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MEASUREMENT OF SAP FLOW IN *AGATHIS BORNEENSIS* (ARAUCARIACEAE) WITH DEEP SAPWOOD

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BECKER, P. 2000. Measurement of sap flow in *Agathis borneensis* (Araucariaceae) with deep sapwood. A quarter section of trunk was removed to enable implanting of probes along the full stemwood radius of *Agathis borneensis,* which does not form dark wood. Sap flow measured by the heat pulse velocity technique was found to occur at depths of at least 120 mm into the stemwood. Mean daily daytime sap flow in this species exceeded 500 kg d^{-1} m^{-2} (stem cross-sectional area) and was substantially greater than typical rates measured on four emergent trees in dipterocarp forest. High water use by *A. borneensis* necessitates deep rooting in this species and may negatively affect other tree species during drought.

Key words: *Agathis borneensis* - sap flow - deep sapwood - sap velocity–depth profile

BECKER, P. 2000. Sukatan aliran sap dalam *Agathis borneensis* (Araucariaceae) dengan kayu gubal yang tebal. Satu suku daripada bahagian batang dibuang untuk membolehkan penanaman prob di sepanjang jejari kayu batang penuh bagi *Agathis borneensis* yang tidak membentuk kayu keras. Aliran sap disukat dengan menggunakan teknik halaju denyutan haba didapati muncul sekurang-kurangnya 120 mm di dalam kayu batang dengan kedalaman sekurang-kurangnya 120 mm. Min aliran sap harian di dalam spesies ini melebihi 500 kg d^{-1} m^{-2} (kawasan keratan rentas batang) dan lebih tinggi daripada kadar biasa yang disukat daripada empat pokok yang baru tumbuh di hutan dipterokarpa. Penggunaan air yang tinggi oleh *A. borneensis* memerlukan pengakaran yang dalam bagi spesies ini dan akan memberikan pengaruh yang negatif kepada pokok-pokok lain pada musim kemarau.

Introduction

The woody core of trees comprises an outer ring containing conductive elements, which are dead at maturity, and some living parenchymatic cells. As the trunk expands outward, its older, inner cells may gradually die, forming a region called heartwood. Typically, this process is accompanied by the deposition of dark coloured extractives and the formation in some angiosperms of tyloses (parenchymatic cell outgrowths into vessel lumina), both of which block the conductive elements (Panshin *et al.* 1964). Sometimes there is an intermediate zone with living cells and colouration like that of heartwood (Panshin *et al.* 1964).

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A dark colour is not a necessary condition for the existence of heartwood, which may fail to form in certain temperate and tropical species (Esau 1977, Ng 1986).

Accurate measurement of sap flow by both the heat pulse velocity and mass flow techniques requires an estimate of the total conductive xylem area (Pearcy *et al.* 1989), which does not necessarily correspond to sapwood area. Thus, sap flow in *Nothofagus* trees of temperate rain forest was confined to the outer 20 mm of sapwood although histochemical sapwood depth was 32–82 mm (Kelliher *et al.* 1992). Marshall (1992), on the other hand, advocated a functional determination of the extent of conducting tissue for the heat pulse technique after detecting sap flow in dark wood of *Eucalyptus marginata*. This may have been an artefact of heat transfer from sapwood to heartwood (Swanson 1994).

Measurement of sap flow in *Agathis borneensis* V. Sl. (Araucariaceae) is complicated by the fact that it attains diameters exceeding 1 m (at 1.3 m above ground) and yet forms no dark wood. This species is a strong dominant of coastal heath forests on deep podsols in Sarawak and Brunei (Newbery 1991), and characterising its water use is an important aspect of a study in progress to compare the water and nutrient relations of heath and dipterocarp forests. Initial heat pulse velocity measurements with probe sensors implanted radially from the trunk surface to a depth of 55 mm into the sapwood failed to define the innermost extent of conductive tissue. Therefore, an invasive approach was adopted in which a quarter section was removed from the bole to enable measurements along the entire radial profile.

Materials and methods

This study took place in May 1994 during a rainy period when rainfall during the previous 30 days exceeded 130 mm. Two *A. borneensis* (code-named PROF1/2) within a relict patch missed by the 1992 fire near the southern border of Badas Forest Reserve (4.568 °N, 114.415 °E; 16 m above sea-level, Becker & Wong 1992) were selected as being near the median size (0.49 m dbh) of trees ≥ 0.3 m dbh in the 0.96-ha University plot there (Davies & Becker 1996).

