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3   **Topographical and seasonal trends in transpiration by two co-occurring**

4   **eucalyptus species over two contrasting years in a low rainfall environment**

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26 **Abstract**

27 Understanding the strategies that confer resilience on natural woodlands in drought-

28 prone environments is important for the conservation of these and similar ecosystems.

29 Our aim in this 2-year study we assessed traits (sapwood area, sapwood density and

30 leaf area index) that control transpiration in *Eucalyptus camaldulensis* and *E.*

31 *microcarpa* in a natural forest in which topographical variation created two topsoils of

32 sandy clay (clay), in the depression that was prone to periodic ponding, and of loamy

33 sand (sand), on the terrace. On the clay, the differences between the two species in

34 their hydraulic attributes were large and rates of water use were widely divergent. *E.*

35 *camaldulensis* that was dominant on this soil had about half the rates of sapflow,

36 transpiration per land area (E_c) and canopy conductance as those of *E. microcarpa*.

37 This was in marked contrast to the sand where water availability was persistently low

38 and variations in sapwood density, sapwood area and canopy conductance were

39 narrow resulting in almost identical rates of water use for the two species, despite *E.*

40 *microcarpa* dominating the stand. Contrary to many previous studies, sapwood

41 density was positively correlated with E_c in these eucalyptus species, suggesting that

42 dense sapwood provided a safeguard against possible xylem embolism and to sustain

43 E_c in this low-rainfall environment with prolonged dry seasons. Also, the proportion

44 of trunk area assigned to sapwood was inversely with trunk size. Single functions

45 were developed for predicting E_c by integrating its response to micrometeorological

46 and soil-water conditions. We concluded that trait variation is less likely where the

47 trees are under persistent water-stress than where the stress is shorter and less intense.

48

49 **Keywords:** drought, flooding, sapwood area, sapwood density, soil-water,

50 transpiration

51   **Introduction**

52

53   Remnants of native woody vegetation are an important resource for understanding

54   pre-existing eco-hydrological processes on highly disturbed landscapes. Such

55   understanding is critical to devising effective management and revegetation strategies.

56   In the semi-arid Australian environments, where European settlement resulted in large

57   scale land clearance, remnants of woody vegetation are a testimony to their capacity

58   to adjust their transpiration in accordance to short- and long-term variability in rainfall

59   and meteorological conditions over the millennia. Adjustment of transpiration

60   involves manipulation of traits at ecological (population density), structural (leaf area

61   index, rooting depth), anatomical (size and density of water conducting tissues,

62   density and location of stoma), physiological (stomatal conductance) and biochemical

63   (osmotic adjustment) levels. These issues have been reviewed in recent years

64   (Wullschleger et al., 1998; Bucci et al., 2004; Meinzer, 2003; Baldocchi and Xu,

65   2007). Disparate species may modify several of these traits to variable degrees to

66   maintain transpiration in a given environment, resulting in *functional convergence*

67   (Meinzer, 2003), i.e. attainment of similarity in transpiration through different

68   strategies. For instance, the concept of *functional convergence* was used to explain

69   the similarity between *Melaleuca spp* and *Eucalyptus spp* in their transpiration per

70   unit leaf area in a contiguous forest despite an apparent large difference in their leaf

71   area index (LAI); this was because the large LAI in melaleuca was compensated for

72   by a larger sapwood area in the eucalypts (Kelley et al., 2007).

73

74   Differences in soil-water availability due to variable soil texture and/or local rainfall

75   can cause permanent structural and physiological changes in the hydraulic apparatus

76   of woody species (Alder et al., 1996; Hultine et al. 2005; Kelley et al. 2007; Mitchell

77   et al., 2008). Alder et al. (1996) showed that trees on a dry slope experienced reduced

78   canopy conductance stemming from reduced hydraulic conductance in the stem and

79   root due to xylem embolism in their roots and stem in a particularly dry year. Hultine

80   et al. (2005) found increases in the dimensions of conducting tissues, including

81   sapwood density, for the desert mesquite (*Prosopis velutina*) growing on fine loamy

82   clay compared with those on a coarser loam due to differing water relations between

83   the two soil types. Amongst stem anatomical changes, those in sapwood density are

84   known to impact on the capacity for water conduction and for withstanding prolonged

85   exposure to limited soil-water supply. For instance, high sapwood density constrains

86   water conductivity, but enhances avoidance of xylem embolism (Koch and Fredeen,

87   2005; Mitchell et al., 2008; Stratton et al., 2000). Thus species with dense sapwood

88   are able to maintain water conduction at much lower leaf water potentials and, hence,

89   lower levels of soil-water availability, than species having low sapwood density.

90   Small variations in sapwood density are known to cause large variations in hydraulic

91   properties, including vulnerability to xylem embolism, and capacity to respond to

92   transient micrometeorological conditions (Bucci et al., 2004; Stratton et al., 2000;

93   Koch and Fredeen, 2005).

94

95   The wide spectrum of soil-water supply experienced in landscapes subjected to short,

96   but frequent flooding or ponding exposes plants to a large range of soil-water

97   potentials that enhance the capacity for extracting water across an extended range of

98   soil-water availability (Sperry and Hacke, 2002). This is achieved through enhanced

99   osmotic adjustment (Alder et al., 1996) so that plants that experience frequent

100   flooding are able to tolerate quite lower soil-water potential (-3.5 MPa) before wilting,

101   compared with non-flooded plants (-3.1 MPa) (Myers and Neales, 1984). Akeroyd et

102   al. (1998), for instance, found that transpiration in eucalypt trees growing on plains

103   subjected to a high frequency of flooding was more responsive to transient changes in

104   vapour pressure deficit, because they maintained higher water potential, than trees

105   growing on the plains with infrequent flooding. Similar responses have been found in

106   other tree species such as cottonwood (*Populus fremontii*) in which transpiration by

107   trees that experienced perennial flooding was more sensitive to vapour pressure

108   deficit, despite reduced sapwood area and LAI, relative to those subjected to

109   intermittent flooding (Gazal et al., 2006).

110

111   Recent studies in the arid environments of Australia, however, found trait variation

112   amongst plant species to be particularly limited under arid conditions (Mitchell et al.,

113   2008; O'Grady et al., 2009). Mitchell et al. (2008) found limited trait variation on soil

114   with prolonged poor water supply, where convergence of water use strategies was

115   more likely, compared with soil having good water storage capacity. Understanding

116   these trade-offs amongst traits that control water use by trees, is important to

117   management of regional water resources, salinity control and environmental health. In

118   this paper, we analyzed transpiration for two co-occurring eucalypt species that

119   dominate a remnant forest in which the terrain caused strong differences in soil

120   texture and hence water supply in southeastern Australia. Our objectives were to (1)

121   quantify transpiration by the trees and characterize its relative sensitivity to

122   micrometeorological and soil water conditions, and (2) identify the dominant traits

123   that control transpiration in the two species under extended drought conditions.

124

125

126 **Materials and methods**

127

128 *The site*

129 This study was undertaken at the Reef Hills State Park (36° 36' S, 145° 56' E or AMG

130 Zone 55, Easting 403442, Northing 594857) located near Benalla in Victoria,

131 Australia. It covers 2032 ha and the vegetation can be generally classified as Heathy

132 Dry Forest (Muir et al., 1995). Annual rainfall for the district is about 670 mm with

133 almost one third of this falling during winter (June –August) when cold westerly

134 winds dominate and mean daily temperature falls below 10 ^{o}C; occasionally the

135 minimum temperature falls to 0 ^{o}C and frosts occur especially from mid winter to

136 early spring. Summers are generally warm to hot with daily mean temperature of 20.6

137 ^{o}C, and also generally dry except for occasional heavy storms. The park was heavily

138 grazed after the cessation of mining in the early decades of the twentieth century, but

139 there has been no record of heavy grazing or wildfires in recent decades. Declaration

140 of the park as a reserve alleviated grazing and has facilitated recovery of the native

141 vegetation and the dominant tree species are approximately 50 years old and have

142 produced substantial sapling undergrowth (Meers and Adams, 2003). There was

143 limited routine harvesting of wood for fuel and timber up until 1988 when the practice

144 was stopped. The park forms part of Box-Ironbark forests and woodlands of almost

145 three million hectares that covers almost 13% of the state of Victoria in Australia

146 (Parks Victoria, 2007).

