TRANSPIRATION IN MOUNTAIN BEECH ESTIMATED SIMULTANEOUSLY BY HEAT-PULSE VELOCITY AND CLIMATISED CUVETTE

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ABSTRACT

Water vapour loss as measured for foliage in a climatised cuvette and xylem sap-flow as calculated from stem heat-pulse velocity (HPV) measurements in mountain beech (**Nothofagus solandri** var. **cliffortioides** Hook. F. Poole) are compared over a seven-hour period.

A close correlation was obtained between branch transpiration and heat-pulse velocity under the prevailing conditions of low moisture stress. The HPV technique appears to be applicable to mountain beech, a hardwood with a diffuse-porous vascular transport system. Tentative extrapolation of results to total crown transpiration and total stem sap-flow gave similar results.

INTRODUCTION

The heat pulse technique (Marshall, 1958) has met with only limited success when used to estimate quantitative transpiration of coniferous trees. Correlations between daily patterns of transpiration rate or volume and heat-pulse velocity have generally been high with correlation coefficients greater than 0.9 (Decker and Skau, 1964; Doley and Grieve, 1966; Wendt, Runkles and Haas, 1967; Swanson, 1972; Lassoie, Scott and Fritschen, 1977). An important part of the problem appears to lie in the lack of thermal homogeneity near the heat-pulse sensing apparatus placed within functioning xylem (Heine and Farr, 1972). Swanson and Whitfield (1980) have been able to accommodate this non-homogeneity as well as the flow disruption caused by the wound around the sensors.

The purpose of the work reported here was to ascertain if the heat-pulse technique as developed for coniferous species with tracheid-flow xylem can be used in a diffuse-porous hardwood such as mountain beech (*Nothofagus solandri* var. *cliffortioides* Hook F. Poole) with a vascular-flow xylem. An opportunity arose to do this in conjunction with the study of photosynthesis and transpiration in mountain beech.

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METHODS

A 6-metre tall moutain beech tree (22 years; 11 cm d.b.h.) was selected for study in an open-growing natural stand on a moist site with good drainage in Craigieburn Forest Park, New Zealand (Lat. 43°10'S, Long. 171°41'E) at 900 m elevation. This and three similar trees were instrumented with one set each of 0.16-cm diameter heat-pulse probes at 1.0 and 2.0 cm from the cambium (Swanson, 1962; 1967; 1974). Values of t_0 obtained at half hourly intervals were converted to uncorrected heat-pulse velocity (HPV) using equation (1):

$$\mathrm{HPV} = 1800\ (1.0\text{-}0.5)t_0^{-1}\mathrm{cm\ hr^{-1}} \qquad (1)$$

where t_0 = time in seconds for the temperature difference between the two sensor thermistors crossing zero after heat-pulse application (details Swanson, 1962).

These values were corrected to true heat-pulse velocity (HPVR) using equation (2):

$$\mathrm{HPVR} = a + b\ (\mathrm{HPV}) + c\ (\mathrm{HPV})^2 \qquad (2)$$

where coefficients a, b, c, vary with wound width. For wound width of 0.44 cm and 0.50 cm values for coniferous wood are — coefficient a, 1.525 and 1.630; b, 1.225 and 1.611; and c, 0.280 and 0.300 respectively (Swanson and Whitfield, 1980). The same coefficient values have been used for mountain beech. Wound width in mountain beech was indicated by darkly stained xylem in cross-sections cut through the heat-pulse sensor zone. The stained width was 0.45 cm to 0.50 cm wide and free from infection, the stain indicating non-functioning xylem as a result of oxidation (P. Gadgil, pers. comm.). The cross-sectional area of sapwood "sampled" by the 1 cm and 2 cm deep sensors was estimated to be 49.5 cm^2 and 51.0 cm^2 respectively. Marshall's equation (3) then allows a total sap flow calculation to be made in equation (4):

$$\text{sap flux } Q = pb\ (m + 0.33)\ \mathrm{HPVR\ cm^3\ cm^{-2}h^{-1}} \qquad (3)$$

where pb = 0.76, sapwood density of sample tree
m = 0.53, moisture content of sample tree

$$\text{Mountain Beech tree } Q = 0.66\ (49.5\ \mathrm{HPVR}_{1.0} + 51.0\ \mathrm{HPVR}_{2.0})\ \mathrm{cm^3h^{-1}} \qquad (4)$$

