Impacts of fire on forest age and runoff in mountain ash forests

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Abstract. Runoff from mountain ash (*Eucalyptus regnans* F.Muell.) forested catchments has been shown to decline significantly in the few decades following fire – returning to pre-fire levels in the following centuries – owing to changes in ecosystem water use with stand age in a relationship known as Kuczera's model. We examined this relationship between catchment runoff and stand age by measuring whole-ecosystem exchanges of water using an eddy covariance system measuring forest evapotranspiration (ET) combined with sap-flow measurements of tree water use, with measurements made across a chronosequence of three sites (24, 80 and 296 years since fire). At the 296-year old site eddy covariance systems were installed above the *E. regnans* overstorey and above the distinct rainforest understorey. Contrary to predictions from the Kuczera curve, we found that measurements of whole-forest ET decreased by far less across stand age between 24 and 296 years. Although the overstorey tree water use declined by 1.8 mm day^{-1} with increasing forest age (an annual decrease of 657 mm) the understorey ET contributed between 1.2 and 1.5 mm day^{-1}, 45% of the total ET (3 mm day^{-1}) at the old growth forest.

Additional keywords: eddy covariance, *Eucalyptus regnans*, sap flow, transpiration.

Introduction

The future availability of water for cities fed by forested catchments is a critical issue in light of worsening water shortage problems globally (Ma *et al.* 2008). Streamflows into water catchments are dependent on the inputs of water from rainfall, but also, critically, on losses through evaporation from the catchment and transpiration from vegetation. Therefore, runoff into these catchments can be affected by changes in evapotranspiration, which may result from either forest succession or deforestation. A reduction in forest cover due to anthropogenic deforestation or disturbance, such as fire, normally results in a short-term increased runoff into catchments, and the re-establishment of forest cover most often decreases the runoff. These modifications in runoff have been attributed to changes in sapwood area (Vertessy *et al.* 1995, 1997; Roberts *et al.* 2001). Forested catchments return to their initial pre-disturbance state through succession of vegetation (Hibbert 1967; Swank *et al.* 2001), resulting in the runoff returning to the pre-disturbance levels. Hornbeck *et al.* (1993) using 11 water catchments in north-eastern USA (Fernow, Leading Ridge, Marcell and Hubbard brook) showed that after deforestation water yield levels increased by up to 250 mm year^{-1}, returning to the initial levels after 7–25 years.

In Australia, a significant amount of research has taken place on the affect of fire on the water yield changes in eucalypt-dominated water catchments. The most significant of these was by Kuczera (1987), which describes the relationship between mean annual water yield and stand age for a mountain ash (*Eucalyptus regnans* F.Muell.) forested catchment by using rainfall-runoff data from fire affected mountain ash forests. Kuczera's study showed that shortly after a catastrophic fire there was by a distinct period (15–20 years) where water yield decreased (300–400 mm), because of tree growth. After this time, water yield increased to pre-fire levels, taking up to 200 years to fully recover (Vertessy *et al.* 2001). The increase in water yield was due to the replacement of mature forests with younger rapidly growing stand. In eucalypt forests, it is common for a younger regrowth stand to use more water than an old-growth forest because of the rapid growth of the young stands and natural thinning of the mature stands (Andreassian 2004).

In Melbourne, Australia potable water is obtained from 1570 km^2 (157 000 ha) of forested catchments located in the Victorian Central highlands (Melbourne Water 2006) and Melbourne Water Corporation uses water from these

catchments to supply water for ~2.8 million customers (Melbourne Water 2006). Mountain ash forests cover half of the catchment area yet this area yields ~80% of the stream flow that makes up Melbourne's water supply. This is because mountain ash forests tend to grow on higher rainfall sites where the mean annual rainfall exceeds 1200 mm (Vertessy *et al.* 1995, 2001; Haydon *et al.* 1997; Melbourne Water 2006).

Since mountain ash trees are a significant vegetative cover in the catchment, they are an important factor in the future of water availability for the city of Melbourne. For example, past studies have shown that the presence of mountain ash trees radically alter the water balance of water catchment areas and that different aged mountain ash stands created by fire or logging have different total tree water use (Langford 1976; Kuczera 1987; Jayasuriya *et al.* 1993; Vertessy *et al.* 1995, 1996, 1997, 2001; Watson *et al.* 1999; Cornish and Vertessy 2001). Hence, bushfires are a crucial, yet infrequent component in the development and life cycle of mountain ash forests and the hydrological cycle. For mountain ash seedlings to survive and grow they need to be exposed in soil with direct sunlight, an environment best created by bushfires (Vertessy *et al.* 2001). Without fire driven regeneration, mountain ash forests would die out in several hundred years through gradual succession to rainforest species (Haydon *et al.* 1997; Vertessy *et al.* 2001). In the 20th century, bushfires have burnt through the Melbourne water catchment areas in 1926 and 1983, which has resulted in the conversion of 80% of the forest in the catchment from old growth (several hundred years of age) to regrowth stands (Vertessy *et al.* 2001). This regeneration process goes through several different successional stages; pole (15–30 years post fire), spar (30–100 years), mature (100–300 years) and old growth (300+ years) (Museum Victoria 2002).

Following fire there is a mass 'seed rain' followed by germination, high growth rates of young *E. regnans* individuals, and intense competition for light and nutrient resources, resulting in thinning over time. Tree thinning continues for the life of the stand but at an almost exponentially decreasing rate (Fig. 1) (Ashton 1976). After

100–200 years large canopy gaps form (Jayasuriya *et al.* 1993; Vertessy *et al.* 2001) that serve to decrease overstorey leaf area (Fig. 2*b*), sapwood area (Fig. 2*a*) and stem density. As a consequence, when *E. regnans* stands age, less water is lost through transpiration by the overstorey, leading to increased runoff into water catchments (England and Attiwill 2006).

Due to this species' importance for commercial timber as well as its dominance of headwater forests in Victoria, a significant amount of study has been has been conducted on mountain ash forests, especially forest hydrological properties. The amount of runoff from *E. regnans* forests into the catchment is known as the water yield and has been closely related to stand age, due to changes in evapotranspiration (ET) over time (Langford 1976; Kuczera 1987; Watson *et al.* 1999; Vertessy *et al.* 2001). An idealised curve developed by Kuczera (1987) describes the relationship between mean annual water yield and stand age for a mountain ash forested catchment by using rainfall-runoff data from fire affected mountain ash forests (Fig. 3). Kuczera's study shows that shortly after the catastrophic fire in 1939 there was a rapid decline in catchment yield of 580 mm over a 27-year period. After this time, water yield was predicted to return to pre-fire levels, taking up to 200 years to fully recover (Vertessy *et al.* 2001).

