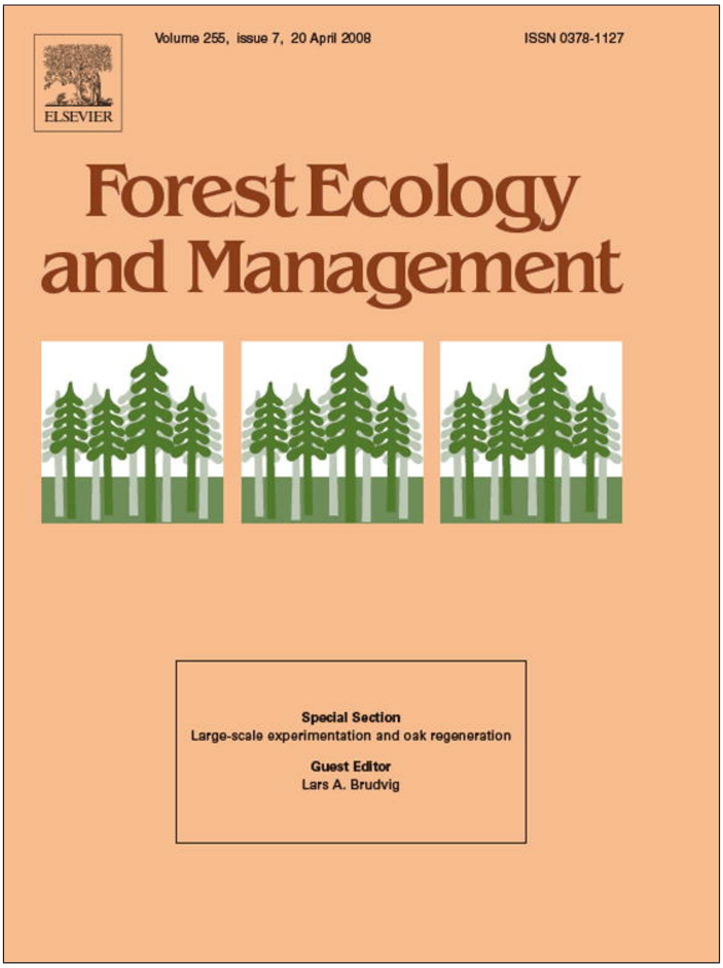
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Full length article

Thinning effects on pine-spruce forest transpiration in central Sweden

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Abstract

This study analyses the effects of thinning on stand transpiration in a typical mixed spruce and pine forest in the southern boreal zone. Studies of transpiration are important for models of water, energy and carbon exchange, and forest management, like thinning, would change those processes. Tree transpiration was measured by the tissue heat-balance sapflow technique, on a reference plot and a thinning plot situated in a 50-year-old stand in central Sweden. Sapflow was measured during one season (1998) on both plots before thinning, to establish reference values. In winter 1998/1999 24% of the basal area was removed from the thinning plot. Thinning was done so as to preserve the initial species composition and the size distribution. The measurements continued after thinning during the growing seasons of 1999 and 2000. The climate showed remarkable differences between the 3 years; 1998 was wet and cool, with frequent rain, and the soil-water content was high throughout the year. In contrast, 1999 was dry and warm, and the soil-water content decreased to very low values, *ca*. 5–6% by volume. In 2000, the weather was more normal, with variable conditions. Stand transpiration was similar on both plots during the year before thinning; the plot to be thinned transpired 6% more than the reference plot. After thinning, transpiration was initially *ca*. 40% lower on the thinned plot, but the difference diminished successively. When the following drought was at its worst, the thinned plot transpired up to seven times more than the reference plot. During the second season after thinning, the thinned plot transpired *ca*. 20% more than the reference plot. The increased transpiration of the thinned plot could not be attributed to environmental variables, but was most probably caused by changes in biological factors, such as a fertilization effect.

Keywords: *Pinus sylvestris*; *Picea abies*; Thinning; Sap flow; Forest management; Drought

1. Introduction

Questions about anthropogenic effects on the environment, through manipulation of the vegetation, have become increasingly topical in recent decades. The partitioning of absorbed radiation into sensible and latent heat at the Earth's surface is a key process for the climate (Sellers et al., 1997; Higgins and Schneider, 2005). This partitioning is readily changed by disturbances or management, which may affect climate. The hydrological cycle is a further example of a global mechanism that is vulnerable to changes in the composition and structure of vegetation through several feedback interactions (Hutjes et al., 1998). The strong link between the hydrological and the carbon cycle also emphasizes the need for a thorough understanding of the mechanisms that regulate the states and fluxes of water in vegetation (Sellers et al., 1997).

Thinning is a common silvicultural practice, aimed at increasing the dimensions and quality of trees harvested at the end of a rotation. It also has an economic justification, because it normally provides the forest owner with a net income. The net income of thinning has been reduced, but factors like; relatively easy terrain and mostly a performed pre-commercial thinning, make thinning in Sweden still profitable (Pettersson, 1993). In Sweden, thinning normally is carried out at 10–30-year intervals, 20–40% of the trees being removed on each occasion (Skogsstyrelsen, 1989a,b). About 1% of Swedish forests are thinned annually, and about one-third of the total harvested volume in Sweden is derived from thinning (Swedish National Forest Inventory).

Mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) are common in moderately fertile forests in Sweden. Pine is always found in the overstory,

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whereas spruce normally grows both in the overstory and as an understory. Spruce is preferentially removed at thinning, compared to pine, since spruce is more valuable as pulpwood but less valuable as sawn timber, which changes the natural species composition.

The effect of thinning on tree and stand growth and structure has been widely investigated in Swedish forestry (Näslund, 1971). Its effect on water uptake and transpiration has received less attention, although a few studies in other countries exist. Morikawa et al. (1986) showed, for instance, that transpiration of stands of *Chamaecyparis obtusa* Endl. was reduced in direct proportion to the reduction of basal area, and Breda et al. (1995) found similar results in sessile oak (*Quercus petraea* (Matt.) Liebl.). In the latter study, transpiration on the thinned plot returned to the same level as that on the reference plot in the second year after thinning. With Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Black et al., 1980) and Loblolly pine (*Pinus taeda* L.) (Stogsdill et al., 1992), there was little or no effect of thinning on stand transpiration, compared to an unthinned stand during dry conditions. And recently Vesala et al. (2005) found no effect of thinning on total transpiration in boreal *P. sylvestris*.

