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The effects of water availability on transpiration, water potential and growth of *Picea abies* during a growing season

Emil Cienciala*[,a], Anders Lindroth[a], Jan Čermák[b], Jan-Erik Hällgren[c], Jiří Kučera[b]

[a]*Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden*
[b]*Institute of Forest Ecology, University of Agriculture, CZ-644 00 Brno–Soběšice, Czech Republic*
[c]*Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden*

Abstract

Transpiration, pre-dawn shoot water potential and growth of Norway spruce trees were measured for one growing season, under three water regimes, giving a seasonal water input of 696 mm (irrigated), 579 mm (control) and 270 mm (drought). Potential transpiration was calculated from the Penman–Monteith equation, using maximal canopy conductance as a function of vapour pressure deficit. Sap flow was measured by a tree-trunk heat balance method and the data were expressed per unit ground surface. This allowed calculation of canopy conductance (g_c) for the three treatments. The median of the daytime g_c was about 1.1 cm s^{-1} for non-limiting water conditions, and about 0.5 cm s^{-1} for the conditions of a moderate water deficit. Pre-dawn water potential did not decrease until daily transpiration rates were substantially reduced, with corresponding g_c of 0.2 cm s^{-1}. The type of control which limits transpiration is discussed. The basal-area growth was related closely to the amount of water infiltrated into the soil. The estimated long-term tree water-use efficiency (the total dry matter produced per unit of water transpired) was on average 4.8 g kg^{-1}, with insignificant differences between the treatments. Seasonal transpiration reached 380 mm, 325 mm and 209 mm for the irrigated, control and drought treatment, respectively.

1. Introduction

Artificially planted stands of Norway spruce, still very common in central and

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* Corresponding author. Tel.: (+46)-18-672562. Fax: (+46)-18-673440.

northern Europe, are vulnerable to both increased industrial pollution and to climatic spells with profound drought. There are many studies on spruce, but the local soil and climatic conditions often demand a separate investigation to be performed to answer questions about ecological stability and production of the spruce trees and stands in a particular region. Also, the literature offers only limited quantitative information on how the growth is related to the transpired water.

Although exchange of water vapour between plants and atmosphere has been studied for a long time it is still not easy to measure water uptake and water loss accurately on intact plants in the field. Recently, Kaufmann and Kelliher (1991) described various approaches to estimating canopy transpiration in forest stands. Besides climate, the water vapour exchange between trees and the atmosphere is controlled by stomata and depends on the boundary-layer conditions of the foliage. In tall forest canopies, where the mixing of air is generally good, and the temperature and humidity variation through the canopy is small, transpiration will be controlled mainly by stomata and vapour pressure deficit (Jarvis and McNaughton, 1986). Hence, forest transpiration can be estimated from measurements of climate and stomatal conductance under such conditions (Kaufmann, 1984; Running, 1984; Jarvis et al., 1985). In studies of canopy transpiration, the Penman–Monteith equation (Monteith, 1965) is often used. On the whole-tree level, total water flux can be estimated using tree-trunk heat balance (THB) method.

This study follows previous work at the site, where measurements by the THB method were used to estimate canopy conductance (g_c), which was then used with the Penman–Monteith equation to give transpiration under non-limiting soil water conditions (Cienciala et al., 1992). Here, the focus was primarily on the effects of water availability on transpiration and increment using various water treatments and long-term measurements. The estimation of the relationships of g_c to soil water deficit and to pre-dawn water potential, and of the long-term water-use efficiency were the main objectives of this work.

2. Materials and methods

2.1. Site, plant material and treatments

The site is located in Skogaby, southwest Sweden, 30 km southeast of Halmstad (56°33.5'N, 13°13.5'E) at an altitude of about 100 m. The sandy till topsoil had a pH of 4.0, increasing to 4.5 in the subsoil, and it is poor in base cations and rich in aluminium. The climate is rather humid, with annual precipitation around 1100 mm. The mean (1931–1960) annual air temperature was about 7°C. The Norway spruce (*Picea abies* L. Karst.) monoculture stand was 24 years old (in 1990) and was a second rotation forest. Basic stand characteristics were: stem basal area 34 m^2ha^{-1}; mean height 13.5 m; 2400 trees ha^{-1}. The stand had one closed canopy layer only, with projected leaf area index (LAI) of 9 (K. Wiklund, personal communication, 1992) and no understorey vegetation. The mean diameter at the breast height (dbh) was 13 cm and the distribution of size was symmetrical. Approximately 90% of the

root system was within the upper 20 cm of the soil; the rest was found in the next 50 cm (H. Persson, unpublished results, 1991). Air temperature, air humidity, wind speed, solar radiation and precipitation were measured at height of 2 m in an open clearing of 80 m by 80 m about 400 m from the trees being studied. A comparative wind speed measurement was made 1 year later (in 1991), when an anemometer was placed 2 m above the top of the canopy. Thus, wind speed was corrected according to the linear relationship assessed between the two locations, so as to represent the conditions above the canopy.

