July (Figure 12). On 8 July, when the transpiration rate of the two stands began to diverge, the soil moisture was 11.9% in the reference stand; this value was reached on 25 July on the thinned plot, and corresponds quite well to the time at which that plot began to deviate relative to the Penman evaporation (Figure 12). Irvine *et al.* (1998) reported the same threshold value for transpiration reduction in Scots pine, but it should be pointed out that individual variation was large in the present study (see above and Paper II).

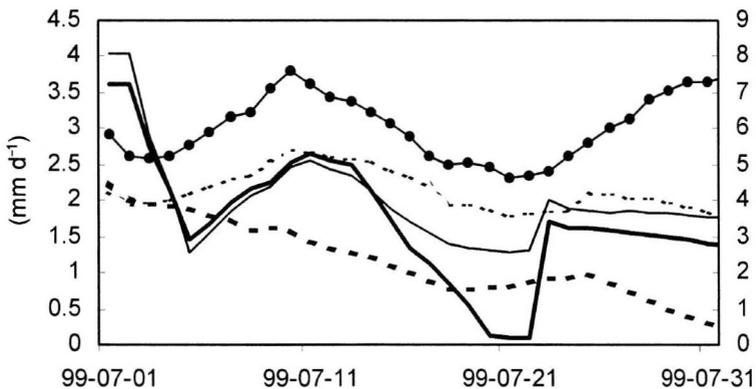


Figure 12. Seven-day running means of Penman potential transpiration (bullet line, right y-axis), depletion of soil water at the 0–50 cm level, after exclusion of rainy days (continuous lines) and transpiration (dashed lines) for the thinned (thin lines) and reference (thick lines) plots.

In 2000, the transpiration was *ca.* 20% higher on the thinned plot compared to the reference plot; spruce transpiration, in particular, had increased most (Figure 11). The variation in transpiration of individual trees was, however, large on the thinned plot in 2000 (Figure 9), and the difference was therefore not significant. From other experiments, it has been reported that it took between two (Breda *et al.*, 1995) and five years (Aussenac & Granier, 1988) until thinned plots had reached the same level as the reference plot. However, it should be pointed out that the thinning intensity was higher in those studies. The high transpiration on

the thinned plot, compared to the control in 2000, is difficult to explain. Reasons for it could be (a) better access to water, as a result of less interception, (b) increased photosynthesis and stomatal conductance, as a result of the nutrient flush from thinning residues, or (c) that the reference stand had reduced needle mass or function, as a result of the severe drought. The MAESTRA model simulated a 20% lower transpiration on the thinned plot after thinning, if no parameters were changed (Paper V). A simulated increase in the nitrogen content was the most efficient way of increasing transpiration. A 50% increase in N gave 16% higher transpiration, and if leaf transmittance and reflectance were also increased, a 22% higher transpiration resulted. Increases in needle N concentration after thinning, of 40%, have been observed in pine and spruce (Mugasha *et al.*, 1991; Hökkä *et al.*, 1996).

Stand growth and water-use efficiency

During the drought in 1999, the trees actually shrank between successive readings, as a result of the dehydration of the stems (Figure 13). This shrinkage, and the subsequent recovery, were significantly higher for trees in the reference stand, which supports the findings from the transpiration measurements, that the drought was more severe on the reference plot.