The effects of thinning on transpiration have also been theoretically analysed by Jarvis (1975) and Whitehead et al. (1984). An interesting feature of their analysis of thinning is that it is thought to reduce the vulnerability of drought as the interception and competing for water will decrease, which has also been shown in field studies (Aussenac and Granier, 1988; Gracia et al., 1999). It has also been shown that the transpiration reduction starts at quit low soil-water content (SWC) but that the response then is very steep (Lagergren and Lindroth, 2002). As a consequence, a small thinning effect on SWC can have a substantial effect on the transpiration. South-eastern Sweden is regularly exposed to summer drought, and extreme weather conditions are predicted to become more frequent in the future (Karl et al., 1995; Fulton, 1999). A possible initial strategy for meeting an increased risk for drought could be to increase the fraction cut in thinnings and to reduce the interval between thinnings.

The development of sapflow methodology (see Swanson, 1994) for the measurement of tree water uptake, has made it possible to study the effects of thinning on water uptake and transpiration at both tree and stand level, at a high temporal resolution.

The expected response of a moderate thinning could be summarized in a few hypotheses. (i) The first response to thinning would be a reduction in the transpiration at the stand level, the reduction should, however, be less than the fraction of removed trees as the remaining trees will get more light (Jarvis, 1975; Whitehead et al., 1984). (ii) Over the following years the transpiration rate should gradually increase to the pre-thinning level in time with a reoccupying of the canopy space (Jarvis, 1975; Whitehead et al., 1984). (iii) As a consequence of reduced transpiration and interception, the soil-water content should increase and the stand should be less sensitive to drought (Lagergren and Lindroth, 2002). The hypothesises were tested in a mixed Swedish coniferous forest, where the very dry growing season in 1999 made it possible to also study the third hypothesis.

2. Materials and methods

2.1. Site and stand

The thinning experiment was situated in the Norunda forest, central Sweden (60°05′N, 17°29′E, 45 m a.s.l.). The stand was *ca*. 50 years old and naturally regenerated. The soil is a deep, boulder-rich, sandy glacial till. The area is basically flat, but small-scale (0–25 m) undulation creates differences of 2–3 m in elevation, which cause large differences in soil moisture in the rooting zone. The mean annual temperature at the nearest weather station is 5.5 °C (1961–1990), and the mean precipitation is 527 mm.

The stand was a mixture of Scots pine (*P. sylvestris* L.), Norway spruce (*P. abies* (L.) Karst.) and some downy birch (*Betula pubescens* Ehrh.) (Table 1). There were also a few specimens of silver birch (*B. pendula* Ehrh.), and in the wetter parts, common alder (*Alnus glutinosa* (L.) Gaertn.). The field-layer vegetation was in both plots dominated by *Vaccinium myrtillus* L. (*ca*. 27% coverage) but the reference plot had a higher coverage of grass (20% compared to 2%). In 1997 coordinates were assigned to all trees >5 cm in diameter at 1.3 m on a 120 m × 120 m thinning plot and on a 120 m × 60 m reference plot, and their diameter was measured. The height and the length of the live crown were measured on a sample of 115 pines and 85 spruces. The plots were located next to each other and were selected to have similar species composition; they were also on the same level in the landscape. The reason for different size of the plots was that the experiment first was designed with two thinning intensities but as a large heterogeneity was revealed we decided to concentrate the recourses to one thinning plot.

The leaf-area index of the stand was estimated three times a year, by means of a plant canopy analyser (LAI-2000, Li-Cor Inc., Lincoln, NE, USA). A fixed grid of 18 positions in the reference plot and 25 in the thinned plot was used. The

Table 1
Stand characteristics of the reference and the thinned 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 (m^2 ha^{-1})	Pine (%)	Spruce (%)	Deciduous (%)	SD (trees ha^{-1})	*D* (cm)	*H* (m)	Distance (m)
Reference	28.9	64	33	2.8	872	19.9	16.9	2.23 (0.61)
Thinned before	29.1	57	40	3.4	939	19.2	16.7	2.10 (0.61)
Thinned after	22.0	56	40	3.6	703	18.9	16.5	2.58 (0.71)

Distance is the average distance to the closest neighbouring tree with its standard deviation in parenthesis.

Table 2
Leaf-area index determined by LAI-2000 and by allometric functions and specific leaf area for the 3 years

	Reading	1998				1999				2000			
		1	2	3	Mean	1	2	3	Mean	1	2	3	Mean
Thinned	LAI-2000	4.6	4.5	4.7	4.6	3.4	3.5	3.3	3.4	3.5	3.5	3.4	3.5
	SE	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	LAI allometric				5.2				3.9				
Reference	LAI	5.2	4.9	5.3	5.1	5.0	5.2	4.7	5.0	5.2	5.0	4.8	5.0
	SE	0.3	0.2	0.2	0.2	0.1	0.2	0.2	0.2	0.1	0.2	0.1	0.2
	LAI allometric				4.9				4.9				

In 1998 LAI-2000 measurements were made on 24 July, 17 August and 16 September. In 1999, on 23 July, 13 August and 18 October. In 2000, on 16 June, 13 August and 2 October.

measurements were corrected for foliage clumping by multiplying the measured values by 1.65, as suggested by the manufacturer. A value of about 2.5 has been found for spruce (Stenberg, 1996), but as the stand was pine dominated and the woody fraction relatively large the lower value was preferred. For validation, LAI was also calculated from the needle biomass derived from the stand inventory and allometric biomass functions (Marklund, 1988) multiplied by specific leaf area (SLA, m^2 leaf area/kg dry leaf weight). From a study in an adjacent 70-year stand (Morén et al., 2000), SLA of 5.01 and 7.36 was calculated for pine and spruce, respectively. The LAI estimates are given in Table 2.

2.2. Thinning

In November 1998, the stand on the thinning plot was thinned. The trees were felled by motor-saw, and extracted by a forwarder. This is not the standard forestry practice today, but was used to reduce possible damage to the trees. The same strip-road system was used as in the previous thinning in the winter of 1990/1991. There was a snow cover of *ca*. 15 cm at the time of thinning, but the soil was not frozen. Trees were selected with three aims in mind: first, to remove trees of poor quality, *i.e*. damaged or with a low growth potential; secondly, to maintain the size and species mixture constant; and thirdly, to distribute the removals evenly over the area. The thinning removed 24% of the basal area and 25% of the leaf area (based on needle mass) (Tables 1 and 2).

2.3. Sapflow measurements

Sapflow was measured by the heat-balance method (Cermak et al., 1973, 1982; Kucera et al., 1977), employing 12-channel tissue heat-balance sapflow meters (P690.3 and P4.1, Environmental Measuring Systems, Brno, Czech Republic), which are complete with data loggers. The working principle of the two models is identical. A set-up with five electrodes for heating, a heating power of 1 W and automatic compensation for natural gradients was used (see Lundblad et al., 2001). Whole-tree sapflow, Q, was scaled up from the measured segment by the ratio between the circumference of the outer xylem at the position of the electrodes and the width of the heated segment (8 cm).