Three types of water regime were considered: drought, control and irrigated. The plots were squares of 45 m by 45 m located next to each other, with stand characteristics that were practically equal. On the drought-treated plot (D), a construction covering two-thirds of the area below the canopy was set up at the beginning of the growing season (1 April). On the irrigated plot (I), a sprinkler system was used to give an even distribution of water. The amount of irrigation was determined by the SOIL model (Jansson and Halldin, 1979), and aimed at keeping the soil water deficit below 20 mm of water during the growing season. Total irrigation for the year was 117 mm. The control plot (C) was untreated. The estimated seasonal totals of soil-surface infiltrated water were 696 mm, 579 mm and 270 mm on Plots I, C and D, respectively.

Weather conditions during the growing season were fairly typical for the region, with no extremes of rain or dry periods (Fig. 1). Vapour pressure deficit was tem-
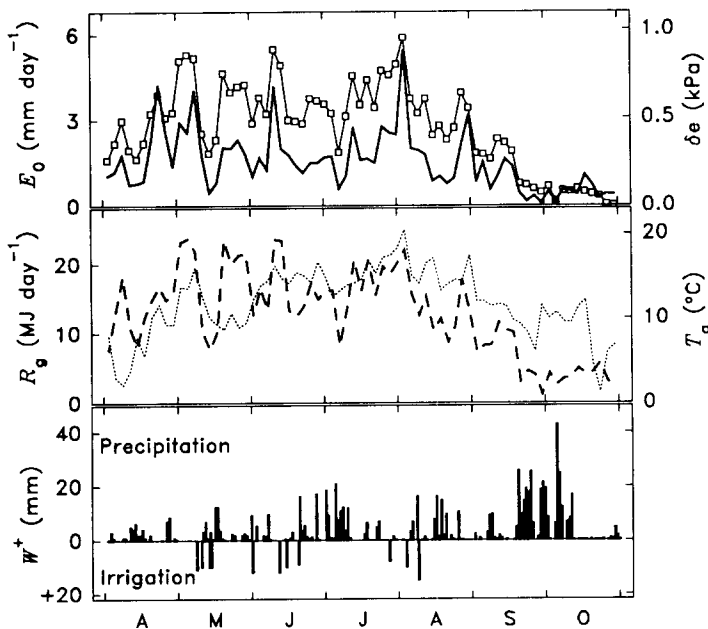

Fig. 1. Climatic variables (3-day mean values) for the growing season at the site. Top: Penman open-water evaporation (E_0, □), and vapour pressure deficit (δe, solid line). Middle: global radiation (R_g, dashed line) and air temperature (T_a, dotted line). Bottom: daily precipitation and irrigation for Plot I (W^+).

porarily high in early August (maximum daily mean 1.9 kPa). During warmer and drier periods, open water evaporation calculated according to Penman (1948) reached 4–5 mm day^{-1} and the total for the growing period (190 days) was 561 mm.

2.2. Measurements of sap flow

Sap flow was measured continuously during the growing season by the THB method with internal heating, where heat is applied to a stem segment using 3–5 electrodes inserted into conductive xylem tissues (Čermák et al., 1973; Kučera et al., 1977). The instruments were made in the Institute of Forest Ecology, Brno (currently commercially available from Ecological Measuring Systems, Brno). There were two measuring points on opposite sides of the trunk at breast height (1.3 m above ground level), to take account of possible variation of sap flow within the stem. Five trees were used for sap-flow measurements: two in Plot I, two in Plot D and one in Plot C. These trees were co-dominant within the stand, with heights of 13.5–15.0 m and dbh of 15.7–18.6 cm.