147

148 We chose a single block of approximately one hectare (62 x 160 m) that was

149 dominated by *Eucalyptus camaldulensis* (Red River Gum) and *E. microcarpa* (Grey

150 Box) and an understorey dominated by *Acacia pynantha* (Golden Wattle) and *A.*

151   *meamsii* (Black wattle) with seasonal groundcover of *Joycea pallida* (Wallaby Grass)

152   and isolated tussocks of *Poa sieberiana* (Tussock-grass). The soil had a duplex profile

153   of coarse textured topsoil underlain by heavy textured clayey subsoil. Salinity

154   measured as electrical conductivity increased from an average of 0.15 dS/m in the

155   near-surface layer to 0.7 dS/m at 3 m depth. The bulk density (Mg/m^3) rises from 1.21

156   in the top 0.2 m layer to 1.43 at 0.5 m depth and 1.75 at 1.0 m; the density was >1.5 at

157   depths below 1.0 m. Site elevation was approximately 190 m above sea level with a

158   gentle slope towards the north north-west of about 1:400.

159

160   The chosen block was split into two distinct zones each of approximately 0.5 ha with

161   contrasting soil textural characteristics (Table 1). The eastern half had a top profile of

162   sandy clay lying in a depression having a gentle slope (~2%) that levels out at about

163   2.0 m; it is prone to ponding due to runoff from the surrounding area. The western

164   half of the block is a terraced alluvium Riverine plain commencing from the edge of

165   the depression and has a topsoil of loamy sand. The surface soil in both cases is

166   underlain with a silty clay middle layer over clay loam profile. Henceforth, the two

167   soils will simply be referred to as clay and sand in this paper. While *E. camaldulensis*

168   accounted for 75% of trees on the clay in the depression, *E. microcarpa* constituted

169   over 90% of trees on the sand on the terraced plain. *E. camaldulensis* is the most

170   widely distributed of eucalypts, commonly found along banks of rivers and seasonal

171   inland streams, and is the most popular eucalypt used in plantations world-wide

172   (Brooker, 2002). *E. microcarpa* tends to be associated with environments that have

173   poor draining clay soil and is considered one of the most high water users (Hookey et

174   al., 1987). Although, the clay was ponded for several months in the winter of 2005

175 prior to commencement of this study in 2006, there was no such episode during the

176 study being reported here.

177

178

179 **Measurements**

180

181 *Tree characteristics*

182 A census of all young and mature trees, including the shrubs, and measurement of

183 their diameter at breast height (DBH) was undertaken in May 2005. Leaf area index

184 (LAI) was made twice in spring (14 September 2006) and summer (20 December

185 2007), using the photographic technique reported previously (Fuentes et al., 2008).

186

187 *Soil water*

188 Water stored in the soil profile was measured with a neutron probe (CPN, 503 DR

189 HYDROPROBE) using pre-installed aluminum access tubes to six metre depth and

190 were spaced at 5 or 10 m intervals across the two soils and were monitored at

191 fortnightly intervals throughout the study period. Each soil types had 10 access tubes.

192 The probe was calibrated using gravimetric determination of soil-water (A. Rab,

193 unpublished data).

194

195 *Transpiration from tree canopy*

196 We used heat-pulse sensors (SF 300, Greenspan Technology, Australia) to monitor

197 sapflow in trees of each species on the clay and the sand. We chose large mature trees,

198 and each was supplied with two probe-sets consisting of a heater and a pair of

199 thermistors. These were implanted into the trunk to a depth of 25 mm, after removal

200   of the bark. The two probe heads installed on to the opposite sides of the trunks and

201   separated by a vertical distance of at least 1.5 m. Installation and maintenance of the

202   logging units followed standard procedures (Yunusa et al., 2008; Zeppel et al., 2006).

203   Core samples were taken from the trunk to estimate wood density and ratio of

204   wood:water (Yunusa et al., 2000). Additional measurements of sapwood area and

205   thickness of heartwood and bark were made on fallen trees, and were used to develop

206   models for predicting trunk tissue diameters from their circumference. The models

207   were then used to estimate dimensions of bark, heartwood and sapwood for the study

208   trees from their trunk circumference. Mean values for these key parameters for the

209   chosen trees are given in Table 2. Transpiration expressed in depth of water (E_c, mm)

210   for any given period was calculated using equation 1 (Akeroyd et al., 1998):

211

212     $$E_c = \frac{V S_b}{S_t A} \tag{1}$$

213

214   in which V was the mean volume of sapflow (V, L/tree) over the time interval, S_t

215   mean sapwood area per tree (m^2), S_b sapwood area for all the tress in the whole

216   block, and A the block area (m^2).

217

218   The sapflow data were used to estimate canopy conductance (g_c) following Monteith

219   and Unsworth (1990):

220

221     $$g_c = \lambda E_c \gamma / \rho C_p D \tag{2}$$

222

223 in which λ is latent heat of vaporization that was taken as constant (2.45 MJ kg^{-1},

224 Monteith and Unsworth, 1990), γ is psychrometric constant (0.066 kPa $^{\circ}$C^{-1}), ρ is the

225 density of air, C_p is the specific heat capacity of air (0.001 MJ kg^{-1} $^{\circ}$C^{-1}) and D vapour

226 pressure deficit of the air (kPa). The g_c was used to calculate the coupling coefficient

227 (Ω) as given by McNaughton and Jarvis (1983):

228

229 $$\Omega = \left(1 + \frac{\gamma}{(\Delta + \gamma)} \cdot \frac{g_a}{g_c}\right)^{-1}$$ (3)

230

231 where g_a is aerodynamic conductance (m s^{-1}) calculated from wind data (Monteith and

232 Unsworth, 1990) and Δ is the slope of the curve relating vapour pressure to

233 temperature (kPa $^{\circ}$C^{-1}).

234

235 *Weather variables*

236 Temperature, humidity, wind speed, solar radiation and rainfall were monitored with

237 an automatic weather station. Potential evapotranspiration (E_{pot}) was calculated using

238 the Priestley-Taylor equation (Priestley and Taylor, 1972). These weather data were

239 also used to calculate equilibrium evapotranspiration (E_{eq}) as a measure of the upper

240 limit for transpiration rate in the absence limited soil water supply and advection

241 (McNaughton and Black, 1973):

242

243 $$\lambda E_{eq} = \frac{\Delta(R_n - G)}{\Delta + \gamma}$$ (4)

244

245 in which R_n is net radiation (MJ m^{-2}) and G is ground heat flux (MJ m^{-2}).

246 **Results**

247

248 *Tree characteristics*

249

250 The two species differed in their trunk and canopy characteristics (Table 2). On both

251 soils, *E. camaldulensis* had larger trunks and sapwood area, but lower sapwood

252 density, than *E. microcarpa*. The wide range in the sapwood area for both species on

253 clay was due to the presence of younger trees; whereas the sand had predominantly

254 mature trees. Mean sapwood area of the instrumented trees was larger on the clay than

255 on sand, more so for *E. camaldulensis* (47%) than for *E. microcarpa* (27%). About

256 10% of the trunk cross-sectional area was occupied by sapwood in both species on the

257 clay and increased to 19% for *E. camaldulensis* and to 12 % for *E. microcarpa* on the

258 sand. Total sapwood area for all the trees and shrubs was 1.79 m^2 on the clay and 1.17

259 m^2 on the sand.

260

261 There were strong positive linear relationships between the depths of heartwood or

262 sapwood area with trunk circumference for the two species on both soil types.

263 Although the sapwood area was significantly correlated with the trunk circumference

264 in both species, the values for the parameters in their linear regressions were different

265 for the two species:

266 *E. cam*: sapwood area = (0.014 x trunk circumference) + 0.00054; $r^2 = 0.76$ (5a)

267 *E. mic*: sapwood area = (0.011 x trunk circumference) - 0.0008; $r^2 = 0.72$ (5b)

268

269 , *E. camaldulensis* maintained a larger sapwood area at all values of the circumference

270 than *E. microcarpa*; the intercept in this regression was larger for *E. camaldulensis*

271   due to its thicker bark than for *E. microcarpa* (see Table 2). There was a significant

272   correlation ($r^2 = 0.59$) between bark thickness and trunk circumference for *E.*

273   *camaldulensis*, but not for *E. microcarpa* (data not presented). Ratio of sapwood

274   area/trunk sectional area declined was inversely correlated with sapwood density (Fig.

275   1).