Previous studies have also shown that vegetation succession following fire produces an increasing understorey leaf area as the overstorey leaf area declines (Vertessy *et al.* 2001). These studies have suggested that the understorey ET is negligible because the understorey is decoupled from the bulk atmosphere, being shaded by the tall (85 m) *E. regnans* canopy, more humid, with less turbulent mixing and reduced evaporative demand (Vertessy *et al.* 2001). Therefore, if it is assumed that the understorey ET is negligible then Kuczera's curve is easily explained by the observed decline in overstorey stem density and leaf area index (LAI) with stand age after the initial 30-year peak. The initial decline in catchment yields over the first 30 years is explained by the rapid growth of mountain ash trees following disturbance and increasing stem densities and leaf area.
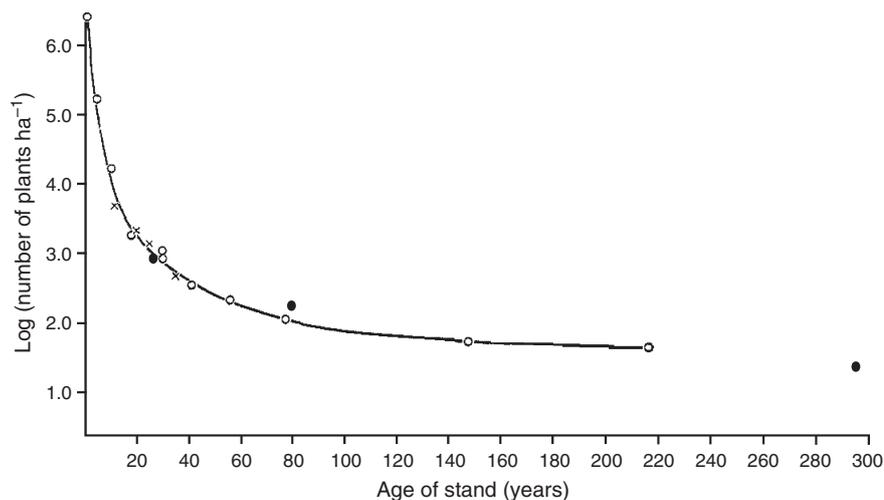

Fig. 1. Relationship between density of trees (plants ha^{-1}) and the age of the stand (years). ○ 1953 assessments; × 1974 reassessments; overlaid with: ● stem density data from this study (Ashton 1976; pp. 399).
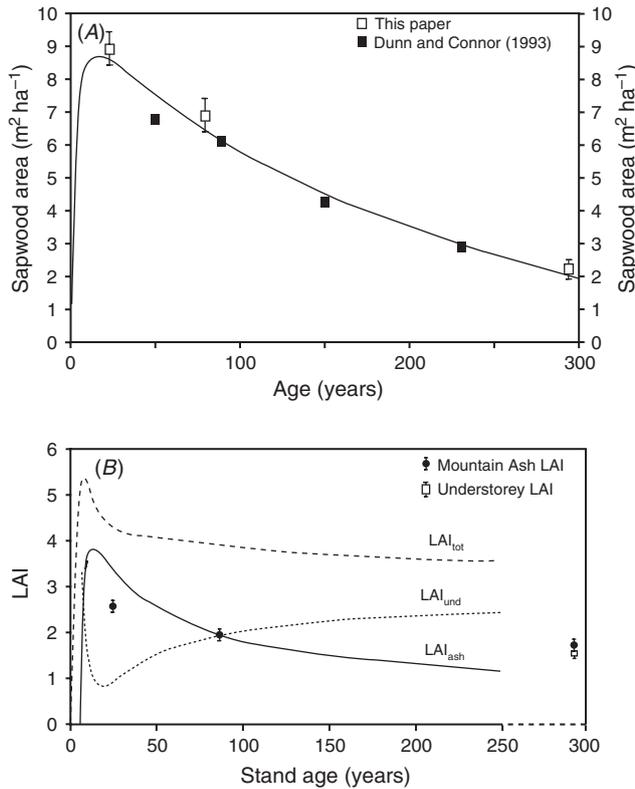
Fig. 2. (*A*) Change in sapwood area with stand age, data from this paper (open squares) plotted with data from Dunn and Connor (1993) (closed squares). Best fit equation $y = (a + c \ln x + e(\ln x)^2)/(1 + b \ln x + d(\ln x)^2)$, $a = 0.0037$, $b = 0.0069$, $c = 6.267$, $d = 0.0113$, $e = -1.014$, $r^2 = 0.94$. (*B*) Age-dependant trends in total LAI (LAI$_{tot}$), mountain ash LAI (LAI$_{ash}$) and understorey LAI (LAI$_{und}$) in the Maroondah catchment, Central Highlands, Victoria (Vertessy *et al.* 2001; pp. 19), compared with mountain ash LAI data (closed circles) and old growth understorey LAI data (open squares) from this study.

Vertessy *et al.* (2001) noticed reportable differences in their estimate of water balance due to their inclusion of changes in understorey transpiration, calculated using the sap-flow method, but for a 240-year-old forest, the understorey transpiration accounted for only 16.6% of the site water use. Their study also showed the annual canopy interception of rainfall and annual soil and litter evaporation decreased by 7.5 and 1.6%, respectively, from a 15 to a 240-year-old stand, illustrating that the major component affecting the yield in water catchments is the transpiration of the dominant mountain ash trees.

Recent studies such as Watson *et al.* (1999) and Vertessy *et al.* (2001) using a range of methods from water balance models to sap-flow techniques to investigate overstorey water use have supported the initial findings by Kuczera (1987). In the case of sap-flow measurements this has been predominantly focussed on the tall overstorey trees (Whitehead and Beadle 2004). However, all these measurements are either indirect or measuring only a single component and there have been no direct measurements of total forest ET undertaken in this forest type to date.

The objectives of this research were to (1) measure sap flux in mountain ash stands of three different ages to determine the effect of forest age on mountain ash water use and compare results with tower based estimates and previous studies; (2) measure the water use of the understorey of an old growth mountain ash forest using sap-flow and tower measurements to more fully investigate the contribution of the understorey to total forest water use on total; (3) scale up sap flux measurements to canopy transpiration to compare results with eddy covariance measurements from the old growth stand.

Materials and methods

Site description

All field measurements were conducted in the Wallaby Creek Melbourne Water catchment, located near Kinglake, ~45 km, north-east of Melbourne, in south-eastern Australia (Fig. 4). Three suitable sites were selected that are typical of
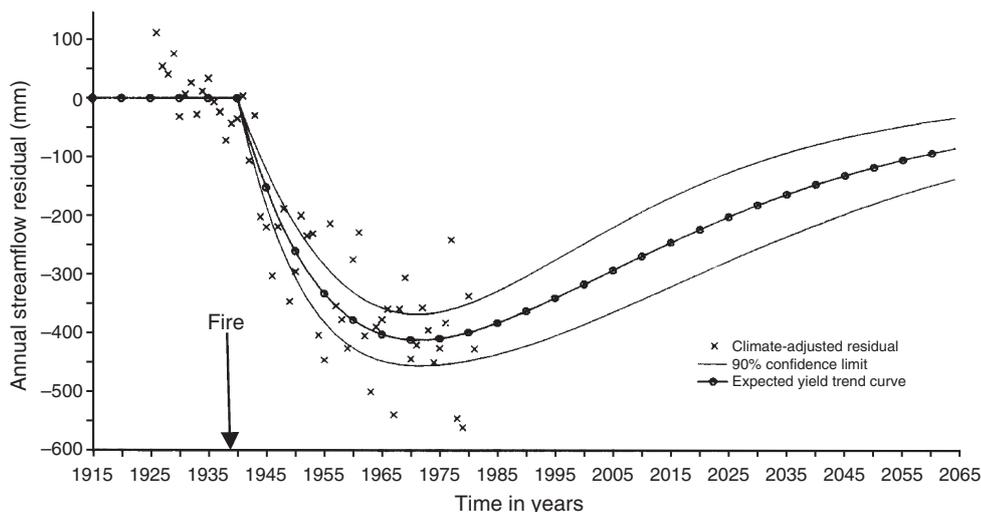