2.3. Calculation of transpiration per unit ground surface from tree sap flow

Sap flow (Q_{wt}) measured by THB method on individual sample trees was converted to transpiration per unit ground surface (E_Q) based on an approach of Čermák et al. (1988). E_Q is calculated using a linear relationship of Q_{wt} to basal area:

$$E_Q = SQ_{wt} \tag{1}$$

where the scaling factor S is

$$S = [(A - A_{min})/(A_R - A_{min})]\beta \tag{2}$$

where A is the average cross-sectional area of the trees on a plot, A_R is the cross-sectional area for the tree where sap flow is measured and β is tree number per unit area. A_{min} is the cross-sectional area of the smallest living trees in the plot. Such a tree had definite size, but practically no measurable sap flow rate, thus transpiration can be assumed with minimal error as zero. The dbh for that tree was 5.5 cm and had not increased during the previous 2 years on the site (the increment of the most suppressed trees is hardly detectable). The minimum time interval for using Eq. (1) should be at least 1 day to avoid a short-time shift between courses of sap flow and transpiration.

2.4. Estimation of potential transpiration and canopy conductance

The calculation of potential transpiration (E) follows the Penman (1953) combination equation in the form given by Monteith (1965):

$$\lambda E = \frac{\Delta(R_n - G) + \rho c_p \delta e g_a}{s + \gamma[1 + (g_a/g_c)]} \tag{3}$$

where λ is latent heat of vaporisation of water (J g^{-1}), R_n is net radiation above the stand (W m^{-2}), G is rate of change of energy storage (W m^{-2}), ρ is density of dry air
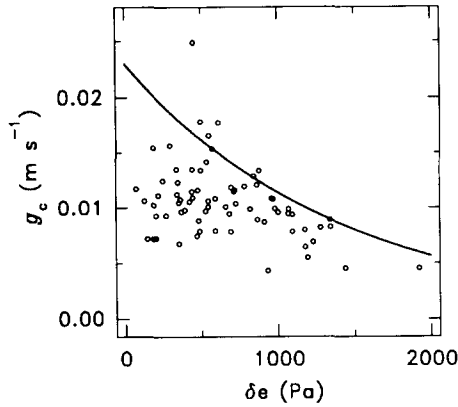
Fig. 2. Canopy conductance (g_c; ○) against vapour pressure deficit (δe). The curve represents the maximum conductance (adapted from Cienciala et al. (1992)).

(kg m^{-3}), δe is vapour pressure deficit at height z (Pa), g_a is aerodynamic conductance (m s^{-1}), s is temperature derivative of saturated vapour pressure function (Pa K^{-1}), γ is psychrometric 'constant' (Pa K^{-1}) and g_c is canopy conductance (m s^{-1}).

It is well known that g_c of forests depends on factors such as air humidity, solar radiation and leaf water potential (e.g. Jarvis 1976; Lindroth, 1985; Stewart and de Bruin, 1985). In a previous work (Cienciala et al., 1992) g_c for the irrigated plot was estimated as a function of air vapour pressure deficit (δe). There is a considerable scatter in the data (Fig. 2) and part of this is caused by other factors affecting g_c. It is likely that the upper range of canopy conductance at the various values of δe would represent potential conditions of Plot I. Therefore, g_c in Eq. (3) was estimated using the maximum g_c values for the irrigated plot (Fig. 2) and expressed as a function of δe:

$$g_c = m e^{-n\delta e} \qquad (4)$$

where parameters $m = 2.3 \times 10^{-2}$ (m s^{-1}) and $n = 7.0 \times 10^{-4}$ (Pa^{-1}) were estimated by eye so as to approximate the curve (solid line in Fig. 2) through the maximum g_c values. The stand had an average leaf area index (LAI) of nine for the period of the growing season. The differences in LAI for Plots I, C and D were estimated to be less than one unit during the period of the growing season (K. Wiklund, personal communication, 1992); thus an equal LAI value was considered for all the plots. Accordingly, the potential transpiration (E) was assumed to be equal for all these plots.

g_c for the three treatments was estimated using an inverse form of Eq. (3) (e.g. Lindroth, 1985). Input data were mean daytime values of weather variables and actual transpiration (E_Q; mm day^{-1}) for the particular plots.

The aerodynamic conductance (g_a, m s^{-1}) was calculated as

$$g_a = \frac{k^2 u}{\{\ln[(z - d)/z_0]\}^2} \qquad (5)$$

The displacement height (d) was set as $0.67h$ and the roughness length as $0.1h$, where h

is stand height, k is von Kármán's constant (0.40) and u is wind speed at height z above the canopy (Brutsaert, 1982). Equation (5) represents only the aerodynamic conductance for transfer of momentum during near-neutral conditions; for transfer of heat and water vapour there is an excess resistance (usually denoted B^{-1}) to be considered. However, the success of Eq. (3) depends on proper assessment of g_c, whereas g_a is less important, because $g_c \ll g_a$, especially for dry weather conditions (Gash and Stewart, 1975). Hence, in the absence of a consistent method for estimating this excess resistance, the estimation of g_a according to Eq. (5) was judged to be of acceptable accuracy.