276

277   *The weather*

278

279   The radiation receipt was largely similar during the two years, except for the months

280   of October to December that received less energy in 2007 than in 2006 (Fig. 2). Daily

281   mean R_s was 248 W m^{-2} for both years. The winter (June – August or days 151–244)

282   was marginally cooler in 2006, when mean temperature was 7.7 $^{\circ}$C compared with 7.9

283    $^{\circ}$C for the same speriod in 2007. However, the summer (November-February) in both

284   years had similar mean daily temperature of 21.8 $^{\circ}$C in 2006 and 22.3 $^{\circ}$C in 2007. The

285   spring to early summer was more humid in 2007 than in 2006, and this was reflected

286   in the lower evaporative demand for this period in 2007. The rainfall in 2006 was

287   particularly low totaling 239 mm or just 36% of the long-term mean. In 2007 monthly

288   rainfall was close to average for the first half of the year and the annual rainfall of 597

289   mm was 89% of the expected, although August to October was dry. This region like

290   many parts of southern Australia has experienced declining rainfall over in the

291   preceding 10 years. However, rainfall in 2005 was 780 mm or about 15% above the

292   long term average, of this 70 mm fell in November and 33 mm in December.

293

294

295

296   *Sapflow in individual trees during adequate soil-water availability*

297

298   Maximum soil-water content during the 2-year study period was observed in the first

299   90 days of 2006, and in this period sapflow was consistently larger for *E. microcarpa*

300   than for *E. camaldulensis* both during the day and night on the clay (Fig. 3). On the

301   sand, the trend in sapflow rates was reversed; being mostly larger for *E.*

302   *camaldulensis* than for *E. microcarpa*. Much of the differences in rates of sapflow

303   between the species on the sand occurred around midday. Daily sapflow on the clay

304   was 2–3 times larger for *E. microcrapa* than for *E. camaldulensis* before rainfall on

305   day 57 after which the former had about 42% higher sapflow than *E. camaldulensis*

306   during the following two days. These differences in sapflow between the species were

307   reversed on the sand, where sapflow for *E. microcarpa* was only between 40 and 72%

308   of that for *E. camaldulensis*. Total sapflow over the 6-day period on the sand relative

309   to that on the clay was only 41% for *E. camaldulensis* and 16% for *E. microcarpa*.

310   There were indications of sapflow by both species during the night on the two soils.

311   Overall, the mean daily sapflow from either species on the sand was about a third that

312   found on the clay, and was significantly correlated with sapwood area and sapwood

313   density (Table 3).

314

315   On average, sapflow attained peak rates at 1320 hrs in *E. cameldulensis* compared

316   with 1440 hrs in *E. microcarpa* on the clay, but on the sand the peak rate was attained

317   at about 1130 hrs for both species. Time interval between the bases of the bell curves

318   (Fig. 3) approximated duration of sapflow during the daylight hours, when sapflow

319   was ≥1.0 L/hr on the clay, was 800 mins for *E. microcarpa* and 775 mins for *E.*

320   *camaldulensis*; the corresponding values on the sand for when sapflow ≥0.5 L/hr

321   averaged 670 mins for both species. Also, sapflow in *E. microcarpa* peaked at 1430 h

322   on the clay and 1130 h on the sand, for *E. camaldulensis* these were at 1320 h and

323   1150 h, respectively.

324

325   *Influence of soil type on daily trends in transpiration during the years*

326

327   The clay was consistently wetter than the sand that had 16% lower volumetric water

328   content (θ) than the clay (Fig. 4). This difference in θ translated to differences in

329   water storage of 12 mm in the top 0.3 m depth of the soil and up to 240 mm over the

330   entire 6 m of the soil profile. Transpiration (E_c) was consistently higher for *E.*

331   *microcarpa* than for *E. camaldulensis* on the clay than on the sand. This was

332   especially so at the start of 2006 when daily E_c on the clay reached 3.2 mm (68 L/tree)

333   for *E. camaldulensis* compared with 4.8 mm (100 L/tree) for *E. microcarpa* (Fig. 4a).

334   These rates declined rapidly to about 0.6 mm (12.8 L/tree) and 1.0 mm (20.9 L/tree)

335   during the cool winter. The two species mostly had similar E_c on the sand, except

336   between days 230 and 290 (in late winter/early spring) when *E. camaldulensis* had as

337   much as 55% higher E_c (0.07 mm versus 0.11 mm d^{-1}) than *E. microcarpa*.

338

339   Rates of E_c in 2007 (Fig. 4b) were 50% of those observed in 2006 on both soils,

340   especially on the clay at the start of the year. At this time E_c for *E. microcarpa* was

341   below one-third and about half for *E. camaldulensis* of those rates observed for the

342   same period in 2006. *E. camaldulensis* was highly responsive to rainfall events on the

343   clay, but E_c for both species rarely exceeded 0.35 mm d^{-1} on the sand. The subdued E_c

344   on this soil was more severe for *E. microcarpa* especially in late winter/early spring

345   (days 230–290) when this species used 40% less water (0.08 mm d^{-1} versus 0.13 mm

346   d^{-1}) than *E. camaldulensis*.

347

348   *Seasonal influence on diurnal trends in transpiration*

349

350   Detailed E_c data for 2-day periods are presented for three contrasting seasons (Fig. 5).

351   On the clay, *E. microcarpa* had higher E_c than *E. camaldulensis* throughout the day in

352   summer and winter. E_c peaked earlier and lasted for a shorter period in *E.*

353   *camaldulensis* than in *E. microcarpa.* In autumn, E_c for *E. microcarpa* occurred

354   essentially in the morning and just before sunset. On the dry sand, E_c was generally

355   higher for *E. camaldulesis* compared with *E. microcarpa* throughout the day in the

356   cool seasons, but this trend was reversed in summer. The low θ on the sand coupled

357   with the prevailing cool conditions in autumn reduced peak E_c to less than 0.025 mm

358   h^{-1} (Fig. 5e). It is noteworthy that on both soils, E_c for either species did not cease at

359   night especially in summer. Daily totals for E_c was lower by as much as 50% in *E.*

360   *camaldulensis* compared with *E. microcarpa* on the clay, but the difference was

361   reversed by several factors (2.5 −7.3) on the sand for these selected dates (Table 4).

362   The difference in E_c for *E. microcarpa* over *E. camaldulensis* was larger in summer

363   than in the cooler seasons.

364

365   To further test the sensitivity of transpiration to prevailing weather conditions,

366   correlations between E_c and the micrometeorological variables presented in Figure 5

367   were calculated. Results are presented for the clay (Fig. 6), because the responses

368   were mostly either not well-defined or were weak and positively linear on the sand. In

369   all cases the relationships were best described with a 2-parameter power function,

370   which showed E_c in the two species to be strongly responsive to both temperature and

371   vapour pressure deficit (D), but not to solar radiation (R_s). E_c in both species

372   responded more strongly to R_s in summer than in the cooler seasons, this was

373   especially so for *E. camaldulensis.* E_c did not increase beyond R_s of 1.8 MJ

374   irrespective of the season. There was a clockwise hysteresis in the E_c response to R_s,

375   especially in *E. microcarpa*. The thresholds in temperature and D at which maximum

376   E_c was observed were much higher for *E. microcarpa* than for *E. camaldulensis*.

377   These thresholds got progressively lower in autumn and winter especially for *E.*

378   *microcarpa.*

379

380   *Influence of soil type on diurnal course in canopy conductance*

381

382   Canopy conductance (g_c) was calculated from the E_c in Figure 5 and the result

383   presented in Figure 7. On the clay g_c attained peak by 1100 hrs in summer. Peak g_c

384   was higher, and its subsequent decline late in the afternoon was more rapid, in *E.*

385   *camaldulensis* than in *E. microcarpa* (Fig. 7). There was often another elevation in g_c

386   just before sunset. On the sand, g_c attained peak by 1100 hrs and remained relatively

387   stable until after 1800 hrs in summer. Also on this soil, peak g_c was about twice as

388   large and attained earlier in autumn and winter than in summer. Daily g_c averages on

389   the clay was larger for *E. microcarpa* by as much as a factor of 3.5 than for *E.*

390   *camaldulensis* (Table 5) during the three seasons. On the sand, however, averaged g_c

391   was 6 −67 % larger for *E. camaldulensis* compared with *E. microcarpa* during autumn

392   and winter. The coupling coefficient (Ω) was generally higher for *E. microcarpa* than

393   for *E. camaldulensis* on the clay, but the trend was reversed on the sand (Table 5).

394

395   Expressing the daily values of E_c as fractions of the equilibrium evaporation (Eqn. 4)

396   largely eliminated the influence of micrometeorological conditions allowing the

397   influence of soil water (θ) to be assessed. The relationship between E_c/E_{eq} and θ was

398   best described with exponential curves for both species (Fig. 8), but the intercept was

399   much lower, while exponent was much larger, for *E. microcarpa* than for *E.*

400   *camaldulensis*.