Fig. 3. Climate adjusted residuals of streamflow for Graceburn catchment with Kuczera's predictive model for expected yield following fire in 1939 (Kuczera 1987; pp. 224).
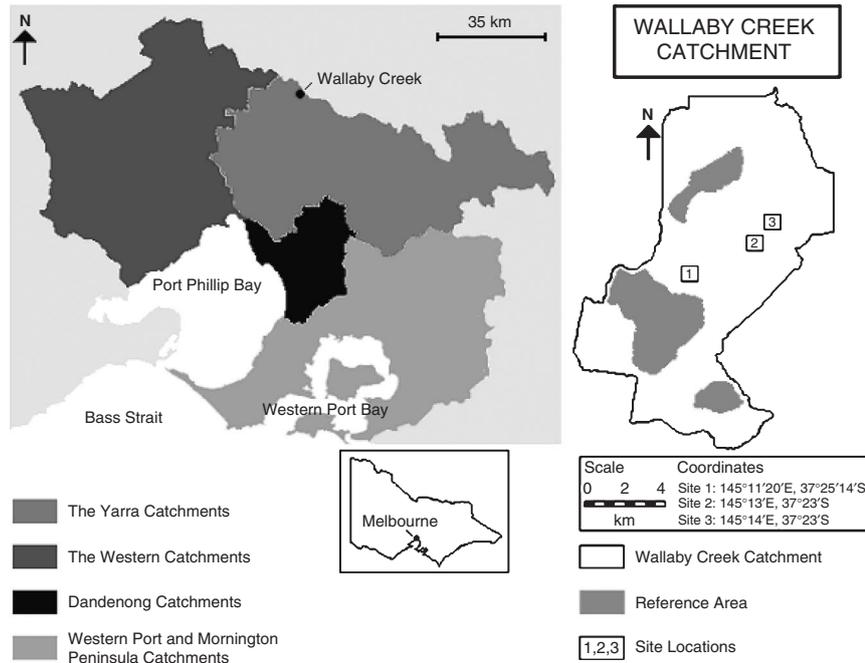
Fig. 4. Location of the Wallaby Creek catchment study site ~45 km north-east of Melbourne, Australia. Site (1) 296 years old/EC tower site; (2) 80 years old; site (3) 24 years old.

Melbourne's water catchment areas representing different age classes (24, 80 and 296 years) of mountain ash (*Eucalyptus regnans* F.Muell.) forest ranging from 660 to 690 m in altitude. Details of these sites are given by Martin *et al.* (2007).

The Wallaby Creek catchment is classified as on the margin of a Mediterranean and temperate climate with warm dry summers and mild winters (Van Pelt *et al.* 2004). It has received an average of 1190 mm of rainfall per year for the past 10 years (1996–2006), with an average of 232 mm (20.8%) occurring during the summer months (December, January and February) (Bureau of Meteorology 2007). The site also receives ~380 mm of snowfall per year (Van Pelt *et al.* 2004). The annual average maximum and minimum temperatures vary between 24.1 and 3.7°C, respectively (Bureau of Meteorology 2007). Mean monthly minimum and maximum temperatures vary between 2 and 8°C in winter, and 16 and 28°C in summer.

Vegetation

Mountain ash trees are straight, grey-trunked trees with smooth-bark for all but the first few metres (Ashton 2000*a*). These trees grow in cool, deep soiled, mostly mountainous areas up to 1000 m in elevation with very high rainfall of over 1200 mm per year (Vertessy *et al.* 1995, 2001; Haydon *et al.* 1997; Melbourne Water 2006). The understory of the old-growth forest is made up of *Olearia argophylla* (Labill.) F. Muell. ex Benth, *Pomaderris aspera* Sieber ex DC., tree ferns (*Dicksonia antarctica* Labill. and *Cyathea australis* (R. Brown) Domin), as well as *Acacia* trees (*A. dealbata* Link. and *A. melanoxylon* R.Brown) (Van Pelt *et al.* 2004). The understorey at the 1926 regrowth site is sparse, and made up mainly of prickly currant (*Coprosma quadrifida* (Labill.) Rob.). The 1982 re-growth site has a very minimal understory compared with the old-growth site and 1926 regrowth sites. More information on the forest and canopy structure at the old-growth site is given by Van Pelt *et al.* (2004) and further

Table 1.   *Eucalyptus regnans* characteristics from each site at the Wallaby Creek sites
DBH, diameter at breast height

Variable	Site age (years)			
	24	80	296	296 understorey
Average stems per ha	898 ± 36	239 ± 10	37 ± 2	278 ± 11
Mean height (m)	21 ± 3	60 ± 5	80 ± 5	8 ± 1
Mean DBH (cm)	26 ± 3	73 ± 3	155 ± 5	14 ± 2
Minimum DBH (cm)	6 ± 3	42 ± 3	95 ± 5	5 ± 2
Maximum DBH (cm)	70 ± 3	121 ± 3	226 ± 5	26 ± 2
LAI	2.62 ± 0.04	2.09 ± 0.04	1.69 ± 0.07	1.67 ± 0.07
Sapwood area ($m^2\,ha^{-1}$)	8.9 ± 0.5	6.9 ± 0.5	2.3 ± 0.2	2.1 ± 0.2
Sap velocity ($cm\,h^{-1}$)	9.1 ± 1.5	12.8 ± 1.1	11.2 ± 1.4	5.0 ± 1.1

information on the history, environment and plant ecology of mountain ash forests is given by Ashton (2000*b*).

The stocking rate, mean height and diameter at breast height (DBH) of *E. regnans* at the three sites are shown in Table 1 and the stocking rate is compared with previous studies in Fig. 1. Tree height was measured using standard forestry techniques (Goodwin 2004), trigonometry and DBH was measured at a height of 5 metres (above the buttress) on the 296-year-old forest and at breast height of 1.3 m on the 24- and 80-year-old forests as well as the 296-year-old understorey. The two dominant species of the understorey of the 296-year-old stand, *P. aspera* and *O. argophylla* had stocking rates of 133 and 145 stems ha^{-1}, respectively (Van Pelt *et al.* 2004).

Soils

The soils of Kinglake and the Hume plateau are rich krasnozemic loams, which are friable, red brown gradational soils with high organic matter contents (15–20%) in the upper 20–30 cm (Ashton 2000*b*). The soil profile at 0–30 cm is a dark brown coarsely friable loam and grades with depth to a red-brown or yellow-brown subsoil clay loam. From a depth of 183–244 cm the soil becomes a sandy loam and from 244–274 cm the soil becomes loamy gravel. Kransnozemic soils provide perfect growing conditions for mountain ash trees as they have a high rate of water infiltration [13–64 mm h^{-1} (Williams 1983)], good aeration and water retention. Mountain ash forest soils are the most productive forest soils in the state of Victoria due to their high organic matter content (Martin *et al.* 2007; Ashton 2000*b*).

Leaf area index

The total single-sided leaf area index (LAI) of each aged stand was measured using an LAI-2000 plant canopy analyser (PCA) (Li-Cor Inc., Lincoln, NE, USA). The LAI-2000 provides a non-destructive means of measuring single sided leaf area using gap fraction theory (Cherry *et al.* 1998). Two PCA's were used; with one left in a clearing, at a range of 1–3 km away from the sites, to record the light conditions automatically every 15 s, whereas the other sensor was used below the canopy. At each site a 200×200 m grid with 20-m spacing was established and LAI measurements (121 spot measurements per site across the grid) were taken. Measurements were taken using the four inner rings of the sensor, confining the PCA's view to a radius of 41 m at the measured height of ~1.5 m. Due to the dense understorey at the 296-year-old stand, the LAI measured was the total LAI (LAI of overstorey plus understorey), however, several recently fallen trees created a 40×40 m gap in the understorey that provided an opportunity to measure the mountain ash LAI only. This overstorey LAI was measured at 20 points in the understorey clearing using the PCA with the quarter view cap and inner ring only to ensure the LAI of only the mountain ash trees above this cleared area was measured.

