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Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements

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Summary

Transpiration of a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand was evaluated by sap flow measurements during a 4-month period. Between-tree variation in sap flow depended on crown class. On a sunny day, total transpiration was 1.6, 8.0 and 22.0 liters day^{-1} for suppressed, codominant and dominant trees, respectively. Transpiration estimated by sap flow fell below potential evapotranspiration when available soil water decreased below 30% of its maximum value. Sap flow measurements gave transpiration values similar to those obtained by the water balance method.

Introduction

Transpiration in trees is difficult to measure under natural conditions because of the large size of trees and the heterogeneity of forest stands. Techniques used to measure transpiration in agronomic species (e.g., energy balance, aerodynamic method) are not readily applicable to tree species because of canopy heterogeneity, topography and the horizontal extension of the forest.

The water balance technique, however, has been widely used for measuring evapotranspiration (E_T) of forest stands. Xylem sap flow determined by the heat pulse method provides another useful estimate of stand transpiration if a large enough sample of trees is measured and proper quantitative procedures are used (Cohen et al. 1981, 1985). However, sap flow measurements rarely have been used to estimate transpiration of an entire stand (Ladefoged 1963, Doley and Grieve 1966). Moreover, the heat pulse technique is not accurate under conditions of low xylem flow.

Granier (1985, 1987) developed a new method of measuring xylem sap flow that gives an accurate and inexpensive estimate of whole-tree transpiration. This method was used in the present study to investigate between-tree variation in transpiration and to estimate stand transpiration. The results for stand transpiration were compared with water balance measurements and potential evapotranspiration (PET) estimated by the Penman formula.

Materials and methods

Study site

The study site was a 24-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.)

Franco) plantation located in the forest of Amance, near Nancy (48°44′ N, 6°14′ E, with an elevation of 250 m). The site has loamy brown soil about 70 cm deep. Two plots were used—a control plot which had not been treated since being planted, and a plot which was thinned 4 years before the beginning of this study. Plot characteristics are given in Table 1. Five trees were selected in each plot: three trees with a diameter close to the mean of the stand, one suppressed tree and one dominant tree.

Table 1. Mean characteristics of the stands.

	Control plot	Thinned plot
Tree height (m)	17.5	17.5
Number of trees per hectare	2545	1384
Basal area ($m^2\ ha^{-1}$)	45.2	31.0
Circumference (cm) at breast height	46.0 ± 8.6	49.7 ± 12.5
Sapwood basal area ($m^2\ ha^{-1}$) at breast height	25.2	17.3

Sap flow measurements

Sap flow measurements were made with an apparatus consisting of two cylindrical probes of 2 mm diameter, which were inserted 2 cm into the sapwood of the bole (Figure 1) (Granier 1985). The probes were inserted one above the other and were

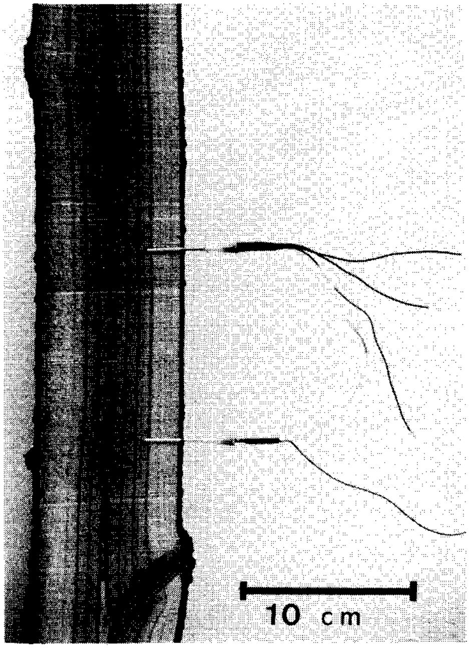

Figure 1. Longitudinal section of a Douglas-fir trunk showing the radial insertion of the two probes into the hydroactive xylem.