Heat pulse velocity measurements and sap flow calculations followed procedures described by Becker (1996), with the following modifications to accommodate the non-standard probe implantations. An approximate quarter section of bole was removed at *c.* 1 m above the ground using a chainsaw to make radial and transverse cuts. The cut faces were coated with automotive grease to minimise drying and the development of artificial moisture gradients. Six probes were implanted perpendicular to one of the 'radial' faces at 30 or 40 mm horizontal spacing. Each probe (Greenspan Technology, Warwick, Qld. Australia) contained two pairs of thermistors spaced 10 mm apart horizontally and located 35–55 mm from the cut wood face. Measurements were taken to enable a scale drawing of the stem in cross-section showing the cut faces and probe locations so that the distance of sensors from the tree centre could be calculated. After sap-flow measurements were completed, a thin radial wedge of wood including the implantation sites was cut away with a chainsaw for sectioning, staining (safranin-o), and microscopic examination. Lumen diameter (mean of minimum and maximum width) was measured at two radial depths with a calibrated ocular micrometer for 30 haphazardly chosen tracheids outside of the 2- or 3-cell-wide band of 'late wood' formed from narrow diameter tracheids.

Heat pulse duration was 1.6 s, and heat pulse velocity was recorded every 0.5 h. If the upstream–downstream temperature difference did not return to zero within 150 s after a heat pulse, sap velocity was considered to be nil (see Becker 1998). Heat pulse velocities were corrected (Swanson & Whitfield 1981) using a mean wound width of 2.0 mm (s.d. = ± 0.06 mm, n = 10), as measured on microscopic sections. No wound reaction was visible other than the crushing of 2–7 tracheids on either side of the hole drilled to accept the probe rods. Artefactual velocity spikes were detected and eliminated by plotting measurements from the two sensors on the same probe against each other. Detailed analyses are presented for only one tree due to technical problems with a logger on the other tree. Because the sensor depths (21–160 mm) for a given probe agreed within 2–8 mm, the two sap velocities measured by each probe were generally averaged prior to subsequent analyses. Sap flow was calculated using a weighted average of the point estimates of sap velocity to integrate the radial velocity–depth profile (Hatton *et al.* 1990). The relative conducting area associated with each probe was calculated on the basis of concentric rings lying midway between successive probes.

Results and discussion

After declining to nearly zero at 82 mm radial depth, sap velocity during peak flow increased sharply and then declined to values just slightly greater than the detection limit dictated by the selected temporal threshold for thermal balance (Figure 1). Irregular sap velocity–depth profiles are often observed (e.g. Becker 1996), but this seems to be the first report of sap flow at a depth of 120 mm although flow at 100 mm depth has been recorded (Köstner *et al.* 1998). Confidence that such sap flow was real is increased by the measurement of sap velocities of 0.040 and 0.027 mm s^{-1} at 80 and 108 mm depths respectively, in the second specially implanted tree (PROF1). While some uncertainty exists concerning the low sap velocities at depths > 120 mm, the velocities measured at intermediate depths of 80–120 mm substantially exceeded the detection limit of 0.019 mm s^{-1} for an extremely conservative temporal threshold of 100 s (see Becker 1998). In this particular case, for the four deepest sets of sensors, the detection limit for the specified temporal threshold (Figure 1) was more conservative than one based on minimum nocturnal sap velocities (see Becker 1998).

Wood at the two innermost implantation sites was more difficult to drill and darkened slightly on exposure to air. Tracheid lumen diameter significantly decreased from 32.9±5.5 μm (mean ± s.d.) at 15-mm depth to 29.7 ± 4.4 μm at 150-mm depth ($t = 2.433$, $p = 0.018$). Because flow rate is proportional to the fourth power of the capillary radius (Zimmermann 1983), even such small differences can have substantial effects. In this case, for the same pressure gradient and sap viscosity, flow through the smaller, inner tracheids would be reduced by one-third relative to that in the outer tracheids. No blockages were detected in the lumina, but flow through the imperforate tracheids of conifers depends on passage through the pits in the cell walls (Panshin *et al.* 1964). Electron microscopic examination would indicate whether the bordered pits of inner tracheids in *Agathis* were aspirated, encrusted or occluded and thus non-functional.