A Koch-Siemens gas-exchange unit with a thermo-electrically cooled cuvette was used to measure transpiration by methods that have been fully described (Koch *et al.*, 1968; Koch and Kerner, 1971). The cuvette enclosed an *in situ* branchlet with 253 leaves while tracking ambient temperature and humidity for a seven-hour period on 30 January 1975. The transpiration system was found to be within ± 5% over a period of several hours when calibrated by the method of Tranquillini and Caldwell (1972). Data sampling proceeded at two-minute intervals. Total foliar diffusive resistance to water vapour (r_{H_2O}) was calculated for the lower surface of foliage in the cuvette from the rate of transpiration and the water vapour-pressure gradient from leaf to air by standard formulae (Sestak *et al.*, 1971).

The sample twig was subsequently removed for determination of leaf area (Thompson and Leyton, 1971) and leaf dry weight. The whole tree was later harvested for determination of total foliage weight and intensive sampling allowed an estimate of total crown leaf-area to be made.

RESULTS AND DISCUSSION

Ten minute mean values for twig transpiration (E) and leaf diffusive resistance (r_{H_2O}) as well as key climatic parameters are shown in Fig. 1. The measurement day was relatively cool and overcast after several days of steady rain. There were brief breaks in the cloud between 10.40 and 11.20 hours and again between 12.50 and 13.00 hours. A moderate breeze ensured the open-growing crown was well ventilated. Other