401

402   *Annual transpiration and rainfall*

403

404   Annual E_c was always higher for *E. microcarpa* than *E. camaldulensis* on the clay,

405   but there was no difference between the two species on the sand (Table 6). Over the

406   two years, daily E_c averaged 0.90 mm (36 L) for *E. microcarpa* and 0.33 (21 L/d) for

407   *E. camaldulensis* on the clay compared with about 0.12 mm for either species, or 5

408   L/d for *E. microcarpa* and 8 L/d for *E. camaldulensis*, on the sand. On the clay the

409   annual E_c for *E. microcarpa* was 23% higher in 2006 than in 2007, but for *E.*

410   *camaldulensis* it was 47% higher in 2007 than in 2006. On the sand, the annual E_c was

411   similar for the two species in both years. The E_c for the whole year was 114% the

412   annual rainfall on the clay, but 19% on the sand, in 2006; these percentages were 36%

413   and 6% in 2007. Annual E_c as a fraction of E_{eq} averaged 16% on the clay and only 3%

414   on the sand, but was just 20% for the whole block.

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419

420   **Discussion**

421

422   *Differences in sapflow among species and sites*

423

424   The trees of *E. camuldulensis* on the clay had consistently lower rate of sapflow (Fig

425   4a) or transpiration (Figs. 5a, 6) than *E. microcarpa*. This was contrary to

426   expectations from the sapwood area produced at any given circumference that was

427   larger for *E. camaldulensis* than for *E. microcarpa* (Fig 1) in addition to the sapwood

428   density that was smaller for the former than for *E. microcarpa* (Table 2). A smaller

429   sapwood density is generally correlated with a larger sapwood hydraulic conductivity

430   (Stratton et al., 2000; Koch and Fredeed 2005; O'Grady et al. 2009), from which a

431   larger rate of sapflow is expected when all else is held constant (Barbour et al., 2004;

432   Bucci et al., 2004). Using the relationship between wood density and conductivity

433   given by Stratton et al (2000) we estimate the hydraulic conductivity of *E. microcarpa*

434   growing on clay to be 4.5 mmol m^{-1} s^{-1} MPa^{-1} and that of *E. camaldulensis* to be 103

435   mmol m^{-1} s^{-1} MPa^{-1}. A smaller wood density is generally correlated with a reduced

436   resistance to xylem embolism (Stratton et al. 2000; Koch and Fredeen 2005). This

437   made *E. camaldulensis* to tightly control its transpiration so as to reduce the risk of

438   embolism arising from extremely low leaf, and hence xylem, water potential. This

439   was evident in the consistently lower g_c in *E. camaldulensis* than in *E. macrocarpa*

440   throughout the day, especially after midday (Fig 8, Table 5), and also in the more

441   restrained increase in E_c in response to rising *D* in *E. camaldulensis* than *E.*

442   *microcarpa* (Fig 7c, f).

443

444   Finally, from the data compiled by Koch and Fredeen (2005) and the wood density in

445   Table 2, it can be estimated that the minimum leaf water potential at the turgor loss

446   point will be higher (- 3.5 MPa) for *E. camaldulensis* than for *E. microcarpa* (-5.0

447   MPa). This further suggested that *E. camaldulensis* controlled its E_c more tightly, to

448   avoid xylem embolism, than *E. microcarpa*. Therefore, *E. camaldulensis* maintained a

449   comparatively low sapwood density allowing potential for high E_c, but the

450   requirement to avoid embolism coupled to the higher water potential at which zero

451   turgor is likely to be attained, made this species quite conservative in its water use on

452   the clay. While the high sapwood density for *E. microcarpa* provided plasticity in its

453   response to variable soil-water supply conditions.

454

455   How do we reconcile these traits with the generally observed inverse correlation

456   between wood density and stem hydraulic conductivity? The majority of previous

457   studies on this issue were conducted in wetter environments (rainfall > 1000mmm)

458   with shorter dry seasons (Barbour et al 2005, Bucci et al. 2004) than the site of the

459   present study. In contrast to the studies with northern hemisphere species, and

460   consistent with the present study (Table 3), Mitchell et al. (2008) observed a weak

461   positive correlation between stem conductivity and sapwood density in an arid (350

462   mm rainfall) environment of Western Australia. Thus, when evaporative demand is

463   high and water supply is moderate or low *and* highly variable, as opposed to

464   predictable as in the savannas (Bucci et al., 2004, Eamus and Prior, 2001), a low

465   sapwood density and hence high conductivity can be maintained if water use is tightly

466   constrained by strong stomatal control.

467

468   The large difference between the two species in their rates of sapflow and E_c observed

469   on the clay was not repeated on the sand (Figs 5a, b, 6). The convergence in rates of

470   water use for the two species on the sand was achieved through convergence in three

471   attributes. First, sapwood density declined in both species on the sand compared to the

472   clay but the decline in E_c for *E. macrocarpa* was much larger than for *E.*

473   *camaldulensis*. Consequently sapwood density converged on this soil. Second,

474   sapwood area per tree declined in both species, but more so in *E. camaldulensis*, and

475   consequently this trait converged. Finally, canopy conductance declined in both

476   species, but more so in *E. microcarpa*, leading to a convergence in canopy

477   conductance. Thus *E. microcarpa* that was the profligate water user on the clay

478   became conservative and closer in its water use to *E. camuldulensis* through

479   convergence of these three attributes on the sand that had lower water holding

480   capacity and water availability than the clay. This convergence in attributes confirms

481   the observation that species occupying sites that experience repeated and prolonged

482   water deficits tend to exhibit a narrow range in their hydraulic traits (Mitchell et al.

483   2008). Thus, in contrast to the response on the clay, the annual water use on the sand

484   did not differ between species.

485

486   The total seasonal E_c (Table 6) for the two species at the two sites further highlights

487   the disparate behaviour of the two species on the two sites. The poor water holding

488   capacity of the sand (run-off), and hence it's lower water availability relative to the

489   clay (run-on) (Fig 5c), was associated with the $10 - 25$ % reduction in LAI and an

490   almost 60 % reduction in basal area (Table 2). Similar reductions have been found in

491   a study of two contiguous forests in which one acted as a run-off and the other a run-

492   on site (Kelley et al., 2007). Consequently the cumulative water-use on the sand was

493   approximately 22 % of that on the clay (100 mm compared to 450 mm) (Table 6). The

494   Huber value for the whole community (H_{Vc}), i.e. ratio of leaf area to sapwood area

495   (Kelley et al., 2007), was larger on the clay (2.95×10^{-4}) than on the sand (2.1×10^{-4}).

496   These are close to values derived from branch-and tree-scale measurements cited by

497   Eamus and Prior (2001). High Huber values are generally associated either with

498   increased aridity of a site or increased transpiration (Mencuccini and Grace, 1995),

499   and reflect increased allocation to sapwood or decreased investment in leaf area.

500   Thus, the larger E_c reflected the increased H_{Vc} on the clay that had larger water

501   availability, relative to the sand. The decreased mean sapwood area per tree was

502   compensated for, to some extent, by an increase in the hydraulic conductivity arising

503   from the reduced sapwood density on the sand.

504

505   *Environmental controls of water use*

506

507   The response of water use by the trees on the clay to micrometeorological variables

508   and soil water showed different sensitivities between species. The conservative

509   pattern of water use in *E. camaldulensis* was reflected in the lower coefficients of the

510   regression of its E_c on R_s, temperature, and *D* (Fig. 6) and on the regression of E_c/E_{eq}

511   on θ (Figs 9). Thus, for any given increase in any of these environmental parameters,

512   the response of E_c, and hence of the stomata, was smaller in *E. camaldulensis* than in

513   *E. microcarpa.* This is well illustrated in the larger coupling coefficient (Ω) for *E.*

514   *microcarpa* than for *E. camuldulensis*. A high Ω is associated with E_c being more

515   sensitive to solar radiation and temperature (Whitehead et al., 1984) than to *D*, and the

516   larger Ω for *E. microcarpa* agrees with the larger slope for the regression of E_c on

517   temperature. It was not possible to determine the response functions on sand because

518   the relatively low rates of E_c limited the scope for the expression of a response to

519   these abiotic variables.

520

521   For both species, the relationship between E_c and either temperature or D was the

522   same across all seasons of the study (Fig. 6), i.e. there was no seasonal acclimation or

523   adjustment in the responsiveness of E_c to these two variables. This is in contrast to the

524   adjustment observed in the response of E_c to R_s that was different for summer,

525   compared with autumn and winter, for both species. This is because at any given level

526   of R_s, temperature and D, and hence E_c, are smaller in autumn/winter than in summer.