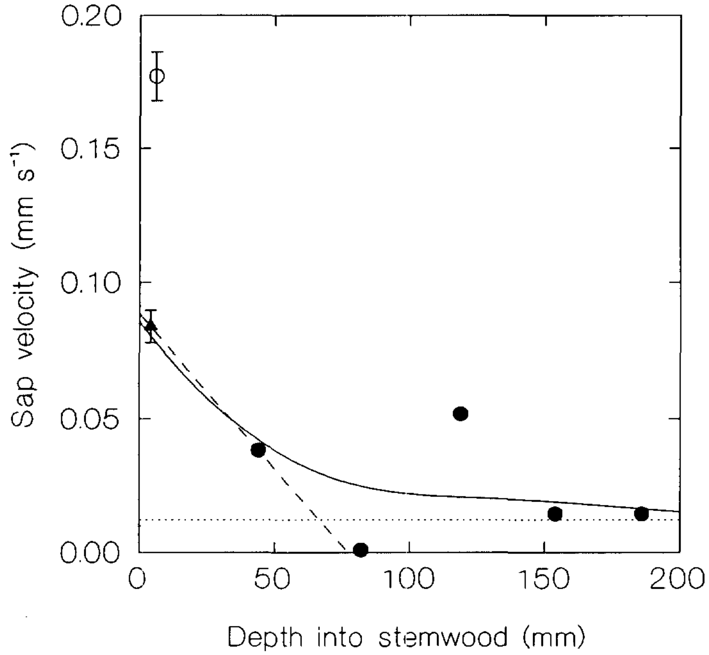

Figure 1. Sap velocity–depth profile for *Agathis borneensis* (tree PROF 2) during 1000–1400 h (solar time) during the first two days of measurement. The full radial depth of stemwood on this tree was 306 mm. Velocities are averages of two sensor measurements except that depicted by the triangle, which excludes extremely high values for one sensor. Error bars (± 2 s.e., n = 16) are shown when they exceed symbol size. The solid line is a smooth curve fitted by distance weighted least squares (Wilkinson 1990) to the values represented by filled symbols. The dotted line shows the minimum detectable sap velocity (0.012 mm s^{-1}) for the adopted (thermal balance) threshold time of 150 s. See text for explanation of dashed line.

Mean sap velocities measured during peak flow by one sensor at the shallowest depth were 3.2 times greater than those for the other sensor just 10 mm away in the same probe and 3 mm radially closer to the cambium. Although comparable variation in sap velocity has been detected among sensors at the same depth but different aspects (Becker, unpubl. data), this observation gives a new perspective on the extremely small spatial scale of variation, and emphasises the importance of representative sensor placement in species with rapidly changing velocity–depth profiles such as *A. borneensis.* Marshall (1958) also reported dye experiments showing that sap flow rates may "differ greatly" at points separated by a few mm. Because the maximum velocities detected in *A. borneensis* were double those typical of other tropical species (Becker *et al.* 1997) and would be extrapolated over a 25-mm-wide band of stemwood, a conservative approach was adopted of excluding the corresponding sensor's values from the sap flow calculations. Thus, only the mean velocity for a single sensor (shown by the triangle in Figure 1) was considered in estimating sap flow in the outermost ring.

Taking the weighted averages of sap velocity measured over the entire profile, and extrapolating from the innermost sensor to the centre of the stem, mean daily daytime (sunrise to sunset) sap flow was calculated as 275 ± 40 kg d^{-1} (mean ± 1 s.d., n = 5 d). Plausible lower and upper bounds of sap flow in the gauged tree were estimated as follows. Extrapolating from the outer two velocities measured in Figure 1 (dashed line), zero sap velocity would be estimated to occur at *c.* 75 mm depth. Sap flow calculated for only the outer 75 mm of stemwood was 206 ± 25 kg d^{-1}, while that calculated for the full profile on the basis of the outer two velocity measurements only was 395 ± 45 kg d^{-1}. The former value must be multiplied by a correction factor of 1.33 and the latter by 0.696 to bring them into line with the first calculation employing the full velocity–depth profile, which might be considered to be the most accurate.