about 10 cm apart. The upper probe contained a heating element of constantan, which was heated at a constant power by the Joule effect. Each probe contained a copper-constantan thermocouple in the middle and these were connected together in opposition. The temperature difference between the two probes was influenced by the sap flux density in the vicinity of the heated probe. Mean sap flux density u along a radius (m s^{-1}) was calculated by calibration with different species (Granier 1985):

$$K = 0.0206\, u^{0.8124} \tag{1}$$

in which

$$K = \frac{T_M - T}{T - T_\infty}$$

is a dimensionless value and depends on: T_M, the temperature of the heated probe, obtained when $u = 0$; T, the temperature of the heated probe when $u > 0$; and T_∞, the reference temperature of the non-heated probe.

As both thermocouples connected in opposition give the temperature difference between the two probes directly, we can use another expression of K:

$$K = \frac{\Delta T_M - \Delta T}{\Delta T} \tag{2}$$

where ΔT_M and ΔT are the temperature differences between the two probes, for no flow and positive xylem flow ($u > 0$) conditions, respectively.

Solving for u and from (1):

$$u = 119 \times 10^{-6} K^{1.231} \tag{3}$$

Total sap flow F ($m^3\ s^{-1}$) is calculated as:

$$F = u\, S_A \tag{4}$$

where S_A is the cross-sectional area of the sapwood at the heating probe (m^2).

To calculate flow accurately, the basic term ΔT_M must be determined separately for each sensor. For a constant loss of heat, ΔT_M is influenced by the thermal characteristics of the wood surrounding the heated probe. For example, ΔT_M for dry wood is usually greater than for wet wood. Further it was assumed that no sap flow occurred at predawn. However, transpiration can occur during the night under favorable climatic conditions. In practice, ΔT_M was estimated over 10-day periods by a linear regression of the daily maximum values of ΔT.

Sapwood area was measured with an increment borer; maximum error was 10%. Sap flow measurements were made hourly from May 29 to September 23, 1984 on the five study trees from each plot.

Water balance measurements

Weekly measures of soil water content were made with an NEA (Nordisk Electrisk Apparatfabrik, Denmark) neutron probe to a depth of 150 cm in aluminum access tubes installed in each plot. The control plot had six tubes and the thinned plot had 11. The maximum extractable water reserve was obtained from field data for the last 7 years, by calculating the difference between the maximum water reserve (when there is no drainage) and the minimum values, measured during the driest periods. For the two plots, the maximum extractable water reserve was 115 mm.

Relative extractable water (REW) in the root zone was calculated as a fraction of maximum extractable water content:

$$\mathrm{REW} = \frac{\theta - \theta_m}{\theta_{FC} - \theta_m} \tag{5}$$

where θ = actual soil water content in the root zone, θ_m = minimum value of θ observed during the driest years, and θ_{FC} = θ at field capacity. A simplified water balance equation was used for calculating of stand E_T:

$$E_T = I - E_i - \Delta S \tag{6}$$

where I denotes precipitation E_i denotes rainfall interception and ΔS is the change in soil water.

This equation was used when drainage and capillary rise were negligible. Hourly values of E_i were estimated using a computer program (Chassagneux and Choisnel 1986).

Weather measurements

Temperature, vapor pressure deficit, global radiation, rainfall and wind speed were recorded automatically at a meteorological station 500 m from the experimental site. Measures were made each minute, and hourly means were calculated. These data were used to calculate evapotranspiration according to the Penman equation. Net radiation was estimated from global radiation measures, distinguishing between clear and cloudy sky conditions (Chassagneux and Choisnel 1986).

Results

Within tree variation in transpiration

Equation (1) states that the total sap flow in a tree is a function of the mean sap flux density and the sapwood cross-sectional area. There are, therefore, two sources of variation in the total sap flow.