527   In all the three seasons, however, E_c showed no further increase with R_s beyond 1.8

528   MJ m^{-2} (500 W m^{-2}) suggesting that stomates were fully opened at this level of

529   irradiance. In dry environments, the role of R_s is mostly confined to that of controlling

530   the opening and closure of stomates, while rates of E_c and stomatal conductance are

531   determined by D (Wullschleger et al., 1998; Lu et al., 2003). The threshold R_s of 500

532   W m^{-2}, attained by 1100 hrs, for these eucalypts was much higher than 200 W m^{-2}

533   found for other tree species in water-limited environments, such as *Pinus radiata*

534   (Yunusa et al., 2005) or *Cryptomeria japonica* (Komatsu et al., 2006). The high value

535   for the eucalypts was consistent with their having evolved in environments of high

536   sunlight and temperature (Brooker, 2002).

537

538   *Summary and Conclusions*

539

540   Small differences in topography resulted in large differences in the characteristics of

541   the top soil profile. The topographic variation modified distribution of rain water

542   generating *run-off* on the terrace and *run-on* in the depression. This produced apparent

543 differences in LAI, sapwood area and hydraulic characteristics between the two

544 species that were common on both soils. On the sand where water availability was

545 persistently low, trait variation was narrow resulting in almost identical rates of water

546 use by the two species. This was in marked contrast to the clay, where the two species

547 showed marked variation in hydraulic attributes and hence divergent rates of water

548 use. We concluded that trait variation is less likely where the trees are under persistent

549 water-stress than where the stress is shorter and less intense.

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552 **Acknowledgement**

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568 **References**

569

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670   coniferous *Callitris* species and a broad-leaved *Eucalyptus* species. Physiol.

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672
673

674   Table 1. Textural characteristics and the limits for volumetric water content (θ)

675   measured during the study for the two soils during 2006–2007 at Reef Hill, Australia.

676

Depth layers (m)	Clay			Sand		
	Sand	Silt	Clay	Sand	Silt	Clay
0.0 – 0.2	49.5	19.4	31.1	74.3	16.6	9.1
0.2 – 1.5	38.0	19.1	62.0	34.3	21.3	65.7
1.5 – 3.0	49.4	15.5	35.2	54.8	15.3	29.9
3.0 – 6.0	28.5	25.1	46.5	64.8	18.8	31.5
Maximum θ (m^3 m^{-3})		0.32 ± 0.034			0.28 ± 0.022	
Minimum θ (m^3 m^{-3})		0.24 ± 0.028			0.23 ± 0.009	

677 Table 2. Mean values (± standard errors) for key trunk characteristics for the trees supplied with sapflow sensors, and for the other

678 trees, on the two soils at Reef Hill.

679

Variables[a]	Clay		Sand	
	E. camaldulensis	*E. microcarpa*	*E. camaldulensis*	*E. microcarpa*
Trees with sapflow gauges				
Mean trunk diameter/tree (m)	0.51 ± 0.15	0.44 ± 0.14	0.34 ± 0.02	0.32 ± 0.15
Mean sapwood area/tree (m^2)	0.023 ± 0.000	0.014 ± 0.002	0.016 ± 0.000	0.011± 0.002
Sapwood area/trunk cross sectional area	0.12 ± 0.04	0.09 ± 0.03	0.18 ± 0.01	0.14 ± 0.02
Sapwood density (kg m^{-3})	0.68 ± 0.16	0.98 ± 0.17	0.58 ± 0.09	0.68 ± 0.05
Bark thickness (mm)	12.5 ± 0.3	6.7 ± 0.1	8.9 ± 0.1	6.5 ± 0.1
Other tree characteristics on the two soil types[a]				
Range in tree sapwood area (m^2)[b]	0.001 – 0.034	0.006 – 0.025	0.003 – 0.021	0.003 – 0.019
Total tree sapwood area (m^2) [b]	1.13	0.55	0.33	0.76
Number of trees	165	70	3	86
LAI (September 2006)	1.14 ± 0.15		1.04 ± 0.08	
LAI (December 2007)	1.23 ± 0.32		0.87 ± 0.16	

680 [a] Each soil type occupied 0.5 ha; [b]Estimated from circumference at breast height

681   Table 3. Correlation coefficients (r) between mean daily sapflow in Figure 3 and stem

682   characteristics for the eight trees.

683

Trait [a]	Sapflow	Sapwood area	Trunk area	Sapwood area/stem area
Sapflow	-			
Sapwood area	0.736*	-		
Trunk area	0.717*	0.995**	-	
Sapwood area/stem area	-0.682	-0.695	-0.636	-
Sapwood density	0.739*	0.401	0.357	-0.733*

684   [a] Coefficients were significant at $p < 0.05$ (*) or $p < 0.01$ (**)

685   Table 4. Daytime mean values for transpiration (E_c) and for the micrometeorological

686   variables for the 2-day periods presented in Figure 5.

687

Variables	Species	Season[a]		
		Summer	Autumn	Winter
E_c (mm d^{-1})				
Clay	*E. camaldulensis*	3.01	0.70	0.87
	E. microcarpa	4.19	0.95	1.63
Sand	*E. camaldulensis*	0.69	0.46	0.51
	E. microcarpa	0.26	0.09	0.07
E_c/E_{eq}				
Clay	*E. camaldulensis*	0.44	0.75	0.61
	E. microcarpa	0.61	0.45	1.13
Sand	*E. camaldulensis*	0.10	0.21	0.36
	E. microcarpa	0.04	0.04	0.05
θ (m^3 m^{-3})				
Clay		0.28	0.26	0.27
Sand		0.28	0.24	0.27
R_s (MJ m^{-2})		18.8	11.8	22.8
Mean temp (^{o}C)		24.1	12.1	7.3
Mean D (kPa)		1.69	0.22	0.12
Mean wind speed (m s^{-1})		2.06	0.65	0.88
Mean E_{eq} (mm d^{-1})		6.9	2.1	1.43

688   [a] The three seasons were: summer, 17 – 18 January 2006; autumn, 19 – 20 May 2006 and winter,

689   7 – 8 June 2007.

690
691

692 Table 5. Mean values for daytime canopy conductance and coupling coefficient (Ω) for

693 the two tree species based on the data presented in Figure 7.

694

Soil type	Species	Season [a]		
		Summer	Autumn	Winter
Canopy conductance (g_c, mm s^{-1})				
Clay	*E. camaldulensis*	2.56	1.07	3.29
	E. microcarpa	4.46	3.93	5.35
Sand	*E. camaldulensis*	0.76	2.49	2.85
	E. microcarpa	0.80	2.34	1.70
Coupling factor (Ω)				
Clay	*E. camaldulensis*	0.50	0.64	0.63
	E. microcarpa	0.64	0.78	0.72
Sand	*E. camaldulensis*	0.21	0.60	0.60
	E. microcarpa	0.23	0.48	0.53

695 [a] The three seasons were: summer, 17 – 18 January 2006; autumn, 19 – 20 May 2006 and winter,

696 7 – 8 June 2007.

697

698

699   Table 6. Summary of water use variables at Reef Hills for the two years of study
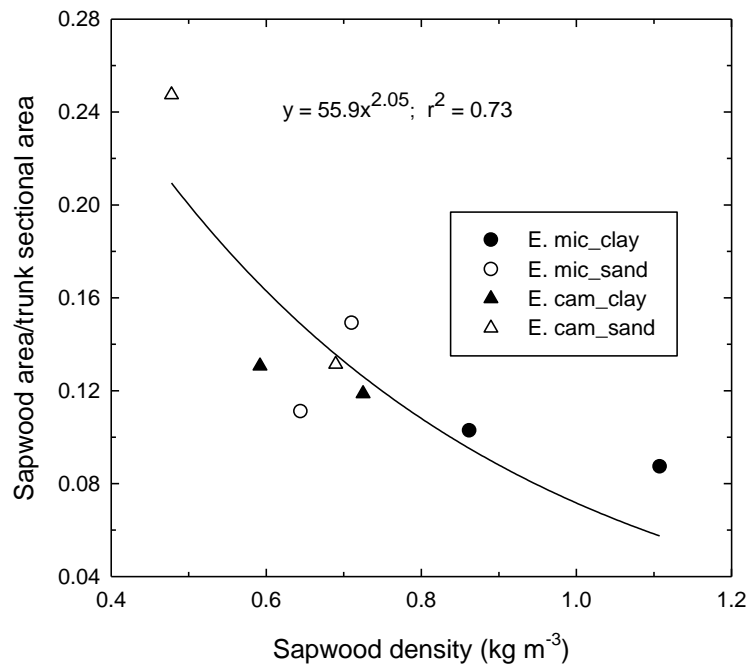
700