2.5. Soil water deficit

The maximum soil water content for the upper 50 cm of the soil was estimated on the basis of soil water retention curves determined for this particular soil. The soil water deficit was calculated as the accumulated sum of actual transpiration minus infiltrated water. It was assumed that the soil was at field capacity on 1 April and gaps in the transpiration data were interpolated using a relationship between actual and potential transpiration from adjacent time periods. The amount of water infiltrated into soil was estimated for each rain event as precipitation minus interception evaporation. The interception evaporation was estimated roughly as a function of precipitation and maximum canopy storage capacity. Amounts of precipitation below the maximum storage capacity were assumed to be totally intercepted; for amounts above, the interception was assumed to equal the maximum storage capacity. The maximum canopy storage capacity was taken as 1.5 mm, the value estimated for another spruce stand in south Sweden by Bringfelt and Lindroth (1987).

2.6. Water potential

Pre-dawn water potential (ψ_p) of 2-year-old shoots was measured by a Scholander-type pressure bomb. Samples from four trees per plot were collected at regular intervals during the season from the middle of the green crown (9–10 m). Immediately after sampling, collected shoots were covered by plastic foil to prevent water loss and measured. The values are means of 3–4 replicates.

2.7. Stem growth and dry matter calculation

Basal area increment was measured using dendrometer bands made of a thin metal sheet. They were placed at breast height on 18 trees (six per plot) and on those trees used for sap-flow measurements. Readings were taken regularly at 1 to 2-week intervals during the period from May to October and any increment outside this period was neglected. Dry matter production was calculated using biomass functions for Norway spruce growing in Sweden (Marklund, 1988). The input variables were dbh, tree height and site index (SI = 32 m; dominant height at 100 years total age) determined on felled trees. The formulae used had a standard deviation of the dependent variable about a regression function of 24%, 22% and 17% for total, above-ground

and stem wood biomass over bark (all in dry weight), respectively. Long-term water-use efficiency (τ) was calculated for three of those trees in which the sap flow was measured. The period used for calculation of τ was from 5 May to 30 September.

3. Results and discussion

3.1. Transpiration at varying water availability

Total of potential transpiration (E) for the period of the growing season (190 days) was 480 mm. Totals of transpiration estimated from sap-flow measurements for Plots I, C and D were 380 mm, 325 mm and 209 mm, respectively (Table 1). Estimated actual transpiration (E_Q) for Plot I was closely correlated with E; similarly, E_Q for Plot C was well correlated with E during most of the season, whereas the correlation between E_Q and E was only occasionally good for Plot D (Fig. 3). The values of E_Q for Plot D were maintained close to E after heavy rains at the end of June, and this recovery lasted through the first 3 weeks of July. Rainfalls at the end of September and the removal of the cover (1 October) also resulted in similar values of E_Q to those obtained for Plots I and C.

The partial drought on Plot D resulted in reduced sap flow: after depletion of water from the upper horizon, the water from deeper layers was probably used, but with evidently limited uptake rates owing to the smaller active root surface there. This resulted in transpiration rates considerably below the potential one, but still with a good correlation to E (e.g. in the beginning of May and in June; Fig. 3). Close to drought-stress conditions might have occurred in Plot D during the period from the end of July to the beginning of August and at the end of September. During these periods, pre-dawn shoot water potential (ψ_p) was also lowered significantly.

Although there is uncertainty in the absolute values of E_Q owing to the small number of sample trees measured, several factors give confidence in the estimated values and the approach used.