Two systems were installed on the thinning plot in June 1997, and one on the reference plot in August 1997. In July 1998 and in May 2000, the systems were reinstalled on new trees. Each system was installed on 10 trees, of which four to six were spruces and the remainder were pines. Sapflow for each tree was based on measurements on two sides as in Lundblad et al. (2001). In May 2000, a fourth system was installed, shared between the plots. In that year, sapflow was measured on 12 pines, 11 spruces and two birches on the thinned plot, and on seven pines, six spruces and two birches on the reference plot.

The trees were selected along 60–80 m long transects, to cover the species and diameter distribution in the stands as well as spatial variation in soil conditions. This strategy was recommended by Cienciala et al. (1999) in a previous study in an adjacent stand.

In 2000, sapflow was also measured on two birches in each plot, to quantify the contribution of deciduous species to total stand transpiration. A simple model, with linearly increasing and decreasing fractions at the beginning and end of the season, respectively, and with a constant fraction during the summer, was used to estimate the contribution of deciduous trees to total stand transpiration during 1998 and 1999.

The gaps in the data, which occurred mainly in 1998 and 2000 (Table 3), were filled by use of the relationship to trees of the same species and treatment a few days before and after the gap. On a few occasions, the other species or treatment had to be used. For 4 days in 1998 the relationship to sapflow measured by the Granier method in an adjacent stand (Lundblad and Lindroth, 2002) with similar characteristics, was used to fill the gaps. For 9 days in 2000 with no sapflow data available the relationship with potential evaporation (E_p) was used (Penman, 1948), these days were not used in the statistical analysis. When sapflow data were used, the correlation with the missing tree was typically *ca*. 0.95, and when E_p was used, it was *ca*. 0.85.

Measured sapflow was scaled up to stand transpiration (E) by use of the quotient between the needle mass of the whole stand (N_{tot}) and the needle mass of the sapflow trees (N_{sap}), as Cienciala et al. (1998)

$$E = \frac{N_{tot} Q_{sum}}{N_{sap} A}$$

Table 3
Number of days on which sapflow measurements malfunctioned divided in different classes

Trees not working	1998		1999		2000	
	Thinning	Reference	Thinning	Reference	Thinning	Reference
0	32	137	83	182	49	74
1–2	54	25	108	25	52	8
3–4	53	0	11	0	2	1
5–7	5	0	0	4	26	21
8–10	15	8	7	2	8	40
11–14	6	–	2	–	7	0
15–19	4	–	1	–	3	13
20–24	8	–	1	–	3	–
25	–	–	–	–	8	–
Total days	177	170	213	213	158	157
Average number of trees not working	4.2/20	0.6/10	1.4/20	0.3/10	4.3/25	4.6/15

where Q_{sum} is the total sapflow in the sapflow trees and A is the area of the stand. Pine, spruce and deciduous trees were treated separately. Needle mass was chosen as the scaling factor as it has shown a linear relationship with no intercept to sapflow (Lagergren and Lindroth, 2004). The biomass functions of Marklund (1988) were used to estimate needle mass of the individual trees. Diameter at breast height, height, length of living crown, and for pine, also the northing in the Swedish coordinate system (RT 90), were the input parameters. For the sapflow trees, all input parameters were measured when they were selected, while for the remainder of the trees, allometric relationships established between needle mass and diameter for the sample of trees, mentioned above, were used.

2.4. Other measurements

Volumetric soil-water content (θ) was measured about every tenth day during the growing season by the TDR technique (Topp et al., 1980), at 16 and 8 positions on the thinned and reference plot, respectively. At each measurement point, one pair of 50-cm steel rods were inserted vertically from the soil surface, and the dielectric of the sensors was measured manually with a 'cable tester' (Tektronix 1502C, Tektronix Corp., Beaverton, OR, USA). Additionally, six other soil moisture sensors (ThetaProbes, ML1, Delta-T Devices, Inc., UK) were installed at 10–15 cm depth, to measure the temporal variation in θ at higher time resolution. Data were recorded every minute by a datalogger and a multiplexer (CR-10 and AM-32, respectively, Campbell Scientific, Inc., NE, USA), and stored as 10-min means. Daily means from the automatically recorded soil moisture sensors were used to obtain daily values of θ between the TDR measurements:

$$\theta_i = \frac{\theta_{\mathrm{TP}_i}\theta_{\mathrm{TDR}_0}}{\theta_{\mathrm{TP}_0}} + \left(\theta_{\mathrm{TDR}_n} - \frac{\theta_{\mathrm{TP}_n}\theta_{\mathrm{TDR}_0}}{\theta_{\mathrm{TP}_0}}\right)\frac{i}{n}$$

θ_i is soil moisture calculated at time i, n is the number of time steps in the ThetaProbe data (θ_{TP}) between TDR measurements (θ_{TDR}) at time 0 and n. R^2 between θ_{TP} and θ_{TDR} was 0.96 and 0.97 for the thinning and reference plots, respectively.

The transpiration response to decreasing soil-water content has been evaluated for individual trees in the reference plot during the dry 1999 season (Lagergren and Lindroth, 2002). The volumetric soil-water content at 0–50 cm depth for the onset of transpiration reduction was 9.9 and 10.3% for the average pine and spruce, respectively. In the present study a common value of 10% is referred to as the critical value for onset of reduced transpiration (CVRT).

Meteorological data were measured on the 100-m "Norunda central tower", *ca.* 500 m from the plot, except precipitation that was measured in a clear-cut area 500 m away (Lundin et al., 1999). When gaps in the time series from the central tower occurred, data from a scaffold tower within the thinned plot, with instruments at 18 m height, were used (Lundblad et al., 2001). About 65% of the meteorological data came from the central tower. Soil temperature at 10 cm depth was measured at 20 points in the thinning plot and 10 points on the reference plot with thermistor probes (107 Campbell Scientific, Inc., NE, USA).

2.5. Statistical treatment

To be able to statistically evaluate the difference in transpiration between the stands the transpiration for each tree was calculated on a ground area basis. The area that each tree was supposed to represent (A_{tree}) was calculated as

$$A_{\mathrm{tree}} = AS\frac{N_{\mathrm{tree}}}{N_{\mathrm{tot}}}$$

where A is the total plot area, S is the share of the total BA for the species of the tree, N_{tree} is the needle biomass of the tree and N_{tot} is the total needle biomass for that species. The difference between the thinned and the reference plots in θ and sapflow was evaluated by Student's t-tests.