Variables[a]	Species	2006	2007
Potential ET (mm)		1792	1633
E_{eq} (mm)		1425	1296
Rainfall (mm)		239	597
E_c (mm)[a]			
Clay	*E. camaldulensis*	99 ± 17 (31)	146 ± 29 (45)
	E. microcarpa	355 ± 36 (69)	289 ± 24 (55)
	Mean	227 ± 22 *(83)*	217 ± 33 *(85)*
Sand	*E. camaldulensis*	44 ± 7 (74)	41 ± 6 (65)
	E. microcarpa	46 ± 6 (26)	34 ± 6 (35)
	Mean	45 ± 8 *(17)*	38 ± 7 *(15)*
Site mean		272 ± 23	255 ± 18
Mean E_c/rainfall			
Clay		0.95	0.36
Sand		0.19	0.06
Site mean		1.14	0.43
Mean E_c/E_{eq}			
Clay		0.16	0.17
Sand		0.03	0.03
Site mean		0.19	0.20

701   [a] Numerals in parenthesis represent percentage contribution by the species to the zonal E_c

702   (normal text) or by each soil to E_c from the whole block (*italics*).

703

704

The plot shows a y-axis labeled "Sapwood area/trunk sectional area" ranging from 0.04 to 0.28, and an x-axis labeled "Sapwood density (kg m^{-3})" ranging from 0.4 to 1.2. The fitted equation is $y = 55.9x^{2.05}$; $r^2 = 0.73$. Legend: E. mic_clay (filled circle), E. mic_sand (open circle), E. cam_clay (filled triangle), E. cam_sand (open triangle).

705

706

707 Fig. 1. Ratio of sapwood area to cross sectional area relative to sapwood density for

708 instrumented trees of *E. camaldulensis* and *E. microcarpa* on the clay or the sand at Reef

709 Hill, Australia.

710

711
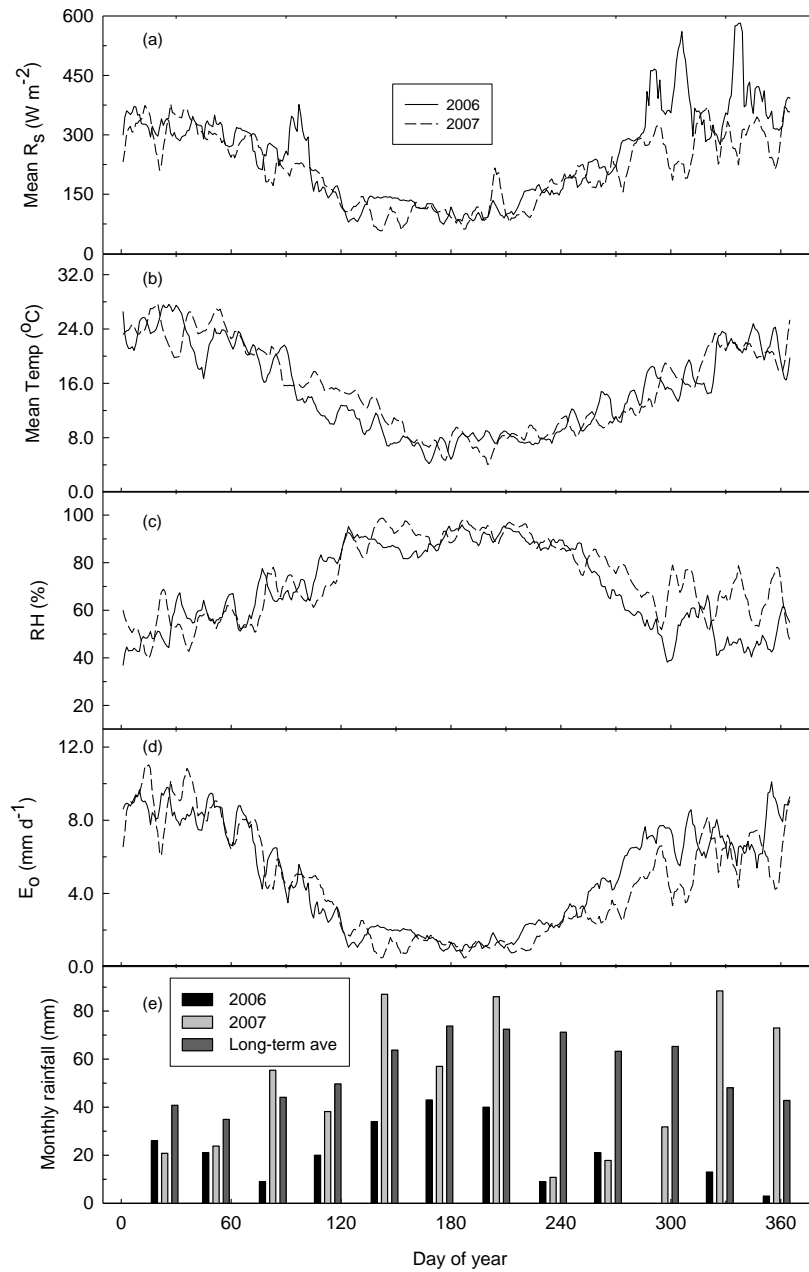
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714

715 Fig. 2. Daily average values for selected weather variables at Reef Hill, Australia, in 2006

716 and 2007: (a) solar radiation, (b) temperature, (c) relative humidity, (d) potential

717 evaporation, and (e) monthly rainfall.

718
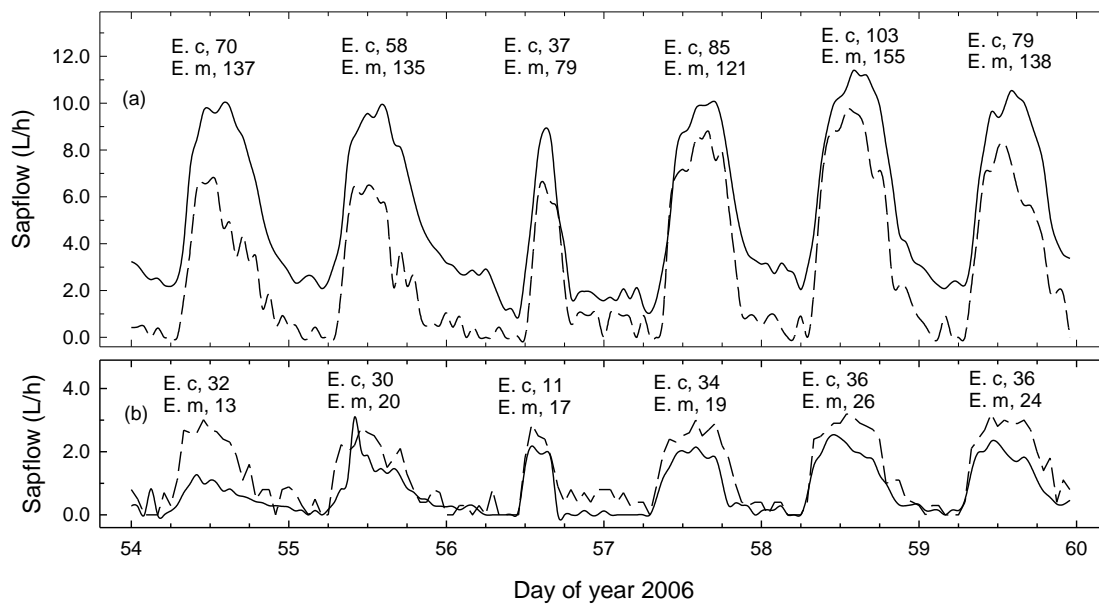
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720

721   Fig. 3. Diurnal trends in sapflow for *E. camaldulensis* (dashed curves) and *E.*

722   *micropcarpa* (solid curves) on the clay (a) and the sand (b) during a selected 6-day period

723   in February 2006 at Reef Hill, Australia. There was an 18 mm rainfall on day 57, daily