Sap flux density (flow per unit of sapwood cross-sectional area) varied according to tree crown class. The diurnal pattern of flow density is given in Figure 2a for three trees in the control plot. Sap flux density was approximately the same for the average tree and the dominant tree. The smallest tree exhibited a maximum sap flux density only half of that of the dominant tree. This difference might be explained by the reduced radiation load on the crown of the suppressed tree.

Sapwood cross-sectional area differed markedly among crown classes. For the 10 sample trees, S_A ranged from 33 to 218 cm^2, i.e., a 6.5-fold variation. This explains why differences in sap flow within tree classes were much greater than flow density differences (Figure 2b). Typical flow rate values were 2.6, 1.0 and 0.2 liters h^{-1} for the dominant, the mean and the suppressed trees, respectively (Figure 2a). Similar differences were reported by Knight et al. (1981) for a closed

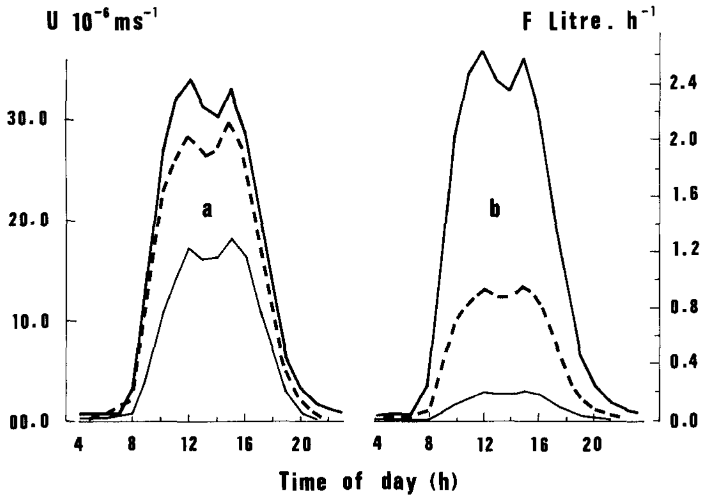

Figure 2. Diurnal pattern of sap flow for three Douglas-fir trees in the control plot. (a) Sap flux density, u; and (b) total sap flow, F. ——— = dominant tree (dbh = 20.4 cm); – – – – – = codominant tree (dbh = 15.9 cm); and ——— = suppressed tree (dbh = 10.8 cm).

stand of *Pinus contorta* Dougl. ex Loud. and by Doley and Grieve (1966) for a *Eucalyptus* stand. On a sunny day, total daily transpiration per tree was 22.0, 8.0 and 1.6 liters for the dominant, mean and suppressed trees, respectively.

Seasonal pattern of stand transpiration

Transpiration of an entire stand can be estimated by considering the contribution of each tree class. For this purpose, both sap flow flux density and the proportion of total stand basal area of sapwood (Table 2) were determined for each tree class in both plots. From these data, hourly and diurnal transpiration rates for each plot were calculated for the 101 days of the experiment. Figure 3 gives the total diurnal transpiration (E) for the control plot from day 166 to day 267. The maximum stand transpiration of 3.6 mm per day can be compared with values of 3.1 to 4.8 mm

Table 2. Proportion of sapwood area of each crown class for the two plots.

Crown class	Control plot			Thinned plot		
	Average dbh[1] (cm)	Average sapwood cross section (cm^2)	Percent of plot sapwood	Average dbh (cm)	Average sapwood cross section (cm^2)	Percent of plot sapwood
Dominant	18.7	150.5	19.9	21.8	208.2	33.6
Codominant	16.0	107.2	48.5	17.8	135.0	45.9
Intermediate	13.3	71.7	22.9	13.8	78.5	14.0
Suppressed	10.5	43.6	8.7	9.9	37.9	6.4

[1] dbh = Diameter at breast height.