3. Results

3.1. Climate

The years 1998–2000 had contrasting weather (Fig. 1). The growing season of 1998 was wet and cool; soil-water content

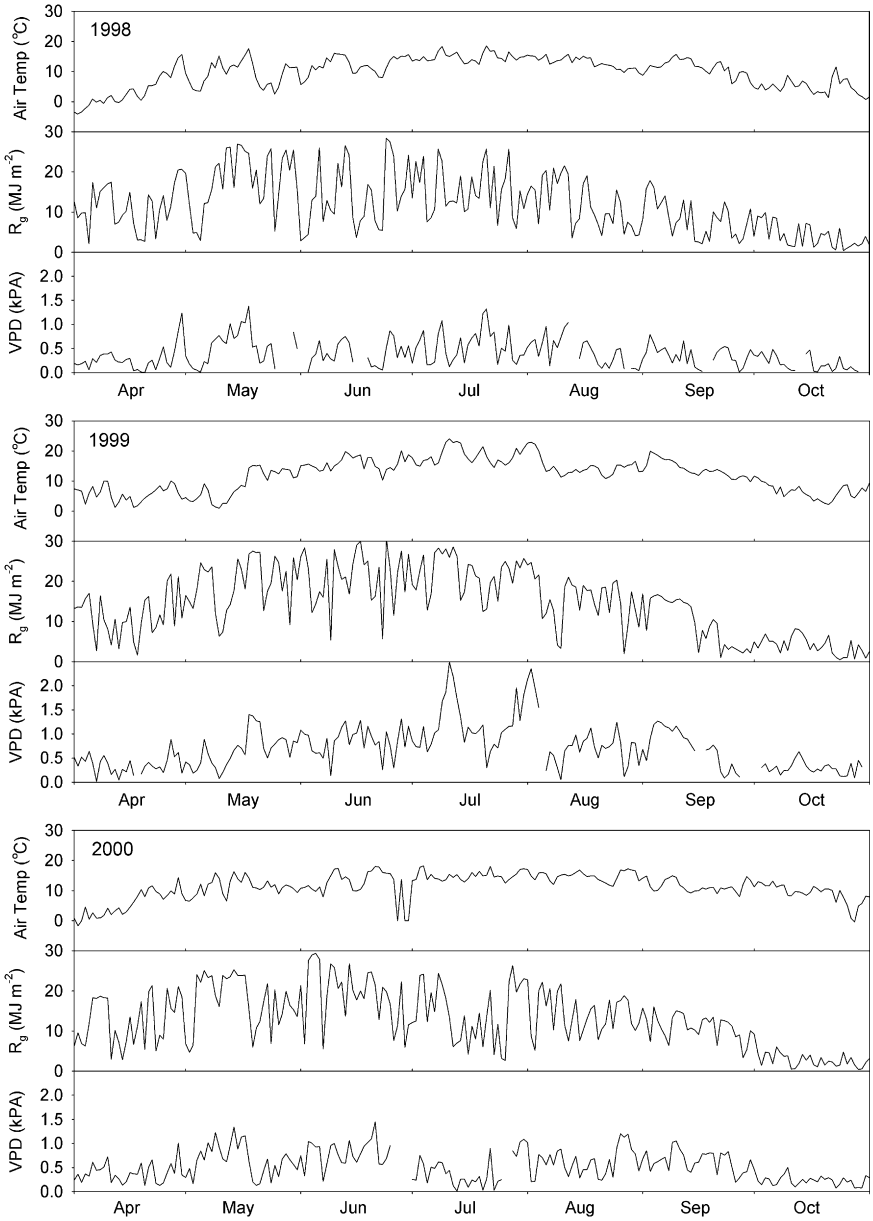

Fig. 1. Meteorological conditions during the growing season in 1998–2000. Daily mean air temperature, daily total global radiation and daytime average vapour pressure deficit.

was high throughout the period as a result of higher than normal precipitation (Fig. 2). The precipitation was also high the following winter and, as a result, the groundwater table reached the soil surface at many points in the spring of 1999. The soil moisture was well above field capacity and close to the porosity of *ca*. 40% (Lundin et al., 1999) (Fig. 2). The summer of 1999 was warm and dry; July had only one-third of the normal precipitation. Consequently, the soil-water content (θ) decreased to a minimum on 4 August (Fig. 2). Some heavy storms recharged the soil-water slightly but after another dry period, lasting about a month, a new minimum θ was attained on 15 September. In 2000, the spring was dry and warm while late June and July were very wet (only 6 days without precipitation in July). The lowest values of θ were found in the second half of June and in the beginning of October.

The differences in evaporative demand between the three seasons are well illustrated by the differences in Penman (1948) evaporation. The wet and cool year 1998 had an estimated potential evaporation of 308 mm for the period June–August, whereas the comparable values of the warm and dry 1999 season was 472 mm, and the intermediate 2000 season was 355 mm (Table 4).

3.2. *Effects of thinning on stand transpiration and soil-water content*

In 1998, the year before thinning, there were only minor differences in transpiration between the two plots (Fig. 3). A maximum transpiration of 4 mm day^{-1} was attained on both plots and on average the transpiration was 6% higher on the