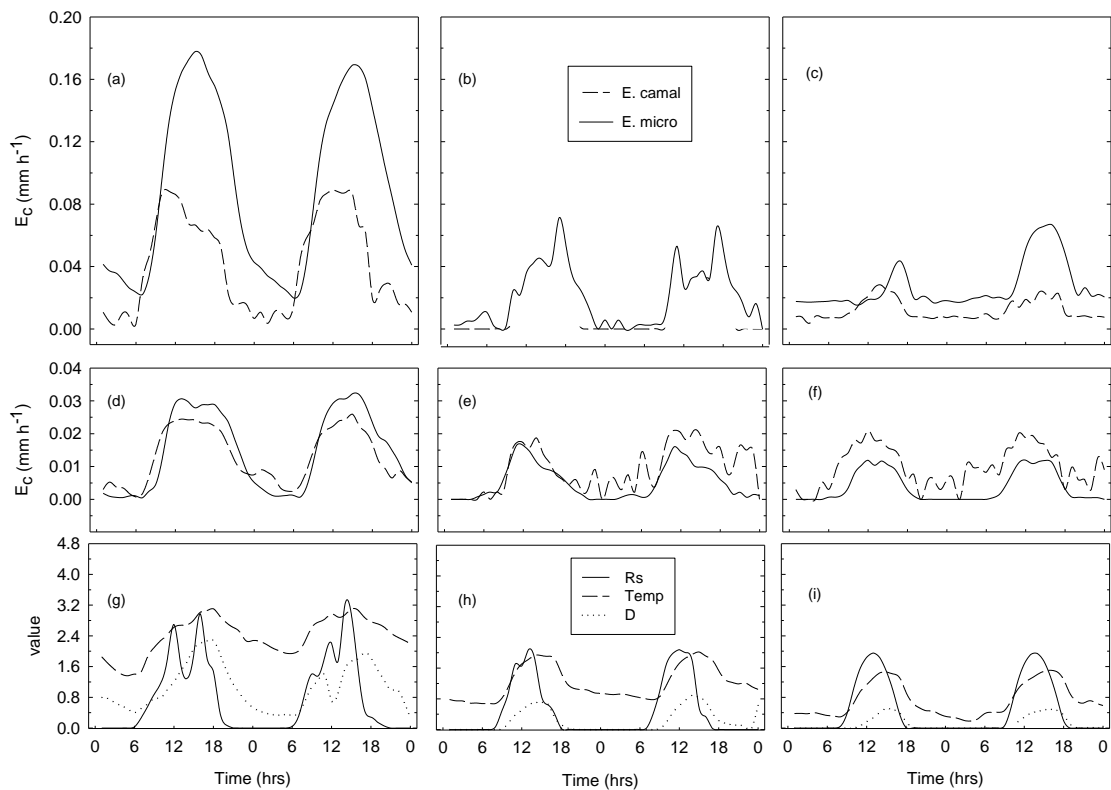724   total of sapflow volumes (litres) are also given for the respective species.
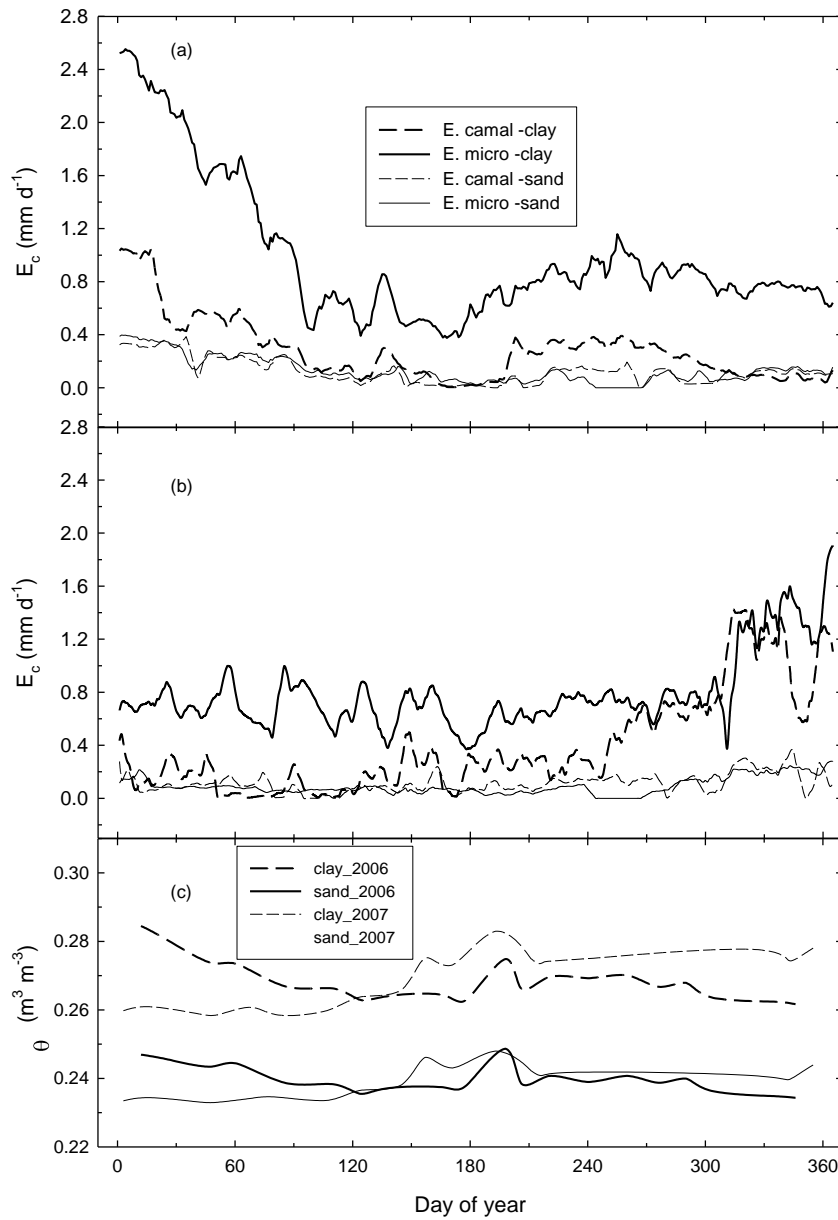
725
726
727   Fig. 4. Five-day running averages for transpiration by *E. camaldulensis* and *E.*

728   *microcarpa* on the clay or the sand at Reef Hill, Australia, in (a) 2006 and (b) 2007, and

729   (c) the mean volumetric water contents for the 6 m profile.

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733 Fig. 5. Diurnal trends in transpiration (E$_c$) rates for E. *camaldulensis* and E. *microcarpa*

734 growing on the clay (a – c) and the sand (d – f) over 2-day periods during summer (a, d,

735 g), autumn (b, e, h) and winter (c. f. i) at Reef Hill, Australia. The corresponding trends in

736 vapour pressure deficit (*D,* kPa), solar radiation (R$_s$, MJ m^{-2}) and temperature (x10^{-1} ^{o}C)

737 are given (g, h, i). The 2-day periods were 17–18 January 2006, 19 –20 May 2006, and 7

738 –8 June 2007. The daily averages for the data are given in Table 4.
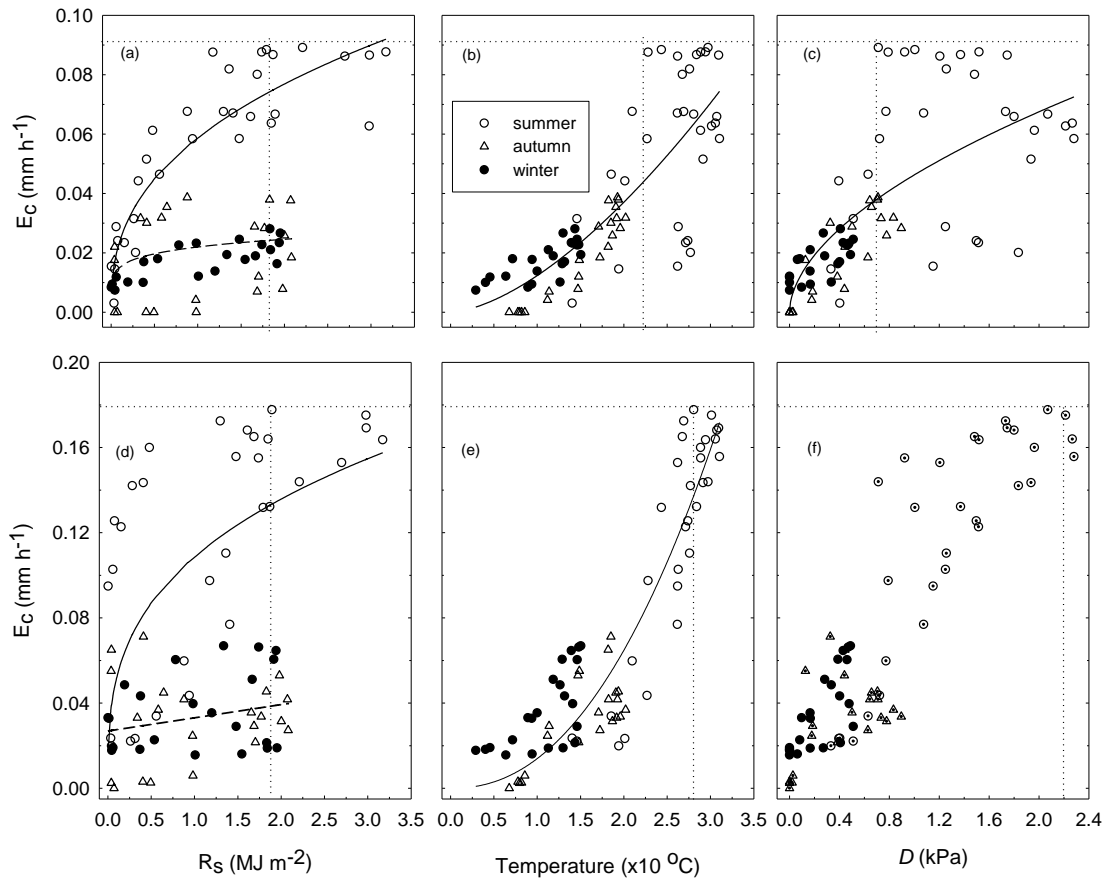
739