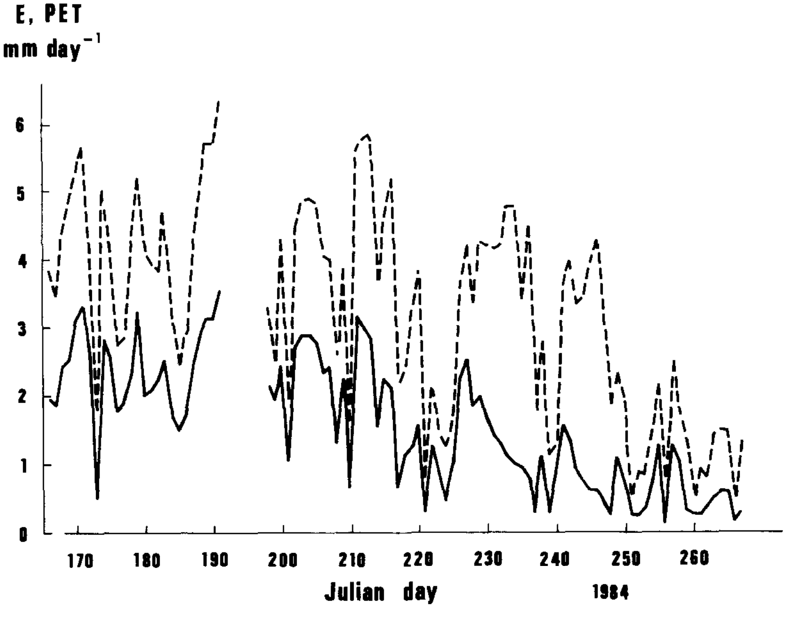

Figure 3. Seasonal variation in transpiration of the control plot (—) compared with Penman evapotranspiration (– – – – –).

day^{-1} found in stands of Douglas-fir by other methods (Whitehead and Jarvis, 1981). The maximum rates of 0.35 mm h^{-1} are slightly lower than those found by other authors. Transpiration of the thinned plot followed the same diurnal pattern as the control plot, but the level of transpiration was lower because of the lower total sapwood basal area. Maximum transpiration of the thinned plot was approximately 2.5 mm day^{-1}.

Total seasonal transpiration (from day 167 to 267) was 169 mm for the control plot and 117 mm for the thinned stand. The ratio of transpiration between the two plots is comparable to the ratio of total sapwood cross section for each plot. Therefore the transpiration per unit of conductive sapwood area was equivalent in each plot.

The relationship between daily potential evapotranspiration (PET) and control stand transpiration (E), estimated with sap flow measurements, is given in Figure 4. From day 166 to 211 the observed relationship was linear:

$$E = -0.11 + 0.60\,\mathrm{PET} \tag{7}$$
$$r^2 = 0.94\,.$$

Deviation from linearity in the relationship between PET and sap flow measures were observed from day 212 to 248, which correspond to periods of water stress. It was also found that E was reduced on rainy days because transpiration stopped when the foliage was wet. The difference between observed transpiration (E) and potential transpiration (E_p) as predicted by Equation (7) is shown in Figure 5. A

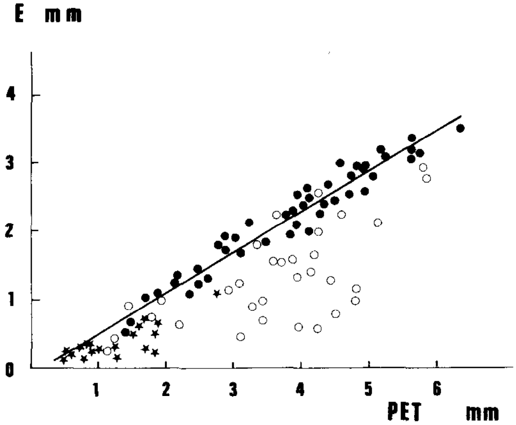

Figure 4. Control plot sap flow (E) plotted against Penman evapotranspiration (PET). ● = days 166 to 211; ○ = days 212 to 248 and ★ = rainy days.