(1) The material was homogeneous; a monospecies and even-aged stand with one closed canopy and no understorey sample trees selected with respect to vitality, social position, size, neighbouring trees, etc. This is reflected by the pattern of relative stem

Table 1
Transpiration on Plots I, C and D: the daily mean of actual transpiration (E_Q); r^2 of the regression between E_Q and potential transpiration (E); seasonal totals of E_Q; ratio of seasonal totals of actual and potential transpiration ($\Sigma E_Q/\Sigma E$), where ΣE was 480 mm

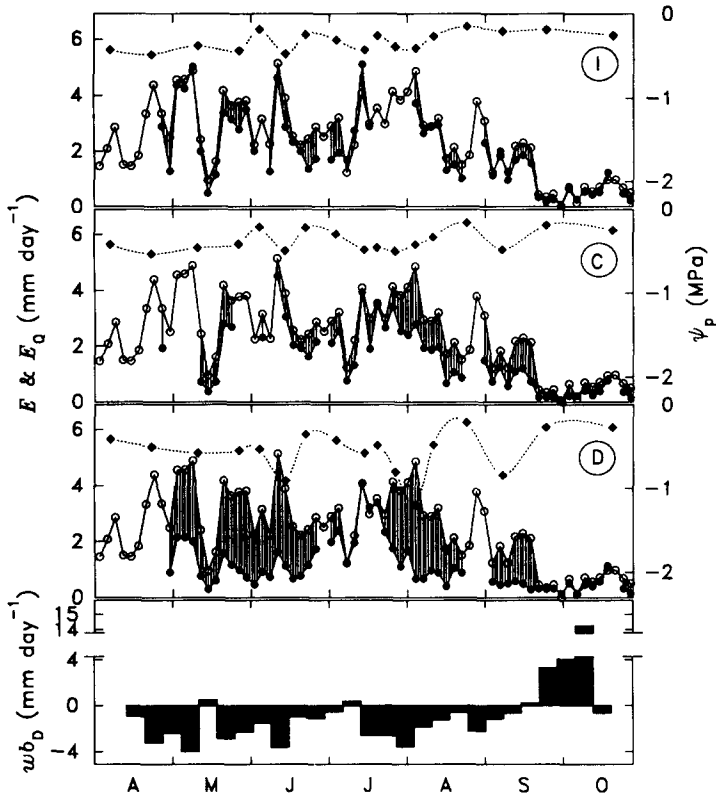|	Plot I	Plot C	Plot D
E_Q (mm)	1.9	1.6	1.1
r^2	0.88	0.88	0.43
ΣE_Q (mm)	380	325	209
$\Sigma E_Q/\Sigma E$ (%)	79	68	44

Fig. 3. Transpiration (E_Q; ●) for irrigated plot (I), control plot (C) and drought-treated plot (D) as compared with potential transpiration (E; ○). Differences between the two variables are shown by vertical shading. All values are means of three successive days. On the right is shown pre-dawn water potential (ψ_p; ◆) in trees from Plots I, C and D during the growing season. Also shown is the daily water balance for the drought plot (wb_D), i.e. infiltration minus actual transpiration.

increment corresponding to other trees within the plot (see the following and Fig. 7 below).

(2) The soil conditions on the plots were homogeneous (P.-E. Jansson, personal communication, 1992).

(3) The transpiration estimated for the periods with sufficient water supply was similar for all the plots; e.g. during the period 23 June–14 July, transpiration totals for 18 days were 46 mm, 40 mm and 41 mm for Plots I, C and D, respectively.

(4) The estimated median values of canopy resistance and ranges for Plots I and C (see below) are in accordance with values reported for other coniferous forests (e.g. Gash and Stewart, 1975; Bringfelt et al., 1977; Lindroth, 1985).

The approach used here is unlikely to hold for a non-even-aged or mixed stand; in such cases, considerably more trees would need to be investigated (e.g. Kelliher et al., 1992; Köstner et al., 1992).

3.2. Canopy conductance and water availability

Median daytime canopy conductance (g_c) for Plot I was 1.1 cm s^{-1}, with 90% of the values in the range 0.7–2.0 cm s^{-1} (Fig. 4). Median conductance of Plot C was 0.8 cm s^{-1} and the range was 0.4–1.4 cm s^{-1}. The variations were larger for Plot D, with 90% of the values between 0.2 and 1.4 cm s^{-1} and a median value of 0.4 cm s^{-1}.

In many modelling approaches it is assumed that g_c also depends on the soil water availability (e.g. Halldin, 1989). Normally g_c is assumed to be unchanged until a threshold value is reached and then it decreases with increasing soil water deficit. The present results indicate that treating the soil as a single compartment is too simple. For instance, after the rainy period at the end of June and the beginning of July, the trees in Plot D recovered and the canopy conductance values were similar to those of the irrigated trees, but the total soil moisture deficit (SWD) was still large on Plot D (Fig. 4). Trees may be capable of transpiring at the maximum rate if enough water is available in the soil layers where most of the roots are situated. Also, an early response of a drought-stressed tree is to increase root growth in deeper layers (Rook et al., 1977), so that the active root surface might be extended deeper quite rapidly. A reallocation of roots downwards was, in fact, detected in Plot D (H. Persson, personal communication, 1991).