740 Fig. 6. Daytime response of transpiration by *E. camaldulensis* (a – c) and *E. microcarpa*

741 (d – f) growing on the clay to solar radiation (a, d) temperature (b, e) and to vapour

742 pressure deficit (c, f) for the 2-day periods shown in Figure 5. The dotted lines are the

743 upper limits for E_c (horizontal) and the threshold values for the meteorological variable

744 (vertical) beyond which no further increase in E_c was observed in summer. Equations for

745 the lines fitted and significance of the regressions at $p < 0.05$ (*) or <0.01 (**) are:

746   (a) $y = 0.059x^{0.389}$ $r^2 = 0.72$** for summer (solid line)

747           $y = 0.022x^{0.171}$ $r^2 = 0.32$* for autumn and winter (dashed line)

748   (b) $y = 0.012x^{1.58}$ $r^2 = 0.64$**

749   (c) $y = 0.005x^{0.009}$ $r^2 = 0.49$*

750   (d) $y = 0.109x^{0.323}$ $r^2 = 0.32$* for summer (solid line)

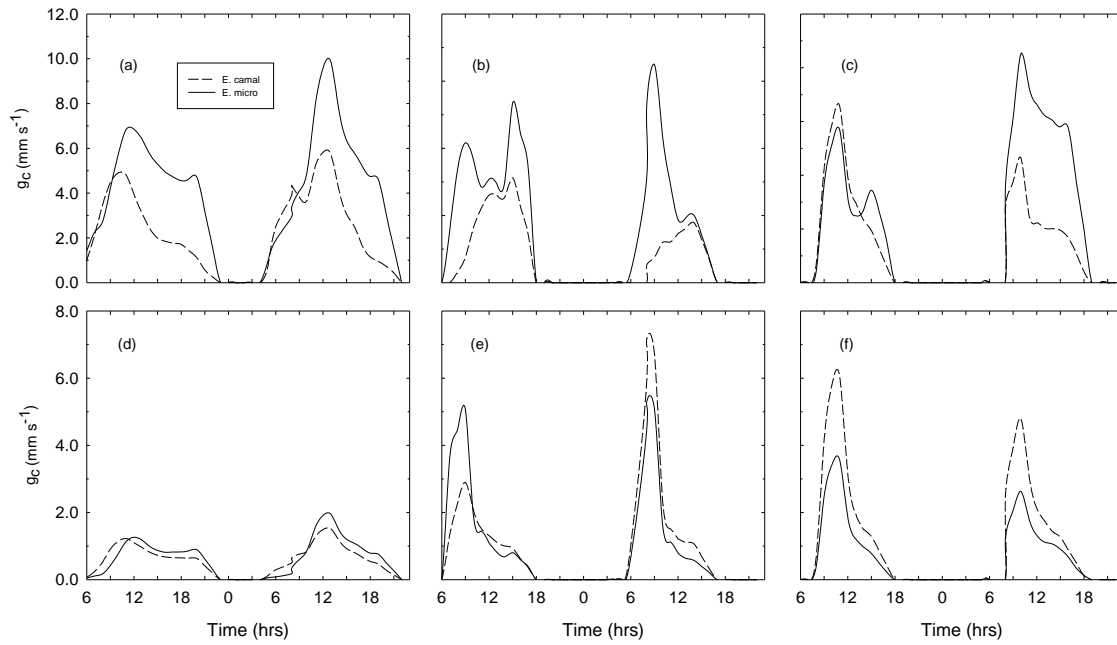751 $y = 0.006x+0.027$ $r^2 = 0.027$ for autumn and winter (dashed line)

752   (e) $y = 0.14x^{2.21}$ $r^2 = 0.85$**

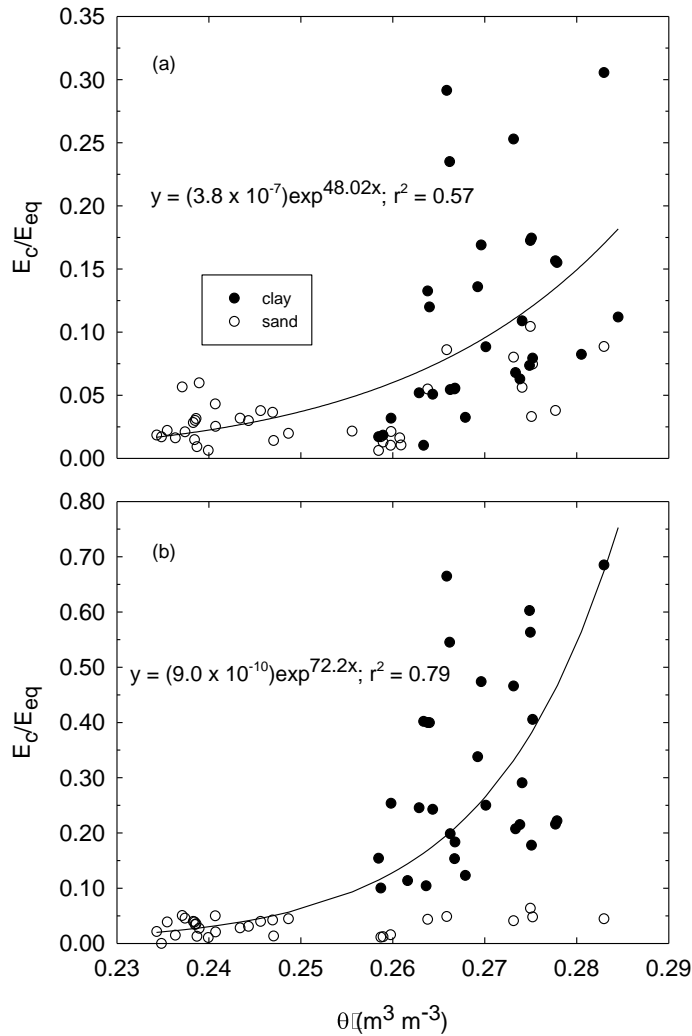753   (f) $y = 0.0091x^{0.86}$ $r^2 = 0.80$**

754

757 Fig. 7. Daytime trends in calculated canopy conductance (g_c) for *E. camaldulensis* and *E.*

758 *microcarpa* growing on the clay (a – c) and the sand (d – f) during summer (a, d), autumn

759 (b, e) and winter (c, f) for the 2-day periods shown in Figure 5. The daily averages for the

760 data are given in Table 5.

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The curves and data points show (a):

$y = (3.8 \times 10^{-7})\exp^{48.02x}$; $r^2 = 0.57$

with legend: ● clay, ○ sand

and (b):

$y = (9.0 \times 10^{-10})\exp^{72.2x}$; $r^2 = 0.79$

Axes: E_c/E_{eq} (vertical), $\theta\ (m^3\ m^{-3})$ (horizontal)

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766
767   Fig. 8. Relationship between relative transpiration (E_c/E_{eq}) and mean volumetric water

768   content (θ) in the 6 m profile of the clay and the sand at Reef Hill, Australia: (a) E.

769   *camaldulensis* and (b) E. *microcarpa*. The curves are fitted lines with their equations

770   given in graph.

771