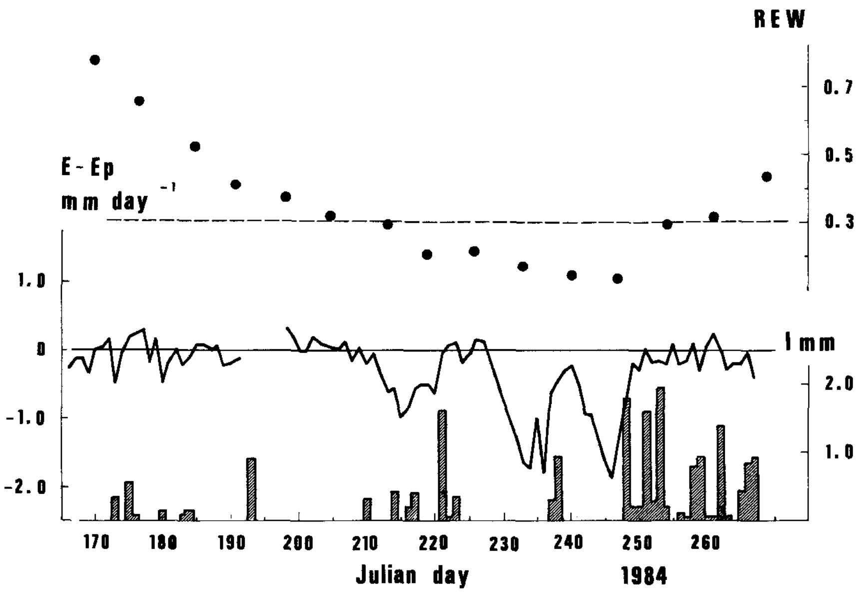

Figure 5. Seasonal differences between measured transpiration (E) and potential transpiration (E_p) predicted by Equation (7). Variation in relative extractable water (REW) in the root zone and incident rainfall (I) are also shown.

substantial negative discrepancy occurred during three periods, indicating that on these occasions transpiration was limited by drought.

Drought was estimated to have started on day 212 when relative extractable water was 0.30, and ended on day 251 when REW was 0.29 in the first 60 cm of the soil. Potential and measured transpiration values were very close on days of water stress after it had rained, even when soil water remained low (day 227 and

241). Choisnel's model (1984) describing transpiration during a drought appears to provide a satisfactory explanation, namely, that rainfall creates a temporary water reservoir, which can be absorbed by trees in a nonlimiting fashion. Exhaustion of this reservoir causes transpiration to decrease to its former rate. For example, between days 221 and 229 incident precipitation amounted to 20.2 mm and net precipitation was estimated as 13.7 mm. During the same period, total sap flow was 12.5 mm, which indicates that the trees had extracted water from the soil at a rate close to the potential transpiration rate. Between days 237 and 242 the same pattern was also observed. The ratio between actual and estimated potential transpiration is plotted against the fraction of extractable water remaining in the root zone (REW) in Figure 6. The relative extractable water reserve at which transpiration starts to decline is 0.3. Black (1979) found a value of 0.4 for Douglas-fir. Figure 5 shows that the difference between observed transpiration (E) and potential transpiration (E_p) predicted by Equation (7) became increasingly negative from day 226 until day 236 after which there was rain. The diurnal pattern of transpiration in the control stand for these 11 days is shown in Figure 7. Throughout this period of decreasing transpiration climatic conditions remained relatively constant. Transpiration on August 23 (day 236) was only 35% of that observed on August 13 (day 226).