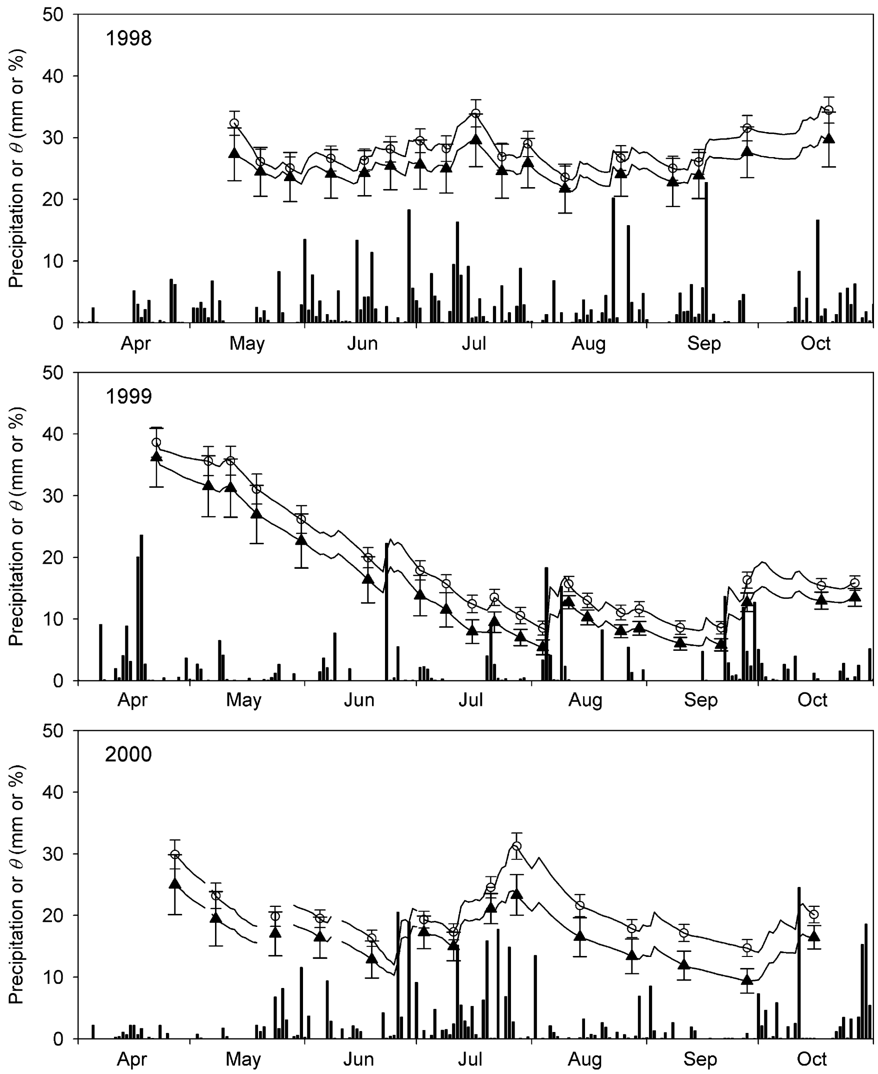

Fig. 2. Daily precipitation (bars) and soil-water content (θ) at 0–50 cm in the thinning (circles) and reference (triangles) plots showing ±S.E. The symbols indicate measured mean values of the TDR-sensors; the lines are derived from the ThetaProbes.

thinning plot (Table 4) but the difference was never significant. The day-to-day variation was large throughout the summer, reflecting the large variation in weather conditions. The volumetric soil-water content (θ) at 0–50 cm showed a small, but almost constant, difference of 3–5%, with the higher values on the thinning plot (Fig. 2). No statistically significant differences in θ were found between the two plots.

Table 4
The sum of the daily Penman potential evaporation (E_p) and measured transpiration for the thinned (E_{thin}) and reference (E_{ref}) plots for the months June, July and August

	1998	1999	2000
E_p (mm)	308	472	355
E_{thin} (mm)	144	159	186
E_{ref} (mm)	136	125	155
E_{thin}/E_p (%)	47	34	53
E_{ref}/E_p (%)	44	27	44
E_{thin}/E_{ref} (%)	106	127	120

At the beginning of the 1999 season, after thinning, the daily transpiration rate in the thinned stand was *ca*. 60% of that on the reference plot (Fig. 4) or 0.5 mm day^{-1} lower in absolute terms (significant $P < 0.05$) (Fig. 3). When looking at the different species the difference was highly significant for pine from middle of April to the middle of June whereas there were no significant differences for spruce during this period (data not shown). The difference decreased gradually until the beginning of July, when the daily transpiration rates were similar (Fig. 4). During this period, θ decreased (Fig. 2), but it was consistently above 10%, the critical value for the onset of reduced transpiration (CVRT) reported by Lagergren and Lindroth (2002). The soil-water content continued to decrease in July; reaching CVRT the 12th and 31st July, in the reference and thinned plots, respectively. At the end of this period the transpiration on the thinned plot, became up to seven times higher than that on the reference plot (Fig. 4) and the difference was significant (Fig. 3). The quotient between transpiration and Penman potential evapotranspiration showed a similar linear