These correction factors may then be applied to sap flow measurements made during a very dry period on another tree (B0666) of *A. borneensis* of similar stem size but implanted by the standard procedure (Table 1). Because of the thick bark of *A. borneensis,* the maximum sensor depth for standard implants is about 55 mm, which is apparently inadequate to characterise the sap velocity–depth profile. Crown-relative sap flow in B0666 was substantially lower than in PROF2 due to the former's larger crown size. However, stem-relative sap flow has been shown to be more effective in eliminating residual size effects, at least for *Dryobalanops aromatica* and *Nothofagus* spp. (Becker & Kelliher, unpublished data). Corrected stem-relative sap flow was 12–22% lower in the tree (B0666) measured during the dry period than that (PROF2) measured in the wet period. This may merely reflect errors arising from the application of approximate correction factors. The difference might be real, however, because peak sap velocity and mean daily sap flow were both observed to decline over the full extent of the measurements during the dry period (Becker 1996), probably as a consequence of developing soil water deficits.

As a first approximation, water use by emergent *A. borneensis* during the rainy season and midway during dry periods seems likely to fall between the extreme estimates of 650 and 850 kg d^{-1} m^{-2} (stem cross-section). The lower limit includes the estimate for PROF2 when only the outer 75 mm of stemwood is taken to be conductive. It is unknown to what extent cutting the quarter section of trunk to implant probes affected sap flow measurements. Because leaf area was not changed while sap wood cross-sectional area was decreased, it is possible that sap velocities in the remaining sapwood increased. If this happened in direct proportion to the area of sapwood removed, it would conservatively imply a reduction of about 25% to a water-use range of 500–650 kg d^{-1} m^{-2} (stem cross-section) in emergent trees. A potential experimental resolution of this question would be to measure sap velocity as increasingly large sections of trunk are removed.

Table 1. Tree dimensions and mean daily daytime (sunrise to sunset) sapflow. Crown- and stem-related sap flow is the ratio of sap flow to crown or stem area respectively. Stem cross-sectional area is over bark, measured at the implantation height. The measurements on B0666 were made during 5 d in a very dry period (April 1993), while those on PROF2 are from the present study. Measurements on the last four trees were made during 8 d in the rainy season (January 1994) in dipterocarp forest (Becker, unpublished data)

Species	Tree	Projected crown area (m^2)	Stem cross-sectional area (m^2)	Sap flow (kg d^{-1})	Crown-related sap flow (kg m^{-2} d^{-1})	Stem-related sap flow' (kg m^{-2} d^{-1})
Agathis borneensis	PROF2	29	0.327	275	9.48	841
	B0666	44	0.316	234*	5.32	741
	B0666	44	0.316	206+	4.68	652
Pentace adenophora	A0106	171	0.383	231	1.35	603
Shorea faguetiana	A0117	142	0.292	84	0.59	288
Dryobalanops aromatica	A0134	240	0.458	166	0.69	362
Shorea rubella	A0558	311	0.742	182	0.59	245

*Calculated for full stemwood profile and multiplied by 0.696 correction factor.

+Calculated for 75-mm deep profile and multiplied by 1.33 correction factor.

Estimates of water use in dipterocarp forest during the wet season by four species implanted with two or three sets of instrumentation show values that are typically half that of *A. borneensis* (Table 1). The difference is greatly exaggerated if sap flow is expressed relative to crown area, due to the narrow, deep crowns of *Agathis*. If *A. borneensis* does have exceptionally high water use, even in drought, this implies that it is quite deep-rooted because the upper metre of a deep humus podsol supporting heath forest dominated by this species was almost depleted of extractable water after a month without rain (Tyree *et al.* 1998). Bruenig (1996) reported that roots of *A. borneensis* penetrated to 3–5 m depth, sometimes passing into or through the indurated horizon beneath albic arenosols. An interesting question is to what extent high water use by *A. borneensis* increases the water stress experienced by other tree species in heath forest during drought.

Conclusion

Sap flow occurs at depths in the stemwood of at least 120 mm in *Agathis borneensis*, necessitating special techniques to characterise the sap velocity–depth profile for accurate estimates of water use by the tree. Sap flow normalised by stem cross-sectional area was estimated to lie between 500 and 850 kg m^{-2} d^{-1}, which is double the typical values for trees in dipterocarp forests.

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