Transpiration

Transpiration in this study was measured using the heat pulse method (Cohen *et al.* 1985; Dunn and Connor 1993; Hatton *et al.* 1990), between December 2005 and December 2006, which included the summer period of highest water use. Sap flow was measured using sap-flow loggers (Greenspan Technology, Warwick, Qld, Australia) with eight *E. regnans* trees and four

understorey trees at the 296-year-old site measured simultaneously over this period. This enabled the water use of overstorey and understorey trees to be compared, once normalised by sapwood area. In addition, four individuals of mountain ash trees at the 24- and 80-year-old sites were also instrumented to examine rates at the younger sites of contrasting structure. For each individual tree, sampling of sap velocity was undertaken at four different points within the sapwood, with measurements made every 30 min across a range of tree diameters at each site (Becker 1998). This provided a relationship between tree size (DBH) and sapwood area with sap flow, which enabled the water use of individual trees to be scaled to stand water use, following Vertessy *et al.* (1997).

The half-hour measurements of mountain ash sap-flow velocities were multiplied by the sapwood cross-sectional area to calculate the transpiration for individual trees. The sapwood depth and sapwood cross-sectional area of each tree used in this study was determined from cores taken with a 5 mm increment borer, taken at breast height (1.3 m) for trees from the 24-, 80- and understorey of the 296-year-old sites. For the old growth site, the cores were collected above the buttresses at a height of ~5 m. The depth of the sapwood was determined from the core by holding it in front of a bright light source, so that the light was able to pass through the vessels. The open vessels in the sapwood are clearly distinct as numerous pinpoints of light. Few or no pinpoints of light can be seen in the heart wood, where most of these vessels are blocked (Dunn and Connor 1993; Jayasuriya *et al.* 1993; Haydon *et al.* 1997). The sapwood depth of the understorey trees at the 296-year-old site was clearly distinguishable as a change in colour when methyl orange dye was added. To measure the sapwood depth with greater accuracy it was measured at four points around each tree (Dunn and Connor 1993; Haydon *et al.* 1997). Sapwood width measurements were used to determine the implantation depth of the heat pulse sensor probes and to calculate sapwood area.

Eddy covariance measurements of forest evapotranspiration

A 110-m tall guyed mast tower was constructed within the old growth stand to record water, carbon and energy exchange data using the eddy covariance technique as part of a larger study that aimed to quantify the carbon, water and energy exchanges within Australia's temperate forests and the factors regulating them over hourly to inter-annual time scales in order to assess the impact of future environmental change. The eddy covariance tower was installed at an elevation of 690 m, with a site slope of ~3°, with adequate fetch in all directions (>1 km) and has been collecting water and CO_2 exchange data continuously since August 2005. For forests, the method involves the deployment of fast response instruments above plant canopies to measure the covariance of vertical wind velocities and scalars such as CO_2, water vapour and temperature (Baldocchi and Meyers 1998). The system is made up of two main instruments, a sonic anemometer (Model CSAT3; Campbell Scientific Inc., Logan, UT, USA) that measures the turbulent wind field, sonic temperature, sensible heat and friction velocity along with an open path gas analyser (LI-7500, Li-Cor) that measures CO_2 and H_2O concentrations and computes the relevant fluxes. The instrument setup follows that by Beringer

et al. (2007) and Hutley *et al.* (2005). Briefly, there are two eddy covariance systems in operation on the tower; the first is located 95 m above the ground, roughly 25 m above the mountain ash canopy which measured the net exchanges between the whole ecosystem and the atmosphere. The second is located 25 m above the ground and measures fluxes from the understorey (8.3 m above the understorey canopy) and the surface. Obtaining flux data from the two different heights allows differentiation between the overstorey canopy and understorey (vegetation and soil) in terms of CO_2 and H_2O fluxes. These systems sampled flux variables at 20 Hz and recorded half hourly mean fluxes and were strictly quality controlled and gap filled following Beringer *et al.* (2007). Neural network (NN) models were produced for gap filling the flux variables using Statistica software package (Statsoft, Tulsa, OK, USA) following Papale and Valentini (2003) and Beringer *et al.* (2007).

In addition to the eddy covariance systems, net radiation is measured every 30 min by measuring the incoming (Pyranometer CM7B; Kipp and Zonen, Delft, The Netherlands) and outgoing (Pyrgeometer CG2; Kipp and Zonen) radiation fluxes at a height of 110 m. There is also a temperature, CO_2 concentration, relative humidity and pressure profile system that run vertically along the tower (HMP45C; Campbell Scientific Inc.). These profiles were measured at heights of 2, 5, 10, 20 and 45 m.

Results

Leaf area index and sapwood

LAI and tree stand density decreased with forest age (Table 1). At the old growth stand (296-year-old) the LAI of the overstorey and understorey were similar, 1.69 and 1.67, respectively (Fig. 2*b*). Understorey LAI was calculated as total forest LAI (3.36), measured at 121 points, minus the overstorey LAI, measured at just 20 points. Sapwood area for the *E. regnans* trees and the two dominant understorey species were estimated from species specific regression equations for each site derived from data collected in this study. A relationship between sapwood area and DBH of individual trees showed a strong relationship ($r^2 = 0.90$) that allowed the stand sapwood area to be calculated by measuring DBH of individuals in the 200×200 m plot (Fig. 2*a*). The total sapwood area of the mountain ash trees was 8.89 ± 0.51, 6.87 ± 0.52 and 2.25 ± 0.23 m^2 ha^{-1} for the 24-, 80- and 296-year-old sites, respectively. The two major understorey species at the old growth site (*Olearia* and *Pomaderris*) had a sapwood area of 0.91 ± 0.21 and 1.23 ± 0.21 m^2 ha^{-1}, respectively.

Mountain ash sap velocity and transpiration

We measured the sap velocity during the summer months to be 9.05 ± 1.5, 12.8 ± 1.1 and 11.2 ± 1.4 cm h^{-1} for the 24-, 80- and 296-year-old stands, respectively. Values of hourly transpiration (Fig. 5) were summed to calculate the daily transpiration rates of the mountain ash trees from the different aged stands. During Melbourne's summer months (December, January and February) the average transpiration from the mountain ash trees at the 24-year-old was 51 L day^{-1} $tree^{-1}$. At the 80-year-old site the average daily transpiration was 251 L day^{-1} $tree^{-1}$ and the 296-year-old site average transpiration was 317 L day^{-1} $tree^{-1}$. During the winter months (July and August) the average
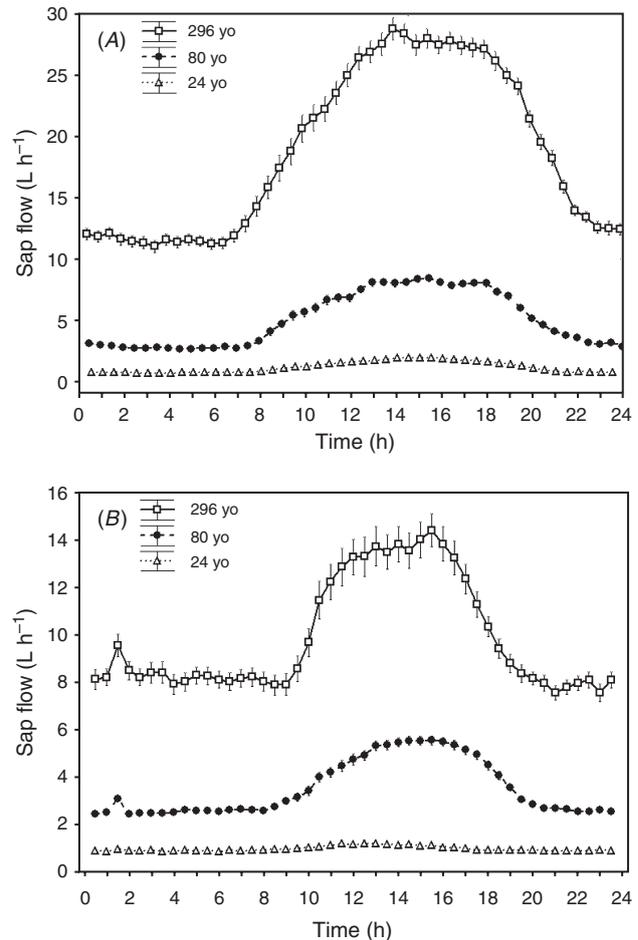