If longer time periods are considered, e.g. half-monthly averages, a dependence of canopy conductance on bulk soil moisture deficit (SWD) can also be seen in the data, although the spread of the data is rather large (Fig. 5). Three points deviated from the relationship in Fig. 5: these coincide with the recovery period after heavy rains at the
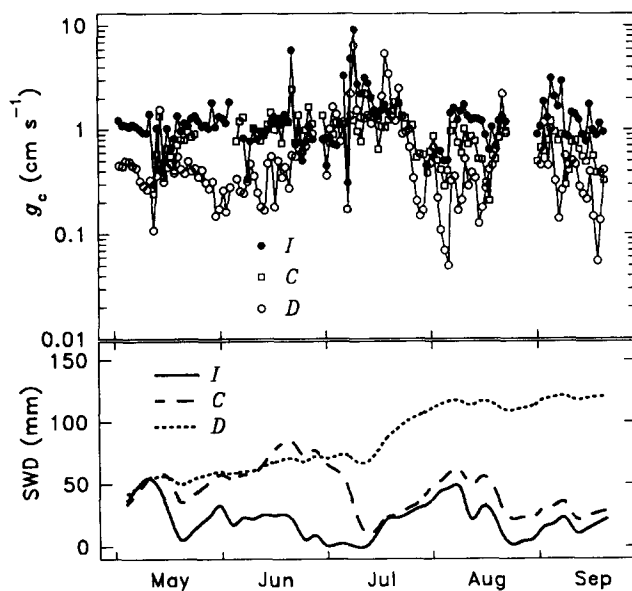

Fig. 4. Top: canopy conductance (g_c) in the irrigated (I), control (C) and drought (D) plots, respectively. Bottom: soil water deficit (SWD) on irrigated (I), control (C) and drought-treated (D) plots during the period 1 May–18 September.
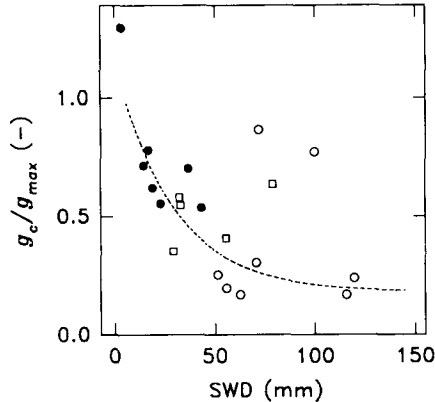
Fig. 5. Half-monthly mean values of normalised canopy conductance (g_c/g_{max}) on irrigated (I; ●), control (C, □) and drought-treated (D; ○) plots against the corresponding mean soil water deficit (SWD). The curve is fitted by eye.

end of June and the beginning of July. The conductance values were normalised, i.e. divided by the corresponding means of maximum conductances (g_{max}) to reduce the climatic influence on the relationship. Normalised conductance (g_c/g_{max}) decreased rapidly for even small values of SWD. For the range of SWD between 0 and 70 mm, g_c/g_{max} was reduced by a factor of about five. Stewart and de Bruin (1985) found that the surface conductance of a pine forest in England decreased by a factor of about 1.5 when going from a wet soil (SWD from 30 to 61 mm; SWD was estimated for the top 90 cm of the soil) to a dry soil (SWD from 68 to 77 mm). The difference between these results for pine and those for spruce obtained in the present study might be a manifestation of a species difference: pine is more drought tolerant than spruce and the relatively rapid decrease of canopy conductance with increasing SWD for spruce can be interpreted as a developing drought stress.