Discussion and conclusion

Transpiration flow estimated by the sap flow technique was compared with values obtained by neutron probe measures. Although cumulated water consumption

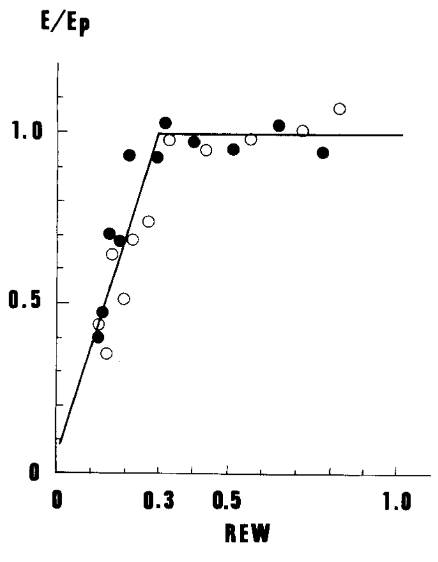

Figure 6. Relationship between actual and potential transpiration (E/E_P) and REW. Each point is a weekly average. ● = Control plot; ○ = thinned plot.

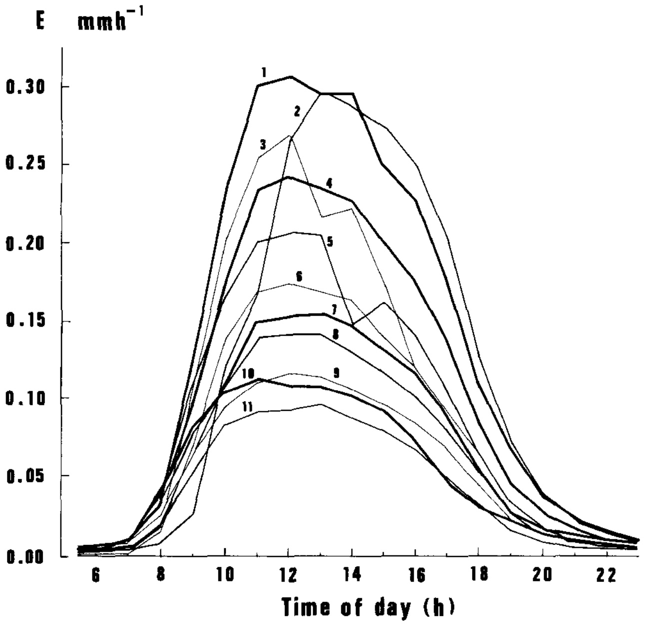

Figure 7. Mean transpiration of the control plot during an 11-day period of drought.

values for the whole season as measured by the two methods gave similar results (Table 3), values for some weekly periods differed markedly because of errors in estimation by the water balance method during periods of heavy rain.

Furthermore, for both seasonal and diurnal periods, variations in water content within the tree can cause differences between inflow (change in soil water reserve) and sap flow in the bole (Schulze et al. 1985, Granier 1987). The available water volume in the bole is also species specific. In addition, the exchangeable water volume within the stand increases with both stand density and age (Jarvis 1975). Waring and Running (1978) have shown large (more than 12 mm) seasonal varia-

Table 3. Comparison of E_T calculated from water balance measurements with total sap flow in the control plot.

Period (Julian days)	E_T (mm)	Sap flow (mm)
157–164	8.5	5.6
164–170	9.3	10.4
170–185	34.4	28.2
185–191	12.7	12.1
198–205	11.6	13.1
205–219	18.4	23.2
219–233	17.6	16.0
233–247	12.7	9.8
Total	125.2	118.4

tions of the sapwood water reserve in an old Douglas-fir stand.

Transpiration declines severely when the extractable water in the root zone drops below 30%. At this point, the mean water potential of soil in the first 60 cm is −0.17 MPa. Diameter growth stops at a value of approximately −0.2 MPa (Aussenac et al. 1984). Therefore growth of Douglas-fir is already affected at relatively high values of soil water potential, whereas needle water potential does not decrease unless drought is more severe.

Errors in the estimation of transpiration of a whole stand using the sap flow method depend on how representative the selected sample of trees is. To estimate transpiration in a relatively homogeneous stand, such as the one studied here, five trees appear to be sufficient because the sap flow density, except in suppressed trees, was relatively constant among the trees (Kline et al. 1976).

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