Fig. 5. Ensemble average of the diurnal pattern of sap flow for mountain ash trees at the three different aged sites (24, 80 and 296 years old), (*A*) for summer period 8 December 2005 to 5 February 2006, (*B*) for winter period 1 May 2006 to 30 May 2006 for 296-year-old and from 26 July 2006 to 10 September 2006 for 80- and 24-year-old sites. Standard error bars shown.

transpiration was 43, 109 and 163 L day^{-1} $tree^{-1}$ for the 24-, 80- and 296-year-old stands, respectively.

From the annual data we calculated the average canopy transpiration rates for the 24-, 80- and 296-year-old mountain ash stands to be 3.32, 2.91 and 1.52 mm day^{-1}, respectively, over the study period. From these measurements the mean annual transpiration was estimated to be 1212, 1051 and 555 mm $year^{-1}$ for the 24-, 80- and 296-year-old stands, respectively.

Dunn and Connor (1993) calculated that 69% of total annual potential evapotranspiration occurred during the six warmest months, with 31% occurring during the six coolest months, giving a ratio of 0.45. Using the data collected in this study, it was estimated that 65% of the measured total transpiration occurred during the warmest months with only 35% occurring during the coolest.

The transpiration data in Fig. 5 also showed a positive night-time sap-flow rate for all measured trees, accounting for ~35 and 50% of total sap flow during summer and winter months, respectively. In general, it is often assumed that stomata close at sunset; however, the stomata of some plants stay partially open,

allowing night-time transpiration (Dawson *et al.* 2007; Marks and Lechowicz 2007). The primary driver of nocturnal transpiration is vapour pressure deficit (VPD) with strong links to high night-time temperature and available soil moisture. Even if the stomata are closed at night-time, sap flow may continue, due to the refilling of stem and branch capacitance, as this water may have been drawn on during high photosynthesis times (Benyon 1999; Phillips *et al.* 2003; Snyder *et al.* 2003).

In addition, the diurnal graphs of transpiration for the old-growth mountain ash trees show a slight plateau between 1400 to 1600 hours local time (Fig. 5), suggesting a possible hydraulic constraint in water use. This occurs as water stored in the trunks and branches of the trees is used for photosynthesis early in the day and when the evaporative demand is greatest (around solar noon) the tree cannot supply water fast enough because of the suction required to draw up water through the trunk from the soil (Goldstein *et al.* 1998; Dawson *et al.* 2007).

Understorey transpiration

Values of tree transpiration were also summed to calculate the daily transpiration rates of the two main understorey species at the old growth site. The transpiration from *O. argophylla* had a mean value of 20 L day^{-1} during summer and 14.5 L day^{-1} during winter. Scaling this to stand level, the *O. argophylla* had a transpiration rate of 0.59 mm day^{-1}. The main understorey species *P. aspera* transpiration had a mean value of 26 L day^{-1} during summer and 17.1 L day^{-1} during winter, giving an average transpiration rate of 0.84 mm day^{-1} after scaling to stand level. The total transpiration from the two main understorey trees was 1.43 mm day^{-1}, only 0.34 mm day^{-1} less than the dominant mountain ash stand. However, it should be noted that the *P. aspera* and *O. argophylla* only account for 90% of the total understorey leaf area, with the other 10% being from *Acacia* spp., *D. antarctica* and *C. australis*. Hence, the total understorey transpiration could be greater than measured.

Total transpiration

The annual time series of 30-min sap-flow and eddy covariance data were pooled to produce monthly water use values (Fig. 6*a*). The data show a significant seasonal variation in total water use that follows a very similar trend to potential ET (Fig. 6*b*). The understorey ET was a larger proportion of the total in summer than winter, presumably because of much higher soil evaporation in summer.

The annual ET of the 296-year-old site from the whole forest and overstorey were derived from the cumulative monthly totals, and the annual transpiration from the understorey was calculated as the cumulative monthly difference between the total ET measured by the eddy covariance tower and the mountain ash transpiration as measured by the sap-flow method (Fig. 6*a*). The whole-ecosystem ET was 1077 mm year^{-1} at the 296-year-old site (Fig. 7). The 20-year-old stand had no understorey, but the 80-year-old site had an estimated understorey LAI that was 10% of the overstorey LAI. After taking this into account, the total forest transpiration for the 80-year-old site was estimated to be 3.2 mm day^{-1} or 1168 mm annually. The transpiration from the 20-year-old site was 3.32 mm day^{-1} or 1212 mm year^{-1}. The
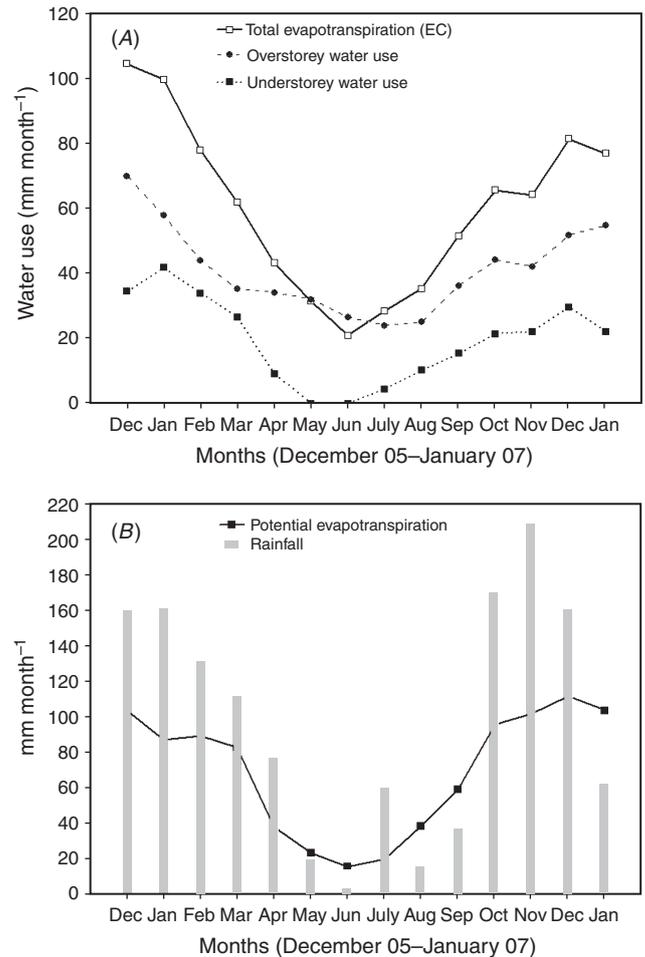
Fig. 6. (*A*) Comparison between the monthly whole-forest evapotranspiration (mm) as measured by the eddy covariance tower, the monthly water use by mountain ash trees (mm) as measured by sap flow and the understorey water use (mm). Understorey water use was calculated as the residual of the total and overstorey measurements. (*B*) Comparison between monthly potential evapotranspiration and rainfall for the 296-year-old site from December 2005 to January 2007.

result was that the total forest transpiration shows a decreased by only 135 mm annually across the chronosequence (Fig. 7).