3.3. Pre-dawn shoot water potential at varying water availability

Pre-dawn shoot water potential (ψ_p) was highest in trees on the irrigated plot and slightly lower or similar in the control plot (Fig. 3). The lowest pre-dawn water potential, -1.2 MPa, was measured in early August in drought-stressed trees. At that time, the lowest actual transpiration (E_Q) with respect to potential transpiration was observed in both drought and control plots. Transpiration less than potential transpiration was often measured without any indication of lowered values of ψ_p (Fig. 3), and this behaviour has also been reported for other woody plants (Garnier and Berger, 1987). ψ_p cannot be considered as a good indicator of water deficit for the stand studied here. The use of cumulative ψ_p can, similarly, be prone to errors. Plants with partially droughted root systems may exhibit decreased stomatal conductance in spite of unchanged leaf water and turgor potential, possibly as a result of hormonal signals from the roots to the shoots (Zhang and Davies, 1990; Davies et al., 1990; Harris and Outlaw, 1991). A preliminary analysis by mass spectrometry of Abscisic
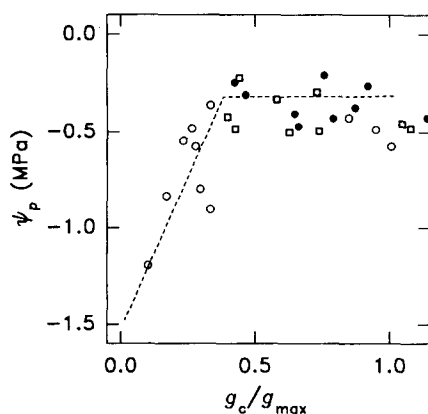
Fig. 6. Pre-dawn water potential (ψ_p) against relative canopy conductance in Plot I (●), Plot C (□) and Plot D (○). The lines are fitted by eye.

acid (ABA) concentration showed much higher values in both xylem sap and needles of drought-stressed as compared well-watered trees (J.E. Hällgren and E. Cienciala, unpublished results, 1990).

Whether the control over transpiration is mainly chemical or is related to water potential can vary within one species depending on the degree of water deficit. It is not known with certainty which process was controlling transpiration here, but the relationship between pre-dawn water potential (ψ_p) and relative canopy conductance (g_c/g_{max}, the ratio of actual to potential canopy conductance; Fig. 6) suggests the following hypothesis for the functioning of trees with regard to the control of water loss. The first phase is mainly hormonal control for relatively small soil water deficits. During this phase there is no correlation between g_c/g_{max} and ψ_p. When g_c/g_{max} decreases below a certain limit (approximately 0.4), a linear relationship between g_c/g_{max} and ψ_p can be observed. This may indicate a second phase, representing large water deficits, when the control is mainly hydraulic.

3.4. Available water and growth

The relative stem area increment of trees was highest in Plot I, slightly lower in Plot C, and half that of the increment of the irrigated plot in Plot D. The relative increment of the trees utilised for sap-flow measurements did not differ from that of the other sample trees (Fig. 7). The periods of more intensive growth corresponded closely to the periods of increased water infiltration (Fig. 7). The close correlation of growth with the amount of infiltrated water confirms the earlier conclusion of Hsiao (1973) that growth is the process most sensitive to water deficits. The simplified measurement of stem increment does not throw any light on the question of changed partitioning of carbohydrates, which may be used preferentially for root growth or extension growth (Schulze, 1986). However, increased root growth at deeper layers was observed in Plot D compared with Plots I and C (H. Persson, personal communication, 1991).

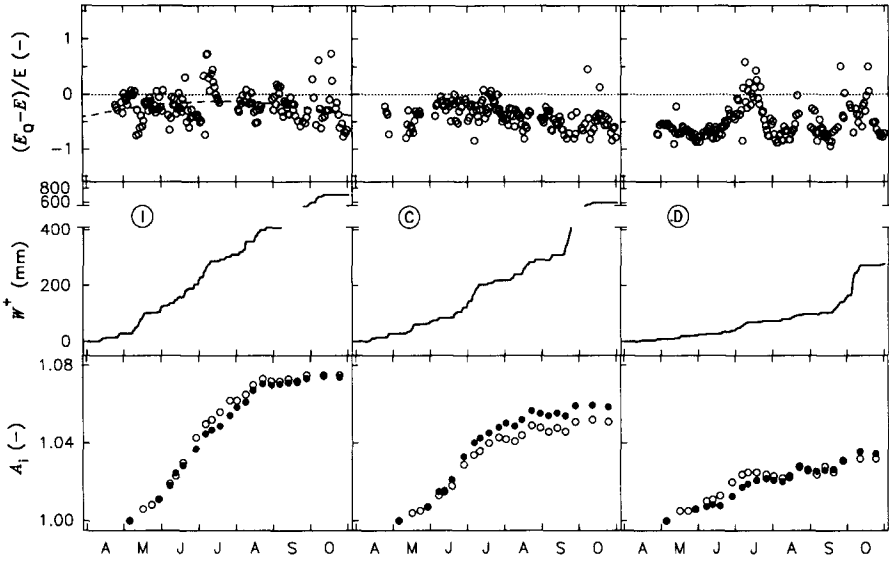The long-term tree water-use efficiency (τ; ratio of dry matter production per water