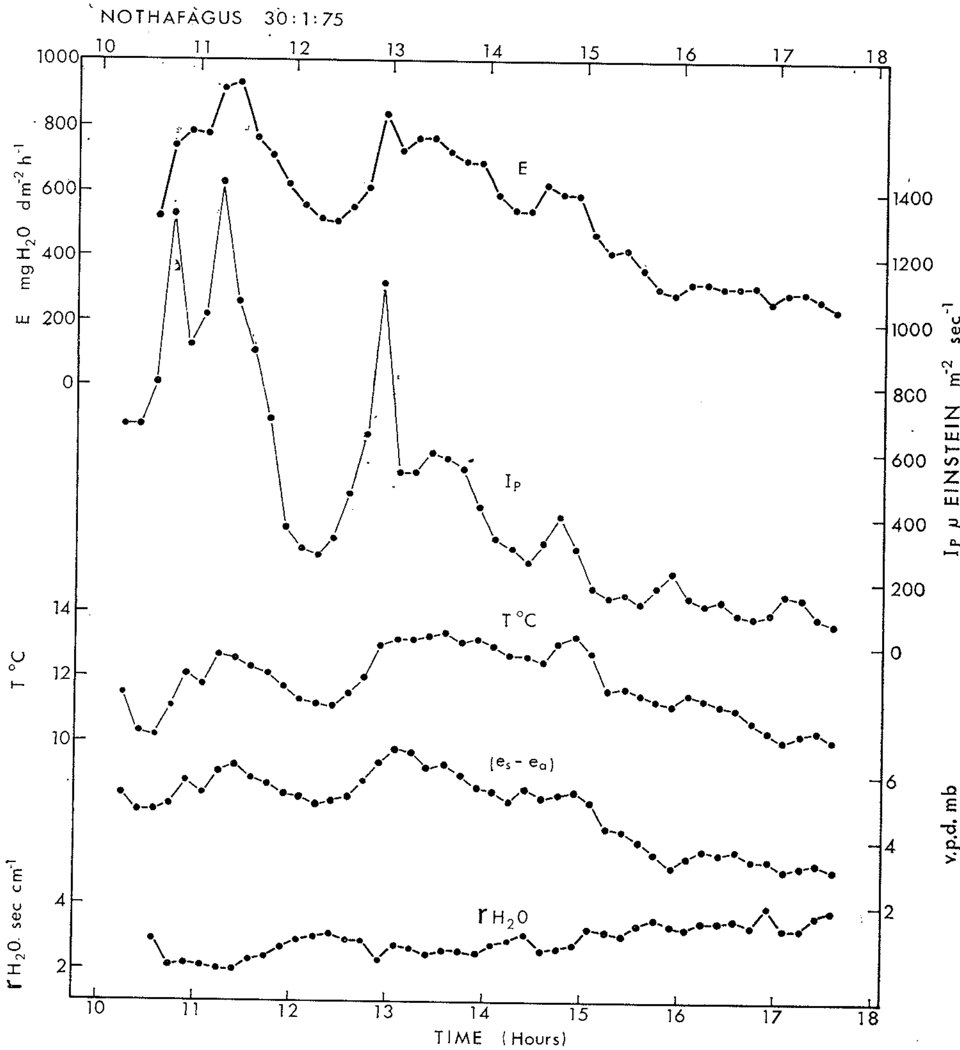

FIG. 1—Transpiration (E $mgH_2Odm^{-2}h^{-1}$) and leaf diffusive resistance to water vapour (r_{H_2O} s cm^{-1}) for 1.31 dm^2 of mountain beech foliage (**Nothofagus cliffortioides**), on 30.1.75 at 900 m a.s.l. Craigieburn Forest Park. Photosynthetically active radiation measured in μ Einstein with LiCOR Quantum sensor, temperatures in °C with platinum resistance bulbs, vapour pressure deficit ($e_s - e_a$) in mb determined from ambient air and its dew-point temperatures.

air temperatures. Soil moisture was near field capacity and the low values for r_{H_2O} (min. 2, max. 4 sec cm^{-1}) indicate the tree was not subject to moisture stress (pre-dawn xylem water potential *ca.* —2 bar).

Under the prevailing conditions r_{H_2O} showed only minor changes during the day with a small general increase as a photo-active response to declining light. Transpiration was thus largely determined by the water vapour pressure deficit.

In Table 1 we present half-hourly real and extrapolated data for heat-pulse velocity and transpiration measurements. The regression of cuvette branch transpiration (E) on uncorrected heat-pulse velocity at 1.0 cm into the sapwood (HPV 1.0) resulted in:

$$E = 128 + 91\ HPV_{1.0}\ (r^2 = 0.88\ .\ P = 0.01) \quad (4)$$

A plot of branch transpiration and $HPV_{1.0}$ against time of day (Fig. 2) clearly shows a similarity of pattern though in relative magnitude transpiration peaked before mid-day and HPV after mid-day. HPV thus lagged a little behind transpiration. This agrees well with other heat-pulse studies on coniferous trees showing a close correspondence between heat-pulse velocity and water-vapour loss under low moisture stress conditions (Decker and Skau, 1964; Swanson, 1972; Lassoie *et al.,* 1977). It would thus seem reasonable to assume that the heat-pulse technique has a similar degree of applicability for use with a diffuse-porous vascular-flow hardwood tree such as mountain beech as that found to date for conifers. Under high water stress conditions correlations between HPV and transpiration tend to be much poorer seemingly due to increased time lags involving stomatal response and delayed recharging of tree moisture levels (Swanson, 1972; Lassoie *et al.,* 1977).

Any extrapolation of twig transpiration to the whole tree crown must be treated with caution (Table 1). The tree crown should be intensively sampled for variation in foliage transpiration if confidence is to be placed in estimated crown water-loss. A suitable porometer able to sample *in situ* twigs in full light was not available for this purpose. However, weather conditions prior to and during twig measurement in the cuvette favoured a tentative attempt to estimate crown transpiration from the twig

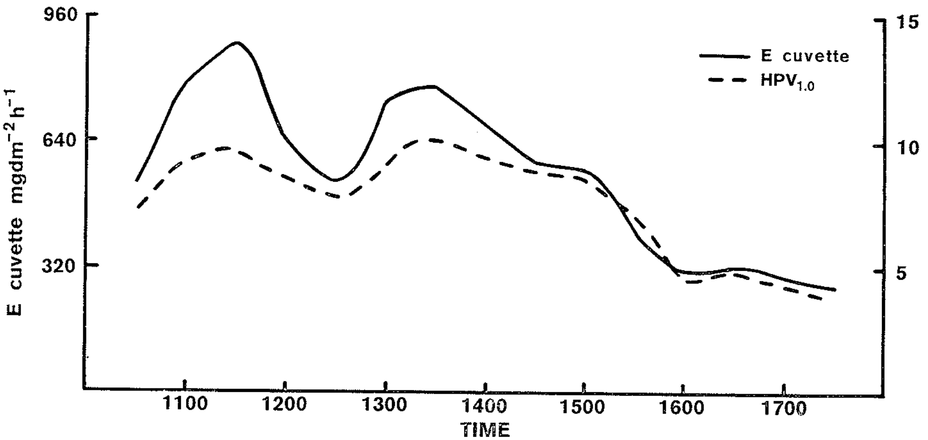

FIG. 2—The measured daily course of branch transpiration (E) and stem heat pulse velocity at 1.0 cm into the sapwood of mountain beech.