Comparison with eddy covariance estimates of forest ET

Mean sap-flux transpiration for summer (December, January and February) 2005–06 was compared with the eddy covariance transpiration for the same period (Fig. 8). Tree transpiration was remarkably similar between the eddy covariance (1.64 ± 0.1 mm day^{-1}) and sap-flux methods (1.79 ± 0.1 mm day^{-1}) and any difference was likely due to errors in scaling. The understorey transpiration from the eddy covariance system was 1.47 mm day^{-1} which was only 0.04 mm day^{-1} more than the estimated rate from the sap-flow method. This provides confidence in the sap-flow methodology and the scaling from trees to plot.

The potential evapotranspiration (PET) was calculated for the 296-year-old stand using the Penman–Monteith equation and data from the eddy covariance tower following Beringer *et al.*
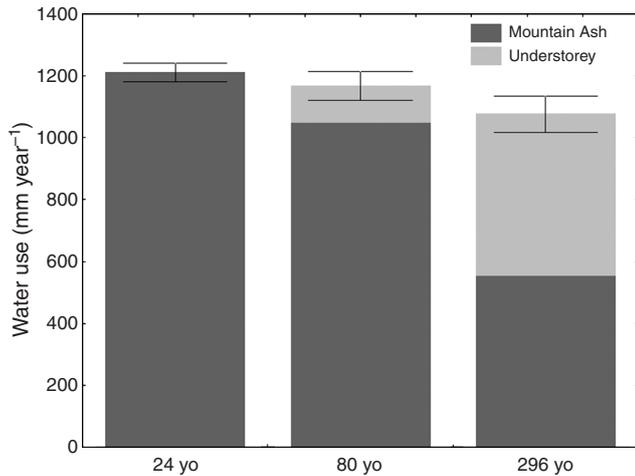
Fig. 7. Change in average annual forest transpiration with stand age, with overstorey and understorey water use given for each site. Standard error bars shown.
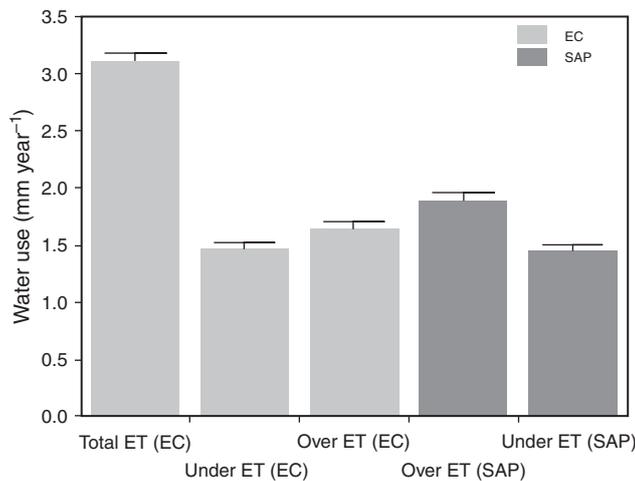

Fig. 8. Comparison of total ET from the ecosystem and understorey ET (vegetation plus soils) measured using the eddy covariance (EC) for summer (December 2005, January and February 2006). The overstorey ET is calculated as the difference between the total and understorey measurements. The scaled sap-flow measurements are shown for December, January and February. Standard error bars shown.

(2005). PET was 860.9 ± 6.9 and was less than the annual rainfall (1175 ± 9.8) for that period illustrating the 'wet' nature of these cool wet temperate forests. Hence, the potential runoff of the 296-year-old stand was estimated as $314 \, \text{mm year}^{-1}$.

Discussion and conclusions

The results of LAI, stem densities and sapwood area of the mountain ash trees from this study are highly consistent with previous studies, as illustrated when plotted with results by Dunn and Connor (1993), where stand sapwood area was measured at the nearby North Maroondah catchment for four different age classes of mountain ash forests, at 50, 90, 150 and 230 years of age (Fig. 2*a*). The sapwood area is essentially zero after fire and

reaches a peak at ~30 years, after which time sapwood area declines steadily with forest age (Fig. 2*a*).

Dunn and Connor (1993) observed that the mean sap velocities in the stems of mountain ash trees in stands aged 50, 90, 150 and 230 years for spring/summer months were 11.5, 11.4, 9.9 and $11.8 \, \text{cm h}^{-1}$, respectively (Dunn and Connor 1993). We concur with the conclusions by Dunn and Connor (1993) and Haydon *et al*. (1997), who stated that sap velocity does not vary significantly with forest succession for mountain ash stands. They also estimated a maximum summer time transpiration rate of 1.9 and $0.8 \, \text{mm day}^{-1}$ for the 50- and 230-year-old stands, respectively. Annually, this resulted in a difference of 383 mm, which was expected to be observed as an increase in water yield. Vertessy *et al*. (2001) showed a similar result with an estimated annual ET difference of 383 mm between a 20- and 220-year-old mountain ash forest, using a water balance method. These two results are much less than the 765 mm difference estimated by Haydon *et al*. (1997) for a 20- *v*. 220-year-old forest, possibly due to a failure to account for changes in understorey transpiration. Kuczera (1987) showed a similar difference to this with a 580 mm decline in stream flow after forest regeneration from bushfire.

Our results have shown a decrease in sapwood area and transpiration of the overstorey trees, highly consistent with previous studies, but our results contradict past assumptions that the ET from the understorey is negligible. We found that for the old growth site, understorey transpiration makes up 48% of the total in summer, consistent with the ratio of understorey to total forest LAI (Table 1). From our results, we suggest that the water use across different stand ages (after maximum leaf area is reached at ~24 years old) declines only slightly, with a decline of $364 \, \text{mm y}^{-1}$ between the 24- and 296-year-old stands.

Assumed negligible understorey transpiration has previously been attributed to low VPD (high relative humidity) within the moist understorey environment that provides a minimal water vapour gradient. However, we were able to measure the relative humidity and vertical gradient using our tower profile. We found that the relative humidity was around 62% and not close to
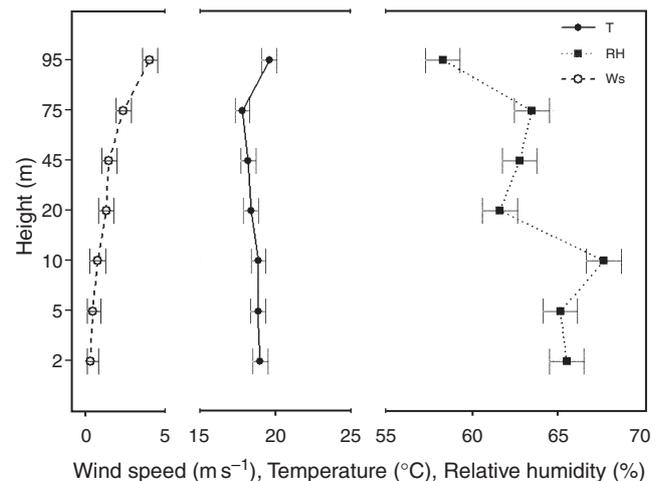

Fig. 9. Comparison of wind speed (m s^{-1}), temperature (°C) and relative humidity (%) at the different measurement heights (2, 5, 10, 20, 45, 75 and 95 m). The overstorey canopy height was 80.44 m and the understorey was 8.3 m.