Fig. 7. Relative transpiration ($(E - E_Q)/E$; ○) for irrigated (I; upper left), control (C; upper middle) and drought (D; upper right) plots. (For details on dashed line for Plot I (upper left), see text.). Also shown are cumulative values of infiltrated water (W^+, solid line) in Plots I, C and D (middle left, centre and right, respectively), and relative basal area increment (A_i) of measured trees on Plots I, C and D (●), as compared with the mean A_i of another six trees (○) from the particular plots (bottom left, centre and right).

unit transpired) was 5.0 g kg^{-1}, 4.7 g kg^{-1} and 4.6 g kg^{-1} for trees on Plots I, C and D, respectively, i.e. on average 4.8 g kg^{-1} for the total biomass produced. The differences in τ between treatments were small (Table 2). These differences, which were more pronounced for above-ground and stem biomass, are not significant with respect to the standard deviation of the biomass functions used. The literature does not offer much comparison of long-term water-use efficiency (τ) values for trees. Čermák et al. (1991) reported values of τ to be 2.5 (2.1) g kg^{-1} and 2.4 (2.2) g kg^{-1} for total and

Table 2
Long-term water use efficiency (τ) for measured trees on Plots I, C and D, all in grams of dry matter produced per kilogram of water transpired

	Irrigated	Control	Drought
Total transpiration (kg per tree)	3014	2144	1212
Total dry matter increment (kg per tree)	15.1	10.0	5.6
τ For total biomass (g kg^{-1})	5.0	4.7	4.6
τ For above-ground biomass (g kg^{-1})	4.1	3.7	3.7
τ For stem wood over bark (g kg^{-1})	3.1	2.7	2.9

The calculation was performed for the continuous period of $n = 149$ days (5 May–30 September); the sum of transpiration included 120, 119 and 136 measured days for trees on Plots I, C and D, respectively; the missing values for n were calculated using parameters of linear regression of the actual daily sap flow to potential transpiration. The total transpiration and total dry matter production for particular trees is also given.

above-ground (in parentheses) biomass production for large oak (*Quercus robur*) trees (dbh more than 60 cm, height about 30 m) for 2 wet years. Polster (1950) reported water-use efficiencies of 2.9 g kg^{-1}, 3.2 g kg^{-1}, 3.3 g kg^{-1}, 3.9 g kg^{-1}, 4.3 g kg^{-1}, 5.8 g kg^{-1} and 5.9 g kg^{-1} for *Quercus robur*, *Betula verrucosa*, *Pinus sylvestris*, *Larix europaea*, *Picea abies*, *Pseudotsuga menziesii* and *Fagus silvatica*, respectively. From this range of values, τ for spruce agrees best with the present findings. Noticeably, this is also the case of τ for oak given by Čermák et al. (1991).

A slightly bent pattern in the seasonal trend of relative transpiration for Plots I and C can be observed (shown by dashed line for Plot I in Fig. 7—top left). This is probably caused by seasonal changes of LAI, which had an equivalent pattern with maximum leaf development in June–July. The assessment of E according to Eqs. (3) and (4), however, does not compensate for these changes.

4. Conclusions

(1) Transpiration is limited below the potential rate for spruce trees if soil water is not available in the upper layer where most of the roots are situated, i.e. in conditions of small or moderate water deficit. Trees subjected to drought stress for short periods are capable of recovering and maintaining transpiration at the potential rate if enough water is infiltrated into the upper layer where most of the roots are situated.

(2) The canopy conductance of spruce for non-limiting soil water conditions was about 1.1 cm s^{-1}, and about 0.5 cm s^{-1} for conditions of moderate water deficit. The values for non-limiting water conditions were similar to those of pine.

(3) For longer time periods (half-month) there is a good relationship between canopy conductance and bulk soil water deficit. The canopy conductance increases by a factor of about five from a dry soil (close to the wilting point) to a wet soil (close to field capacity).

(4) Pre-dawn water potential is a poor indicator of water deficit.

(5) Pre-dawn water potential did not decrease until daily transpiration rates were substantially reduced, with corresponding relative canopy conductances of about 0.4.

(6) Growth of spruce is sensitive to soil water deficits and there is a good correlation between growth and infiltration of water into the soil. The long-term water-use efficiency estimated for the total dry matter produced was on average 4.8 g kg^{-1}, and it was similar for different water regimes.

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