TABLE 1—Heat-pulse velocities (measured, HPV and corrected, HPVR), stem sap-flow (Q) and half-hourly transpiration rates (E), calculated for mountain beech tree No. 250, 30 January 1975; tree ht 6 m, age 22 years, wt. oven-dried of leaves 5.55 kg, total crown leaf-area 32 m^2 (one side). HPVR is given for two wounding widths about sensor (W = 0.44 cm and 0.50 cm)

Time hr	Measured HPV cm hr^{-1} at 1.0 cm	Measured HPV cm hr^{-1} at 2.0 cm	Corrected HPVR w = 0.44 cm cm hr^{-1} at 1.0 cm	Corrected HPVR w = 0.44 cm cm hr^{-1} at 2.0 cm	Sap Flow Q cm^3 hr^{-1}	Corrected HPVR w = 0.50 cm cm hr^{-1} at 1.0 cm	Corrected HPVR w = 0.50 cm cm hr^{-1} at 2.0 cm	Sap Flow Q cm^3 hr^{-1}	Branch Transpiration E mg $dm^{-2}h^{-1}$	Tree Transpiration E cm^3 hr^{-1}
1030	7.2	5.9	24.9	18.5	1436	28.8	21.6	1668	537.6	1680
1100	9.1	7.4	35.8	25.9	2041	41.1	30.0	2353	785.0	2453
1130	9.6	7.8	39.1	28.1	2223	44.7	32.4	2551	894.2	2793
1200	8.6	6.7	32.8	22.3	1822	38.6	25.9	2100	644.2	2013
1230	7.8	6.0	28.1	18.9	1554	32.4	22.1	1802	537.6	1680
1300	8.9	6.9	34.6	23.3	1915	39.7	27.0	2206	743.4	2323
1330	10.0	7.9	41.8	28.7	2332	47.7	33.1	2673	770.2	2407
1400	9.4	7.3	37.8	25.4	2090	43.2	29.4	2401	676.2	2113
1430	8.8	7.2	34.0	24.9	1949	39.0	28.8	2244	585.6	1830
1500	8.5	6.8	32.2	22.8	1819	37.0	26.4	2097	569.6	1780
1530	7.0	5.4	23.8	16.3	1326	27.6	19.1	1545	409.6	1280
1600	4.5	3.7	12.8	9.9	748	14.9	11.7	881	312.6	977
1630	4.8	3.8	13.9	10.2	797	16.3	12.1	940	321.0	1003
1700	4.4	3.3	12.3	8.6	691	14.5	10.2	817	296.6	927
1730	4.3	3.8	12.0	10.2	735	14.1	12.1	868	275.2	860
$\bar{x}$	7.6	6.0			1565			1810	557.2	1741
Total water flow (litres) in 7 hrs					11.0 1			12.7 1		12.2 1

leaf diffusive resistance to water vapour transfer (r_{H_2O}) were similar throughout the tree-crown on the day of measurement. Also the inner crown is assumed to have received adequate light for stomatal response to be similar to that of the outer measured twig.

In Douglas fir water movement in sapwood was not uniform and varied with depth past the cambium and with the stem quadrant (Lassoie *et al.*, 1977). Generally, defining and quantitatively determining the conducting cross-sectional area of trees, together with the wounding effects of sensor installations, pose problems when attempting to quantify HPV data. The findings in this respect by Swanson and Whitfield (1980) for coniferous wood have been applied to mountain beech resulting in the corrected HPVR values presented in Table 1. Total tree sap flow (Q) for the seven-hour period from 1030 to 1730 hours were thus estimated to lie between 11.0 and 12.7 litres by heat-pulse determinations. This compared favourably with 12.2 litres from an extrapolation of cuvette twig transpiration (E) to the tree crown.

These results indicate that the theory developed by Marshall (1958) when modified for finite sensors (Swanson and Whitfield, 1980) is not restricted to tracheid-flow systems. More intensive tests with mountain beech and other vascular-flow tree species would be useful in establishing the range of applicability of the heat pulse technique.

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