saturation during daylight hours (0800–1700) in summer (December, January and February) (Fig. 9). In addition, there was a clear water vapour gradient. There was little difference in air temperature within the canopy and wind speeds decreased monotonically. Further, the measured turbulence was modest, as measured by the so called friction velocity (u^*) derived from the eddy covariance system that averaged $0.26\,\mathrm{m\,s}^{-1}$ during the day with a peak of over $0.5\,\mathrm{m\,s}^{-1}$. The overstorey u^* measurements had an average value of $0.99\,\mathrm{m\,s}^{-1}$ with a peak around $1.05\,\mathrm{m\,s}^{-1}$. Many studies have shown that u^* values greater than around $0.1\,\mathrm{m\,s}^{-1}$ represent conditions of sufficient turbulent transport to capture fluxes (Aubinet *et al*. 2005; Papale *et al*. 2006). Hence, the values shown for mountain ash forest suggest that canopy mixing was occurring and that turbulent exchange from the understorey is significant from this canopy layer, as demonstrated by the measured water fluxes using both sap-flow and eddy covariance techniques.

The consequence of this higher than expected total forest ET of older stands is that catchment runoff may not increase substantially with stand age once the forest is mature and LAI has peaked. Kuczera's curve is somewhat unique in the literature because it shows no immediate increase in runoff following disturbance, in contrast to most studies of catchment disturbance (fire or clear-felling), which show an initial increase in yield following fire, then followed by a decline in yields associated with vigorous regrowth and then a small decline in ET back to pre-disturbance levels (Jayasuriya *et al*. 1993; Watson *et al*. 1999; Cornish and Vertessy 2001). A local example is given by Watson *et al*. (1999), who showed that after clear felling, 78% of mountain ash forest in the Picaninny catchment (Central Highlands of Victoria), the annual water yield increased by ~300 mm after 2 years and then decreased by up to 200 mm as the forest matured (<25 years old) (Fig. 10). Our result of a 135 mm year^{-1} reduction in annual ET between 24 and 296 years old is more consistent with Watson *et al*. (1999), who showed that the difference from 25-year-old to pre burn levels was on the order of 150 mm year^{-1}.

These findings provide additional information that can be used to further interpret and refine the relationships suggested by Kuczera. Their catchment yield curve was developed using a simple, two parameter model fit to observed catchment data from
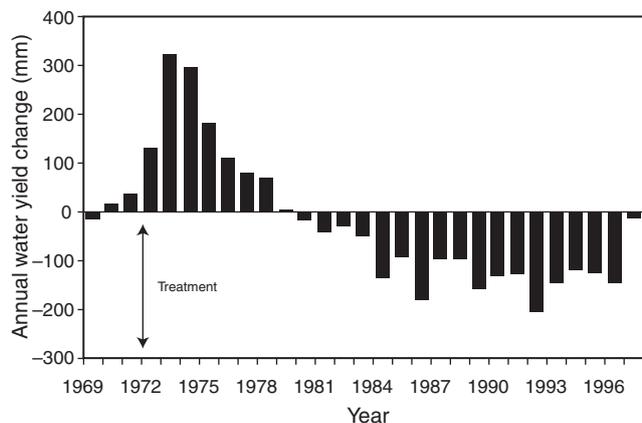
before and after fire and is therefore an empirical relationship based on a single fire event in 1939. Kuczera's curve has been supported by some water balance studies but has lacked an ecological or plant physiological interpretation. However, our results are the first direct observations of total forest ET across a chronosequence and suggest that the decline in ET may not be as large as predicted by Kuczera's curve but are more consistent with other studies of forest disturbance locally and worldwide. The Kuczera curve has maintained some prominence in State government water resource management (Department of Sustainability and Environment 1998) and it is, therefore, important that better understanding of the forest hydrology these important Melbourne's water catchments be obtained and any uncertainties reduced. This is especially important given climate change scenarios and potentially permanent declines in mean annual rainfall for south-eastern Australia (Whetton *et al*. 2002). Process-based soil vegetation atmosphere transfer (SVAT) models could aid in the interpretation of the available data and will provide the most gain when coupled to hydrological catchment models. Such an effort will require integration of the hydrological approach (water balance and catchment models) with an ecosystem ecology approach (ecosystem fluxes and ecological models). This will be crucial to capture future environmental change including climate change, drought, disturbance (fire) processes and changes in the water use efficiency of vegetation with increasing atmospheric CO_2 levels.

Acknowledgements

References

Andreassian V (2004) Waters and forests: from historical controversy to scientific debate. *Journal of Hydrology* **291**, 1–27. doi: 10.1016/j.jhydrol.2003.12.015

Ashton DH (1976) Development of even-aged stands of *Eucalyptus regnans* F.Muell. in Central Victoria. *Australian Journal of Botany* **24**, 397–414. doi: 10.1071/BT9760397

Ashton DH (2000*a*) The big ash forest, Wallaby Creek, Victoria – changes during one lifetime. *Australian Journal of Botany* **48**, 1–26. doi: 10.1071/BT98045

Ashton DH (2000*b*) The environment and plant ecology of the Hume Range, Central Victoria. *Proceedings of the Royal Society of Victoria* **11**, 185–278.

Aubinet M, Berbigier P, Bernhofer CH, Cescatti A, Feigenwinter C *et al*. (2005) Comparing CO_2 storage and advection conditions at night at different carboeuroflux sites. *Boundary-Layer Meteorology* **116**, 63–94. doi: 10.1007/s10546-004-7091-8

Baldocchi D, Meyers T (1998) On using eco-physiological, micrometeorological and biogeochemical theory to evaluate carbon dioxide, water vapor and trace gas fluxes over vegetation: a perspective. *Agricultural and Forest Meteorology* **90**, 1–25. doi: 10.1016/S0168-1923(97)00072-5

Becker P (1998) Limitations of a compensation heat pulse velocity system at low sap flow: implications for measurements at night and in shaded trees. *Tree Physiology* **18**, 177–184.

Benyon RG (1999) Nighttime water use in an irrigated *Eucalyptus grandis* plantation. *Tree Physiology* **19**, 853–859.

Fig. 10. Mean annual water yield changes after a 78% clear fell logging in the Picaninny catchment, Central Highlands, Vic., 1969–98. Based on analysis reported in Watson *et al*. 1999 (from Vertessy *et al*. 2001; pp. 16).

Beringer J, Chapin FS, Thompson CC, McGuire AD (2005) Surface energy exchanges along a tundra-forest transition and feedbacks to climate. *Agricultural and Forest Meteorology* **131**, 143–161. doi: 10.1016/j.agrformet.2005.05.006

Beringer J, Hutley L, Tapper N, Cernusak LA (2007) Savanna fires and their impact on net ecosystem productivity in North Australia. *Global Change Biology* **13**, 990–1004. doi: 10.1111/j.1365-2486.2007.01334.x

Bureau of Meteorology (2007) Bureau of Meteorology webpage. Available at www.bom.gov.au. Accessed 20 January 2007

Cherry M, Hingston A, Battaglia M, Beadle C (1998) Calibrating the LI–COR LAI-2000 for estimating leaf area index in eucalypt plantations. *Tasforests* **10**, 75–82.

Cohen Y, Kelliher FM, Black TA (1985) Determination of sap flow in douglas-fir trees using the heat pulse technique. *Canadian Journal of Forest Research – Revue Canadienne De Recherche Forestiere* **15**, 422–428.