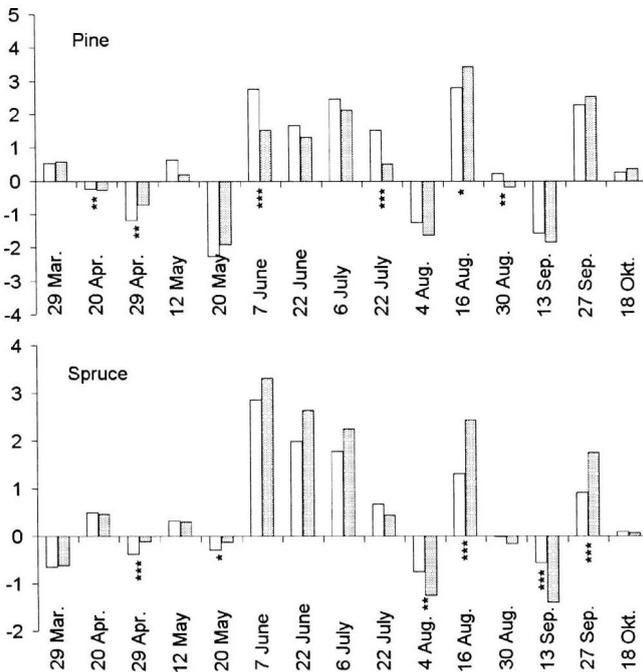


Figure 13. Average change in circumference between two subsequent readings of the dendrometer bands; the date represents the second reading. The asterisks represent significant differences. Open bars: thinned plot, filled bars: reference plot.

Mean BA growth (1998–2000) for the reference plot was $0.77 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$ (Table 4); this is very close to what could be expected for a stand of that age, site index and species composition (Table 18-19 in Agestam, 1985). In 1998, BA growth was 13% lower on the thinning plot than on the reference plot, for both pine and spruce. In 1999, the dry year after thinning, BA growth was 85% and 93% of the growth in 1998 for the thinned and reference plots, respectively. The quotient between growth on the two plots was reduced by only 7%, even though BA was reduced by 24%. The drought apparently affected growth, since the trees certainly received sufficient heat and radiation in 1999. The mean temperature for April to October 1999 was $0.6 \text{ }^\circ\text{C}$ higher, and total radiation 12% higher, than in 2000, but growth on the reference plot was only 70% of that in 2000. In contrast to transpiration, growth in pine was more affected than that in spruce during the dry year. One reason for this may be that spruce starts its growth slightly earlier in spring (Figure 7 in Paper IV), and could therefore better utilise the favourable conditions in May and July. The small reduction in the quotient between the two plots may also have been caused by the very wet conditions in 1998. The thinning plot was somewhat wetter, and some of the trees were exposed to an almost saturated soil for most of the growing season (Figure 5). Reduced availability of oxygen to the roots can lead to reduced nutrient and water uptake, hence to reduced photosynthesis and growth (Kozłowski *et al.*, 1991). In 2000, growth was higher than in 1998 on both plots, and the quotient between the plots was 13% lower than before thinning.

Table 4. Basal area growth ($\text{m}^2 \text{ ha}^{-1} \text{ year}^{-1}$) for the years 1998 to 2000, and the quotient between growth in the thinned and the reference stands

	1998	1999	2000	Mean
Thinning Pine	0.41	0.31	0.45	0.39
Thinning Spruce	0.21	0.22	0.26	0.23
Sum Thinning	0.62	0.53	0.71	0.62
Reference Pine	0.47	0.36	0.58	0.47
Reference Spruce	0.24	0.30	0.36	0.30
Sum Reference	0.71	0.66	0.94	0.77
Thin./Ref. Pine	87%	86%	78%	83%
Thin./Ref. Spruce	87%	74%	74%	77%
Thin./Ref. Sum	87%	81%	76%	81%

The long-term water-use efficiency (WUE) for aboveground growth was calculated by dividing BA growth by transpiration for the period 19 May to 30 September in each year (Figure 14); this was a period when sapflow was measured in all years. The growth unit should normally be units of mass, but since BA growth is almost linearly correlated to the increase in mass over a few years, this approach allows simple direct and relative comparison. In 1998, WUE was quite similar across species and plots, with the exception of spruce on the thinning plot, which was *ca.* 30% lower than the others (Figure 14). In 1999, WUE for pine decreased on both plots, while it increased on both of the spruce