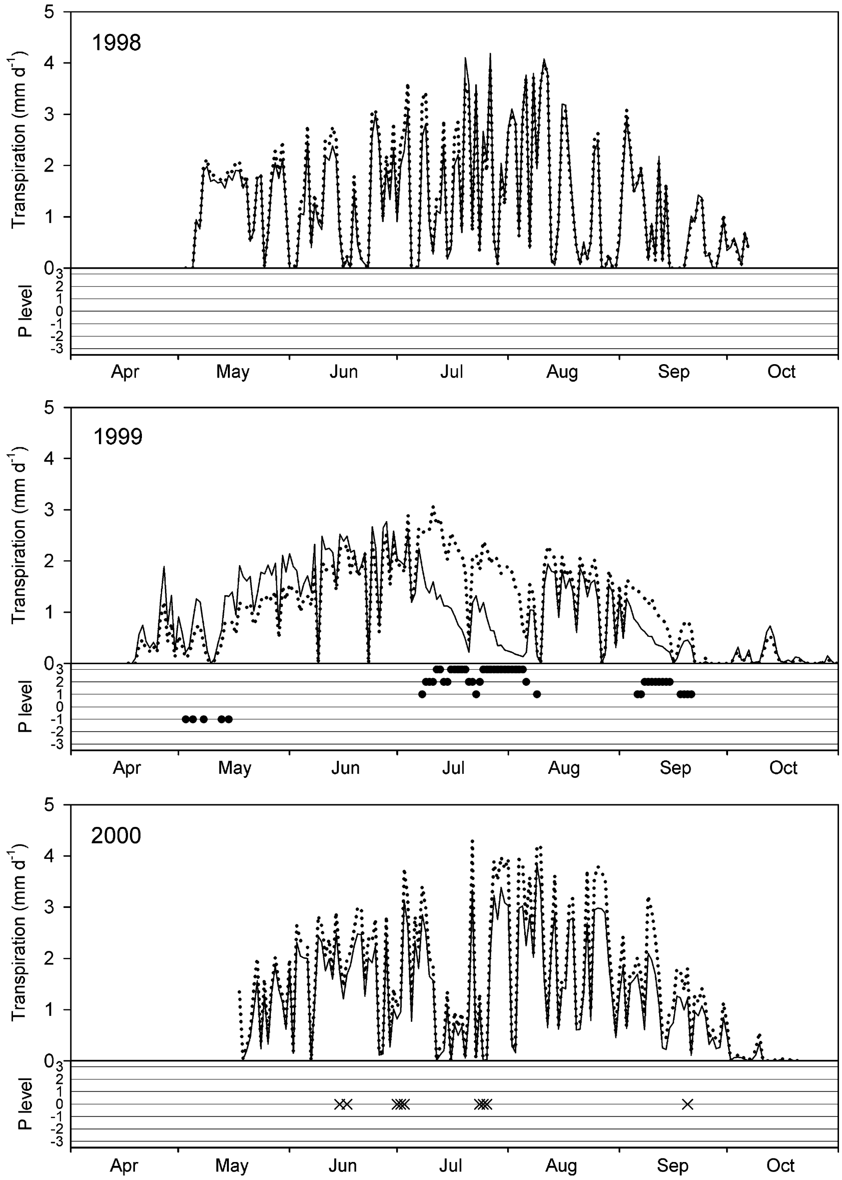

Fig. 3. Daily transpiration rates for the reference (dotted line) and thinning (solid line) plots. The P level is the level of the probability for equal transpiration (0 if $P > 0.05$, 1 if $0.05 > P > 0.01$, 2 if $0.01 > P > 0.001$ and 3 if $P < 0.001$), a positive value means that the transpiration for the trees in the thinning plot was higher than in the reference plot and *vice versa*. In 2000 the crosses shows data were no sapflow was available but the flow was calculated from the relationship to Penman potential evaporation.

relationship to θ for both treatments for θ below CVRT (Fig. 5). The decrease during the second drought period, however, started at lower θ (Fig. 5). For the period in August with temporarily higher θ, the thinned plot transpired *ca*. 20% more than the reference plot (Fig. 4).

In the year 2000, the second season after thinning, the transpiration of the thinned plot was higher than that of the reference plot throughout the season (Fig. 3). The difference was, however, not significant, which was mainly a consequence of very large variation in individual transpiration on the thinned plot. The variation was largest for spruce with standard deviation two to three times that on the reference plot, spruce also showed the largest difference in absolute average transpiration. The soil-water content fell only slightly below CVRT on the reference plot during 8 days in the latter half of September. The transpiration of the thinned stand was 120% of that of the reference stand in this season (Table 4).

In total for the three summers, the transpiration of the thinned plot was 73 mm higher than that of the reference plot, *i.e*. 17.5% (Table 4). In a comparison of the two seasons after thinning, the transpiration of the thinned plot exceeded that of the reference by 65 mm, *i.e*. 23%. There was, however, a difference by 6% before the thinning and if this is considered the ‘‘thinning effect’’ would be a 16% increase.

3.3. *Effects of thinning on species contribution to stand transpiration*

Since sapflow was measured on birch during the year 2000 only, it was not possible to analyse the effects of thinning on this

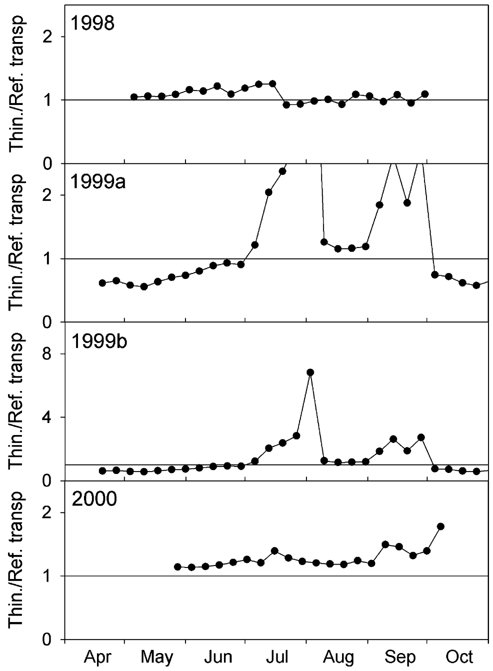

Fig. 4. Quotient between transpiration in the thinning and reference plots showing also the 1:1 line. In 1999 there are two plots with different scales to show the high quotient during the drought.

species. The relative contribution of deciduous trees (measured on birch) to total stand transpiration increased during May, and reached a maximum of about 10% on the thinned plot and 7–8% on the reference plot in the end of June (Fig. 6). The sapflow measurements began as late as 19 May in 2000; therefore, the estimated contribution by deciduous trees in the spring is uncertain. As the deciduous trees' share of the total stand BA (Table 1) was about half of their contribution to total transpiration, the measured birch trees transpired about twice as much as equally sized pines or spruces. The fraction then decreased slowly until the end of August when leaf senescence accelerated and the fraction decreased more rapidly.

In general, pine contributed slightly more to total stand transpiration on the reference plot than on the thinning plot, both before and after thinning (Fig. 7). The minimum

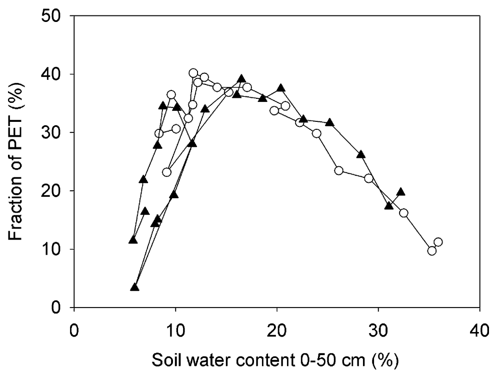

Fig. 5. Relationship between 1-week averages of the volumetric soil-water content at 0.50 cm and the measured transpiration's fraction of Penman potential evaporation. Data shown is from May to September 1999, open circles thinned plot, filled triangles reference plot.

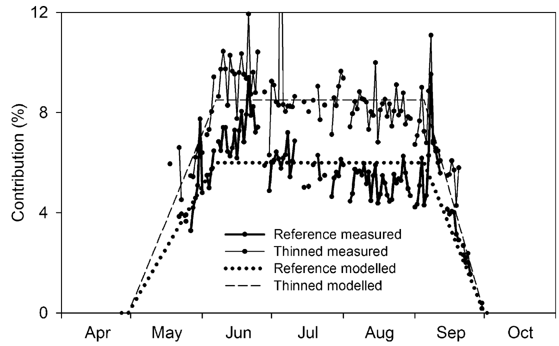

Fig. 6. Measured and modelled relative contribution to stand transpiration by deciduous trees for the thinned and reference plots, respectively, in 2000. Days with less than 0.5 mm total stand transpiration are excluded.

contribution by pine was in the first spring after the thinning when it was only 30%. Then a maximum pine contribution was attained in the beginning of August 1999, shortly before some heavy rainstorms interrupted the drought. At that moment, pine contributed *ca.* 70% in the thinned stand and 80% in the reference stand. The peak in pine contribution during the September drought was much more pronounced in the reference stand. In the year 2000, the contribution of pine was more evenly distributed over the season, with corresponding values of *ca.* 55 and 60%, respectively.