Cornish PM, Vertessy RA (2001) Forest age-induced changes in evapotranspiration and water yield in a eucalypt forest. *Journal of Hydrology (Amsterdam)* **242**, 43–63.

Dawson TE, Burgess SSO, Tu KP, Oliveira RS, Santiago LS, Fisher JB, Simonin KA, Ambrose AR (2007) Nighttime transpiration in woody plants from contrasting ecosystems. *Tree Physiology* **27**, 561–575.

Department of Sustainability and Environment (1998) 'Forest management plan for the central highlands.' (Department of Natural Resources and Environment: Melbourne)

Dunn GM, Connor DJ (1993) An analysis of sap flow in mountain ash (*Eucalyptus regnans*) forests of different age. *Tree Physiology* **13**, 321–336.

England JR, Attiwill PM (2006) Changes in leaf morphology and anatomy with tree age and height in the broadleaved evergreen species, *Eucalyptus regnans* F.Muell. *Trees* **20**, 79–90. doi: 10.1007/s00468-005-0015-5

Goldstein G, Andrade JL, Meinzer FC, Holbrook NM, Cavelier J, Jackson P, Celis A (1998) Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant, Cell & Environment* **21**, 397–406. doi: 10.1046/j.1365-3040.1998.00273.x

Goodwin AN (2004) Measuring tall tree heights from the ground. *Tasforests* **15**, 85–97.

Hatton TJ, Catchpole EA, Vertessy RA (1990) Integration of sap flow velocity to estimate plant water use. *Tree Physiology* **6**, 201–209.

Haydon SR, Benyon RG, Lewis R (1997) Variation in sapwood area and throughfall with forest age in mountain ash (*Eucalyptus regnans* F.Muell.). *Journal of Hydrology* **187**, 351–366. doi: 10.1016/S0022-1694(96)03016-8

Hibbert AR (1967) Forest treatment effects on water yield. In 'International Symposium of Forest Hydrology'. (Eds WE Sopper and HW Lull) pp. 527–243. (Pergamon: Oxford)

Hornbeck JW, Adams MB, Corbett ES, Verry ES, Lynch JA (1993) Long-term impacts of forest treatments on water yield – a summary for northeastern USA. *Journal of Hydrology (Amsterdam)* **150**, 323–344.

Hutley LB, Leuning R, Beringer J, Cleugh HA (2005) The utility of the eddy covariance techniques as a tool in carbon accounting: tropical savanna as a case study. *Australian Journal of Botany* **53**, 663–675. doi: 10.1071/BT04147

Jayasuriya MDA, Dunn G, Benyon R, Oshaughnessy PJ (1993) Some factors affecting water yield from mountain ash (*Eucalyptus regnans*) dominated forests in south-east Australia. *Journal of Hydrology* **150**, 345–367. doi: 10.1016/0022-1694(93)90116-Q

Kuczera G (1987) Prediction of water yield reductions following a bushfire in ash-mixed species eucalypt forest. *Journal of Hydrology* **94**, 215–236. doi: 10.1016/0022-1694(87)90054-0

Langford KJ (1976) Change in yield of water following a bushfire in a forest of *Eucalyptus regnans*. *Journal of Hydrology* **29**, 87–114. doi: 10.1016/0022-1694(76)90007-X

Ma ZM, Kang SZ, Zhang L, Tong L, Su XL (2008) Analysis of impacts of climate variability and human activity on streamflow for a river basin in arid region of northwest China. *Journal of Hydrology* **352**, 239–249.

Marks CO, Lechowicz MJ (2007) The ecological and functional correlates of nocturnal transpiration. *Tree Physiology* **27**, 577–584.

Martin D, Beringer J, Hutley LB, McHugh I (2007) Carbon cycling in a mountain ash forest: analysis of below-ground respiration. *Agricultural and Forest Meteorology* **147**, 58–70. doi: 10.1016/j.agrformet.2007.06.008

Melbourne Water (2006) Protecting Melbourne's water catchments. Available at http://www.melbournewater.com.au. Accessed 10 January 2007.

Museum Victoria (2002) Fire and the forest. Available at http://www.mov.vic.gov.au/forest/fire/forest.html. Accessed 10 January 2007.

Papale D, Valentini A (2003) A new assessment of European forests carbon exchanges by eddy fluxes and artificial neural network spatialization. *Global Change Biology* **9**, 525–535. doi: 10.1046/j.1365-2486.2003.00609.x

Papale D, Reichstein M, Aubinet M, Canfora E, Bernhofer C *et al.* (2006) Towards a standardized processing of net ecosystem exchange measured with eddy covariance technique: algorithms and uncertainty estimation. *Biogeosciences* **3**, 571–583.

Phillips NG, Ryan MG, Bond BJ, McDowell NG, Hinckley TM, Cermak J (2003) Reliance on stored water increases with tree size in three species in the Pacific Northwest. *Tree Physiology* **23**, 237–245.

Roberts S, Vertessy R, Grayson R (2001) Transpiration from *Eucalyptus sieberi* (L.Johnson) forests of different age. *Forest Ecology and Management* **143**, 153–161. doi: 10.1016/S0378-1127(00)00514-4

Snyder KA, Richards JH, Donovan LA (2003) Night-time conductance in C-3 and C-4 species: do plants lose water at night? *Journal of Experimental Botany* **54**, 861–865. doi: 10.1093/jxb/erg082

Swank WT, Vose JM, Elliott KJ (2001) Long-term hydrologic and water quality responses following commercial clearcutting of mixed hardwoods on a southern Appalachian catchment. *Forest Ecology and Management* **143**, 163–178. doi: 10.1016/S0378-1127(00)00515-6

Van Pelt R, Sillett SC, Nadkarni NM (2004) Quantifying and visualizing canopy structure in tall forests: methods and a case study. In 'Forest canopies'. 2nd edn. (Eds MD Lowman, HB Rinker) pp. 49–72. (Elsevier Academic Press: San Diego)

Vertessy RA, Benyon RG, O'Sullivan SK, Gribben PR (1995) Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiology* **15**, 559–567.

Vertessy RA, Hatton TJ, Benyon RG, Dawes WR (1996) Long-term growth and water balance predictions for a mountain ash (*Eucalyptus regnans*) forest catchment subject to clear-felling and regeneration. *Tree Physiology* **16**, 221–232.

Vertessy RA, Hatton TJ, Reece P, O'Sullivan SK, Benyon RG (1997) Estimating stand water use of large mountain ash trees and validation of the sap flow measurement technique. *Tree Physiology* **17**, 747–756.

Vertessy RA, Watson FGR, O'Sullivan SK (2001) Factors determining relations between stand age and catchment water balance in mountain ash forests. *Forest Ecology and Management* **143**, 13–26. doi: 10.1016/S0378-1127(00)00501-6

Watson FGR, Vertessy RA, Grayson RB (1999) Large-scale modelling of forest hydrological processes and their long-term effect on water yield. *Hydrological Processes* **13**, 689–700. doi: 10.1002/(SICI)1099-1085(19990415)13 : 5<689::AID-HYP773>3.0.CO;2-D

Whetton PH, Suppiah R, McInnes KL, Hennessy KJ, Jones RN (2002) 'Climate change in Victoria: high resolution regional assessment of climate change impacts.' (Department of Natural Resources and Environment: Melbourne)

Whitehead D, Beadle CL (2004) Physiological regulation of productivity and water use in *Eucalyptus*: a review. *Forest Ecology and Management* **193**, 113–140. doi: 10.1016/j.foreco.2004.01.026

Williams J (1983) Soil hydrology. In 'Soils: an Australian viewpoint'. pp. 507–530. (Academic Press: London)