plots; the increase was most remarkable for spruce on the reference plot, which almost doubled its WUE as compared to 1998. In 2000, WUE increased relative to 1999 on both pine plots, while it decreased for spruce. Considered over the three years, WUE showed the largest variation on the reference plot, for both pine and spruce; this was probably an effect of the severe drought to which this plot was exposed in 1999. WUE on the thinned plot varied less, and showed a small decrease after thinning. This indicates that trees on the thinned plot allocated more of their growth to parts other than the stem at breast height, which is a natural reaction, to utilise the newly available space. However, the opposite has also been observed, since an increased exposure to wind can stimulate growth in the lower part of the stem after thinning (Farrar, 1961; Burton & Smith, 1972). In the present study, the thinning intensity was, however, low; the area was flat, and the surrounding stands at least as tall: hence the wind load on the thinned trees can scarcely have increased because of thinning. Apparently, growth and transpiration were affected differently by the contrasting conditions during the three years, but also by thinning.

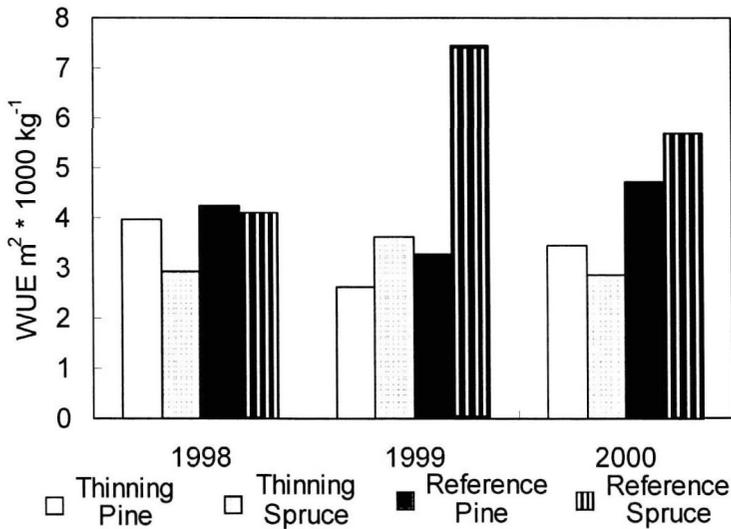


Figure 14. Relative water-use efficiency (WUE), calculated by dividing the basal area growth by total transpiration for the period 19 May to 31 September in each year.

Conclusions

The studied stand was rather inhomogeneous with respect to tree size, species composition and soil properties, and the experimental design did not include any replication or grades of thinning. It is therefore impossible to draw general conclusions from this experiment about the effect of thinning. Many interesting

results have, however, been produced concerning sapflow systems, and about the response of individual trees and stands to thinning and drought.

- The Granier and Cermak methods gave different results when the original Granier calibration was used. With new coefficients, both methods gave results in accordance with eddy correlation measurements. Since no satisfactory explanation was found for the discrepancy, it is recommended that Granier sensors should be tested against an independent method, when they are used in new conditions.
- Tree conductance for pine is more sensitive to changes in vapour pressure deficit, radiation and temperature, than that for spruce.
- The reaction to decreasing soil water content can vary widely between individual trees in a stand. Pine tends to maintain transpiration better than spruce at low soil moisture.
- The variation in sapflow increases after a disturbance such as a thinning. This was shown by the fact that it was hard to find a biometric quantity with a good correlation to sapflow after thinning.
- Ten years after a thinning, sapflow and stem growth may still be affected in the area around a strip-road system. Spruce is generally negatively affected, whereas the pattern is not as clear for pine.
- In the first period after a thinning, transpiration may be reduced to a higher degree than the reduction in BA, especially for pine.
- During a drought, a thinned stand is less sensitive to the decreasing soil-water content, with respect to transpiration.
- Water-use efficiency, defined as BA growth per unit of water transpired, may be reduced in the early years after thinning. This may probably be explained by a change in growth allocation.
- Growth is less affected than transpiration in a dry year.
- Increased nitrogen concentration in the needles is a likely explanation of why a thinned stand, shortly after thinning, can transpire at the same or at a higher rate, than an unthinned stand.

For a forester, it has been very interesting to combine my former field of forest management with the new field of biogeophysics. In future research, it would be interesting to follow this stand in further years, and to delve deeper into the carbon fluxes.

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