4. Discussion

In general the stated hypothesis of thinning responses on transpiration were confirmed; transpiration was initially reduced, the transpiration gradually recovered and the thinned stand was less sensitive to drought. The interruption of the recovery phase by the dry period makes it harder to distinguish the plain effects of thinning but a few results in parity with or deviating from, the hypothesised responses will be discussed.

4.1. Initial decrease after thinning in 1999

The initial response after thinning was a reduction by more than 40% relative to the reference plot (from +6% to −38%) for a reduction of the basal area (BA) by only 24% (Fig. 4). A few reasons for this ''overreaction'' can be stressed: (1) it is known that trees left in a thinning can get some sort of post-thinning stress, mainly as a result of a light shock for shade adopted needles (Harrington and Reukema, 1983). (2) The thinning operation could physically have damaged the remaining trees. Thinning was carried out at temperatures below 0 °C; the felling crew complained that the stiffness of the branches made felling difficult. Although measurements with the Plant Canopy Analyser in 1999 confirmed that leaf area had not been reduced by more than the expected *ca.* 25% (Table 2), branches and needles on the remaining trees may nevertheless have been damaged. (3) The roots may have been damaged, since the soil was not frozen and there was only a thin snow cover during the thinning operation. (4) The remaining trees on the thinned plot may have been more sensitive to the additive stress of night-time freezing temperatures that occurred in the beginning of

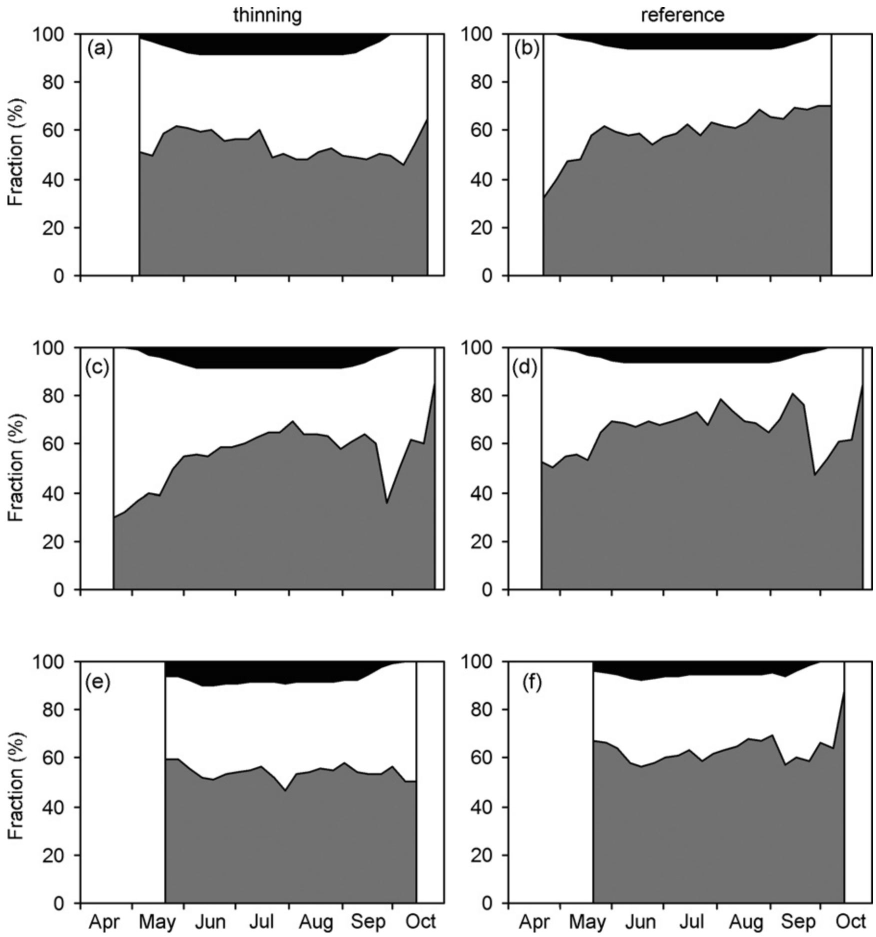

Fig. 7. Fraction of the total transpiration from the different species, pine (grey), spruce (white) and deciduous (black), calculated from 1-week sums. (a) Thinning plot 1998, (b) reference 1998, (c) thinned 1999, (d) reference 1999, (e) thinned 2000 and (f) reference 2000.

May after a warm ending of April (Bergh et al., 1998; Aussenac, 2000). The low pine contribution in the thinned plot in the spring directly after the thinning (Fig. 7) could be an indication of some sort of damage.

4.2. Recovery after the thinning in 1999

Transpiration of trees on the thinned plot recovered rapidly from the initially strong reduction in transpiration rates following thinning (Fig. 3). Stand transpiration of the thinned plot exceeded that in the reference plot from 4 July, except for a few days in October 1999, though the difference was only significant during the drought periods. Similar results were found for lodgepole pine (*P. contorta*) where the leaf area based transpiration increased from 80 to 200% of the reference during the first 3 months after thinning (Reid et al., 2006). In a loblolly pine (*P. taeda*) thinning experiment, the 50 and 75% removals of BA resulted in reductions of 29 and 43%, respectively, in stand transpiration, compared to the reference, during the first wet growing season. During the second, dry season, transpiration was reduced by only 12% in both treatments (Stogsdill et al., 1992). Breda et al. (1995) observed a similar response in sessile oak (*Q. petraea*), in that removal of 35% of BA resulted in a 25% reduction in transpiration in the first year after thinning while it was equal to the reference value in the second year.

Irvine et al. (1998) showed that stomatal conductance recovered in the year following a drought treatment in Scots pine. In that study, growth was significantly reduced in the year following the drought, whereas in the present studied stand, growth in both treatments in 2000 was better than that in 1998 (Lagergren and Lindroth, 2004). A simple form of light use efficiency showed higher values in 2000 than in 1998 for the reference stand while it was the opposite for the thinned stand (Lagergren, 2001). The rapid recovery of transpiration of the thinned plot to that of the reference in the present study may possibly be explained by the relatively light thinning compared to worldwide thinning practices.

4.3. Drought in 1999

The effect of drought on transpiration on both plots in the summer of 1999 was remarkable (Fig. 5). Transpiration during the driest days at the beginning of August fell to almost zero on the reference plot (Fig. 3), and the thinned plot also responded strongly. The similar relationships to volumetric soil-water content (θ) (Fig. 5) confirm that there was a difference in θ between the plots, even if not significant. The very steep relationships also show that quite precise measurements of θ are needed if results will be compared to other studies. The use of water pressure instead could be a better way as the pressure change rapidly at low θ. The relationships in the present study (Fig. 5), however agree with other studies' transpiration response to θ (Stewart, 1988; Irvine et al., 1998; Ewers et al., 2001). Furthermore, during a 1-month drought period in August, the thinned stand transpired *ca*. 45 mm more. Although there was a difference in soil-water content between the plots, this difference was practically constant throughout the period of drought, so that the thinned stand did not deplete the stored soil water more than the reference stand. About 40 mm of rain fell during this period, mainly in two large storms, and it is possible that increased throughfall and infiltration on the thinned plot made up part of the difference. However, there is much uncertainty as to how the soil-water content behaved in the deeper horizons. In the thinning study by Stogsdill et al. (1992), the most significant difference in θ was found in the deepest measured soil layer (90–122 cm). The difference in response to θ at the first and second drought period (Fig. 5) also indicates that there might be another layer than 0–50 cm that is more important in the stomata regulation.

4.4. Increased transpiration in 2000

The *ca*. 20% higher transpiration in the thinned stand, compared to the reference, during the second season after thinning could be attributed to the drought in the summer of 1999 that effected transpiration far more in the reference stand. A normal reaction of trees to severe drought is leaf-shedding (Kozlowski et al., 1991) which could have reduced the potential for transpiration in the following year. However, leaf-area measurements with the Plant Canopy Analyser did not indicate that this had happened (Table 2). The LAI-2000 may, however, be insensitive to leaf-shedding in a conifer forest (Stenberg et al., 1994). Transpiration of the reference stand in the year 2000 was, however, at the same level, relative to the Penman evaporation, as it was in 1998 (Table 4). The transpiration of the thinned stand relative to the Penman evaporation, on the other hand, increased from 47 to 53%. Thus, the increase in transpiration in the thinned stand was not only in relation to the reference, but also with respect to the variables driving transpiration.

Thinning not only affects transpiration in the hydrological cycle, but also interception, evaporation and throughfall. A reduction in leaf area reduces the capacity of the canopy to store intercepted water and therefore, the evaporation of intercepted water is reduced. Teklehaimanot et al. (1991) found a linear relationship between tree spacing and boundary layer conductance per tree resulting in a higher rate of interception evaporation at wider tree spacing. An earlier drying of the canopy could affect transpiration positively, though the change in the evaporation of intercepted water is probably of minor importance to transpiration. The effect on throughfall could have a larger impact, since an increase in throughfall will increase the amount of water that infiltrates into the soil (e.g. Zahner, 1968). This, in turn, will increase the amount of water available for transpiration. An indication that this was actually the case is the fact that the mean difference in soil-water content between thinned and reference plots increased from 2.9% in 1998 to 4.1% in 2000, in spite of an increase in transpiration. On the other hand, an increase in water availability is important only when soil-water content limits transpiration, which in 2000 was only the case for the latter half of September (Fig. 2). It is therefore unlikely that increased throughfall is the reason for the increase in transpiration on the thinned plot relative to the reference. However, it may be important in a year when water is limiting for transpiration as in 1999.

The light regime of the stand is directly affected by thinning and the amount of absorbed light in the canopy per unit of ground area will inevitably be reduced. However, it is reasonable to assume that the amount of light absorbed per tree or per unit of needle mass will increase but that this only partly compensates for the reduction in leaf area. This, in turn, implies that canopy conductance will decrease similarly, hence also transpiration. The increased transmittance of sunlight below the canopy and a deeper snow cover normally increase the soil temperature after thinning (Braathe, 1957), but no effect to soil temperature has also been reported (Son et al., 1999). In the present study soil temperature measured at 10 cm depth was similar both before and after thinning, and showed no effect of thinning. This implies that the increased net radiation was primarily utilised to increase the convective heat fluxes from the field- and ground-layer vegetation.

The possible explanations discussed above are insufficient to explain the increase in transpiration of the thinned stand relative to the reference stand. A factor, which may have an effect, is the growth of the canopy to occupy the space made available by thinning. This process normally takes 4–8 years, and there was no indication from the leaf-area measurements (Table 2) that this had occurred. Increased conductivity of the stems after thinning is also something to consider. According to the pipe theory (Shinozaki et al., 1964a,b) reduced competition could increase the hydrological conductivity of the newly formed xylem, while a drought would have the opposite effect (Deckmyn et al., 2006). The newest xylem is important for the water transport (Nadezhdina et al., 2002) but it is not likely that this alone could account for the increased transpiration in 2000. Another explanation may be the fertilization effect created by the large input of organic material, needles, branches and dead roots (Wollum and Schubert, 1975). This will stimulate photosynthesis, which in turn will increase canopy conductance, and thus increase the transpiration rate per unit needle area (Gough et al., 2004), perhaps to such an extent that it more than compensated for the 24% loss of needle area in the present study. One argument in favour is that most of the forests in this part of Sweden are known to be nitrogen-limited; the Norunda forest is no exception. The reaction of needle nitrogen concentrations to thinning is normally a rapid increase, followed by a dilution as the needles become larger (Vesterdal et al., 1995; Hökkä et al., 1996). The implication is that thinning can actually increase transpiration to a level above that in the unthinned situation.

4.5. Uncertainties

Uncertainty in the estimates of transpiration should also be considered. The standard deviation for spruce on the thinned plot was two times larger than that for the reference plot in 2000 (*ca*. 30% lower for pine), which is the reason why the difference in transpiration was not significant (Fig. 3). The variation in sapflow density also increased significantly in a sessile oak stand after thinning (Breda et al., 1995). The reason for increased variation in spruce transpiration could be that their shallow root system is more sensitive to damage. Spruce has also a deeper leaf area distribution that will benefit more from the reduced competition for light, compared to pine. The total effect can probably be very different for individual spruces (Lagergren and Lindroth, 2004). A larger than normal sample of trees for sapflow measurements should therefore be used in future thinning studies. Cermak et al. (1995) recommend 6–12 measured trees per species which means that the number of measured trees in the reference stand was somewhat low in 1998–1999 (five trees per species).

5. Conclusions

The initial response at the beginning of the first season following thinning was a decrease in transpiration that was larger than the reduction in leaf area. This was followed by a successive recovery up to the level of the reference transpiration.

The thinned stand was much less affected by drought than the reference during a severe drought the first year after thinning.

A thinned stand can be stimulated such that transpiration increases above the level of the unthinned stand during the second season after thinning. A possible mechanism may be that the thinning activity itself causes a fertilization effect.

The sapflow technique is well suited to this type of study on relatively small plots. A larger sample of trees than normal is however recommended as the variation in sapflow after thinning increased.

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